The tympanic region of the mammalian skull

by P. N. van Kampen*

[p.466]

VI. Tubulidentata

Wall of the middle ear

The tympanic bone of *Orycteropus* (Fig. 31) contributes neither to the construction of the wall of the middle ear cavity nor to the wall of the external ear tube. The tympanic has the form of a slightly slanted, large, thick, and dorsally incomplete ring. The anterior crus broadens into a plate whose lateral margin ends ventrally with a short process. The point of the posterior crus is very thin and at its end bent into a hook-shape.

Except for the Processus Folii, the tympanic bone is not fused with any bone. It also lies entirely free, the ends of the two crurae excepted. The anterior crus immediately behind the glenoid fossa abuts with the squamosal; the posterior crus covers the tympanohyal laterally, but remains separate from the squamosal.

The tympanic and the ear drum form the external wall of the middle ear cavity. The inner wall is entirely formed of the promontorium, which ends in a sharp crest.

Between the tympanic an petrosal there remains an additional open fissure, which according to Hyrtyl is closed during life only by a membrane. An ossified tympanic tube is thereby not distinct on the skull.

The alisphenoid extends between petrosal and tympanic and forms the anterodorsal wall of the middle ear cavity.

Arterial course

Hyrtyl (1850) describes a stapedial artery, “which reaches the drum-cavity through a hole in the posterior wall in the middle ear bone; it rises onto the promontorium towards the stapes via a fairly deep groove, moving to the upper wall of the ear cavity, and ultimately into the braincase, between the crurae of the stapes.” The groove for this artery lies orally from the fenestra cochleae; the foramen spinosum, through which the artery leaves the middle ear cavity, is probably the small opening, which is evident on the border between the tegmen tympani and squamosal (see fig. 31 "f. sp.").

Concerning the course of the carotid itself, after it gives off the stapedial artery, I find no information. According to the descriptions of Hyrtyl, one could conclude that this artery is missing. However, as Hyrtyl himself says, his investigation was based on an “extremely mangled skull” and may not be very reliable. As far as evident from the skull, the internal carotid is preserved for its entire extent: a deep groove travels from posterior to anterior over the promontory, and from this branches a much shallower groove for the stapedial artery. Anteriorly on the promontory, the former groove ends near the carotid foramen; contrary to Rapp (1852) this is not missing. Its identity as such is demonstrated by the fact that it travels through the basisphenoid.

Judging by this groove, the carotid most likely runs through the middle ear. Because the ventral wall of the middle ear is lacking, this is not certain in a dry skull.

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Epitympanic sinus
Several researchers have described the epitympanic recess in the squamosal. This is not very large and has a wall that except for a few low bands is smooth. It communicates with the middle ear cavity with a very broad pneumatic foramen, which lies largely anterior to the epitympanic recess. According to Hyrtyl (1850) this foramen is closed by a strong, fibrous diaphragm, to which stick the neck of the malleus and the long crus of the incus. As a result, the epitympanic recess forms a part of this sub-cavity.

Following Hyrtyl (1845) and Huxley (1864) the part of the alisphenoid which borders the middle ear cavity has a concavity, which serves to enlarge the middle ear and is a continuation of a concavity in the squamosal. In the skulls I have examined, at least among those which show a suture between the alisphenoid and squamosal, this kind of participation of the alisphenoid in the middle-ear cavity is not an issue.

Hyoid skeleton and facial canal
"The fallopian canal" writes Huxley (1864, p. 253), "[quote in English bottom p. 468]."

This hook-like process is a short tympanohyal. It lies in the posterior wall of the middle ear cavity, inside of the point of the posterior crus of the tympanic. According to Parker's description (1886b), it ossifies independently.

The point of the tympanohyal is free; the stylomastoid foramen is therefore only incompletely enclosed in bone.

Summary
The ventral wall of the middle ear cavity of the Orycteropodidae shows the simplest-possible condition, since there is no ossification. From this perspective they correspond to the Sirenia, with whom also the form of the large and thick tympanic ring shows a superficial similarity; the tympanic is not broadened either interiorly or laterally.

Through the possession of a stapedial artery and the form of a short tympanohyal, *Orycteropus* is reminiscent of the lowest mammals. Correspondences with the other so-called "edentates" (Pholidota, Xenarthra) consist only regarding those points in which these taxa retain primitive characteristics. Only the epitympanic sinus in the squamosal is more particularly a derived feature of edentates (*Manis*, *Bradypus*, *Myrmecophaga*); but is also evident in other mammals and thereby can be explained as nothing more than convergence.

[p. 636]

XIII. Cetacea

<u>Delphinidae</u>, <u>Delphinapteridae</u>

The area of the petrotympanic
Before the bulla itself is described I will provide a short description of the surrounding petrotympanicum, which among the Cetacea many deviations from the normal type are apparent. This description has been repeated, most recently and thoroughly from Beauregard (1893 for *Delphinus delphis*) and Boenninghaus (1904 for *Phocaena communis*).

The petrotympanic (Fig. 83) is not sutured to the rest of the skull, rather ligamentously joined with it. Following the normal pattern it is surrounded by the squamosal, exoccipital, and alisphenoid. These bones enclose on either side of the skull base a deep, irregular trough in which the petrotympanic lies. Medially, the wall of the trough is composed of the basioccipital and its strongly raised edge, the basioccipital process.

The basioccipital process is separated posteriorly from the paroccipital process by a break, the basioccipital incisure von Boenninghaus. The paroccipital process is a short but broad lamellar process, which with its concave anterior surface composes the posterior wall of the groove. The squamosal articulates directly with the exoccipital and borders the trough laterally. This bone is characterized by a strong part behind the glenoid fossa, which in addition is covered by the exoccipital. The superficial aspect of the meatus is externally short, although rather broad, and a posttympanic process is absent. From the medial wall of the glenoid fossa arises a free, medially directed, flattened process, the falciform process (Beauregard), which ventrally along the alisphenoid helps to enclose the anterior wall of the trough and which must be regarded as the Pars entoglenoid of the squamosal. The remaining anterior wall of the trough, above the falciform process, is composed of the alisphenoid. This anterior wall is not as complete and much lower as the other walls of the depression and forms only an incomplete separation.

The braincase-directed floor of the trough is normally only closed in part by the parietal, which is so extended along the squamosal on its inner side, that it excludes not only this bone from the braincase but also is apparent in the base of the trough and laterally composes some of its floor (fig. 83). It may however occur that the floor of the trough (as among physeterids) is almost completely closed; Huxley (1864) indicates as much for *Delphinapterus* and *Orca*, and following the illustrations of von Beneden and Gervais (1880) is also the case for many other genera. Following Huxley, this closure occurs due to extension of the alisphenoid. Incidentally, the floor will also become more and more closed, where it is initially wide open, through extension of the surrounding bones in old age. This is consistent with the rule, which according to Boenninghaus (see p. 218) is generally valid for the cranial openings in *Phocaena*.

The external entrance to the described depression is for the most part closed by the petrotympanic, which extends laterally to the squamosal, medially almost to the basioccipital process, which entirely covers the inner wall of the bulla. The petrotympanic separates the opening to this in two: one is the anterior lacerate foramen, before the petrotympanic; and another, more posteriorly situated, which is directed towards the floor of the hyoid and Facialis [nerve]. The medial part of the opening occurs together with the basi-paroccipital incisure, and allows the passage of the vagus and glossopharyngeal nerves, plus the jugular vein, and thereby comprises a posterior lacerate foramen.

The petrotympanic and middle ear [p. 638]
The bony ventral wall of the middle ear is entirely composed of the tympanic, and generally fuses with the petrosal early in ontogeny.

The tympanic (fig. 83) shows among the various delphinids and delphinapterids few differences. It is extensively described, in particular by Beauregard (1894) for *Delphinus delphis* and by Denker (1902) and Boenninghaus (1904) for *Phocaena phocaena* (communis), while additionally, in the systematic literature, countless more or less comprehensive descriptions are scattered. A bulla is constructed, which in the rule among sea-living mammals is very hard and thick-walled. Especially the medial lip is unusually thick. This lip has an inwardly uneven edge, within which a broad fissure (petrotympanic fissure) opens between it and the promontorium. In addition there are two features that provide the bulla its characteristic external appearance. First, the posterior underside is divided into two lobes by a deep, elongate groove; “de des deux lobes l’externe repond au fond de la gouttiere tympanique; il est donc creux; l’interne au contraire est plein et forme tout entier par la levre interne massive” (Beauregard 1894). The groove is filled with connective tissue (Bonninghaus). And thereby the Orificium tubae, which is nothing more than the anterior part of the petrotympanic fissure, is particularly broad and high; as a consequence the bulla is anteriorly stretched into a half-canal and takes on an elongate appearance. In *Globicephalus* this anterior elongation is sharply pointed.

The external ear opening lies as a consequence of this groove-shaped extension of the bulla in the posterior half of the bullar external wall. There is a very short external ear opening, which has frequently been overlooked by previous authors, although not always as Boenninghaus believes; also Flower has spoken for example often about a “meatus auditorius externus”. Also Beauregard describes it comprehensively, however without having recognized it, so it seems, as an external ear opening. Its wall is externally uneven. Anterior and ventral walls comprise a sharp angle with the eardrum and thereby also a meatal recess. This comprises the most conspicuous [ansehnlichsten] part of the bony auditory meatus, which in addition is through the thickness of the walls somewhat elongated. Insofar as the anterior and ventral lips of the ear tube are externally separated through a deep groove, which is directed ventrally from the anteroventral angle of the meatal opening, both lips have on their own the external appearance of a distinct process: the anterior lip is the sigmoid process (“apophyse sygmoïde”) of Beauregard, the short, cusp-shaped ventral lip is the Processus conicus posterior (“apophyse conique postérieure”) of Beauregard, the Processus medius of Boenninghaus. The first lip is in the ventral half of its concave surface directed towards the middle ear (Beauregard); the concavity is directed exteriorly from the tympanic sulcus and comprises thereby a small bulge of the external ear tube. In contrast, the cavity (similarly described by Beauregard) of the posterior conical process communicates with the middle ear under the sulcus and, as a consequence, the latter protrudes somewhat towards the interior of the middle ear (fig. 83). The auditory canal possesses in addition a small posterior and dorsal wall: the former is composed of the stem of the posterior process of the tympanic (to be described later), the latter of an approximately horizontal ledge, which from this process (in *Delphinus delphis* in contrast from the mastoid, according to Beauregard) extends anteriorly and remains separate from the sigmoid process only via a narrow fissure. Both parts (stem and ledge) of the posterior process protrude in *Tursiops* a bit farther exteriorly from the tympanic membrane. This is not the case for the stem in *Phocaena* and therefore in this place a defect in the auditory tube is present (Boenninghaus).

Via the aforementioned narrow fissure, the external auditory tube communicates, as described by Beauregard, with a second opening, which similarly leads to the middle ear and dorsally is enclosed by the petrosal (tegmen tympani). This opening, the petrotympanic aperture (“orifice petro-tympanique” of Beauregard, hiatus epitympanicus Boenninghaus), which communicates via an air-sinus with the middle ear, leads to the epitympanic recess where the malleus and incus are visible from the outside. Boenninghaus regards this opening as “one of the unique openings of the whale ear,” the origins of which are due to a strong distension of the lateral wall of the bulla, which also results in the removal of the tympanic membrane from the hammer. “Hence with them [i.e., the distensions] the ring of the tympanic membrane...

[***Bottom of p. 639 cut off***]

[top of p. 640, starting “so entstand...”]

...thus arose a fissure, the epitympanic hiatus, between this incision and the periotic” (*loc. cit.* p. 257). This fissure would however just as well arise without the enlargement. It corresponds with the area that among all mammals is evident between the pars tensa of the tympanic membrane and the margin of the tegmen tympani, and which normally is enclosed via the squamosal and Membrana flaccida. When the petrotympanic occupies its normal position in the skull, it is evident that in this area the squamosal abuts with the tegmen tympani and comprises a roof over the petrotympanic aperture, while farther anteriorly a fissure remains free for the air-sinus. This roof, composed of the squamosal, is the original lateral wall of the epitympanic recess, which has undergone some reduction, probably in relation to the creation of an air-sinus. A similar condition is apparent among many ungulates and is therefore not a unique characteristic of cetaceans.

Anterior to the sigmoid process, the margin of the bulla is thickened and turned interiorly, forming a process directed towards the middle ear. This is the “apophyse conique antérieure” of Beauregard. Boenninghaus referred to it as the Processus tubarius, because it served to attach the eustachian tube and appropriately enables comparison with the similar process of some ungulates. It adheres to the tegmen tympani (to the processus anterior periotici of Boenninghaus). Between this process and the sigmoid process is a small opening, the glaserian fissure, lying between the edge of the bulla and the tegmen tympani (Boenninghaus). Boenninghaus calls the processus tubarius and the sigmoid process together the processus anterior ossis tympanici. This process helps to border a depression in the outer wall of the petrotympanic; medially it is closed by the processus tubarius, posteriorly by the processus sigmoideus, and dorsally by the edge of the tegmen tympani. In its floor lies the glaserian fissure. This groove is the “Schalltrichter” (sound-funnel) of Boenninghaus.

Beyond here, the petrosal and tympanic are only connected in one other place. Behind and above the auditory meatus, the tympanic has a broad and massive process (processus petrosus Denker, processus posterior Boenninghaus), which adheres to the bulla via a narrow connective part. In *Globicephalus* this process is long, sideways directed and pointed, and shows through this strong development similarity to physeterids. The connective part is often pierced by a posteriorly directed opening, the posterior aperture (“orifice postérieur”) von Beauregard, and the process is connected to the tympanic through two bony crurae that are oriented laterally to one another. The opening permits an air sac of the middle ear to pass through (see below). The air sac is present for example in *Delphinus delphis* (Beauregard) and *Tursiops tursio*, and is absent in *Phocaena phocaena* (Boenninghaus; Denker mentions it here, but can mean nothing else except the posterior end of the petrotympanic fissure) and *Globiceps* (Beauregard).

Interiorly and anteriorly, a similar process of the petrosal attaches itself to the Processus petrosus (Processus tympanicus of Denker). This appendage is to be considered as the Pars mastoidea. Among young animals, both processes, that of the petrosal and that of the tympanic, are separated by a joint. Later they grow with one another and comprise a short, thick, cusp-like process, directed posteriorly and slightly exteriorly. It is this process that primarily holds the petrotympanic onto the skull, specifically on the border of the exoccipital and the squamosal, along a more-or-less visible border formed of these two bones. Only the part of the process that belongs to the tympanic is externally visible, in the angle composed of the inferior border of the squamosal and exoccipital. In contrast the mastoid is totally covered, as noted by Beauregard.

The internal carotid conducts itself according to the descriptions of Beauregard and Boenninghaus in *Delphinus* and *Phocaena* as follows: embryonically it is well developed, but by adult animals rudimentary. It reaches via the posterior lacerate foramen the posterior wall of the petrotympanic; and near the facial nerve and under the fenestra rotunda it enters the middle ear between the tympanic and petrosal. Due to the persistent opening of the petrotympanic fissure, there is no sharply enclosed posterior carotid foramen present. Rather, it is in the caudal portion of the fissure itself into which the carotid enters. Inside the middle ear the carotid runs lengthwise along the promontory, surrounded by a venous corpus cavernosum, which penetrates the middle ear via the petrotympanic fissure. The carotid leaves the middle ear again through the anterior end of the petrotympanic fissure, tunneling through the pneumatic vestibule (see below), and follows its way towards the carotid foramen of the skull.

A stapedial artery is absent.

Long since documented are the large air sacs of the Delphinidae, which are composed of protuberances of the mucosa of the middle ear, and which are connected through its various openings of this cavity's wall. Because the air sacs have only walls of tissue, only the way in which the cavity communicates with the middle ear will primarily be addressed. After the last and most comprehensive description of the whale ear of Boenninghaus, there are in *Phocaena phocaena* two systems of this sinus to distinguish:

The anterior cavities move out from a central chamber, the pneumatic vestibule. The latter communicates with the eustachian tube and with the orifice of the eustachian tube directly with the middle ear. This is probably the cause of the large breadth of the eustachian opening. A part of these cavities is received in a concavity of the pterygoid.

The posterior cavities move directly out from the middle ear. To these belong:

> The peribullar pneumatic sinus (between tympanic and basioccipital process), which communicates with the middle ear through the petrotympanic fissure, ventral from the above-mentioned corpus cavernosum.
>
> The peripetrosal pneumatic sinus, which surrounds the petrosal and connects with the middle ear at its posterior end, between the facial nerve and carotid artery, once again through the petrotympanic fissure.
>
> The paroccipital pneumatic sinus ("sac postérieur" von Beauregard) is small and lies in the concavity of the paroccipital process. In *Phocaena* it is an appendix of the peripetrosal sinus; in *Delphinus* it is linked with the middle ear through the posterior aperture (missing in *Phocaena*) (Beauregard).

The epitympanic pneumatic sinus ("sac moyen" von Beauregard), similarly small, extends primarily under the falciform process of the squamosal and communicates with the middle ear through the epitympanic hiatus. It is therefore to be considered a protuberance of the flaccid membrane.

Hyoid bone and facialis canal

The facial nerve proceeds in the normal fashion from the tympanic aperture lengthwise along the periotic through a furrow which ends in the stylomastoid foramen. This opening is surrounded only by the petrosal and is linked with the caudal end of the petrotympanic fissure, from which the opening therefore comprises a bulge. Immediately external to the stylomastoid foramen the facial nerve turns laterally and makes a furrow on the posterior process of the petrotympanic. In *Tursiops tursio*, the dorsomedial margin of the stylomastoid foramen has a deep, narrow lateral buckling (narrow only through a communication with the edge), which probably presents the fossa for the stapedius muscle.

According to previous data from Hallman and others, the hyoid apparatus is fastened to the exoccipital. Stannius (1846, p. 367) disputed this interpretation and found in both fetal and adult specimens of *Phocaena* and *Monodon* the normal attachment of the hyoid apparatus to the petrotympanic. This contradiction is explained by the fact that both connections may be found: Flower (1885) describes this for *Globicephalus melas* as follows: "[quote here in English, middle of p. 643]." The hyoid shows in this perspective therefore great correspondence with the Sirenia and is, as in the latter group, opisthotrematic. However, I have never successfully found in either *Globicephalus* or other species a tympanohyal.

<u>Platanistidae</u>

The surroundings of the petrotympanic

As far as can be determined from the literature, (particularly Eschricht 1851, Flower 1869c, and Anderson 1878), the surroundings of the petrotympanic in platanistids is not that different from that of delphinids. The greatest difference is that in *Platanista*, the synclinal depression for the anterior aspect of the petrotympanic is in a similar way enclosed in part through the hollowed-out pterygoid, as is the case in balaenids. *Inia*, however, does not show this peculiarity; while in *Stenodelphis* (*Pontoporria*) *blainvillei* an intermediate form between the two is present (Flower). The processus falciformis ("hook of Camp," from Eschricht) is according to Eschricht strongly developed in *Platanista*.

Anderson describes in Platanista a posterior tympanic process, "[quote in English, top of p. 644]"

The floor of the depression is in *Inia* (Flower) and *Platanista* (Eschricht) wide open as in *Phocaena*. However, according to Anderson, the opening is in older specimens of *Platanista* divided into anterior and posterior lacerate foramina.

The petrotympanic

The petrotympanic itself also corresponds for the most part with delphinids, as described particularly in the comprehensive, but not very precise, descriptions of Anderson and further in that of v. Benenden and Gervais (1880), so that I need not describe this structure comprehensively. The tympanic is anteriorly pointed (as in *Globicephalus* among the delphinids), and in *Inia* less so than in *Platanista* (Flower).

In contrast to the delphinids, the petrotympanic in *Platanista* does not fall out due to maceration, but rather is held in place by the surrounding bones. According to Eschricht, this condition arises via the strong development of the falciform process. According to Anderson, the pterygoid also contributes; he describes at least the anterior portion of the petrosal as "[quote in English, middle of p. 644]." This condition comprises a resemblance between the Physeteridae and the Balaenidae. The posterior process of the petrotympanic seems also to be slightly more developed in *Platanista* than in delphinids, at least according to the descriptions of Eschricht and Anderson. The latter author describes the mastoid as follows: "[quote in English, bottom of p. 644]." Along with this Anderson also describes the posterior process of the tympanic, which is supposedly much less developed than the pars mastoidea; if this is correct, then it would comprise a difference from physeterids, in which the reverse is true. In contrast to Eschricht, Anderson (and also Hyrtyl 1845) indicates that the attachment of the petrotympanic arises from the posterior process.

In *Inia* and *Stenodelphis* the petrotympanic has a similarly loose connection with the skull as in delphinids (Flower).

Hyoid apparatus and facial nerve canal

Eschricht describes in *Platanista* a connection of the cartilage of the anterior hyoid horn with the paroccipital process, totally in correspondence with delphinids.

Physeteridae

The surroundings of the petrotympanic

The surroundings of the petrotympanic do not deviate greatly from the Delphinidae. According to Beauregard (1893), this region of the skull in *Physeter macrocephalus* is in almost complete correspondence with *Delphinus*. A comprehensive description is therefore redundant; only may it be pointed out that a falciform process is also present and already described and illustrated in *Physeter* by Camper (1820, p. 108, tables 20 & 22). In contrast to delphinids, the falciform process contributes to the attachment of the petrotympanic to the skull. "The Camper's hook of the temporal bone" says Eschricht (1849) in his description of *Hyperoodon*, "clasps the Labyrinth so firmly, that even when the labyrinth is totally broken, it still requires a certain grasp of the hand to avoid breaking the Hook."

The opening, through which the floor of the cavity (in which the petrotympanic lies) communicates with the braincase, is according to the description of v. Beneden et Gervais (1880, p. 368) divided into three small openings in *Hyperoodon*, so that "[quote in French, top of p. 646]". The remaining ziphiines are according to those researchers, as far as has been studied, in this regard not much different from *Hyperoodon*, in contrast to balaenids and platanistids.

The petrotympanic
The petrotympanic itself also shows generally a great similarity with that of the Delphinidae. In *Mesoplodon*, according to v. Beneden and Gervais, the petrosal and tympanic are not fused with one another.

The lengthwise-directed furrow on the inferior side of the bulla behaves differently: "[quote in English, top of p. 646, Flower 1879]

I am not familiar with any comprehensive description of the area of the external ear opening; but as far as can be determined from the illustrations, particularly those of Flower (1874), there are no important from the Delphinidae, except that the communication between external ear opening and the epitympanic hiatus seems farther along, as is the case in the Balaenidae.

A marked difference with the Delphinidae is that the petrotympanic, although not fused with the skull, is nevertheless inserted between the surrounding bones so that it does not become detached during maceration. The falciform process is here the primary cause because it lies under the tegmen tympani and keeps it in place. In his description of *Hyperoodon*, Gerstäcker (1887) states "to this contributes in addition a flat, jagged extension of the lower root of the pterygoid, which pushes diagonally before the inner wall of the periotic, without directly touching it." In addition the petrotympanic is held in place by the strong development of the posterior process of the tympanic. Flower (1869b) describes this condition (which seems first to have been recognized by Eschricht 1849 in *Hyperoodon*) in *Physeter* as follows: "[quote in English, top of p. 647]." The process lies thus on the same place as the respective process of the Delphinidae and is, as here, externally visible. The pars mastoidea is, in contrast, covered and not larger as among the Delphinidae; it seems not to fuse with the process of the tympanicum. At least in *Hyperoodon* this process possesses no posterior aperture (Beauregard 1894: 395).

Flower (1874) states concerning the posterior process of the tympanic of *Berardius arnouxi*: "[quote in English bottom p. 647]." I believe, however, that the possibility of such a special connection between the tympanic and mastoid can in fact be discounted. Firstly, one would have to accept this separation between petrosal and mastoid, for which not a single example is known; and additionally it is possible to view the process, considering it as a part of the tympanic, as a highly modified part of the external auditory tube. Its root lies, as in the Delphinidae, immediately behind the external ear opening. The process is thus a growth of the posterior margin of the external ear opening and is therefore morphologically best seen as the posterior lip of an ossified ear tube. Its abnormal position may be explained by the fact that the posttympanic process and the mastoid, which in other mammals separate the external ear tube from the exoccipital, are lacking (or are reduced); as a consequence the ear tube lies directly against the exoccipital.

Cuvier and Laurillard mention (in Cuvier's *Anat. Comp*. II, p. 374) in *Mesoplodon bidens* ("*Delphinorhynchus micropterus*") a free "mastoid," not fused with the petrosal. v. Beneden (1863) names this also for "*Ziphius indicus*" and v. Beneden and Gervais illustrate it for *Mesoplodon sowerbensis* (= *bidens*) and mention it also for other species of *Mesoplodon*. For *Mesoplodon bidens* they describe it as follows: [quote in French, middle of p. 648]. Malm (1886) and Aurivillius (1887) describe this so-called "mastoid" as fused to the tympanic without a suture, which incidentally seems to be the case following the description of the specimens investigated by v. Beneden and Gervais. In any event, the place and form of the "mastoid" as depicted in their figures (plate XXVI fig. 1b and LXII fig. 1b) is totally in concordance with the place and form of the tympanic posterior process of the other Physeteridae (a concordance which was also noted by Hyrtyl and Eschricht); and from their illustrations of the tympanic (plate XXVI fig. 4 and 4a) it is clear that this process is also present in M. bidens, although it is not named in the text. I regard it therefore as unquestionable that the so-called "mastoid" is nothing other than the posterior process of the tympanic. Even in case it at times is not bound to the tympanic and possibly free, the demonstrated shape and form sufficiently demonstrate that it is this process, which then in any case would have been secondarily cut-off from the tympanic.

Hyoid skeleton and facial canal

Concerning the course of the facial nerve and the connection of the hyoid skeleton to the skull I find no precise data; most likely both taxa do not deviate from the Delphinidae.

Balaenidae, Balaenopteridae

The surroundings of the petrotympanic

As mentioned by Beauregard (1893 p. 199) for *Balaenoptera rostrata*, the surroundings of the petrotympanic in *B. musculus* is in the main the same as in the Delphinidae. The most important differences (for both *B. rostrata* and *B. musculus*) are as follows:

The pterygoid comes between the alisphenoid and falciform process; it contains an additional cavity, which creates an extension directed anterior to the depression in which the petrotympanic lies. Beauregard describes this cavity in the pterygoid as follows: "[quote in French, middle of p. 649]." With this broadening of the pterygoid, the falciform process has attained in some respects a different position: it is oriented more anteriorly and abuts with its point an anteriorly reaching part of the pars entoglenoid of the squamosal. Between the two an opening is formed, which according to Eschricht (1849) and Beauregard permits passage of the trigeminal.

The most noteworthy difference from the Delphinidae is a strong extension of the surface of the meatus. As a result, this extension has the form of a long, exteriorly and posteriorly directed groove, the anterior or posterior wall of which is formed of the similar, broadly developed posterior glenoid process and paroccipital process. This groove is divided lengthwise into two narrower grooves by the border of the squamosal. The anterior groove lies therefore completely in the squamosal; the posterior groove is made up partly of the squamosal and partly of the exoccipital, and the fissure between the bones runs along its floor. In this second groove lies a process of the petrotympanic, as in the corresponding but much shorter groove of odontocetes; through the anterior groove runs the exterior ear opening, according to Beauregard.

Judging according to the description of Eschricht and Reinhardt (1861), *Balaena* seems to correspond in all major points with *Balaenoptera*.

The petrotympanic and the middle ear cavity

The following description applies especially for *Balaenoptera*; *Balaena* corresponds for the most part with the former, as far as can be determined from the literature (Eschricht and Reinhardt, v. Beneden and Gervais, among others). The inferior wall of the bulla does not show the lengthwise groove of the Delphinidae, although otherwise the inferior wall corresponds generally with this family. Here too is the inner lip thick and the outer lip thin. The surroundings of the external ear tube, also described by Beauregard (1894), shows a number of differences: the sigmoid and posterior conical processes are not excavated, and the bony margin of the sigmoid process, which among delphinids separates the external ear tube from the tympanic incisure, is lacking. As a consequence, the two openings are united into one. The tympanic sulcus is sometimes conspicuous and has then the same position as in delphinids; in other cases it is not present. Presence/absence may be dependent on age.

As among the Physeteridae, the petrotympanic is kept in place by the surrounding bones. This occurs by way of two processes, which are absent in young animals and develop gradually (v. Beneden and Gervais, *l.c.* p. 72). The anterior process is oriented anteriorly and medially and is nothing more than a continuation of the thick, massive tegmen tympani. It is as in physeterids covered and kept in place by the falciform process in tandem with the pterygoid.

The other bone is the posterior process. It lies in the previously described groove between the squamosal and exoccipital and is correspondingly very long and directed exteriorly and posteriorly, forming an angle with the long axis of the bulla. Its beginning helps to delimit the external auditory opening, and it is visible externally throughout its entire length. A posterior aperture (in *Balaeonoptera*) is absent (Beauregard). This process was already very strongly developed in *Plesiocetus* (v. Beneden and Gervais).

In the illustration presented by v. Beneden and Gervais (plate I, fig. 10) as a petrotympanic of a young *Balaena australis*, the posterior process is strongly reminiscent of that of the Delphinidae. It is composed through the junction of a mastoid with a tympanic process. Only later does the process grow, as the above authors mention for *B. mysticetus*, to its definitive adult size. However, they do not indicate to what extent the two original components contribute; among skulls of fully grown individuals they appear fully ankylosed and without any recognizable border. The correspondence with the Physeteridae makes it however very likely that, as inferred by Eschricht (1849, p. 46), only the tympanic comprises the process and that therefore (as assumed by Hallmann) the usual name "mastoid" is for this structure inappropriate.

The eustachian tube and air sacs have been described by Beauregard (1894, p. 396) for *Balaenoptera rostrata*. The system of the anterior cavities is composed solely from a single sinus, housed by the concavity of the pterygoid. Incidentally, the sinuses are, at least in their relation to the middle ear cavity, the same as in those of the Delphinidae. Relating to the aforementioned broad communication between external ear opening and tympanic incisure, the wall of the epitympanic sinus has united with the pars tensa of the tympanic membrane: together they form the familiar pocket-shaped "ear drum" of the Mystacoceti [*sic*].

Hyoid skeleton and facial canal

The facial nerve runs from the stylomastoid foramen laterally in a groove, which forms with the exoccipital the posterior wall of the posterior process (Beauregard 1893). In the same groove also runs the cranial end of the hyoid skeleton, as described in Eschricht's description (1849) of *Pterobalaena minor* (= *Balaenoptera rostrata*). In a young fetus, he stated, the end of the stylohyal thrusts itself "as a thin strand of cartilage deep between the occiput and the bulla, without making it easy for anyone to indicate where it is fastened. In older fetuses and more so in older postnatal individuals, the ossified elongate portion of the hyoid is anchored to the occiput by a strong mass of connective tissue. But when this connective tissue is carefully examined, it results ... that it is not actually the cartilaginous end of the hyoid that is here connected [ansitzt??], in that this much more, particularly in the tender fetus, deeply projects between the occiput and bulla, in a channel of the latter bone, behind and running parallel with the external ear tube, in order to finally anchor on the bulla. This deeply hidden cartilaginous strand, the true cartilaginous, external end of the posterior hyoid bone, is evidently often observed in the course of examination of the ear mechanics of baleen whales, without however being recognized for what it actually is. In the "lectures on comparative anatomy" of Ev. Home, it is illustrated in plate 101, the caption for which however indicates that its external connections have not been observed. In older individuals, external bands of connective tissues increase in strength, while the deep-lying cartilaginous end becomes smaller, until finally in adult age it may disappear without a trace" (*l.c.* p. 127).

From this description it emerges that the condition deviates from the Delphinidae only in that through the expansion of the paroccipital process the anchor-point of the stylohyal on the exoccipital is moved laterally.

Flower (1885) also names a tympanohyal as "[English quote, bottom of p. 652]."

Zeuglodontidae, Squalodontidae

From the data present in the literature, it emerges that the bullae from *Zeuglodon* and *Squalodon* already possessed the form of typical cetacean bullae. The surroundings seem however in zeuglodontids to be much more normally constructed than in recent cetaceans, as is particularly visible from the figures and description of *Protocetus atavus* given by Fraas (1904). The condition here is reminiscent of the Carnivora (a comparison oft made by Fraas) and ungulates; a basioccipital process is missing and the bulla is not sunk in a cavity, but projects from the skull. Furthermore, there appears to be a present mastoid process, which is similar to that of pinnipeds.

Summary

As Boenninghaus (1904) correctly observed, the tympanic of toothed whales (the same can be said for baleen whales) shows the same elements as that of other mammals: its form, which at first glance seems so different, is easily traceable to the form of a normal mammalian bulla. The parts of the external ear tube, the glaserian fissure, the tubal process, can all be traced to the normal bulla, as for example occurs among the Ungulata. Even the groove in the inferior wall of the tympanic of most odontocetes similarity with the vagina processus hyoidei. This groove is however, following Boenninghaus, filled with connective tissue and does not accommodate the hyoid skeleton.

The deviations from the normal condition are explainable as direct or indirect adaptive occurrences. In the first category belong probably traits seen in other aquatic mammals, including hard and thick bones, whereby among other effects is caused the peculiar form of the inner lip.

In the second category must be considered the deep openings in the wall of the middle ear, which certainly admit the corpus cavernosum and air sacks. As a consequence arises the petrotympanic fissure and is expanded to the tubal orifice. The latter causes the anteriorly directed, groove-like extension, through which the bulla attains its elongate form, and through which the porus acousticus comes to lie on the posterior half of the side wall.

Most distinctive is the posterior wall of the ear tube, which is transformed into a thick, massive process, the posterior process, which in turn unites into a whole with the pars mastoidea. The purpose of this is to anchor the petrotympanic to the skull, which incidentally in the interest of auditory function (see Boenninghaus) is only very loose or may even be lacking.

This process brings to the families of Cetacea important differences among each other. The element composed in part of the mastoid always remains small and not visible from the surface of the skull (only in *Platanista* is it supposedly, according to Anderson, better developed). In contrast the posterior process of the tympanic is developed to different degrees. In the Delphinidae it is relative small, button-shaped and lies only loosely in a depression on the skull. In physeterids, it is much larger, bulb-shaped and sufficiently united with the squamosal and exoccipital that the petrotympanic remains solidly anchored to the skull. The same is true of the balaenids with the following difference: the process here becomes narrow and long in relation to the normal configuration of the bordering skull elements.

The other differences in form of the tympanic can serve to distinguish genera and species and therefore, particularly because the bone due to its hardness easily remains intact, are very important for systematics. “Le tympanal,” write v. Beneden and Gervais, “[quote in French, p. 654].” In terms of comparative anatomy, however, these differences have only minor importance.

[p. 583]

2 Artiodactyla

Suidae

Bulla ossea

The bulla ossea is always well developed, but biggest in *Sus* (fig. 67) and *Babirussa*. It is usually longest in its vertical dimension; however, the vertical axis is slightly tilted, so that the tip of the bulla is anterior to its base. Only in *Dicotyles* is the bulla low and does not protrude, or (in young animals) only slightly protrudes, under the fossa glenoidea; its height is about the same as its width, and it is not laterally compressed. In all other extant genera, the bulla protrudes far under the fossa glenoidea and is more or less laterally compressed. In *Dicotyles*, *Sus*, and *Babirussa*, the tip is usually slightly pointed, in *Potamocherus* sharply pointed. In *Phacochoerus* it is rather comb-shaped due to a flattening of the bulla.

The bulla is separated from the base of the skull by the small foramen lacerum posterius, the big foramen lacerum anterius, and the foramen ovale. The foramen ovale is not closed along its entire circumference, but rather forms an indentation in the posterior margin of the alisphenoid. It is usually only partially separated from the foramen lacerum anterius by a small process of the alisphenoid. Foramen lacerum anterius and posterius are connected by a narrow or wide gap. The posterior part of the bulla touches the base of the processus paroccipitalis, except in *Dicotyles*, where a gap remains open between the two structures. The margin of the bulla is not fused to the petrosum, but there is no gap between them either, contrary to Huxley (1864, p. 256).

As mentioned before, the vertical axis of the bulla is slightly tilted to the front, so the upper front wall of the bulla covers the ostium tympanicum tubae, which lies between the bulla and the petrosal. This wall of the bulla has a shallow groove (Sulcus tubarius) that forms the lower wall of the bony tuba. The tuba is described by Denker (1899) for *Sus scrofa* as a cylindrical channel “which lies on the outer surface of the front inner wall of the bulla (“Paukenkapsel”) and extends towards the front, inwards, and slightly downwards. The roof of the tuba is formed by a small bony plate that protrudes from the lower surface of the petrosal, whereas the other walls of the tuba belong to the bulla ossea, and therefore to the os tympanicum. These other towers far above the upper wall at the pharyngeal end of the tuba. The roof, however, continues after the cavum tympani until it reaches the front inner margin of the fossa pro tensore tympani. In contrast, the lower, outer and inner walls end 1-2 mm before the margin of the tympanic membrane.” Leidy (1869) describes a long processus styliformis on the small bulla of *Elotherium*.

There is no canalis or sulcus caroticus.

According to Parker (1884), an “os bullae” is involved in the genesis of the bulla of the pig, in addition to the tympanicum. He describes it as follows for an embryo of 6 inches in length: “It will be seen in the lower view that there is an additional bone clinging to the inner edge of the tympanic; this wedge and two smaller ossicles which I shall describe in the next stage are the feeble counterparts of the auditory ‘bulla’ of the ‘Felidae’ and their congeners.” In the following stage (newborn animals), the smallest of the two smaller “ossa bullae” is described and depicted as laying against the chorda tympani on the level of the fenestra cochleae. The other one seems to be laying further down against the petrosum, “in front of the Stylohyal.” The significance of these two ossicles is unclear; judging from the rather vague description they only play a very minor role in the development of the bulla. It is also impossible to say by Parker’s description which role the biggest of the three “ossa bullae” plays in this respect, and whether it forms the entire wall of the bulla or whether the tympanicum also contributes to this. In his figure of the head of the 6-inch embryo, the entotympanicum is small, while in the next stage (the newborn animal) it is no longer mentioned. I looked for it myself in different sized embryos. In younger stages, there is a gap between annulus and petrosum that is closed by connective tissue; this wall soon ossifies, but I could not find a border between this ossification and the tympanicum. Therefore, the entotympanicum is free for only a very short period of time.

There also does not seem to be a cartilaginous stage before the ossification. Parker, too, mentions: "the bullar ossifications are found in a very soft stroma of connective tissue and not in thin cartilage." This disproves the statement by Hallmann: "The *Paukenring* [ring-shaped bulla at an early stage] in a certain age of the embryo is located in a cartilage that already has the shape of the bulla."

The bulla is much lower and by this shaped much more normal in the beginning as compared to later.

Outer auditory canal
The outer auditory canal is very long and of cylindrical shape. It runs in the back along the root of the high processus zygomaticus, in an oblique direction and strongly upwards, so that the porus acusticus points upwards (fig. 67).

Its wall apparently comprises only part of the tympanicum: In *Dicotyles* certainly only the lower and back wall are formed by the tympanicum, and also in Sus the roof seems to be formed by the squamosum, as pointed out by Denker. The tympanal part and the squamosum are fused entirely, so their boundaries mostly cannot be detected for sure.

Eschweiler (1904) writes about the pig: "The upper wall of the auditory canal […] shows a big incision close to the attachment site of the tympanic membrane, so there is only a membranous wall of the auditory canal in this place in a specimen with soft tissues." This membranous wall is of course nothing else but a pars flaccida; the incision is an incisura tympanica (as Eschweiler points out, too).

Furthermore, the entire auditory canal is surrounded by the squamosum with the help of a well-developed processus posttympanicus that, under the auditory canal, attaches to the back edge of the fossa glenoidea and fuses with it. Its tip, however, stretches further ventral along the side wall of the bulla and the basis of the processus paroccipitalis and fuses with the bulla (and usually with the processus paroccipitalis as well). The fusion of the processus jugalis and processus posttympanicus therefore produces a situation that is comparable to a part of the Rhinocerotidae. There is, however, a difference: The meatus spurius is formed by the fusion of the processus posttympanicus and the processus postglenoideus in Rhinocerotidae, whereas in Suidae the fusion takes place with the processus zygomaticus above the articular surface. A processus postglenoideus is only present in *Dicotyles*, but here it protrudes freely under the false auditory canal.

There is another correspondence with *Rhinoceros* as well as with other ungulates: The small mastoid is excluded from the outer surface of the skull because of the fusion of squamosum and exoccipitale. In *Elotherium*, the mastoid was visible from the outside, following a description by Scott (1898b).

The fused processus zygomaticus and processus are connected directly to the sides of the bulla, so the cylindrical auditory canal is surrounded only by the Squamosum from its beginning. Only in *Dicotyles*, a canal remains open between the above-mentioned processes and the lower wall of the tympanal auditory canal. It opens to the outside in two places: first, in a foramen below the outer auditory opening; second, in an opening lateral to the bulla. Turner (1848) seems to have confused this latter opening with a foramen postglenoideum that he describes for *Dicotyles*. However, I cannot find such a foramen in *Dicotyles*, neither can Cope and Kopetsch. It is also missing in all other extant genera.

Auditory bulla
In extant genera, the bulla is pneumatized; the air cells communicate with the middle ear space via numerous small openings (fig. 67). As Scott (1899, p. 28) points out, this structure most likely evolved independently from those of the Tylopoda and Tragulidea because the tertiary *Perchoerus* had a hollow bulla. The small bulla of *Elotherium* was hollow (Scott, 1898b).

The separating walls in the bulla of Sus don't develop secondarily but are present from the very beginning of the swelling.

The recessus epitympanicus is described by Denker (1899) in *Sus scrofa* as follows: "Separated by a narrow bony bridge from the lateral edge of the half-canal for the nervus facialis and the outer border of the fossa pro tensore tympani, there is a cavity above the medial end of the upper wall of the auditory canal which freely communicates with the tympanic cavity. This is to be interpreted as the recessus epitympanicus. Only a small part of the roof of this cavity belongs to the os petrosum; it is mainly formed by the os squamosum which advances from the outside under the petrosal." A sinus epitympanicus is therefore missing.

Hyoid arch and canal for the facial nerve
The entrance of a vertical canal is found between bulla, processus posttympanicus and processus paroccipitalis. Only in *Dicotyles* is this entrance not completely separated from the foramen lacerum posterius, for here the processus paroccipitalis does not touch the bulla (fig. 68). The facial nerve comes from the apertura tympanica canalis facialis, runs in the normal way through the tympanic cavity in a sulcus and leaves it between bulla and petrosal. It then exits to the exterior through this above-mentioned canal.

The long and (compared to most other ungulates) thin tympanohyal protrudes more towards the inside in the same canal or in a more or less deep groove (vagina) in the posterior wall of the bulla that is connected to the canal. (In *Dicotyles*, this groove is sometimes completely separated from the canal.) The tympanohyal originates as usual from the perioticum and is free over its entire length. It breaks easily and is often missing in macerated skulls.

Vrolik (1872) states that in the pig embryo, the proximal end of the hyoid arch lies exterior of the annulus tympanicus, thus exactly like what I described for the horse (p. 582). After mentioning that in humans the annulus lies exterior of the hyoid arch, he continues: "In the cow and pig, things are different. In these animals, the homologous structure of the above-mentioned cartilaginous rod lies above the annulus tympanicus; thus, their position is exactly reversed as compared to humans. In the pig, the annulus reaches a considerable size and grows around the rod." But the difference is less marked than Vrolik believes: The very first part of the Reichert-cartilage lies also in the pig interior to the tip of the rear part of the annulus, just like in humans. However, it soon arches backward and around the rod. Thus, here we find a transition between the general condition in humans and other mammals and the modified state in the horse.

Parker (1874, p. 322) says that the tympanohyal in the pig ossifies from two nuclei, but Ficalbi (1886/87, p. 121) only mentions one ossification point.

[p. 588]

<u>Hippopotamidae</u>
Bulla ossea

The bulla of *Hippopotamus amphibius* L. is shaped in a Suidae-type way, but unlike in Suidae it is not compressed in direction about perpendicular to the long axis of the skull. The two flat lateral sides are separated through the quite sharp lower edge of the bulla. The bulla ends in a pointed process of normal length which points downwards in an oblique angle in the front, and a shorter point in the back. The bulla protrudes only slightly under the fossa glenoidea. In young animals, where it is not yet compressed, it is therefore more similar to *Dicotyles*.

A wide gap remains open between the base of the skull and the bulla. It is formed by the fused foramina lacera, which are not separated from the Foramen ovale. Lateral to the foramen lacerum, the posterior wall of the bulla is fused with the inner root of the processus paroccipitalis.