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The Auditory Region (Ossicles, Sinuses) in Gliding Mammals and Selected Representatives of Non-Gliding Genera

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ABSTRACT

Gliding does not leave an imprint on the auditory region. A well-developed sinus system and specialized auditory ossicles are probably a necessary pre-adaptation for gliding. Some non-gliding genera, which belong to the same families, have an equally developed sinus system and equally specialized auditory ossicles. *Acrobates* shows specialization not found in other Phalangeridae. The generalized mallei of marsupials, insectivores, and rodents are quite similar. The specialized mallei in marsupials, insectivores, rodents, and Dermoptera differ greatly in their morphology. The stapes of some insectivores and that of many rodents are similar. A septum bullae indicating the border between the entotympanic and the tympanic process of the alisphenoid is present in some marsupials; a similar septum in the same location between a possible entotympanic and the tympanic process of the basisphenoid is seen in some insectivores. The name "septum sphenoideum" is suggested for this structure which is found in some gliders and non-gliders.

INTRODUCTION

This paper, dealing with the auditory region of mammalian gliders, is done prior to a study of that region in the Chiroptera. This sequence is observed because gliding is looked upon as a possible prestage for active flight. A study of the auditory region in gliders is not found anywhere in the literature. Van Kampen (1950) mentions only cursorily the presence of sinuses in some gliders; as does van der Klaaw (1931) in his compilation arranged by structural categories. Doran (1879) in his extensive work on the auditory ossicles describes the ossicles in some of the gliders.

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The following study deals especially with the sinuses and the auditory ossicles. A comparison is made with those of related non-flying taxa. Generalized ossicles of non-gliders and the specialized ossicles of gliders are compared and a morphological description of the auditory region of selected specimens is given and illustrated by drawings or photos. I have given special consideration to the septa within the sinuses. This investigation is intended to determine a possible influence of gliding on the morphology of the auditory region.

METHODS

After studying the external features of the ear region, the middle ear with its sinuses was exposed (Segall, 1969b). The ossicles in most cases were described only to such an extent as they could be seen in situ. In some cases the isolated ossicles could be studied. The angle of the ossicular functional axis with the Frankfurter horizontal was determined in as many instances as the limited material permitted. The ossicular functional axis is an imaginary line which runs from the distal end of the short crus incudis, through the malleolar-incudal articulation to the upper insertion of the lamina on the head of the malleus. The stapedia ratio is the ratio between length and width of the stapedia plate or of the fenestra ovalis (Segall, 1970). The term "generalized" resp. "specialized" is used only with reference to structures of the auditory region. The term "posterior crus incudis" is often used instead of "short crus incudis" and the term "stapedial crus" instead of "long crus incudis." As with the ossicular functional axis, the stapedia ratio was noted whenever possible.

MATERIAL

The following specimens of the recent mammal collection of Field Museum of Natural History and the American Museum of Natural History (AMNH) were studied.

Gliding marsupials:

Petaurus norfolcensis 60954, 53736

Petaurus breviceps 60907

Schoinobates volans volans 60906

Acrobates pygmaeus AMNH 37185

Acrobates pygmaeus 60898

Non-gliding marsupials

Protemnodon eugenii 41339

Vombatus ursinus tasmaniensis 98887

Didelphis albiventris 24154
Dasyurus viverrimus 81523
Dromiciops australis 50074
Isoödon obesulus 35327
Caenolestes obscurus 70876
Caluromys lannata 70994
Caluromys philander 22208
Phalanger 53970
Trichosurus vulpecula 60934
Pseudocheirus herbertensis 60910
Pseudocheirus lemuroides 60926
Dactilopsida trivingata picata 08363

Gliding rodents

Glaucomys volans 48283
Petaurista petaurista melanotus 98533
Hylopetes n. nigripes 63031
Anomalurus fraseri 88208, 88209

Non-gliding rodents

Oryzomys melanomys 18511
Peromyscus c. crinitus 02530
Callosciurus flavimanus bouhotei 36689
Callosciurus flavimanus juvenis 63041
Sciurus hudsonicus 43950
Sciurus niger 57325
Nannosciurus m. borneanus 18040
Nannosciurus philippines 92785
Citellus grammurus v. 11223
Citellus l. tridecemlineatus 51738
Cryptomys 47383
Geomys bursarius illinoensis 51617

Dermoptera

Cynocephalus variegatus peninsulae 82615, 68785
Cynocephalus volans 56504

MORPHOLOGY

The morphological characteristics of generalized and specialized rodent ossicles will be considered below. Those of the marsupials and insectivores have been dealt with before (Segall, 1970). A description of the ossicles of *Cynocephalus* follows in the descriptive part of this paper.

MALLEUS

The rodent malleus shows variations within the order. The generalized malleus as seen in *Oryzomys* (fig. 1A) is characterized by a relatively small head; saddle-shaped articulation directed postero-dorsad; sharp capitular crest; long angular neck; large sub-quadrangular lamina; well-developed apophysis orbicularis; an anteriorly open angle of about 100° between neck and manubrium;

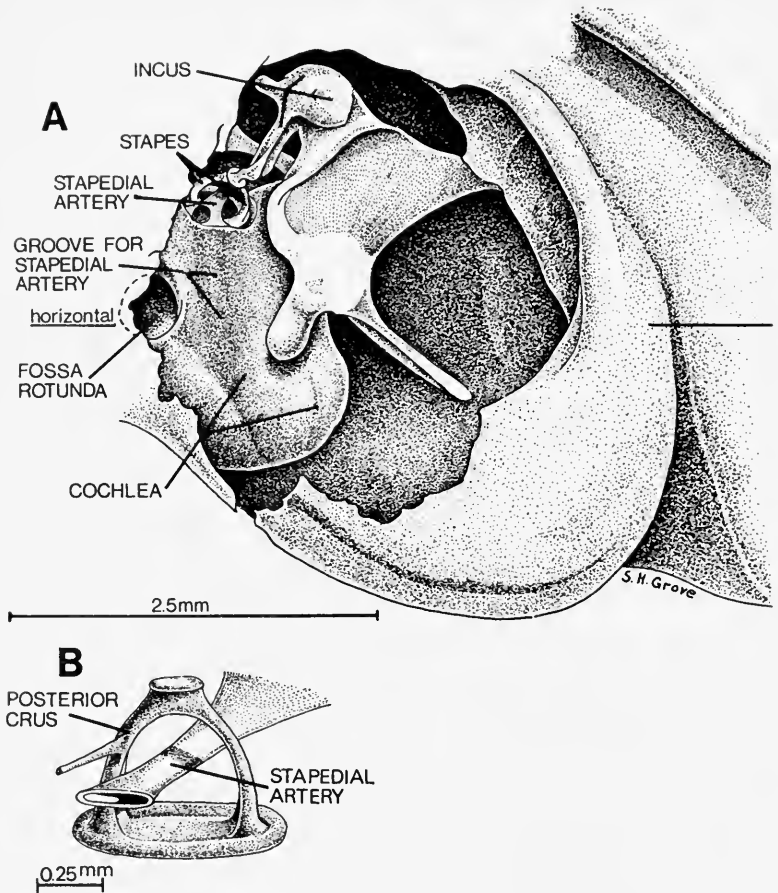


FIG. 1. *Oryzomys melanomys columbianus* (18511). A, Latero-ventral view of right middle ear (obstructing bone removed). B, Right stapes.

a slender, distally spatulated manubrium directed antero-ventrad. The ossicular functional axis forms an angle of about 15° with the Frankfurter horizontal.

All rodent gliders have specialized mallei, e.g., *Glaucomys* (fig. 2A). The malleus head is flattened latero-medially; its dome-like upper extremity reaches higher into the recessus epitympanicus than the incus. The large saddle-shaped articulation faces caudad. Anteriorly the head diminishes in size so that, seen from above, it has a pear-shaped appearance. A neck is practically absent and the triangular lamina is fused with the tympanic. The head is

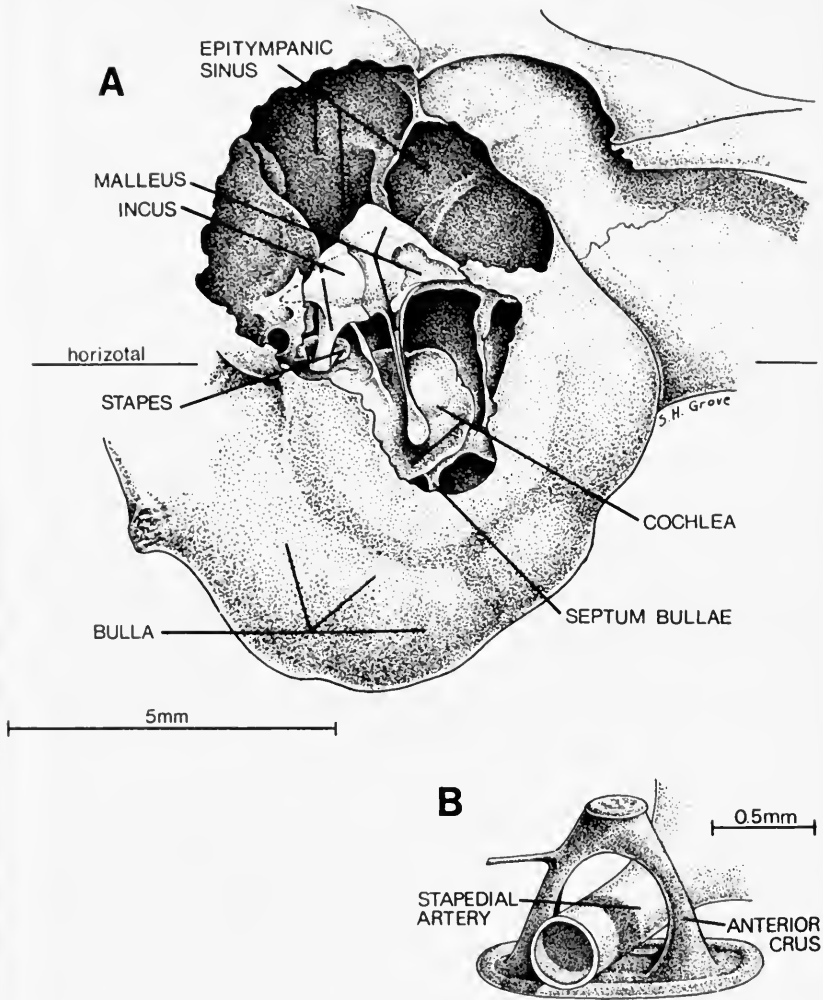


FIG. 2. *Glaucomys volans* (48283). A, Lateral view of right middle ear (obstructing bone removed). B, Right stapes.

slightly bent medially against the saber-shaped, ventrally directed manubrium, which has on the lateral side of its proximal end a prominent processus brevis and below a muscular process at its medial side. Neck and manubrium are essentially aligned. The anterior and posterior sides of the manubrium are flat; its distal end spatulated.

INCUS

The generalized incus, as seen in *Oryzomys*, has a robust body (fig. 1A). The posterior finger-like crus is short and rests in the epitympanic recess. The ossicular functional axis forms an angle with the Frankfurter horizontal of about 15° . The stapedial crus has a concavity anteriorly which is reminiscent of the stapedial crus in some insectivores, is longer than the posterior (short) crus and through the lenticular process is in articular contact with the stapes head.

The specialized incus, as seen in *Glaucomys*, also has a robust body (fig. 2A). The posterior (short) pointed crus, which is about equally long, sometimes even longer than the stapedial crus, reaches into the fossa incudis located in the posterior inferior wall of the epitympanic recess; the ossicular functional axis is about parallel with the Frankfurter horizontal. The anterior side of the stapedial crus incudis is slightly convex, not concave as in the generalized form (*Oryzomys*).

STAPES

The generalized stapes has slightly curved crura and the stapedial ratio in *Oryzomys* and *Peromys* is about 1.4, which gives the plate an oval shape (figs. 1B, 14).

The specialized rodent stapes, as in *Glaucomys* which has straight, long, divergent crura, is triangular in shape (fig. 2B). The stapes plate is elliptical and the stapedial artery is enclosed in a bony canal. The stapedial ratio is about 2.2.

BULLA

The bulla in all rodents studied is completely ossified in generalized as well as in specialized auditory regions.

SINUSES

Van Kampen (1905) defines an auditory sinus as a cavity which communicates with the cavum tympani and which does not contain any organ necessary for the hearing function. Sinuses develop by invasion of the mucosa of the middle ear into the surrounding bone (Wittmaack, 1918). Sometimes the sinuses are already present at birth, sometimes they develop afterward. Arranged according to their position they are the hypotympanic sinus or bulla below; the

epitympanic sinus above; the mastoid sinus posteriorly; and the zygomatic sinus anterolaterally. Sometimes the paroccipital also contains a small sinus. The sizes of the sinuses vary greatly. The epitympanic sinus is connected through the foramen pneumaticum with the epitympanic recess, which contains the head of the malleus and a part of the incus. This foramen pneumaticum shows great variation in size. Sometimes it is so large that one cavity leads to the other gradually without any distinction. This also applies to the hypotympanic sinus or bulla. It may be separated from the cavum tympani by a nearly complete septum or there may be no separation present at all. The lumen of a sinus may be empty or septa of different height and number may divide the cavity. The septa have various origins. Most of them are lamellae that persist while the surrounding bone becomes absorbed (Van Kampen, 1905). Some sinuses are cellular, others are taken up by spongiöse bone. The morphology of the contents of the sinuses necessarily influences the sound.

In both marsupials and rodents, the gliding genera will be dealt with first, the related non-gliding forms afterward.

GLIDING MARSUPIALS

Petaurus 53736, 60954

The tympanic forms the lower half of the external canal, which consists of a steep ascending recessus meatus and a cylindrical part directed laterad. The upper half of the canal is formed by the bullous squama. Medially and posteriorly the tympanic continues to the paroccipital process and supplies in that way a part of the ventral bulla wall. The anterior part of the bulla is formed by the tympanic process of the alisphenoid, which is bordered posteriorly by a whitish line that corresponds to a septum on the inside of the bulla. In front of the antero-superior end of the external canal is the antero-laterad-facing postglenoid foramen. The opening for the Eustachian tube is antero-medially in the bulla.

The inside of the bulla shows the above mentioned low septum, stretching from the antero-lateral end of the cochlea, past the antero-lateral side of the Eustachian tube to the underside of the sulcus tympanicus. This septum, which is outlined on the ventral side as the above mentioned whitish line, separates the tympanic process of the alisphenoid from the entotympanic (see p. 56).

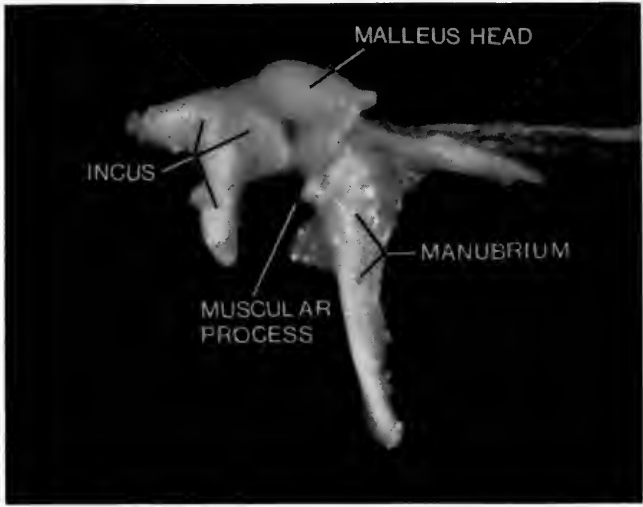


FIG. 3. *Petaurus norfolcensis* (60954). Medial view of left malleus (damaged) and incus.

A bony wall separates the epitympanic recess incompletely from the sinus epitympanicus; the latter continues antero-laterally into the postzygomatic sinus. All sinuses are cellular, except the bulla.

Seen dorso-medially, the pear-shaped head of the malleus is pointed anteriorly (fig. 3). Its capitular crest continues to nearly the distal end of the short neck. A processus brevis is hardly discernible. About the same level on the medial side of the manubrium is a muscular process. The small lateral side of the manubrium is flat and its ventral end is spatulated.

The robust posterior (short) crus incudis has about the same length as the sturdy stapedial crus.

The columella-like stapes divides close to its elliptical plate into the two crura. There is an opening between the crura, the size of which corresponds to the diameter of one crus. The vestibular surface of the plate is only slightly convex. The stapedial ratio is about 2.0.

Schoinobates volans volans 60907, 60906. Figure 4.

The external auditory canal consists of a long, steeply ascending recessus meatus, which projects into the bulla and a nearly horizontal, cylindrical part. The tympanic forms slightly more than the lower half of the canal, which is directed laterad and slightly caudad.

Its upper wall is supplied by the squamosal. The tympanic continues on the ventral side of the bulla to the basis of the paroccipital process, thus forming a part of the inflated bulla wall. The anterior part of the bulla is formed by the inflated tympanic process of the alisphenoid. The posterior end of this process turns dorsad and forms a low septum on the inside of the bulla, which separates the tympanic process of the alisphenoid from the entotympanic. The septum is highest close to the cochlea and diminishes in height laterad. Medially, it shields the Eustachian tube from the lateral view. Posteriorly, the bulla is separated from the cellular mastoid. The posterior root of the zygomatic process is also pneumatized. The long, thin, pointed paroccipital process is taken up by a cavity. Medial to the bulla a lengthy strip of the periotic comes to the surface.

The head of malleus and incus reach into the recessus epitympanicus which communicates dorsally with the cellular epitympanic sinus; anteriorly and slightly laterally the latter continues into the zygomatic sinus. Posteriorly and postero-ventrally to the epitympanic sinus is the mastoid sinus. The inside of the bulla is divided

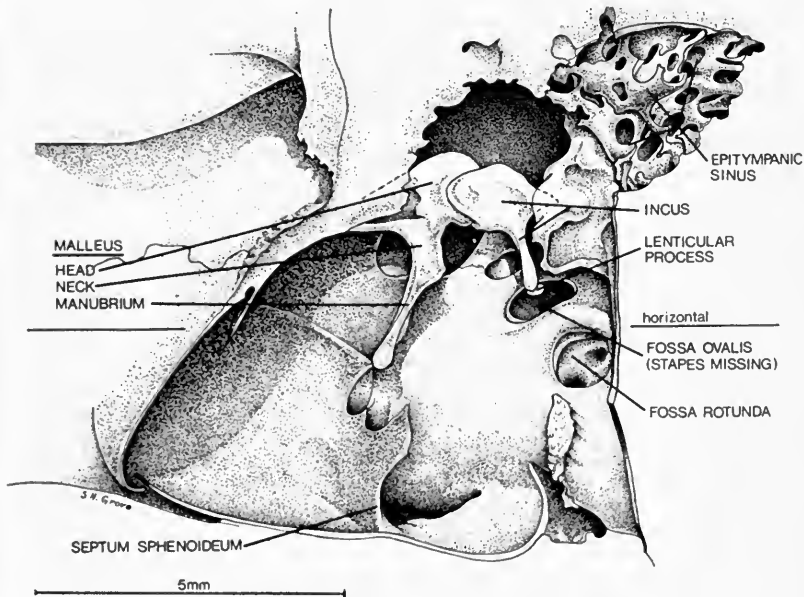


FIG. 4. *Schoinobates volans volans* (60906). Latero-ventral view of left middle ear (obstructing bone removed).

incompletely by a low septum which originates at the anterior tip of the cochlea. Antero-laterally to the inner opening of the Eustachian tube this septum proceeds in a postero-lateral direction to the underside of the sulcus tympanicus. It divides the bulla incompletely into two parts and is visible on the outside wall as a whitish line (see p. 57). All sinuses, except the bulla, are very cellular.

The malleus is similar to that of *Petaurus*; its head seen from above has an elongated, pear-shaped, anteriorly pointed configuration. The elongation is more marked than in *Petaurus*. The articulation is saddle-shaped. The short lamina is triangular. The capitular crest continues into the neck. Head and neck are only slightly bent medially against the manubrium, though less than in *Petaurus*. The neck forms an anteriorly open angle of about 130° with the manubrium. Posteriorly, there is a sharp corner between these two structures. The short process is hardly developed and the small saber-shaped, antero-ventrad directed manubrium has a slightly concave lateral side.

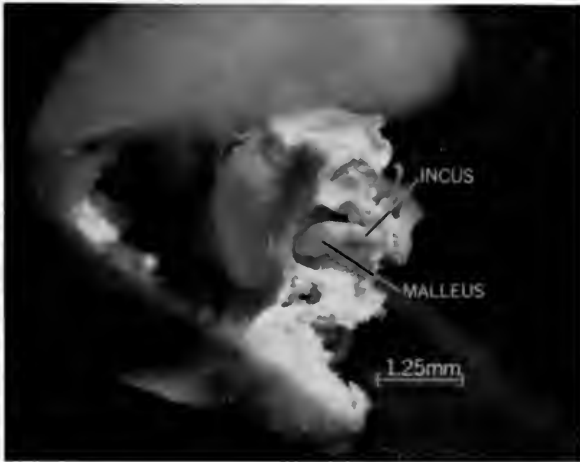
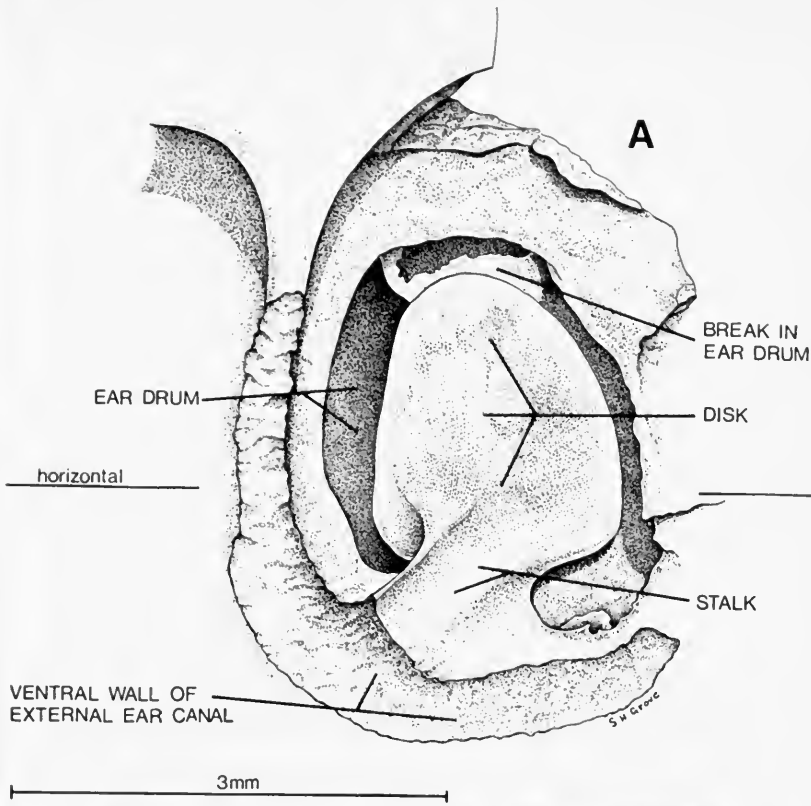
The plump body of the incus continues into a short process, which reaches into the fossa incudis located in the lower end of the recessus tympanicus. The stapedial crus is directed ventro-caudad. The ossicular functional axis is about parallel with the Frankfurter horizontal.

The dorso-ventrally flat columella-like stapes divides close to the plate into the crura, which have a pin-sized opening between them. The stapes ratio is about 2.0.

Acrobates pygmaeus 37185AMNH, 60898FMNH. Figure 5A, B.

The auditory region of *Acrobates* is more specialized than in other Phalangeridae. The tympanic forms approximately the lower half of the oval-shaped external canal, which is directed laterad and slightly dorsad. The upper half of the canal is supplied by the bullous squama, which extends further laterad than the lower wall. The border between these two structures is not clearly marked.

Close to the medial end of the external canal is an attached, nearly vertical, disc-like structure, which is supported by a broad stalk (fig. 5A). This antero-postero flattened stalk extends from the floor of the external canal to the ventral edge of the disk and has a buttress at a right angle to the disk, extending from its ventral edge to the center. It is darkish in color, particularly at its ends, due to air contents. The disk stands in a slightly oblique position with the upper edge reaching further laterad than the lower. It nearly hides



B

FIG. 5. *Acrobates pygmaeus* (37185). A, Disk in left external auditory canal (obstructing bone removed). B, Malleus head and incus body seen in dorso-lateral view (roof of epitympanic removed).

the eardrum from the lateral view and only the edge of the eardrum can be seen. The whitish edges of the disk are slightly thicker than the darkish center.

The function of the disk seems to be mechanical. It may act as a shield for the eardrum against the swift air currents during the gliding act. The structure is unique and there is no report on it in the literature.

Between the tympanic and the basioccipital is a bony structure, probably an entotympanic that fuses with the tympanic and forms about the medial half of the moderately inflated bulla wall. Its anterior border begins slightly medial to the Eustachian tube and stretches in a lateral direction towards the tympanic. Such a border is characteristic of an entotympanic (p. 56).

Posterior to the tympanic is an elongated mastoid; anterior, the bullous alisphenoid. A tympanic process of the alisphenoid is not present. No paroccipital process is visible. The stylomastoid foramen is bordered by the tympanic and the post-tympanic process of the squamosal, and sometimes the mastoid. Some of the structures mentioned in this paragraph are fused with each other and not clearly defined.

To preserve the relationship of this disk to the surrounding elements, the epitympanic sinus was exposed from above. This sinus continues anterolaterally into the zygomatic sinus, posteriorly into the mastoid sinus. All sinuses are very cellular, as in the other Phalangeridae. The extensive sinus system and the air-filled spaces in the disk and its stalk reduce the weight and may so contribute to the buoyancy.

The robust malleus head and incus body are very close to the lateral wall of the recessus epitympanicus; however, there is a slightly larger space between them and the medial wall (fig. 5B). The anteriorly rounded head is slightly bent medially against the manubrium. There is practically no neck present. The manubrium is ventrally directed.

The strong posterior (short) crus incudis lies in about the Frankfurter horizontal; its posterior end rests in the fossa incudis located in the posterior inferior wall of the recessus epitympanicus.

The stapes has the shape of a long, dorso-ventrally flattened rod, which divides close to the plate into the two crura. Between them is an oval opening.

An arteria stapedia is not present in the macerated skull. The plate has an elliptical outline, which is characteristic of a specialized stapes as has been pointed out before (Segall, 1970). The stapedia ratio is about 2.2. Its vestibular surface is bullous. Doran (1879) cites Hyrtl, who used this term to describe the stapes plate in *Phalanger cookii*. Doran states further that "he did not find it in any other marsupial" and that "its morphological value does not appear great as bullate stapes occur sporadically in other higher mammals which are not closely allied to each other as in *Mustela*, *Geomys* and *Hyrax*." Doran and Hyrtl apparently intended the word bullous to indicate the presence of an airspace within the stapes plate. He differentiates this type of stapes from a stapes with a convex vestibular surface which Doran describes in *Chrysochloris*, a configuration which is also present in *Elephantulus*.

Acrobates is a highly specialized phalanger. The dislike structure in the external canal, the shape of the malleus, and the missing tympanic process of the alisphenoid in the formation of the ventral bulla wall distinguish this genus from other Phalangeridae. These characteristics may indicate a longer period of adaptation for gliding than other marsupial gliders have had.

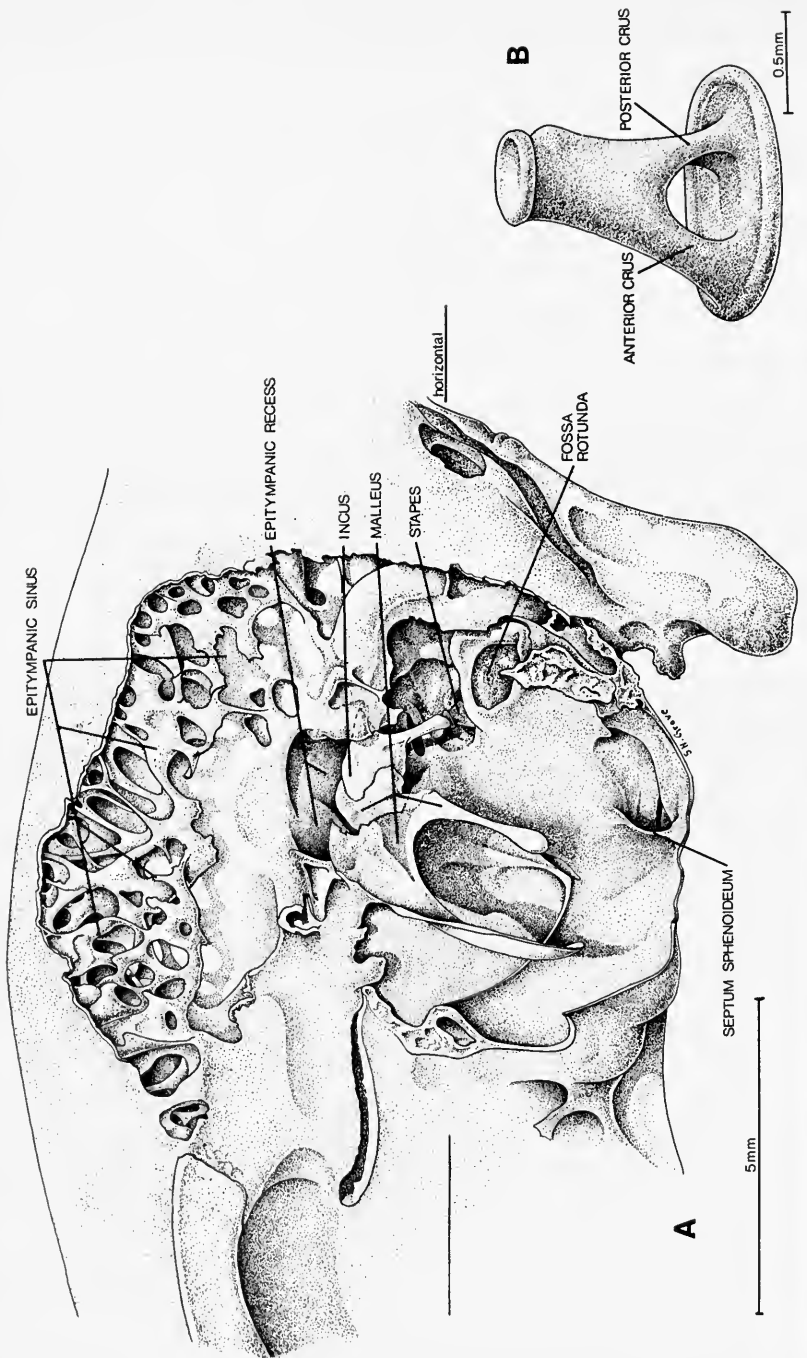
NON-GLIDING MARSUPIALS

Trichosurus vulpecula 60934

The rather flat bulla is limited anteriorly by the alisphenoid; caudal to the tympanic process of the alisphenoid in sutural connection with it is an entotympanic which reaches to the paraoccipital process. The suture is indicated on the inside of the bulla by a septum described below.

The antero-lateral part of the bulla is supplied by the squama (van Kampen, 1905). The external canal consists of a recessus meatus and a cylindrical part and is directed latero-dorsad and slightly posteriorly. The tympanic continues medially, thus contributing a small part of the ventral bulla wall. The mastoid and the posterior root of the zygomatic process are much inflated.

The cavum tympani has large cellular sinuses (epitympanic, mastoid, and zygomatic), while the bulla is only moderately inflated the latter has a septum on its inside, which runs from the antero-lateral side of the cochlea to the sulcus tympanicus. It indicates the border of the tympanic process of the alisphenoid and the entotympanic (see p. 56).



The malleus head seen from above has a less pointed anterior end than the malleus of *Petaurus* and is only slightly bent medially toward the neck. The angle between the articulation surfaces is about 90° . The straight neck is directed postero-ventrally. The small, short lamina is triangular. The neck forms with the antero-ventrally directed manubrium a caudally sharp projecting corner. The short crus incudis rests in the fossa incudis located in the posterior-inferior part of the recessus epitympanicus. The stapedia crus is slightly concave on its anterior side and runs parallel to the neck of the malleus. The collumella-like stapes divides close to the plate into two crura which have an opening between them of about one-third the length of the stapes plate. The stapedia ratio is about 1.7.

Phalanger

The auditory region of *Phalanger* has been described in Segall, 1969b.

Pseudocheirus herbertensis 60910. Figure 6.

P. lemuroides 60926

Approximately the lower half of the external canal is formed by the tympanic; the upper half by the squama. The suture between these structures is clearly defined. The tympanic continues on the base of the skull at first mediad, then mediad and slightly posteriorly to the long paroccipital process, thus forming a part of the bulla wall. Anteriorly, the bulla is supplied by a tympanic process of the alisphenoid and behind the latter and completely fused with it, by an entotympanic. In some specimens the border between these two elements is indicated on the ventral side of the bulla as a white line. The entotympanic is medially in contact with the periotic, which appears as a longitudinal strip on the ventral side of the skull. Posteriorly, the bulla is separated from the mastoid sinus.

The middle ear is surrounded by sinuses; dorsally by the epitympanic sinus which antero-dorsally continues into the zygomatic sinus of the squamosal; posteriorly, by the mastoid sinus. The first two sinuses are very cellular, which gives them a honeycomb appearance. The inside wall of the bulla is smooth with the exception of the septum. This septum diminishes in height from the

FIG. 6. *Pseudocheirus herbertensis* (60910). A, Latero-ventral view of left middle ear (obstructing bone removed). B, Left stapes.

anterior end of the cochlea, antero-laterally to the Eustachian tube toward the sulcus tympanicus, and is indicated on the outside bulla wall as a whitish line described above. Posteriorly to this septum is the entotympanic (see p. 56).

Anteriorly, the head of the malleus is pointed; together with the neck it is bent slightly medially against the manubrium. The crista capituli continues into the neck, which forms a prominent angle on its caudal side with the manubrium. Anteriorly, the angle between the neck and manubrium is about 140° . The small lamina is triangular; a processus brevis is hardly developed.

The body of the incus continues without distinction into the short crus, which rests its distal end in the fossa incudis located in the postero-inferior wall of the recessus epitympanicus. The stapedia crus diminishes in size ventrally; the ossicular functional axis is about parallel with the Frankfurter horizontal.

The columella-like stapes, which divides close to the stapes plate into the two crura, has an opening which apparently is smaller on the dorsal than on the ventral side (fig. 6B). No stapedia artery is present on the desiccated skull and the stapedia ratio is about 2.0.

Dactylopsida trivingata picata 08363

The auditory region is similar to that of other Phalangeridae. Present are: a large tympanic process of the alisphenoid; a well-developed entotympanic; and a relatively large paroccipital process which contains a sinus. There is a long recessus meatus and the sinuses are large and cellular.

Its malleus looks like that of a phalanger with a broad, long neck and an anteriorly open angle between neck and manubrium of about 110° . The latter is directed antero-ventrad.

GLIDING RODENTS

Glaucomys volans 48283. Figure 2.

The dorsad and slightly laterad directed external canal consists of a recessus meatus and a short circular part, which are difficult to separate from each other. The tympanic is fused with the periotic, so that the amount of participation of the two structures in the formation of the ear canal cannot be determined. The much inflated bulla carries two markings on its outside, one on its anterior part, and the other one about its middle. Each corresponds to a septum on the inside of the bulla. These septa run latero-medially; the anterior

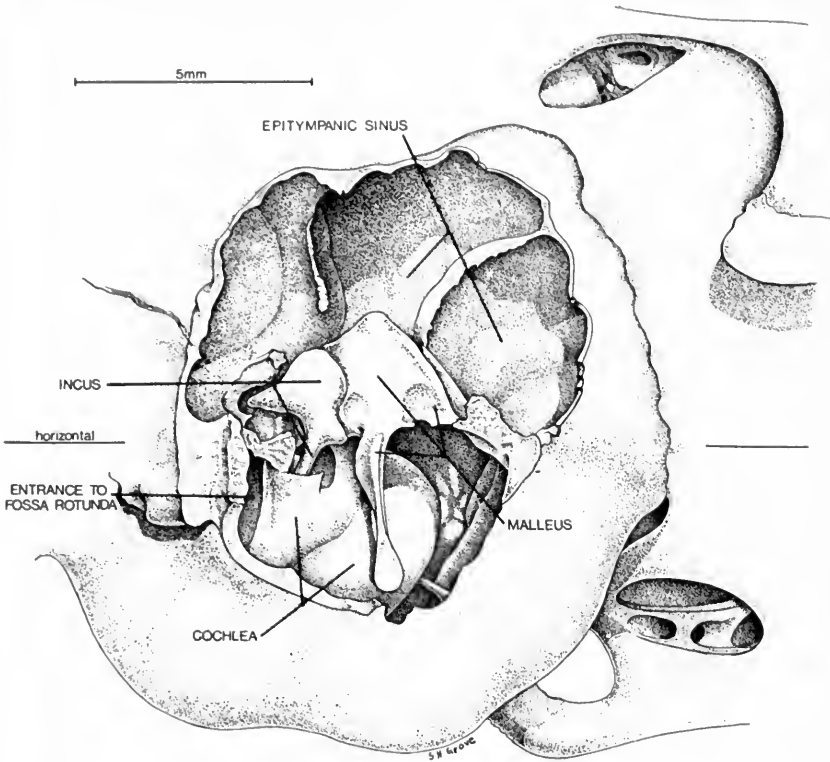


FIG. 7. *Petaurista petaurista melanotus* (98533). Lateral view of right middle ear (obstructing bone removed).

one from the underside of the tip of the cochlea; the posterior from the middle to a point opposite under the sulcus tympanicus. Vertical to the anterior septum another septum branches off which reaches dorsally to the upper end of the anterior tympanic crus. It separates the anterior part of the bulla incompletely into two compartments. The dorso-medial compartment has the inner opening of the Eustachian tube in its floor and continues for some distance caudad into a space medial to the cochlea. There is also a lateral compartment.

Posterior to the bulla is a short paroccipital process. The bulla is separated from the mastoid sinus, which in turn is partly separated from the large epitympanic sinus. The latter is medial to the ossicles in wide communication with the cavum tympani. The smooth walled epitympanic sinus is incompletely subdivided by a

septum and is partly separated by a thin bony wall from the antero-dorsal extension of the bulla. There is no zygomatic sinus present. The sinuses are arranged circularly around the middle ear.

A description of the ossicles has been given in the morphology section of this paper.

Petaurista petaurista melanotus 98533. Figure 7.

The auditory region is very similar to that of *Glaucomys*. Its dimensions are greater, corresponding to the greater size of the skull. The dorsad and only slightly laterad directed external canal consists of a recessus meatus and a cylindrical part. Here, too, the sinuses are arranged ringlike around the cavum tympani, as in *Glaucomys*. Their inner wall is smooth and the septa are very similar to those in *Glaucomys*.

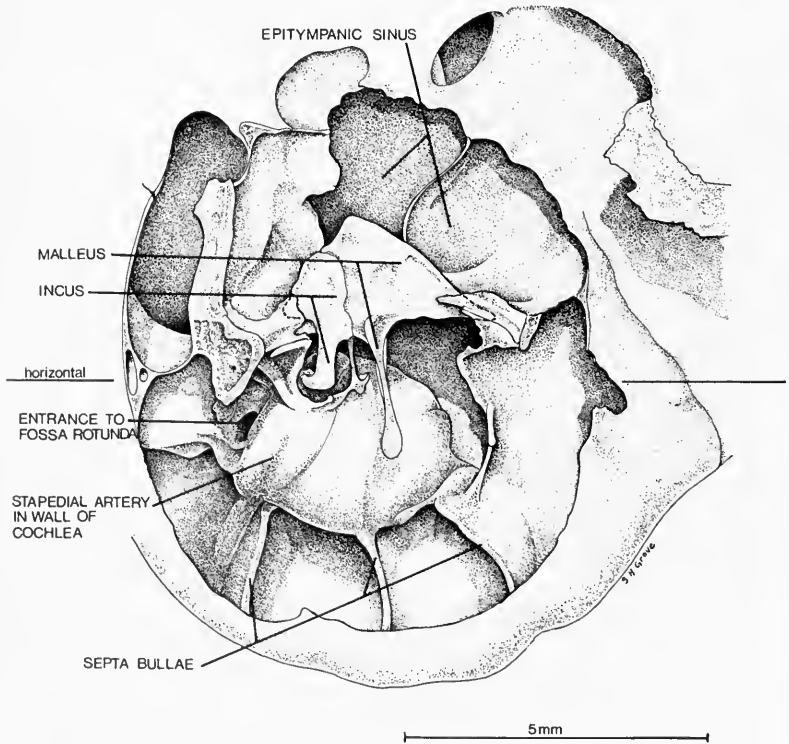


FIG. 8. *Sciurus hudsonicus* (43950). Lateral view of right middle ear (obstructing bone removed).

The auditory ossicles are also very similar to *Glaucomys*. The head of the malleus is bent against the manubrium which has a prominent short process. The pointed posterior processus incudis reaches into the fossa incudis, located in the posterior inferior wall of the epitympanic recess. The distal end of the stapedial crus is directed caudo-medial in addition to the ventral direction and reaches into a dorsally open pocket. This pocket obscures the articulation with the stapes and the stapes itself from a lateral view. A relatively large stapedial artery is present in the same position as in *Glaucomys*.

Hylopetes nigripes 63031

The auditory region of this genus is also very similar to *Glaucomys*. The morphology and topography of the sinuses and their septa are also similar. The same applies to the auditory ossicles, which need no separate description. The arteria stapedia between the crura is enclosed in a bony canal. The stapedial ratio is about 2.2.

Anomalurus fraseri 88208, 88209

The auditory region is generally like that in Sciuridae. It differs in that there 1) are no large septae in the sinuses; 2) is no visible trace of a stapedial artery, nor is there a groove or bony canal for it; 3) is no septum covering the stapes; and 4) is a slightly different form to the head of the malleus with a lower lamina attachment. The stapedial ratio is about 2.2.

NON-GLIDING RODENTS

Sciurus hudsonicus 43950. Figure 8.

Sciurus niger rufiventer 57325

The external canal is formed by the petro-tympanicum. The lower tip of the squamosal reaches the external canal at its upper posterior corner. The bulla is much inflated and shows on its outside three transverse, whitish lines, which correspond to septa on the inside. These septa originate from the underside of the cochlea; the most anterior, close to the tip of the cochlea; the next, from about the middle; and the last from the posterior end of the cochlea. They radiate toward the sulcus tympanicus. The anterior septum has a different morphology and topography than the septum described for some Phalangeridae (see *Discussion*). All septa are very similar to those of the gliding Sciuridae. Dorsally, the epitympanic recessus

is behind the malleus and incus in communication with the sinus epitympanicus, which is incompletely divided by two septa. The posterior root of the zygomatic process is not pneumatized. The cochlea projects with all sides as in *Glaucomys*, except the largest part of its medial side into the cavum tympani. Its fossa rotunda faces caudad.

The ossicles have a very characteristic morphology. The dorsal extremity of the latero-medial flattened head of the malleus is slightly pointed; the malleus reaches higher than the incus; has practically no neck; a short triangular lamina; a saddle-shaped articulation; and a slightly developed short process. The saber-shaped manubrium is only slightly bent medially against the head. It has a slightly concave lateral edge; a muscular process at about the middle of the medial edge; and points practically ventrad.

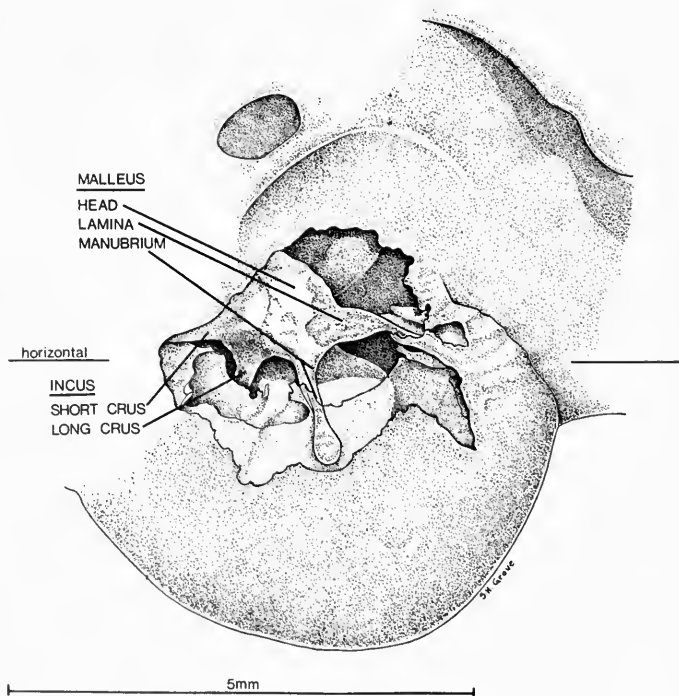


FIG. 9. *Nannosciurus* (92785). Lateral view of right middle ear (obstructing bone removed).

The incus has a robust body and a short posterior crus. The stapedia crus deviates ventrad and slightly caudad and has a longitudinal groove anteriorly.

The deeply set triangular stapes is to a great extent obscured by a bony lamella. The stapedia ratio in *Sciurus niger* is about 2.7. The stapedia artery runs in a bony canal along the lateral edge of the fossa rotunda within the wall of the cochlea to the triangular stapes. It loses the bony canal between the crura.

Callosciurus flavimanus bouhotei 36689

The auditory region is very similar to that of *Sciurus*, therefore, only certain morphological characters will be mentioned. The stapedia crus incudis is directed caudo-mediad beside its ventral direction. The posterior crus incudis is flattened in the horizontal plane. The ossicular functional axis is about parallel with the Frankfurter horizontal. The deeply set, triangular stapes is covered by a bony lamella on its lateral side. The stapes head is elliptical. The anterior crus is slightly convex. The stapedia artery is enclosed in a bony canal, which has a lateral opening under the crura. The stapes ratio is about 3.0.

Nannosciurus (Phillipines) 92785. Figure 9.

The morphology of the auditory region is very similar to that of other Sciuridae. The bulla has no septa and the epitympanic sinus is hardly inflated at all. The morphology and topography of the ossicles is also very similar to that of other Sciuridae. The stapedia crus incudis is directed caudo-medially. The articulation of the stapedia crus with the stapes is in a bony pocket and not visible from the lateral view. The ossicular functional axis is about parallel with the Frankfurter horizontal.

Citellus t. tridecemlineatus 11223, 51738. Figure 10.

The much inflated bulla and the external canal are formed by the petrotympanic. There are two whitish lines on the outside of the ventral bulla wall which correspond to septa on its inside. The ventral end of the squamosal comes very close to the postero-superior angle of the porus acusticus externus. The short paroccipital process is flattened antero-posteriorly and its tip swings antero-medially. The inside of the bulla shows the two above mentioned septa which divide the bulla incompletely into three smooth-walled compartments. One septum runs from the anterior end, the other



FIG. 10. *Citellus t. tridecemlineatus* (51738). Lateral view of left middle ear (obstructing bone removed).

from the middle of the underside of the cochlea ventro-laterally to opposite points of the underside of the sulcus tympanicus. The septum, which divides the antero-dorsal part of the bulla and which has been described in *Glaucomys*, is also present in *Citellus*. Postero-dorsally the bulla continues into a small, smooth-walled mastoid sinus. The recessus epitympanicus continues dorsally into the sinus epitympanicus which is divided incompletely by two septa in compartments. There is no zygomatic sinus present.

The malleus is specialized. Its dome-shaped head continues into a pars cephalica of the processus anterior mallei; the lamina is very small. The articulation surfaces seen from the lateral side form an angle of about 90° with each other. The head is bent only slightly medially against the saber-shaped manubrium. A neck cannot be distinguished. A small processus brevis is present. The manubrium

has sharp medial and lateral edges; is slightly concave laterally; and ends ventrally in a spatula. At about the middle of the medial edge of the manubrium is a muscular process.

The robust incus body continues into a pointed posterior crus. The straight stapedial crus has a concavity on its anterior side; its very distal end is slightly bent medially. The triangular shaped stapes has an elliptical head and between its crura runs a stapedial artery. The artery is enclosed in a bony canal, which is missing under the crura.

Dermoptera

Cynocephalus variegatus 82615. Figure 11A, B.

C. volans 56504

The tympanic forms a recessus meatus and the lower part of the cylindrical ear canal which is directed laterad. The antero-postero diameter of the canal is much smaller than the dorso-ventral diameter and, consequently, has a slitlike appearance in *Cynocephalus volans*. This is less marked in *Cynocephalus variegatus*. There is a long, gradually ascending recessus meatus.

The ear canal is bordered anteriorly by a robust postglenoid process; dorsally by the superficies of the squama; posteriorly by the cellular mastoid process formed by the posterior tympanic process of the squama and the periotic (van Kampen, 1905). The moderately inflated bulla is medial to the tympanic and continues posteriorly into a much inflated cellular mastoid and anteriorly into a short styliform process. Anterior to the latter is a large foramen ovale.

Leche (after van Kampen, 1905) assumes that the bulla is formed by the tympanic. The participation of an entotympanic is questionable. Van Kampen is not sure if the alisphenoid participates in the formation of the tegmen tympani. According to Weber (1928) it does supply a part of the cavum tympani wall.

Malleus and incus described as seen in situ from the ventrolateral view have a very distinct morphology. The articulation between them appears practically flat. On separation, the articulation surface of the incus is slightly concave. The neck of the malleus is very short. Its lamina is narrow; the medially open angle of neck with manubrium is about 135° ; the processus brevis very prominent. The manubrium has flat anterior and posterior sides and is directed ventro-mediad and slightly anteriorly.

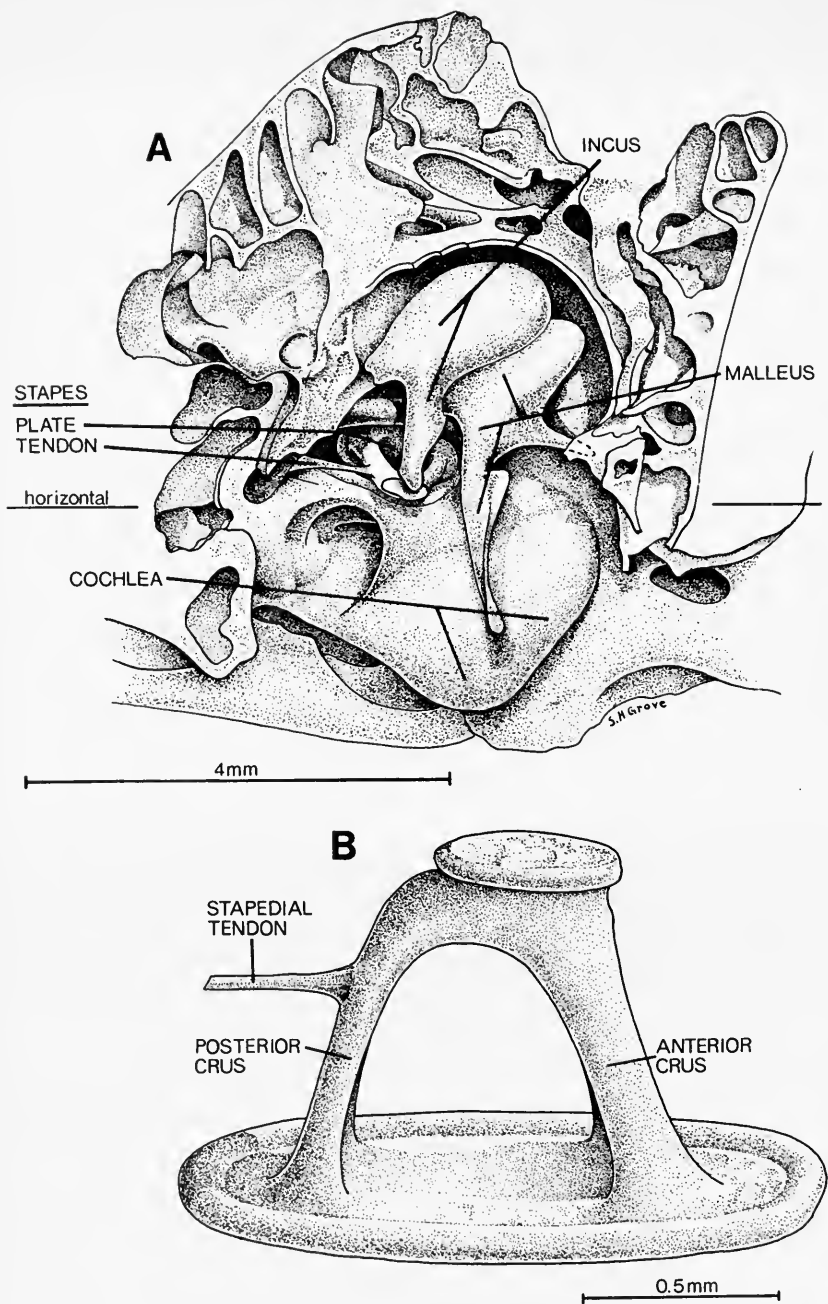


FIG. 11. *Cynocephalus variegatus* (82615). A, Latero-ventral view of right middle ear (obstructing bone removed). B, Left stapes.

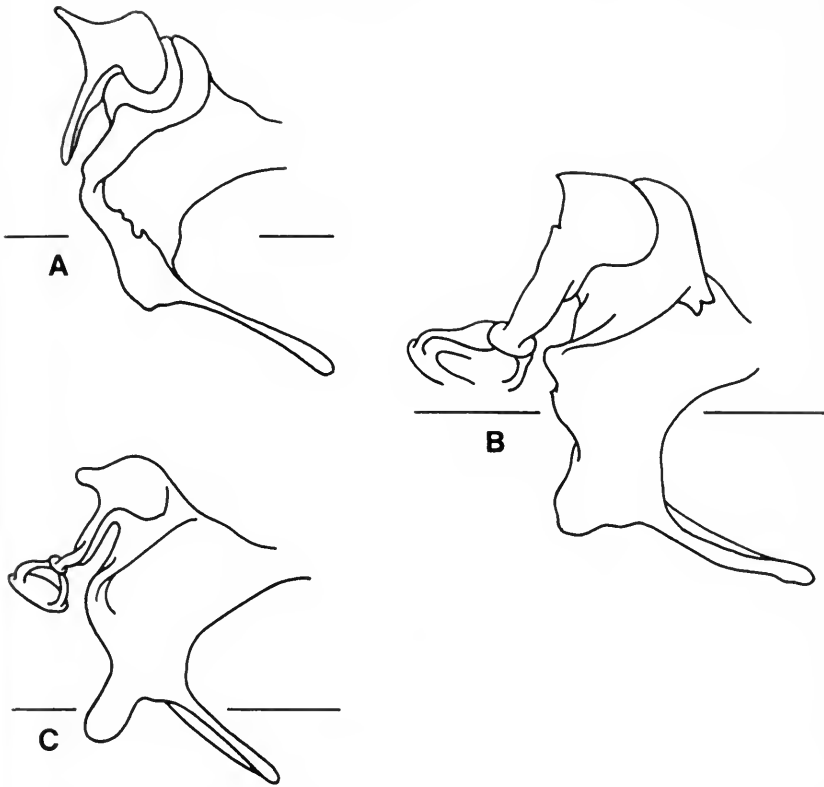


FIG. 12. Diagram of malleus, incus, and Frankfurter horizontal in A, *Didelphis*, B, *Solenodon*, and C, *Oryzomys*.

The incus has a massive body which rises dorsally above the body of the malleus. It extends from dorso-cranial to a ventro-caudad direction. The rudimentary short crus reaches into the fossa incudis in the posterior-inferior wall of the epitympanic recess and the ossicular functional axis is practically parallel with the Frankfurter horizontal.

The stapes head is elliptical, the anterior crus deviates more than the posterior; the elliptical plate has a convex vestibular side and a ratio of about 2.2. No remnant of a stapedia artery can be seen on the macerated skull. The fossa rotunda looks practically caudad. The carotid artery enters a canal in front of the foramen lacerum posterius. This canal is formed by the entotympanic, the periotic, and the basioccipital and leads to the foramen lacerum anterius.

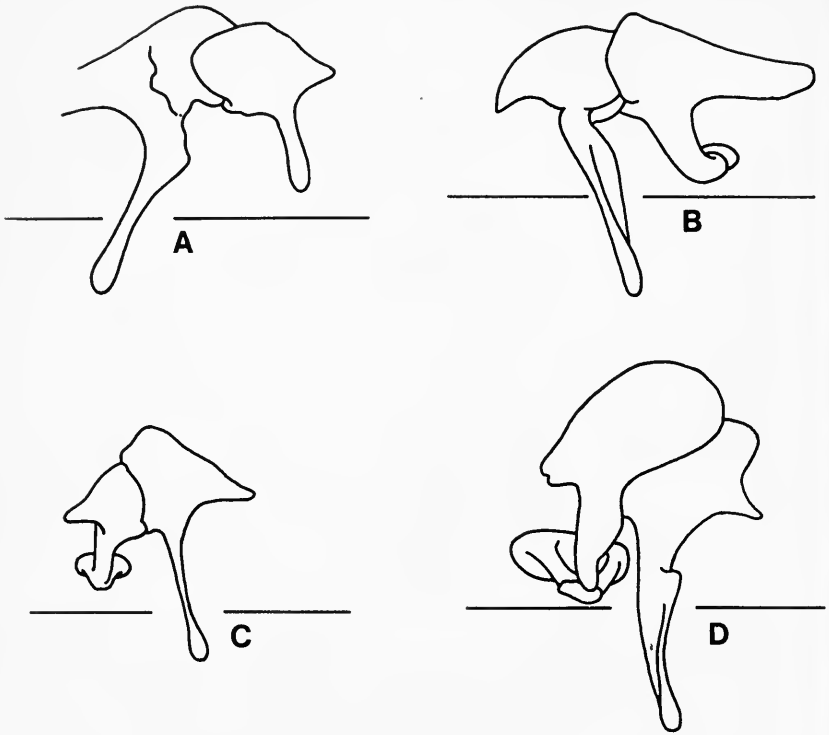


FIG. 13. Diagram of malleus, incus, and Frankfurt horizontal in: A, *Schoinobates*, B, *Tupaia*, C, *Glaucomys*, and D, *Cynocephalus*.

DISCUSSION

OSSICLES

Grossly, the generalized mallei of marsupials, insectivores, and rodents are very similar (fig. 12). This similarity is probably a parallelism based on common ancestry and is of phylogenetic interest.

The specialized mallei, however, of these three orders differ greatly, especially in the configuration of the malleus head; less in the rest of the malleus (fig. 13). The malleus head is a reliable indicator for phyletic differences. This is of taxonomic importance and has been pointed out in a previous study (Segall, 1943).

A similar comparison of the malleus within the order of the Dermoptera is not possible, since this order is represented only by a single living, highly specialized genus.

The mallei of the Sciuridae, gliding and non-gliding genera alike, show great similarity to each other. There is also a great likeness between the gliding and non-gliding Phalangeridae. One may conclude from these facts that the specialization of the malleus in gliders apparently does not correlate with gliding activity.

INCUS

The generalized incus of marsupials, insectivores, and rodents are similar (fig. 12). The posterior crus incudis reaches into the fossa incudis located in the recessus epitympanicus. The ossicular functional axis forms an angle of between 15° and 30° with the Frankfurter horizontal. This angle decreases with specialization (Segall, 1969b, 1970).

There are similarities in the incus between marsupial gliders and rodent gliders. Hardly any, however, exist between the incus of these two orders and that of the dermoptera in which the malleus has also very distinct morphological features (fig. 11A).

In all gliders the fossa incudis is located in the lower end of the posterior wall of the epitympanic recess and the ossicular functional axis runs about parallel with the Frankfurter horizontal. This position is characteristic for all specialized incus, not for the incus of gliders alone.

STAPES

The difference between the generalized and specialized rodent stapes is of interest. The crura of the generalized rodent stapes are somewhat curved (*Oryzomys*, *Perimyscus*), reminiscent of the insectivore stapes (fig. 1B). The stapes plate is oval with a ratio of about 1.5 as in some generalized marsupials and insectivores (fig. 14). Lower stapes ratios are usually found in generalized auditory systems; high ratios in specialized ones (Segall, 1970). Those rodent genera with a low stapes ratio have also a generalized malleus similar to the generalized malleus in marsupials and insectivores (figs. 12, 14). These facts are of phylogenetic interest.

The straight crura of the specialized stapes in rodent gliders are divergent and form a triangle. A similarly shaped stapes can be seen in some insectivores (*Nasilio*). The stapedia ratio in *Glaucomyss* is 2.2, in *Nasilio* 2.0 (fig. 14).

2.2	*ACROBATES DROMICIOPS		*CYNOCEPHALUS	CALLOSCIURUS 3.0 SCIURUS 2.7
2.1	*SCHINOBATES PSEUDOCHEIRUS *PETAURUS	NASILIO ELEPHANTULUS		*HYLOPETES
2.0				*GLAUCOMYS
1.9				
1.8	PHALANGER	HYLOMYS		
1.7				
1.8				
1.5				ORYZOMYS PEROMYSCUS
1.4	DIDELPHIS			
1.3				
1.2				
1.1	DASYURUS			
1.0	TACHYGLOSSUS			
	MONOTREMES	INSECTIVORES	DERMOPERA	RODENTS

Fig. 14. Stapedial ratios. Gliders indicated by asterics.

While there are similarities between the generalized stapes of the insectivores and rodents, there are none between the stapes of these two orders and the marsupial stapes, except in the stapedia ratio. The marsupial stapes has in all forms, generalized and specialized alike, a columella-like shape, similar to that of the monotreme stapes. In most marsupials the columella divides close to the plate into two crura with a more or less oval opening between them. The stapes plate can be practically round, as in *Dasyurus*, with a stapes ratio of 1.1, which increases in the specialized stapes to 2.0, as in *Schoinobates*, and to 2.2 in *Dromiciops*, similar to the stapes ratio in some insectivore stapes, as, for example, 2.0 in *Nasilio* (fig. 14) and 2.5 in *Scalopus*.

The stapes in marsupials shows no trace of an artery between the crura in the macerated postembryonic skull. In all insectivores and in most rodents a stapedia artery or remnants of it are present. In rodents the stapedia artery is usually smaller than in insectivores. The size and the location of the artery during the embryonic stage may influence the shape of the stapes (Werner, 1960). In that stage a stapedia artery is always present, later it may completely disappear; may become rudimentary; or may remain well preserved (Tandler, 1901).

Fossorial insectivores and *Tupaia* have the artery enclosed in a bony canal (Segall, 1970). This is also true in many rodents. In Dermoptera no stapedia artery can be seen in the macerated skull.

The fossa rotunda in Sciuridae is mainly directed caudad. In the generalized auditory regions of some rodents, as in *Peromyscus* and *Oryzomys*, it faces caudo-laterad.

In the generalized auditory forms of rodents, as in *Oryzomys*, the stapedia artery runs antero-laterally to the fossa rotunda in an open groove over the cochlea (fig. 1). In the specialized Sciuridae the artery runs laterad to the fossa rotunda enclosed in a bony canal in the postero-lateral and ventral edge of the cochlea (fig. 8). In insectivores the artery also runs in an open groove over the cochlea, as in the generalized auditory forms of some rodents.

A similarity exists between the generalized auditory region of some insectivores and rodents with respect to the three ossicles and the angle of the ossicular functional axis with the Frankfurter horizontal.

The ossicles of the marsupial gliders have a great similarity to the ossicles of the non-gliding members of the same family. Also,

the ossicles of the rodent gliders are very similar to the ossicles of non-gliding members of the same family.

While the malleus and incus become highly specialized, the stapes remains rather conservative in its morphology. This can be seen in the Dermoptera where malleus and incus are highly specialized. The stapes, however, has kept characteristics similar to the stapes in some insectivores and in bats. This will be discussed in a following study on the auditory region in bats.

SINUSES

Marsupials with a generalized ear region, as *Didelphis*, have a partially bony bulla and no epitympanic or mastoid sinus. In *Dasyurus* the bulla is well developed and a small smooth-walled mastoid sinus is present. All the Phalangeridae, gliders and non-gliders alike, have a large sinus system with small variations in their development. They have a large bulla, which is somewhat bigger in the gliders; an epitympanic sinus; a mastoid sinus; and a zygomatic sinus. The last three sinuses are cellular in contrast to the sinuses of most rodents. In the superficial meatus *Phascalomys* has a large cavity which is divided by a transverse projection into an anterior and a posterior part. *Macropus* also has a concavity in the squama, smaller than in *Phascalomys*. The concavity is in communication with the cavity in the posterior root of the zygomatic process by way of the foramen postzygomaticum.

A septum in the bulla in some marsupials and some insectivores deserves special attention. In *Didelphis*, which has only a very small entotympanic, a large part of the ventral bulla wall is not ossified. The posterior part of the tympanic process of the alisphenoid is turned slightly dorsad. This is also the case in *Caenolestes*, which has a large open space between the alisphenoid process and the periotic. An entotympanic is not present. In *Caluromys* the latter is large and approaches the tympanic process of the alisphenoid closely. The posterior edge of the latter turns slightly dorsad, separating to a slight extent the front section of the bulla cavity from the posterior one. The same condition prevails in *Isoödon*. In some marsupials on the inside of the bulla wall is a low septum located at the border between the tympanic process of the alisphenoid and the entotympanic. It is present in the Phalangeridae (*Phalanger*, *Pseudocheirus*, *Trichosurus*, *Schoinobates*, *Petaurus*) and also in *Dromiciops* (Segall, 1969a). All of them have a completely ossified bulla.

The septum begins at the anterior tip of the promontorium, shields the Eustachian tube antero-laterally and runs to the underside of the sulcus tympanicus. The topography of its medial end is constant. Its further course laterad shows variations. From the location and from the slight upturn of the posterior end of the tympanic process of the alisphenoid above the anterior end of the entotympanic mentioned in some taxa, one may assume that this septum is formed by the tympanic process of the alisphenoid. Its course is often marked on the outside of the bulla as a whitish line. This line is especially clearly marked in *Dromiciops*, where it runs latero-mediad (Segall, 1969a). Again, this line is also clearly visible in *Petaurus*.

There is no septum visible in the bulla of *Macropus*. The tympanic process of the alisphenoid is long and the posterior part of the bulla wall is probably formed by an entotympanic (van Kampen, 1905). Neither is a septum visible in *Phascalomys*, where the tympanic process of the alisphenoid is substituted by a process of the squama. A septum in position similar to that described above is also found in some insectivores, for instance, in *Hylomys*. The importance of this septum and the possible presence of an entotympanic was not recognized during the preparation of my paper on insectivores (Segall, 1970). The name "septum sphenoidium" is suggested for this structure.

Rodents with a generalized auditory region and generalized auditory ossicles have a smooth-walled, flat bulla without any septa (*Oryzomys*, *Peromyscus*) and no other sinuses. *Sciurus*, *Nannosciurus*, *Citellus*, and *Callosciurus* and the rodent gliders with specialized auditory regions have a well-developed sinus system. The sinus wall is smooth in contrast to the Phalangeridae, where the sinuses are cellular, except for their bulla. There is a septum or septa, which subdivides the cavity. Rodent gliders have, in contrast to the *Phalangeridae*, no sinus in the posterior root of the zygomatic process.

The Dermoptera have large sinuses, also, which are very cellular. The posterior zygomatic root is also pneumatized and cellular in this order.

Summarizing, it can be stated that genera with a generalized auditory region have a poorly developed sinus system. A large sinus system is a sign of specialization.

BULLA

In all gliding marsupials, rodents, and Dermoptera the bulla is complete. A complete bulla is a sign of specialization. The completeness of the bulla is generally correlated with the specialization of malleus and incus; to the angle of the ossicular functional axis, which is about zero; and to the relatively high stapedial ratio. There are, however, some rodents in which malleus and incus have retained general characters although the bulla is complete.

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