Auditory Organ of the Whalebone Whales

(Preliminary Report)

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Introduction :—

This is the first report of my studies upon the sensory organs of Cetaceans. The present investigation on the structure of Cetacean auditory organ was begun in 1946, and has made some noticeable progress especially during the Antarctic expedition on board the Japanese whaling factory ship the " Nissin Maru No. 1 " of the Taiyo Fishery Company in the season of 1947—48.

Sensuous life-mode of whales is very much interesting, and important as well, not only from the biological point of view, but also for the practical side of whaling. Their sense of hearing must be very important for maintaining their lives in the water. It is commonly said among whalers

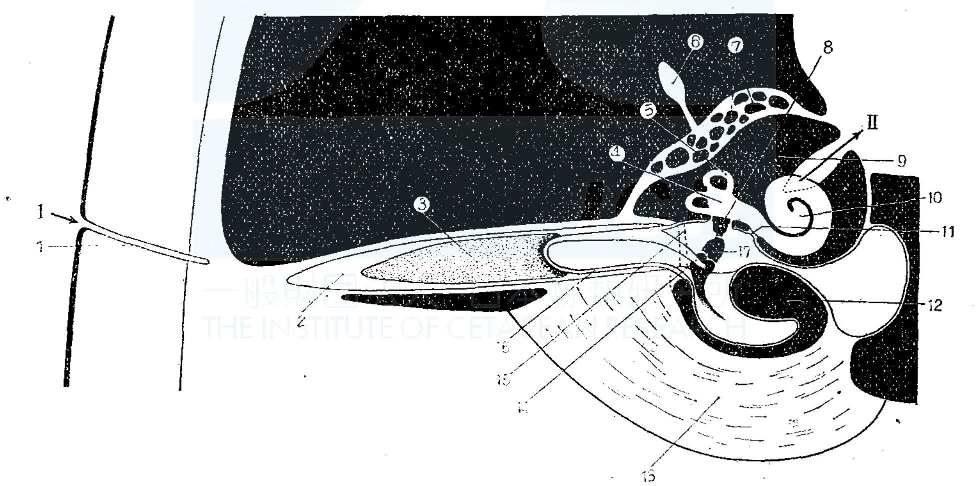

Fig. 1a. Diagram of the auditory organ of *Balaenoptera* in frontal section. ↑I. shows outer ear hole, ↑II. Inner acoustic meatus. 1. Lateral portion and 2. Medial portion of the outer acoustic meatus, 3. Plug of ear-wax, 4. Vestibule, 5. Semicircular canal, 6. Ligamentous cord, 7. Sesamoid ossicles, 8. Stapes, 9. Periotic bone, 10. Cochlear labyrinth, 11. Cochlear fenster, 12. Tympanic bone, 13. Thick fibrous layer of connective tissue, 14. Triangular ligament between the tympanic membrane and malleus, 15. Thin pedicles which fuse the tympanic and periotic bones, 16. Tympanic membrane, 17. Incus.

that whales are very sensitive to the sounds in the water. We can give some examples to make this view easily be accepted, although in this place they are not touched at all.

Materials :—

Materials here treated are confined to two species of the genus *Balaenoptera*, i. e., *Balaenoptera musculus* and *Balaenoptera physalus*, because other species could never be caught by the Japanese in the Antarctic. Being blessed with abundant materials, both adult and foetus, I made observations about the organ macroscopically on board, and brought home some materials for further studies.

Here, merely an outline of my observations will be reported, mainly about the fin whale (*B. physalus*), and further details will be published in the near future together with histological studies, considering at the same time some other members of Cetacea.

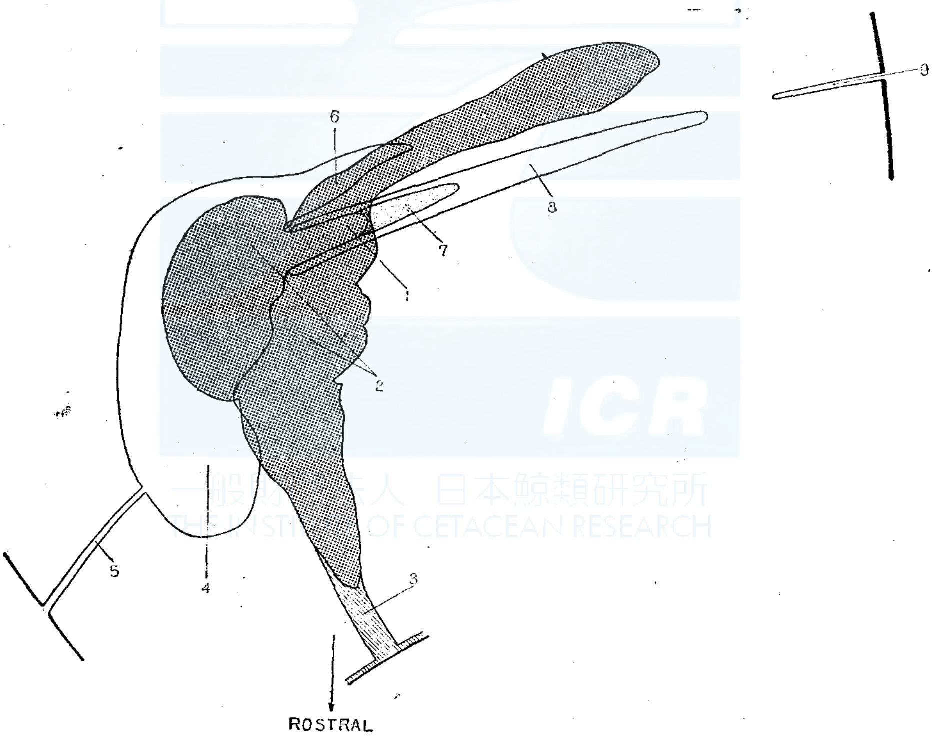

Fig. 1b. Diagram of the auditory organ of *Balaenoptera* in horizontal section, illustrating the topographic relation of the tympanic cavity and its adjoining expansions to the petrotympanic bone, which is shown half-toned in the background. 1. Tympanic membrane, 2. Petrotympanic bone, 3. Rod of connective tissue straining the pro-otic leg to the periost outside, 4. Pterygoid fossa, 5. Eustachian tube, 6. Blind diverticle of the tympanic cavity, 7. Plug of ear-wax, 8. Medial portion, and 9. Lateral portion of the outer acoustic meatus.

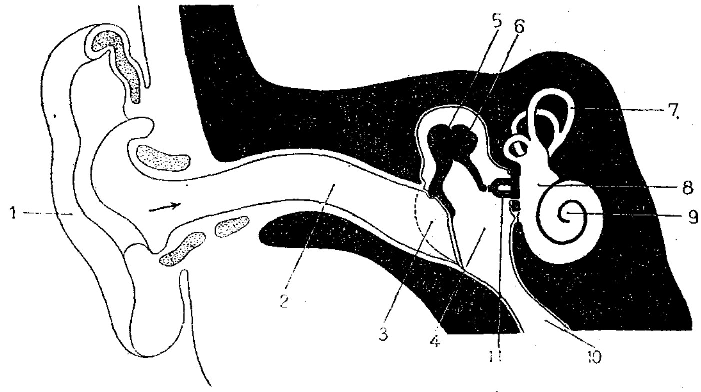

Fig. 1c. Diagram of the auditory organ of the human being in frontal section. 1. Auricle, 2. Outer acoustic meatus, 3. Tympanic membrane, 4. Tympanic cavity, 5. Malleus, 6. Incus, 7. Semicircular canal, 8. Vestibule, 9. Cochlear labyrinth, 10. Eustachian tube, 11. Stapes.

Fig. 1a is a diagram showing the structure of the auditory organ of *Balaenoptera* in frontal section, to be compared with another diagram (Fig. 1c) of the human ear.

Outer Ear :—

The outer ear hole of fin whale is small, opening at the bottom of a longitudinal short groove, which runs parallel to the ventral grooves, and lies about halfway from the eye to the anterior edge of the fore limb (Fig. 2). It is usually a horizontal slit, and admits the little-finger no further

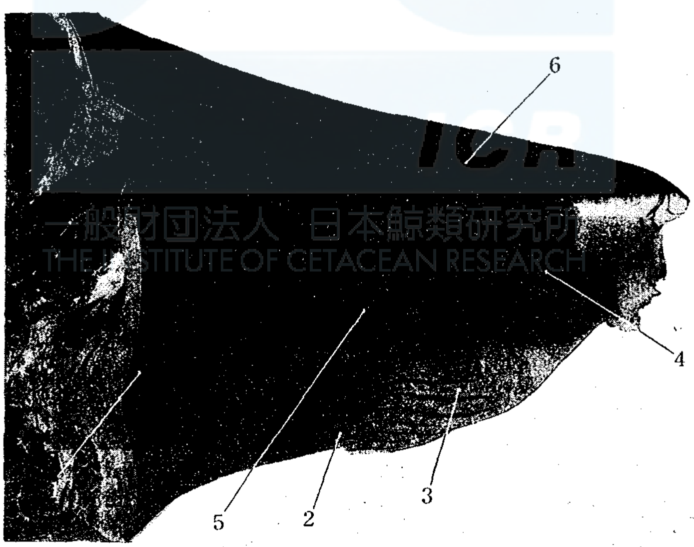

Fig. 2. Head of a fin whale showing the outer ear hole (1) and its topographical relation to the eye (5). 1. Outer ear hole, 2. Ventral grooves, 3. Mandible, 4. Baleen, 5. Eye, 6. Maxilla.

than the third phalangeal joint, measuring about half an inch in diameter.

The outer acoustic meatus is obviously degraded, devided into two portions, the lateral and the medial. Of these two portions, the lateral is far more rudimental and far shorter in length than the medial. The lateral portion is buried in thin blubber, and usually torn off with the blubber at the time of dissection. On the contrary, the medial portion is pretty well preserved in the acoustic furrow, which lies on the lower side of the squamosal bone. In my former observation of a female fin whale at Akkeshi, Hokkaido (1947), the lengths of the two portions measured 13 cm and 45 cm respectively, and to the consequence, the outer acoustic meatus was broken for the interval of about 30 cm. This fact of discontinuance of the acoustic meatus in the whalebone whales, however, has strange enough been missed by some authors worked on this same subject (Lillie, 1910; Hinoura, 1938). And so far as learned by me, Remington Kellogg (1928) alone has presented an accurate description of this fact about the humpback whale (*Megaptera*).

The tympanic membrane is rather thick, and projects outwards about 6 cm into the acoustic meatus in a shape of a finger-sac, slightly flattened in vertical direction; it is connected with the rigid malleus by a ligamentous cord (Fig. 1a and 3). Thus, the membrane obviously lost its original function as a drum, and its outer surface is coated tightly with a plug of ear-wax. With this tympanic membrane, the outer ear adjoins the middle ear.

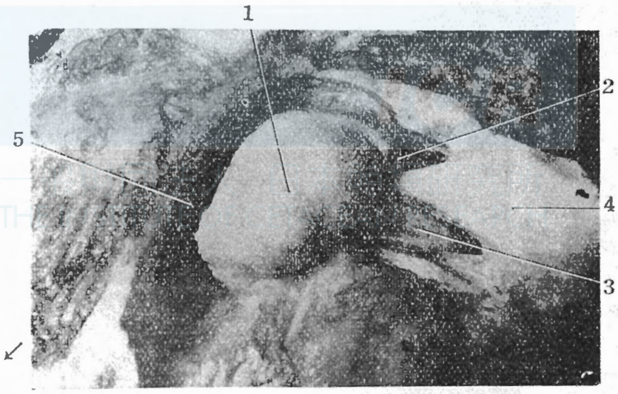

Fig. 3. Photograph showing the tympanic bone and part of the tympanic cavity, together with the tympanic membrane. Ventral view, right side. After removal of the thick fibrous layer partially (4). Arrow shows the rostral direction. 1. Tympanic bone, 2. Blind diverticle of the tympanic cavity, 3. Tympanic membrane, 4. Fibrous layer covering the auditory region from the lower side, 5. Tympanic cavity.

Middle Ear :—

The most conspicuous character of the middle ear of the whalebone whales is the morphology of the tympanic bone, which is also known by the name of "tympanic bulla," and the relation of this bone to the periotic (os perioticum s. petrosum). These two bones are fused together with two thin but broad pedicles as is shown in Figs. 6 and 7. The two bones are, altogether, sometimes called as the petrotympanic (os petrotympanicum) or tympano-periotic. The tympanic membrane is situated in the bony tunnel between these two bones, between these pedicles.

The tympanic bone is very hard like quartz and compact like ivory, and is shaped like a cowrie shell, with a deep depression on its upper surface and lies so as its longitudinal axis to be parallel to that of the whale body. The middle ear cannot easily be seen at the dissection because a particular white, thick and hard layer of connective tissue covers this region from the lower side (Figs. 1 and 3). But, in the region of the tympanic alone, no tight connection exists between this bone and the fibrous layer but a little amount of adipose tissue. The tympanic bone is, therefore, comparatively free from the fibrous layer, and consequently, the heavy tympanic bone is often dislocated by the external force or through inertia when this layer is taken off, for the pedicles are thin and easily broken.

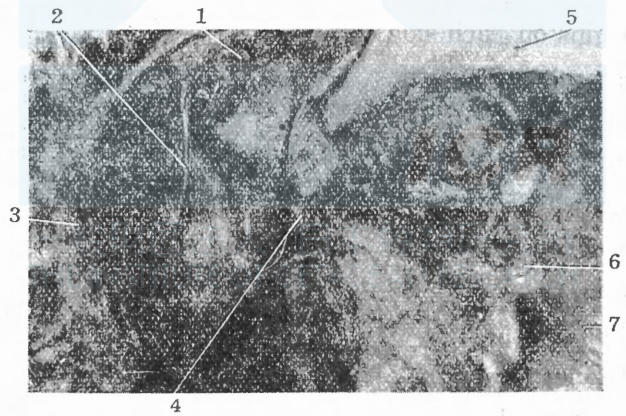

Fig. 4. Photograph of the tympanic cavity in full view (right side, same specimen with Fig. 3). Drawing-out line 4 shows the rostral direction. Photo shows the mucous folds and vesicles on the spherical portion of the periotic bone. Incus is seen in the center, joining with stapes, but the joint between incus and malleus is broken, the tympanic bone being overturned to the right. 1. Vesicular formation, 2. Mucous fold, 3. Medial wall of the tympanic cavity, 4. Incus, 5. Connective tissue, 6. Malleus, 7. Tympanic bone.

Tympanic Cavity :—

The tympanic cavity is, in whalebone whales, a room that lies between the tympanic and the periotic bones, situated likewise to the land animals next to the tympanic membrane (Figs. 1a., 4 and 7). The periotic makes the ceiling of the tympanic cavity with its spherical portion, in which there lies the inner ear, viz. cochlea, vestibule and semicircular canals.

The tympanic cavity has a remarkable expansion in the depression of the tympanic bone; it is also expanded rostrad into the pterygoid fossa and caudo-laterad into a pointed blind diverticle in the above mentioned thick layer of connective tissue (Fig. 1b, 3 and 6). The cavity has also a finger-like expansion in the tympanic membrane, thus, four expansions are attached to the tympanic cavity, of which the pterygoid fossa is the largest (Fig. 1b).

The mucous membrane which covers the tympanic cavity and its expansions is rugged with various folds and vesicular formations. These formations are most complex on the ceiling of the tympanic cavity, that is, the spherical portion of the periotic bone (Fig. 4). The pterygoid fossa is to be considered as an expanded posterior portion of the Eustachian tube. The Eustachian tube begins on each side at the upper lateral wall of the nasal passage instead of the pharyngeal cavity, and runs about 30 cm backwards to somewhat lateral direction to the pterygoid fossa, and joins it at its ventral floor (Fig. 1b).

Tympanic Ossicles :—

Like other mammals, across the tympanic cavity, there lies a chain of the tympanic ossicles: malleus-incus-stapes. Forms of these ossicles are different to some extent from those of the

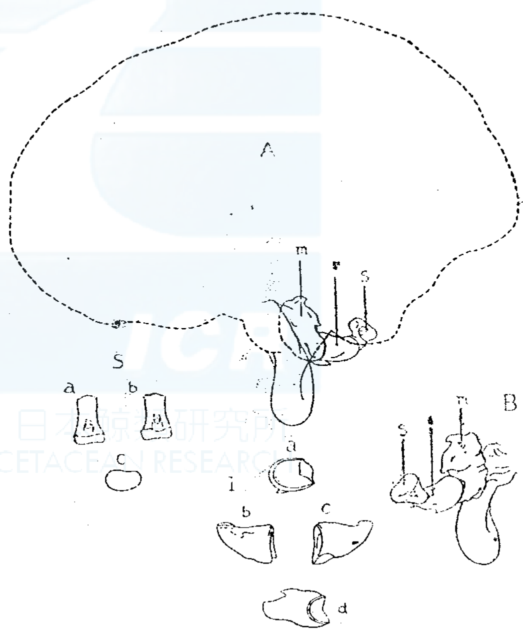

Fig. 5. Tympanic ossicles. Right side. The dotted line shows the contour of the tympanic bone A. (ventral view), and B. (dorsal view) in toto. m. Malleus, i. Incus, s. Stapes. I. Incus seen from: a. Rostro-ventral, b. Lateral, c. Mesial, d. Ventro-caudal. S. Stapes seen from: a. Caudo-mesial, b. Rostro-lateral, c. Basis stapedis.

land mammals. The malleus, above all, is fused to the tympanic bone, and is so located as to coincide with the phonetic focus for the depression of the tympanic bone, which I believe, to function as a resonance box, an amplifier of sounds in the water.

Thus, three ossicles make a continuously articulated bony chain, until finally the stapes inserts its bottom into the vestibular fenster. The connection between stapes and vestibular fenster of the inner ear is not ankylosed, and accordingly, the vibrations of the stapes are considered to be transmitted into the cochlear lymph through the fenster. The tympanic ossicles are shown in Fig. 5.

The chorda tympani of the facial nerve was not observed in the tympanic cavity.

Inner Ear :—

The inner ear, namely vestibule, cochlear labyrinth and semicircular canals, together with inner acoustic meatus containing the auditory and the

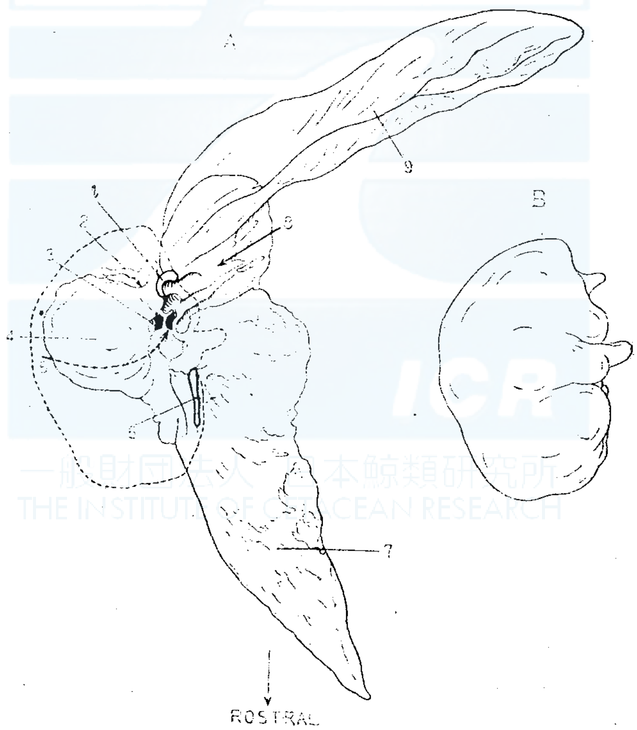

Fig. 6. Petrotympanic bone. Right side, ventral view. The tympanic bone is dislocated to the right (B), to illustrate the labyrinthic portion of the periotic (A). 1. Caudal pedicle, 2. Cochlear fenster, 3. Vestibular fenster, 4. Labyrinthic portion, 5. Facial nerve canal, 6. Rostral pedicle, 7. Pro-otic leg, 8. Furrow for the outer acoustic meatus, 9. Opisthotic leg.

facial nerves, and the Falloppian duct of endolymph, etc., lie in the central spheric portion of the periotic bone. For this reason, the spheric portion is also called as the labyrinthic. The vestibular fenster is situated in a depression on the under side of this dome-shaped labyrinthic portion at its lateral border. The cochlear fenster lies on the posterior surface of the labyrinthic portion, a little distant behind the vestibular fenster (Fig. 6). The cochlear labyrinth measured, in one case of fin whale (77 feet female), 19 mm in diameter, the modiolus being 10 mm in length. The rotation of the cochlear canal is about two and a half as in the human ear. The cochlea exceeds that of the mankind more than twice in each dimension, while the three semicircular canals are not larger than the human case. The bony tissue of the labyrinthic portion is also as hard and as compact as the tympanic bone, but the thin layer that faces to the cochlea is not so compact as its surrounding tissue. Such being the structure, the cochlea is easily broken during chiseling even with the greatest care. But, the medial part of this portion, which is perforated by the auditory nerve, the Falloppian duct and the facial nerve, and which takes part in the formation of the basis of the cranial cavity is as loose as other bones such as vertebrae.

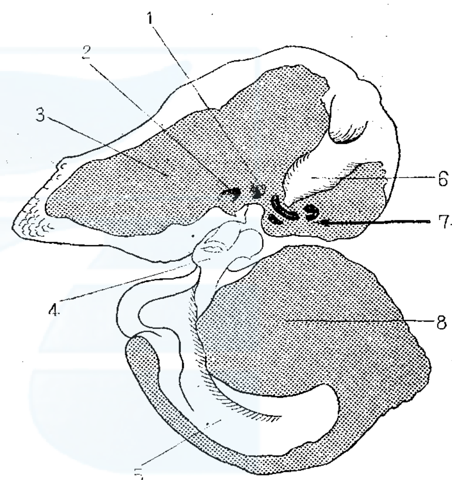

Fig. 7. Petrotympanic bone. Right side, frontal section. 1. Vestibular fenster, 2. Opening of facial nerve canal, 3. Periotic bone, 4. Malleus, 5. Depression of the tympanic bone, 6. Inner acoustic meatsus, 7. Cochlea, 8. Tympanic bone.

The periotic bone has two more portions besides the labyrinthic: the anterior pro-otic and the posterior opisthotic (Figs. 1b and 6). The former is pointed and of pyramid shape, being also hard and compact, and projects into a canal in the squamosal above the roof of the pterygoid fossa, but is coated and connected with a thick sheath of fibrous tissue. These two, making together a rod-shaped process, are connected with the periost of the squamosal through the canal above mentioned to the lateral outside of the squamosal (Fig. 1b). On the contrary, the opisthotic portion lies in the skull firmly between the squamosal and the exooccipital bones. In other words, the three portions may be said that the two of them, the pro-otic and the opisthotic portions form a right angle at the site where the labyrinthic portion lies.

The opisthotic portion is thin and compact at its root, but broadens and extends towards its extremity, and at the same time it diminishes in compactness. These two extremity portions, I would hereafter call as "Legs" (cruri).

How the Organ Functions :—

The problem how the Cetacean auditory organ functions, has been discussed for a recent century. Although many authors such as Buchanan, Claudius (1858), Denker (1902), Boenninghaus (1903), Lillie (1910), Abel (1912), Kellogg (1928) and Hinoura (1938) have set up some theories for this problem, none of them has been hitherto regarded to be perfect and indisputable. The reason why this problem has not been settled is that, the two sub-orders of Cetacea, toothed and baleen whales are often treated equally, in spite of the great difference in structure between them, and that perhaps for the difficulty of dissection, some structures having been missed by some or all authors.

I myself would lay special weight on the structural relations of the above described cruri to the skull and the peculiar ankylose of the tympanic bone to the periotic, and explain the auditory function of the whalebone whales as follows :— In short, the entire petrotympanic bone is set into vibration by the sounds, transmitted through the surface of the body, especially from the head, at that time the opisthotic leg functions as fulcurum and propagating apparatus (Abel), while the pro-otic leg strains the entire organ to the periost outside the skull, and thus, making the vibration more effective, limits vibrations of the petrotympanic to a certain extent. And to make my suggestion more certain, I will mention some other structures which seem to have escaped the notice of previous researchers. Between the upper side of the labyrinthic portion and the under side of the skull, there exist in the fibrous layer, scores of sesamoid ossicles, large and small in size, which seemingly function as buffers and are considered to make the whole organ noiseless. Besides, from this fibrous tissue, a thin but strong cord extends upwards into the squamosal bone of the skull and ends in a swelling (Fig. 1a). Sesamoid ossicles are also observed at the entrance of the pro-otic canal in the roof of the pterygoid fossa, between the pro-otic leg and the squamosal bone.

When the petrotympanic bone is put into vibration, it must be inertially amplified by the tympanic with its heaviest mass through its peculiar attaching mode to the periotic. Of the two flattened thin pedicles, which fuse the tympanic to the labyrinthic portion, the posterior one is situated at right angle to the anterior one (Fig. 6), in order to maintain the heavy mass of the lateral lip of the tympanic at the time of vibration (Fig. 7).

These facts seem to be essential for the functioning of the tympanic as the amplifier of the vibration and as the resonance box.

Moreover, the depression of the tympanic bulla and other expansions of the tympanic cavity may also well be considered to be resonators, and put the malleus into utmost vibration. In both cases, the vibration can be transmitted through the bony chain by the basis of stapes directly into the cochlea. As described before, the ventral surface of the tympanic bone is relatively free from the fibrous layer which covers the entire auditory region from the lower side, This relation makes the tympanic vibrate freely and thus, make my vibration theory in the ear of whalebone whales more reasonable. This fibrous layer, in my opinion, protects the auditory organ from tremendous pressure of sea water, when whales dive down to a great depth.

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