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THE MALLEUS (OSSICULUM AUDITUS) OF THE ANTHROPOID APES

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In an earlier study of the auditory region of the arctoid carnivores (Segall, 1943) the morphology of the malleus was found to be the most useful feature in indicating affinities between genera and families. As is well known, the location of the ossicles within the cavum tympani renders them less susceptible to environmental influence than any other feature of the morphology. This is especially true of the dorsal contour of the malleus, which is in contact with no other structure. In addition, there is no significant difference in the functioning of these bones within mammalian physiology. Thus it seems that the ossicles should be among the most conservative of all morphological structures.

As pointed out in my earlier paper, the distinctive features of any clear value in classification are confined chiefly to the malleus, and for this reason only that ossicle has been considered in the present work. No comparative study of the anthropoid ossicles has been made since Doran's classic treatise (1877).

The material used in this study is in the collection of Chicago Natural History Museum, except the ossicles of *Symphalangus*, which were lent by the United States National Museum. All known genera, and all the important species except *Hylobates lar*, are represented.

The accompanying drawings were made, with the use of a camera lucida, by Miss H. Elizabeth Story, Assistant in the Division of Vertebrate Anatomy. Mr. D. D. Davis, Curator of Vertebrate Anatomy, has provided assistance and valuable advice throughout the course of the study.

GIBBONS

On the basis of the morphology of the malleus the gibbons fall into two groups.

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GROUP 1

DARK-HANDED GIBBON (*Hylobates agilis*)

The head of the malleus is subglobular, with its longest diameter from caudal to cranial and slightly lateral. The cranial end is enlarged. The articulation surface is divided by the prominent vertical ridge into a relatively large external and a small inner part. The articulation plane covers the posterior and a small part of the adjacent lateral faces of the head of the malleus. There is a pointed anterior process and a small muscular process. The handle is slightly curved in its entire length, and its tip is spatulate.

GRAY GIBBON (*Hylobates cinereus*)

The head is subglobular. In dorsal outline it is somewhat elongated cranio-caudally but does not diminish cranially. The longest diameter is from caudal to cranial and slightly lateral. The external part of the articulation plane is only slightly larger than the inner part. The vertical ridge is not very marked. The anterior process is short and the muscular process hardly visible. The handle is sturdy and is curved along its whole length. Its tip is spatulate.

Hylobates cinereus is included in Group 1 although its articulation facet does not show the characteristics of that group.

MUELLER'S GIBBON (*Hylobates muelleri*)

The shape of the head is as in *H. agilis*. The longest diameter is directed from caudo-medial to cranio-lateral and thus is rotated more laterally than in *H. agilis*. Its cranial end is globular and continues in a very short, ventrally directed process. The articulation plane is very similar in all its characters to that of *H. agilis*. The neck is very short. There is a muscular process. The handle is slightly curved along its whole length, and its lower end is spatulate.

HOOLOCK (*Hylobates hoolok*)

The form of the head resembles that of *H. agilis* but is more angular. The process seen on the cranial face in *H. muelleri* is here elongated into a vertical ridge. The articulation plane is very similar to that of *H. agilis*. The neck is short, with a short pointed anterior process. The muscular process is rudimentary. The lower end of the handle is slightly curved and spatulate.

KLOSS'S GIBBON (*Brachitanytes klossi*)

The form of the head is very similar to that of *H. agilis*. As in that species the longest diameter is directed from caudal to cranial

and slightly lateral, and the cranial end is subglobular. The configuration of the articulation plane is identical with that of *H. agilis*. There is a short neck, with a small anterior process. The muscular process is very short. The handle is slightly curved in its whole length, and the tip is not spatulate.

GROUP 2

SIAMANG (*Symphalangus syndactylus*)

The head of the malleus is oblong in outline and is only slightly narrower cranially. It continues cranially into a short sharp process

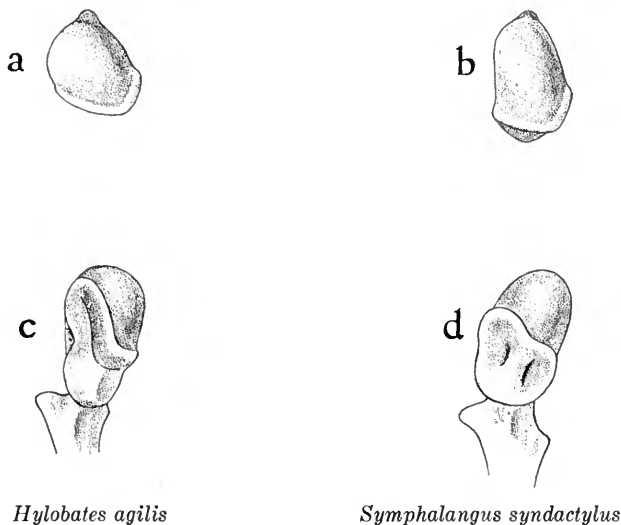


FIG. 15. Mallei of gibbons, showing characters of Groups 1 and 2. a, b, dorsal view of head; c, d, articulation facet. Left malleus, $\times 8$.

directed cranio-ventrally. The long diameter of the head is directed approximately cranio-caudally. The articulation surface is heart-shaped, with the external part only slightly larger than the internal. The vertical ridge projects very slightly. It covers only the caudal face of the head. There is a short anterior process and a rather well-developed muscular process. The handle is straight, except that its lower end is slightly bent and spatulate.

BUFF-CHEEKED GIBBON (*Hylobates concolor gabriellae*)

The long diameter of the head is approximately cranio-caudal. The head is slightly shorter than in the preceding species and has a

more oval outline. The articulation plane is as in *Symphalangus*. There is a small muscular process, and the lateral process is as in *Symphalangus*. The handle is practically straight, its lower end slightly bent and spatulate.

WHITE-CHEEKED GIBBON (*Hylobates concolor leucogenys*)

The head is elongated and more irregular in outline than in any other form examined. The longitudinal axis is approximately cranio-caudal. The cranial end of the head is pointed. The articulation plane is approximately heart-shaped. The anterior and lateral processes are well developed. There is a very small muscular process. The handle is straight, its lower end curved and spatulate.

The mallei of the gibbons fall into two distinct groups, distinguished by several characteristics. The first group includes *Hylobates agilis*, *H. cinereus*, *H. muelleri*, *H. hoolok*, and *Brachitanytes klossi*. The hoolock exhibits the characters of this group, except that the head is much more flattened. The articulation plane in *H. cinereus* is more like that of Group 2, but the globular form of the head and the curvature of the handle conform with Group 1.

Group 1 is characterized as follows:

- (1) The longest diameter of the head is directed from caudo-medial to cranial and slightly lateral.
- (2) The cranial end of the head is enlarged and globular.
- (3) The articulation plane covers the caudal face and a small part of the adjacent lateral face of the head. The vertical ridge is prominent and is close to the inner border of the articulation plane. The external facet is much larger and more elongate than in the second group.
- (4) The handle is curved in its whole length. It is spatulate except in the one specimen of *Brachitanytes* available for examination.

The second group includes *Symphalangus syndactylus* and *Hylobates concolor*. The characters of this group are less clearly seen in *H. concolor leucogenys* than in the others, but this form belongs to the group.

Group 2 is characterized as follows:

- (1) The head is elongated like a cylinder, diminishing slightly in size cranially.

- (2) The longest diameter of the head is directed approximately cranio-caudally.
- (3) The articulation plane covers the caudal end of the head. It is heart-shaped. Its vertical ridge is less prominent than in Group 1. The external facet is only slightly larger than the inner.
- (4) The handle is straight, its lower end slightly curved and spatulate.

Miller (1933) united all the gibbons under the generic name *Hylobates*. On the basis of various morphological characters, supported by zoogeographic considerations, he recognized four groups (subgenera) among the gibbons. His subgenus *Nomascus* contains the Indo-Chinese forms of *Hylobates*, and his subgenus *Hylobates* the Indo-Malayan forms of *Hylobates*. *Symphalangus* and *Brachitanytes* are reduced to subgenera. The morphology of the malleus supports the distinctness of Miller's subgenera *Nomascus* and *Hylobates*, but not of *Symphalangus* and *Brachitanytes*. The malleus indicates that *Symphalangus* has close affinities with *Nomascus*, and *Brachitanytes* with *Hylobates* (subgenus), and we have therefore recognized two groups in place of the four proposed by Miller.

GREAT APES

CHIMPANZEE (*Pan satyrus*)

The head of the malleus is oval in outline. The long axis is directed from medial and slightly caudal to lateral and slightly cranial. The articulation surface is heart-shaped. The vertical ridge dividing it into a larger outer and a smaller inner part is situated near the middle of the articulation plane, slightly closer to the inner border. The neck is short and flattened latero-medially. The sigmoid ridge is only slightly visible. The processus gracilis is very small. There is no lamina extending from this process to the neck. Internal to the processus gracilis is a minute muscular process. The handle is longer and more curved than in man. The lateral side of the handle is rounded, and its distal end is spatulate. The lateral process is directed laterally and slightly dorsally. In all details the malleus is very similar to that of man.

ORANG (*Pongo pygmaeus*)

The head of the malleus is more angular in outline than in the chimpanzee. The long axis is directed from medial and slightly

caudal to lateral and slightly cranial. The cranial face of the head is produced into a short process. The upper half of the articulation plane is about equal in size to the lower one, in contrast with man and the chimpanzee, where the upper half is much larger. The neck is flattened in an approximately latero-medial direction. No

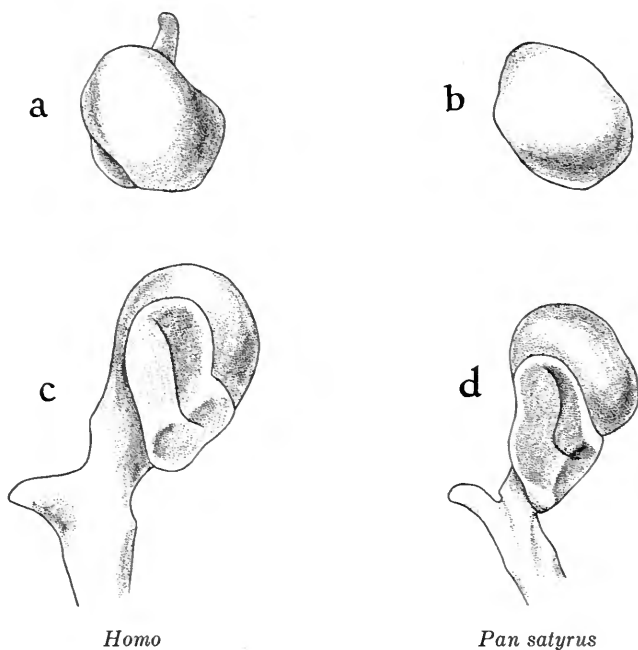


FIG. 16. Mallei of chimpanzee and man, showing characters of Group 1. *a, b*, dorsal view of head; *c, d*, articulation facet. Left malleus, $\times 8$.

sigmoid ridge is discernible. There is a very short *processus gracilis*. The handle shows cranial and caudal faces, separated by a ridge that is not so sharp as in the gorilla. This edge enlarges distally into the slightly bent spatulate tip. Cranially, it continues into a short lateral process.

GORILLA (*Gorilla gorilla*)

The head of the malleus is oval in outline and corresponds in size to the other anthropoids. The long axis is directed approximately cranio-caudally, in contrast to the two preceding genera. There is a sharp vertical ridge on its cranial side. The cranial end is slightly pointed; it is more round in man, the chimpanzee, and the orang. The upper and lower facets are about equal in size, which

gives the articulation plane a quadrangular outline as in the orang. The vertical ridge is in the middle of the plane. The neck is short and flattened in a latero-medial direction. There is a slight sigmoid ridge. The processus gracilis is straight and pointed, and a muscular process is just visible. The angle between head and neck is about

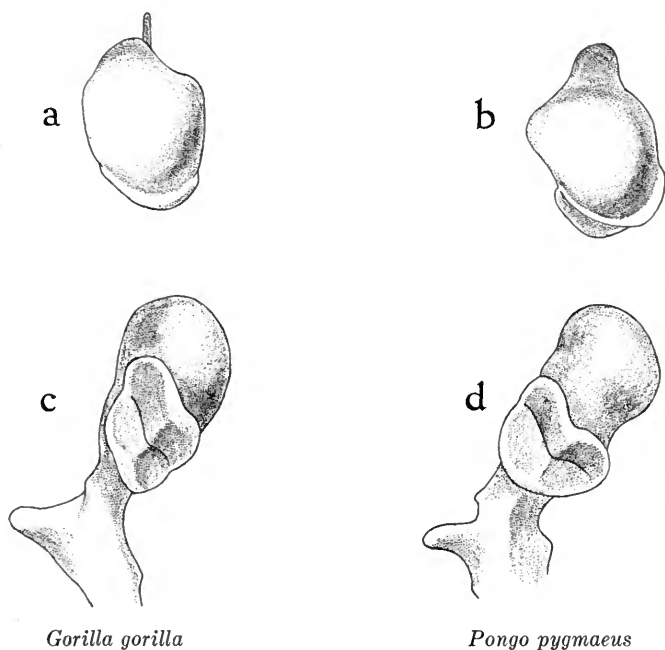


FIG. 17. Mallei of great apes, showing characters of Group 2. *a*, *b*, dorsal view of head; *c*, *d*, articulation facet. Left malleus, $\times 8$.

the same as in the genera already described. The handle is relatively long, and its lower end is curved and spatulate. Its cranial and caudal faces are separated by a rather sharp lateral edge, unlike that in man and the chimpanzee. The edge continues above into the straight, well-developed lateral process and downward into the spatulate tip.

A malleus of the mountain gorilla (*Gorilla beringei*) was also examined. No difference could be detected between this form and *G. gorilla*.

The malleus of the chimpanzee is very similar to that of man in nearly all respects, in accordance with the findings of Doran. This is true of the outline of the head, the direction of its long axis, the

shape of the articulation plane, and the direction of the neck. The gorilla and the orang differ from the chimpanzee-human type in several respects. In a few characters, such as the approximate direction of the long axis, the quadrangular outline of the articulation plane, and the presence of a process on the cranial side of the head, the gorilla and orang approach each other. In other respects, however, such as the outline of the head, they differ not only from each other but from the chimpanzee as well.

Thus in the form of the malleus the chimpanzee is very similar to man, while the gorilla and orang resemble each other, but far less closely than the chimpanzee does man. Two groupings are indicated: (1) man, chimpanzee, and (2) gorilla, orang. It is a curious fact that the first group of gibbons is suggestive of the chimpanzee group, while the second group of gibbons recalls the gorilla-orang type. The similarities are apparent in the dorsal contour of the head, the articulation plane, and the curvature of the handle.

SUMMARY

On the basis of the morphology of the malleus the gibbons fall into two groups: (1) *Hylobates agilis*, *H. muelleri*, *H. hoolok*, *H. cinereus*, and *Brachitanytes klossi*, and (2) *Hylobates concolor* and *Symphalangus syndactylus*.

The remaining anthropoids are likewise divisible into two groups: (1) man and chimpanzee, and (2) gorilla and orang.

Some general similarities were discovered between Group 1 of the Hylobatinae and Group 1 of the remaining anthropoids, and between Group 2 of the Hylobatinae and Group 2 of the remaining anthropoids.

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