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## Contributors

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### ON THE COMPARATIVE ANATOMY

OF THE

## AUDITORY OSSICLES OF THE MAMMAIIA

#### BY

### ALBAN H. G. DORAN, F.R.C.S.

### (Abstract.)

The following observations have been made during the preparation of a series of the small ear-bones of the higher Vertebrata for the Museum of the Royal College of Surgeons of England, an undertaking which was commenced in the autumn of 1874, and is in the course of rapid enlargement up to the present date.

The foundation of the entire series was a small collection of the osseous auditory apparatus of the domestic and common indigenous animals of Germany, purchased by the College of Dr. Max Hübrich, of Munich, a few years since. Following the suggestions of the Conservator, Professor W. H. Flower, F.R.S., the author succeeded in removing from the crania of mammals in the College Museum a sufficient number of auditory ossicula to illustrate the characters of those bones in most of the important subdivisions of that class of vertebrated animals. Numerous additions from rare specimens have been obtained through the kindness of Sir Victor Brooke, Bart., Professor Parker, Professor A. H. Garrod, and other gentlemen.

These observations are now brought forward with the object of demonstrating how far the characteristics of the auditory ossicles of the different orders of the Mammalia accord with those distinctions throughout the whole organization which have assisted anatomists up to the present day in giving a definite position to each member of the class. Dr. Hyrtl has already published a well-known work on the Comparative Anatomy of the Internal Auditory Apparatus of the Mammalia<sup>\*</sup>, but the subject of the ossicula themselves has not been considered in that able treatise quite fully and precisely enough for the present purpose.

All the Mammalia are known to possess three of these small bones, named respectively the *malleus*, the *incus*, and the *stapes*; the two former are occasionally fused. Their form and characters in our own species may be regarded as fairly typical, so that it is advisable to commence the subject by considering the ossicula of *Homo*.

Speaking from the stand-point of comparative anatomy, we may describe the malleus of man as having a well-developed head somewhat compressed antero-posteriorly and expanded laterally. It rises considerably above its articular region, and bulges markedly in an outward direction. The articular surface lies on the posterior aspect of the head very obliquely, so that its external extremity lies much higher than the internal. It is generally spoken of by human anatomists as forming one single saddle-shaped facet; but on comparing it with the same surface in the malleus of most of the lower mammalia, say in a cat or a pig, it will be seen that it is in reality made up of two facets, much less distinct than in those animals, but more marked than in many monkeys. A very faint groove divides them, and runs in the very oblique long axis of the whole surface. The more internal and upper facet above this groove represents that which is almost completely superior in the lower animals, the more external, below the groove, corresponding to their lower facet. Both rise into a high vertical convexity about the middle of the surface, where the latter is a little contracted; their planes slope towards the groove, so that the articular surface appears concave. especially when viewed sideways.

The neck of the human malleus is constricted and shorter than in most of the Mammalia, though longer than in most of the Primates. On its extero-superior aspect is a sharp sigmoid ridge, beginning near the anterior border of the articular surface, and losing itself on the root of the manubrium. This ridge is of the same form, and probably represents the sharply curved entire neck of the malleus of most Carnivora and Ruminants and many other Mammalia, where a bony lamella extends from that portion as far as the processus gracilis. A very faint trace of that "lamina," as it may briefly be called, may be seen extending, in a fully developed foetal human malleus, from the neck to the root of the processus gracilis; but it seems reasonable to infer that the stout, compact portion of the neck in front of the sigmoid ridge represents in a more solid form the lamina referred to. Close to the root of the manubrium, and on the inner side, a very faint eminence, to which the tensor tympani is attached, represents the processus muscularis of some other mammals. The well-known processus gracilis of the malleus of Homo is known to be to a great extent absorbed in the process of extra-

\* Vergleichend-anatomische Untersuchungen über das innere Gehörorgan des Menschen und der Säugethiere. Prague, 1845.

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uterine growth, and hence is far less stable than in animals where it is held together, speaking roughly, by the manubrium.

The manubrium is rather short, and forms with the neck an angle of about 140°. It is broader at the base than in the Simiidæ, and flattened laterally; still the sides are slightly convex. The extremity is slightly recurved and spatulate, and the processus brevis is very well developed.

The body of the incus in *Homo* is well developed and rather longer than deep vertically; the crura are very divergent, and the "processus brevis," or posterior crus, very high in the natural position of the bone, is stout and rather long; the long, slender "processus longus" is gently curved, and bears a small os orbiculare or Sylvian apophysis rather firmly seated on a not very thin pedicle.

The stapes of man is noted for the great width of its aperture, although there is no canal between its crura as in many lower animals. The head is proportionally rather small, and the anterior of the two slender crura is the straightest. The footplate is necessarily wide horizontally, but rather narrow vertically; its outline is reniform, the upper border being convex or arched, the lower is slightly concave in the middle. Its posterior extremity is blunter than the anterior, and it is somewhat convex towards the vestibule.

Comparing the ossicula of Homo with those of the Simiidæ it appears :---

1st. That the ear-bones of *Homo*, *Troglodytes*, and *Simia* closely resemble one another.

2ndly. The malleus of *Hylobates* has greater affinities to the above genera than to the lower monkeys, but the incus and stapes are of a lower type.

3rdly. The ossicula of *Troglodytes niger* are altogether most like those of *Homo*; but in the form of the head and articular surface of the malleus *Simia* most approaches Man. The malleus of the gorilla is less human than the chimpanzee's, the outer segment of the articular surface being wide, whilst its manubrium more resembles that of *Simia*: but the incus and stapes of *T. gorilla* are very much like the same ossicula in *Homo*.

4thly. Taking the characters of these high animals into general consideration, we must conclude that they tend far more towards *Homo* than to the tailed Old-World monkeys.

The ossicula of the CERCOPITHECIDE possess several prominent characters, some of which are absent in certain genera; and they are most marked in *Macacus*. These peculiarities are principally:—in the malleus great shortness and great constriction of the neck, and a manubrium forming a very wide angle with the rest of the bone, possessing both a processus brevis and a processus muscularis, and well dilated at the extremity; in the incus a square or high and narrow body, and in the stapes extremely straight crura; this latter feature is constant.

Semnopithecus in its incus, and in the slight lateral compression of the well-developed head of the malleus, approaches the Simiidæ, but in the characters of the neck and manubrium and of the whole stapes it resembles the other genera of this group. *Cercopithecus* comes next, the head of the malleus being well developed and prominent; but its incus is generally square-bodied or high and narrow. In *Colobus* and *Cercocebus* the head of the malleus is almost as flattened and comparatively illdeveloped as in *Macacus*, and the incus is similar. In *Cynopithecus* and *Cynocephalus* the flattening of the head of the malleus and shortness of its neck and other characters already referred to are as marked as in *Macacus*, and there are no distinctions of the slightest importance between the ossicula of those three genera. In the shortness of the neck and form of the incus the Old-World monkeys resemble or tend more towards the Cebidæ than to Man.

The PLATYRRHINI differ considerably in their ear-bones from the Old-World monkeys, and chiefly in the complete or practical absence of the neck of the malleus in all genera excepting *Ateles*, and the peculiar shape of the neck in that genus. The Hapalidæ have mallei which approach in type the corresponding ossicle in the Lorises (Nycticebidæ), and the stapes, by the partial fusion of its crura, reverts to a condition frequent among the Edentata and Marsupialia. Such fusion may be seen both in *Hapale* and *Midas*, but is not constant.

Whilst Ateles differs from all the other Cebidæ in its malleus, Cebus closely resembles that genus in having a similar incus; but in the absence of neck to the malleus it rather resembles Mycetes. In the high narrow incus Pithecia agrees with Mycetes.

Among the LEMURIDÆ the ossicula of the Galagos, Nycticebidæ, and Propithecus differ hardly at all from the type of the smaller Cebidæ. In Lemur the neck of the malleus, and often a trace of the processus brevis mallei, reappears; and in that genus and the Indrisinæ there is a bony canal between the crura of the stapes not observed in the Galagos and Lorises or in Tarsius. Whilst retaining certain points of resemblance to Lemur, the ossicula of Chiromys decidedly remind the observer of the same bones in certain Rodents, especially the Castoridæ and Sciuridæ.

Among the CARNIVORA the auditory ossicles of the Fissipedia differ completely in character from those of the Pinnipedia.

The ossicula of the terrestrial flesh-eaters bear on the whole a strong general resemblance to one another; still they present some interesting points of distinction in the more typical families. These distinctions are mostly to be found in the malleus. The presence of a lamina of thin bone between the neck of the malleus and the processus gracilis is a constant character, except in *Herpestes* and its allies; and there is always a processus muscularis for the tendon of the tensor tympani, except in the Bears, as Hyrtl has observed.

Putting aside the Ursidæ, which are at once readily distinguished from all other families by the absence of that process, the more typical divisions present certain salient distinctions in the malleus. In the cats and dogs the muscular process is long, slender, and curved; but in the

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Canidæ the manubrium forms a bold curve with the concavity forwards, and its outer surface, towards the membrana tympani, is broad throughout; in the Felidæ this curve hardly exists, and the outer aspect is very narrow. In *Hyæna* and *Proteles* the processus muscularis of the malleus is very stout, blunt-pointed, and almost straight, and the manubrium is curved as in the dogs; its outer aspect is broader near the tip than at the base in the *Hyæna*, but broad throughout in *Proteles*. Hence the mallei of these animals are more canine than feline, particularly that of the Aard-wolf. Among the Canidæ themselves *Lycaon* most approaches the Hyænidæ in the stoutness of its processus muscularis. In all the above families, as well as in the Civets and in the *Cryptoprocta*, the incus is small with slender crura, the posterior almost as long as the processus longus, and the stapes is small and triangular.

The Procyonidæ, Æluridæ, Viverridæ, and Cryptoproctidæ resemble one another in the ill-development of the processus muscularis of the malleus, which, however, is never quite absent. The outer surface of the manubrium in those families is narrow, as in *Felis* and *Ursus*. In the *Ælurus* and the Procyonidæ, including *Bassaris astuta*, the incus has a very short processus brevis, as in the bear; in the Civets and *Cryptoprocta* that crus is well developed, as in the cats and dogs. From the above observations it follows that *Crypt procta* is more Feline than Canine, and more Viverrine than Feline, in the character of its malleus.

The weasels and the other Mustelidæ are known from the rest of the Fissipedia by the extreme narrowness of the lamina of the malleus, and the very wide angle which the rather short manubrium forms with the neck. The processus muscularis of the malleus is as well developed as in the cats and dogs; but the Mustelidæ exceed the bears and the Procyonidæ in the extreme ill-development of the posterior crus of the incus. In the smaller weasels the base of the stapes is generally bullate.

In the genera *Herpestes* and *Suricata* the malleus differs in form from the type existing in the other Viverridæ and the rest of this suborder. The head of that ossicle is more developed, but there is hardly a trace of a lamina. The processus muscularis is not situated on the neck close to the root of the handle as in the other Carnivora, but on the inner edge of the manubrium itself. The incus is of the form seen in *Felis*, *Viverra*, and *Canis*, not of the ursine type.

The ossicula of the Pinnipedia are large, well marked, and readily distinguishable in the different genera.

The Otariidæ are exceptional in having very small ossicula, but they are of dense consistence as in the true seals. The malleus has a head which is concave anteriorly, and the articular surface is of the same prominent character as in *Phoca*. The neck is constricted, and the manubrium rather longer than in the other Pinnipedia. The incus differs from that of all other members of this suborder; in its non-divergent posterior crus and its long, far-reaching slender processus longus it is almost arctoid. On the other hand, the stapes has oftener fused crura without any aperture (as in the dolphins) than in the Phocina.

The walrus possesses a malleus with a head much like that of *Phoca*; but the articular surface is less abnormal in character, and above all the manubrium is extremely short. The incus is phocine; but in the stapes *Trichechus* approaches *Macrorhinus*.

The ossicula of *Macrorhinus* differ very markedly from those of *Cystophora*; in the malleus the former resembles *Stenorhynchus*, whilst in the stapes it is more like *Trichechus*. The stapedes of *Stenorhynchus* and *Cystophora* are more of the *Phoca* type. In the Phocinæ alone is seen a second articulation between the malleus and incus, and this feature is not constant in every species.

Among the UNGULATA the laminated type of malleus prevails; the processus muscularis is rarely quite obsolete, but seldom very long. The incus is very variable in form, and bears important distinguishing features in certain families. A quadrilateral form of stapes, due to great breadth of the head of that ossicle, occurs very frequently.

Among the Perissodactyla *Equus* in its malleus least resembles the remainder of the whole order, the head of that bone being well developed above the level of the articular surface as well as anteriorly, and the lamina is almost obsolete. In the Rhinocerotidæ (where all the ossicula are proportionally very small) and in the Tapirs the malleus has a narrow lamina, not simply extending between the head and the processus gracilis, but running forwards to the very extremity of the latter. All these animals have perfectly triangular stapedes, differing from the form almost constant in the larger Artiodactyla.

In the Tylopoda the malleus resembles that of the pig and its allies in the great anterior development of its head; but unlike those animals the articular surface of that ossicle is wide and shallow, as in the Rhinoceros on the one hand and the larger Ruminants on the other; but it most resembles *Rhinoceros* in the ill-development of the processus muscularis mallei and in the triangular form of the stapes.

In the Suidæ, in *Hippopotamus* and *Phacochærus*, the head of the malleus is greatly produced forwards with a rather deep articular surface; the lamina and the processus muscularis are well developed. The incus has a typical character; the body is very square in form, with the crura short, especially the posterior. The form of the articular surface in *Hippopotamus* and in large specimens of *Phacochærus* differs from the same in the pigs. *Hippopotamus*, though so large, has a triangular stapes, whilst that bone is quadrilateral in the Suidæ, as in the ox and adult sheep.

In *Tragulus* the malleus is indistinguishable from those of many small antelopes and deer, the head not being produced forwards as in the pigs; whilst the incus retains to perfection the square body and short posterior crus of the Suidæ.

The Bovidæ, Antilocapridæ, Camelopardalidæ, and Cervidæ are re-

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markable for the strong resemblance which the ossicula of the adults of the smaller species bear to those of the mature foctus or young of the larger members of those families. The head of the malleus is always ill-developed, the processus muscularis always present, and the manubrium is frequently very long. In the adult *Bos* the great shallowness of the articular facet of the malleus, the bold curve of the manubrium, the very high and well-developed body of the incus with its long and divergent processus brevis, and the quadrilateral form of the stapes are all very distinctive; on the other hand, in the adult *Ovis* the articular surface is deeper and the facets less level than in *Bos*, and the manubrium is almost straight; nor is the body of the incus so developed, although the posterior crus is very long. The stapes is nearly as quadrilateral in a large adult *Ovis aries* as in *Bos*, but it often remains triangular in small sheep.

In the lamb or fully developed fætal sheep the articular surface of the malleus is still deeper cut and the facets more prominent than in the adult; the incus has a shallow body and the stapes is quite triangular. Most of the remaining Bovidæ imitate, in the ossicula of the adults, the types of the ox, the sheep, or the lamb. Thus in the wild sheep, the goats, and many small antelopes, as *Nemorhædus*, *Oreotragus*, and *Saiga*, the ossicula much resemble those of the young Ovis aries; Gazella and its allies are more bovine in the type of the malleus, whilst the stapes is generally triangular, even in the adult; the incus appears quite transitional between Ovis and Bos, the body being almost square; indeed as the posterior crus is sometimes rather short in these antelopes, that ossicle approaches the pig and chevrotain type. Nanotragus, Cephalophus, Neotragus, Tetraceros, and Nanohædus are also balanced in characters between Bos and Ovis.

Kobus, Tragelaphus, Alcelaphus, and Catoblepas lean more, in the general characters of the auditory ossicles, towards Bos; the gnus are remarkable for the great length of the manubrium, which is straighter than in the ox. In the adult Ovibos and Anoa the ossicula are slightly more calf-like than ox-like.

The ossicula of *Camelopardalis* are remarkably like those of *Bos*, and undergo similar changes during the growth of the animal. In *Antilocapra* the ossicula have not strongly defined characters, although perhaps they most resemble those of the medium-sized antelopes. The quadrilateral form of stapes allies it to *Ovis* or *Bos*; the incus, as in *Gazella*, may either be considered intermediate between the form in those two domesticated ruminants, or (as the posterior crus is not long) to relate the prong-horn antelope to the Chevrotains.

In the Cervidæ the malleus always retains in the adult the characters seen in the fully developed fœtal ox, the articular surface having wellmarked facets, and the manubrium being almost straight. The processus muscularis is large in the genus *Cervus*. The body of the incus is always shallow, with an even, stouter, and more divergent posterior crus than in other ruminants. The stapes remains triangular in full-grown large deer. *Moschus* is quite cervine in its ossicula, the shallow body and thick, long, divergent posterior crus of the incus being very different from the square-bodied incus with short crura seen in the Tragulidæ.

Among the RODENTIA we find great variety in the form of the auditory ossicula in different families, as is also the case among the Insectivora. Nearly every type of malleus may be observed among the various subdivisions of the order, such as the large-headed, distinctly necked form of the higher Primates, the neckless variety of the lower monkeys, the laminated type of the ruminants and terrestrial carnivora, and the fused condition of the malleus and incus of the guinea-pig and its allies. The stapes, too, varies, being sometimes large in proportion to the size of the animal, in other cases very small in large species.

The most constant character in the rodent's malleus is the broad, laterally flattened manubrium, with a processus muscularis on its inner edge far from the neck of the ossicle, which may be said to present three prevailing types—the neckless form in the squirrels, the laminated variety of the rats, and the malleo-incudal fusion of the Hystricidæ. The incus varies little, and its processus brevis is always shorter than the anterior crus, and but little divergent. A bony canal between the crura of the stapes is frequent in several families.

Classifying the animals intermediate in the character of the malleus between the genus Sciurus, where it is neckless without a trace of any processus brevis, and Castor, where both neck and process exist, the genera will be found to run as nearly as possible in the following order :--Sciurus, Anomalurus, Marmotta, Tamias and Spermophilus, Pteromys, Myoxus and Castor, the separation of the head from the manubrium becoming more and more apparent in each of these genera towards the last; but, taking other points into consideration, Anomalurus should be placed after the ground-squirrels, having a small stapes with crura not very divergent, as in the Hystricidæ; and Marmotta separates itself from other sciuroid rodents by the peculiar form of its head, which is extremely flattened laterally and projects above the articular surface. In all the above rodents, except Anomalurus, the stapes is large, with wide, thin, divergent crura; and an intercrural bony canal exists in most species.

In the Muridæ the malleus has a well-formed lamina and a manubrium rather broad at the base. The former peculiarity is most marked in *Mus, Hapalotis, Hydromys*, and their allies, where an orbicular process standing out from the front of the neck is a frequent feature, and appears identical with a similar projection in the shrews, and is probably an extreme development of the sharp angular protuberance seen in the malleus of the badger, and in that from a *Bassaris* in the College collection. In *Fiber* the lamina is smaller and the manubrium broader than 1876.]

in *Mus*, so that the malleus more resembles that of *Lepus*. The stapes of this family has generally long, slender, and not very divergent crura, and the intercrural canal is wanting.

In the Hystricidæ the great feature is the ankylosis of the malleus to the incus, already well known to zoologists. It is almost invariable in the adults of that family. The manubrium is very broad, and the inper edge above the processus muscularis is very thick. The varieties among the different genera are trifling: the head of the malleus is produced forwards to an extreme degree in *Aulacodus*, *Capromys*, and particularly in *Chinchilla*, but less so in the porcupines and the agouti. The stapes is always proportionally small, with stout and not very divergent crura; a bony intercrural canal occurs in many genera, but is an inconstant feature in individual specimens of the same species.

As the ankylosis of the two outer ossicles occurs in *Dipus*, whilst the head of the malleus remains small and unproduced, and that bone possesses a wide lamina, it must be considered intermediate, as far as those little bones are concerned, between the Muridæ and Hystricidæ.

As occurs in other orders, the fossorial members of the Rodentia present great peculiarities in their ear-bones. In *Geomys* the malleus somewhat resembles that of *Marmotta*; the stapes is remarkable for the large bulla on its base. *Rhizomys* and *Ellobius* approximate most to the rats, *Bathyergus* to the Hystricidæ, which it exceeds in the degree of fusion of the malleus to the incus, which latter bone, however, differs in form from the same in that family. In *Spalax* the malleus approaches the more central type of *Castor* or *Lepus*; but the stapes is of a very unique type, somewhat similar to that of *Chrysochloris*, except that one crus is quite straight and very divergent.

In both species of ELEPHANT the large ossicula appear rather like the modified ear-bones of certain rodents than like any ungulate. There is neither the lamina or long manubrium mallei, nor the thick and divergent processus brevis incudis, nor the quadrilateral stapes frequent among the large Ungulata; on the other hand the short, broad-based manubrium, the thin, short, and hardly divergent processus brevis of the incus, and the wide intercrural aperture of the stapes are characteristic in *Elephas* and common among the Rodentia.

In the HYRACES the ear-bones bear a slight affinity to those of the horse, but none of any importance to the common types among the Ungulata or Rodentia.

The ossicles of the remaining groups of the Mammalia will be described in a subsequent communication.

