

# Contribution to the Anatomy of the Organ of Hearing of Whales\*

By

MUNESATO YAMADA

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\* この研究中 *Berardius* の一部および *Physeter* の材料採集には、昭和25年度 文部省科学研究費の援助を受けた。なお当時著者は東京大学の大学院学生であつたため、この研究費は形式上小川鼎三教授に交付されたことを附言する (山田致知)。

### Preface

Since Spitzka in 1886, neuro-anatomists have pointed out cetacean sense of hearing to be extremely sensitive from their stand-point as morphologists. It has been recently revealed by Ogawa and Arifuku (1948, p. 12) that there are noteworthy differences between the two cetacean suborders in the acoustic system within the brain stem, and that the odontocete suborder seems to hear far more sensitively than mystacoceti, though the latter seems probably not inferior to the land mammals. They add, in this connection, that discussions on the mystacocete sense of hearing through the study of that of odontoceti are in no way justified. This must be considered in every research concerning whales, ever so much in the present work.

The superior sense of hearing of whales, however, has been seemingly known since far more ancient days because Herodotus wrote in "Persian Wars" a mythological case of Arion and a dolphin which came to his rescue at his enchanting performance on lyre asking for help. According to the myth, Arion was obviously conscious of dolphins to understand his music and believed that one would come to his rescue when he played accordingly. Another case of music-loving dolphins can be quoted from "Daphnis et Chloe". These myths sound to me to be based on some real knowledge of those ancient people rather than fictional origin.

Whaler's experiences, meanwhile, have endorsed this view from their practical side. It has been well known that Faeroe Islanders pursue schools of blackfish shoreward, by firing guns, beating on pans and shouting to frighten them (Kellogg, 1940, p. 70). In the ancient whaling of Japan from fifteenth through the last centuries, they used wooden hammers to beat their boats in making rythmical noise through which they pursued the prey shoreward freely at will for many miles and finally netted and harpooned. In this way, they had caught giant whales such as sperm whale, humpback, gray and right whales. The similar means of pursuing have lasted up to the present to catch blackfish and dolphins among coast whalers of Japan. Laying these particular cases aside, it has been a common sense of whalers that whales are quite sensitive to sounds, and some have tabooed to make any unnecessary noise, even speaking during pursuits. Practically, objections were raised mainly from this stand-point against noise-making Diesel engines to be replaced in whaling catcher boats instead of steam engines. Happily, whales did not mind the sounds of beating engines so much as had been afraid of, and this has led to the successful revolution in whaling history, especially

in establishing the so-called pelagic whaling. It remains, however, still doubtful if whales have been perfectly specialized physiologically to hear the water-borne sounds alone and no longer hear the air-borne ones.

It is granted natural that a large number of anatomists as well as cetologists have participated in the anatomy and physiology of the cetacean organ of hearing of extreme specialization, as Home 1812, Camper 1820, Buchanan 1828, Hyrtl 1845, Claudius 1858, Carte and Macalister 1867, Flower 1867, Beaugregard 1893-94, Denker 1902, Boenninghaus 1904, Lillie 1910-15, Abel 1912, Hanke 1914, Kernan 1918-19, Kellogg 1928, Hinoura 1938, myself 1948 and others. However, some larger animals were only occasionally obtained and hardly examined, and to the consequence, observations easily became fragmental or superficial, or sometimes worsely mistaken; lesser animals, usually delphinidae representatives, to the contrary, are more convenient to treat and have been practically routine material throughout. Thus from various specific data and various stand-points of each author, serious disputes have been brought to the fore, particularly concerning the problem how the organ functions. Above all, the so-called acoustic isolation of the organ from the skull in odontoceti seems to have waited for the re-confirmation or criticisms of my own because the suborder *was* seriously different from mystacoceti, of which two species of the genus *Balaenoptera*, i. e., gigantic blue whale, *B. musculus* (Linnaeus) and common rorqual or fin whale, *B. physalus* (Linnaeus) first came to my study. In the meantime, Pacific beaked whale, *Berardius bairdii* Stejneger, first odontocete whale in my study, has made me strongly suspicious of the isolation in odontocete suborder, and further strongly did sperm whale, *Physeter catodon* Linnaeus. Finally, I faced to some delphinidae animals, from which the view of isolation had been derived by previous authors. They were bottle-nose, *Tursiops truncatus* (Montague); Risso's dolphin, *Grampus griseus* (Cuvier); blackfish or pilot whale, *Globicephalus sieboldii* (Gray) and finless black porpoise, *Neomeris phocaenoides* (Cuvier). The seemingly isolation in the delphinidae family has been thus revealed to be the more highly specialized form than other odontocete families.

The present work deals mainly with my observations on the possibly many species of variety obtainable here at present as well as discussions pertaining to the isolation, pointing out how dangerous it is to consider of one or minor species, regardless of others, particularly those within category not less than family. It must be confessed at the same time that my observations are not exceptional and fragmental as has been critically mentioned of the past contributors including myself. It is for

this reason that other particulars such as the auricular musculature, nerves, blood vessels and wider soft parts altogether are not touched here, because the wholesale preparation is indispensable, which is, however, usually impossible to carry out.

In the meantime, the sensory nerve endings in the external otic region in some species seem to have escaped the previous contributions and will be described simultaneously in the present work. It is of much interest that the vestigial auditory meatus undertakes some new rôle as an independent sensory organ, probably the pressure gauge which must be essential to the cetacean life in the water.

I do not take the present stage of my work as finished because there remain many blanks to be filled up as will be clearly mentioned on each occasion, and also because I would like to have further additions of new species. However, I have only a faint hope that some new animals might bring new data so important in principles as to necessitate some re-writing in a form favorable or unfavorable. The remaining two families of mystacocete suborder, viz., balaenidae and rhachianectidae seem now almost hopeless to meet. Meanwhile, it is another of my enthusiastic desires to examine the fossil cetaceans, particularly archaeoceti, because they may be expected to present more primitive stages of specialization, but this will remain unfulfilled so far as my field of work is constricted in Japan.

### Material and Method

Material treated more or less herewith consists of ten genera, representing three families of odontoceti and one of mystacoceti as follows<sup>1</sup>:

#### Suborder Odontoceti

##### Family Delphinidae:

1. *Prodelphinus caeruleo-albus* (Meyen) from Kawana
2. *Trusiops truncatus* (Montague) from Taiji
3. *Grampus griseus* (Cuvier) from Taiji
4. *Globicephalus sieboldii* (Gray) from Taiji  
*Globicephalus* sp., probably *G. scammonii* (Cope) from  
Ayukawa
5. *Neomeris phocaenoides* (Cuvier) from Yorishima

##### Family Ziphiide:

6. *Ziphius cavirostris* Cuvier from Taiji and Otohama

1) Some other skull specimens in possession of the Department of Anatomy, University of Tokyo, have been studied for simultaneous reference.

7. *Berardius bairdii* Stejneger from Otohama

Family Physeteridae :

8. *Physeter catodon* Linnaeus from Akkeshi

9. *Kogia breviceps* (Blainville) from Taiji

Suborder Mystacoceti

Family Balaenopteridae :

10. *Balaenoptera physalus* (Linnaeus) from Akkeshi and the Southern Ocean

*B. musculus* (Linnaeus) from the Southern Ocean

*B. borealis* Lesson from Akkeshi

All material has come to me by courtesy of our whalers with exception of *Neomeris* which haunts abundantly in the Inland Sea of Japan. The remaining genera of the family delphinidae except *Prodelphinus* came from Taiji of Kii together with *Kogia* and *Ziphius* during summer seasons of 1951-52. The town has been historically famed since the ancient whaling of Japan was originated there to catch whales by use of nets. The town is now famous of the fishery of minor odontoceti, of which *Globicephalus* is most popular. It seems of much interest of cetology that the unusual pygmy sperm whale, *Kogia* has never been reported from there until 1951, in spite that a certain number has been annually caught (Yamada, 1952). Also rare *Berardius* was examined in 1949-50 at Otohama near Chikura of Awa, and grotesque *Physeter* and sei whale, *Balaenoptera borealis* at Akkeshi, Hokkaido in 1950. Two gigantic and important balaenopterids, i. e., *B. physalus* and *B. musculus* were studied chiefly during two seasons of the Antarctic whaling as 1947-48 and 1948-49 on board a whaler "Nisshin Maru No. 1".

The organ was usually dissected at whaling stations and necessary material has been brought back for further study after fixation in 10% formalin solution. This has resulted the mentioned fragmental observations for the dissection at the whaling stations had to be usually done quickly not to hinder the flensing operation. Now my sincere thanks are indebted to the authorities concerned as well as the friendly workers to their good assistance and co-operation, without which adequate and timely dissection would have been utterly impossible.

Most of the observations was macroscopic, but it was very often necessary to use some instruments as saws, axes, and chisels, and in laboratory work, dental lathe with burs, abrasive points, wheels and discs has been indispensable to fenestrate or to remove the extremely hard and dense bony tissues without destroying the interior or gross relations.



For histology, the sections were stained by haematoxylin and eosin after routine embedding in celloidin, but for staining nerves I applied the pyridine-method of Bielschowsky. Concerning the internal ear, the observations remain insufficient, particularly in histology due to the difficulties to get fresh materials and to prepare the satisfactory sections<sup>1</sup>. It is for these reasons that this region is here put aside.

### Chapter 1. External Ear

#### 1. External Ear Hole:

The opening of the external auditory meatus, porus acusticus externus, is in odontoceti so minute that "one can not introduce the lead of a pencil" (Kellogg, 1928, p. 204) through it, as has been described previously by all researchers. The opening is generally situated caudad or ventro-caudad from the eye<sup>2</sup> (fig. 1), but is really so minute

1) The preferable fixation by injecting the proper fixatives was impossible. And in the decalcifying procedure, the gas bubbles were quite harmful to the tissues.

2) In *Kogia* the aperture is situated behind the eye but a little distance above the eye level.

Fig. 1. Position of the external ear hole of various cetaceans. From top to bottom: *Neomeris*, *Ziphius*, *Kogia*, *Balaenoptera (musculus)*.

and practically closed that one can hardly recognize it. In *Physeter*, the opening can be probed with less difficulty with a finger around the suspicious spot because there is felt less resistance to pit the finger due to the well developed peri-meatal lymphoid tissues as will be mentioned later. While in *Balaenoptera* of mystacoceti, it is not hard to mark the opening because it is, although small, much wider than odontoceti and often lies in a short and shallow groove which runs horizontally and parallel to the peculiar longitudinal grooves on the throat and chest regions, about halfway from the eye to the anterior edge of the fore limb. The opening is as big, in *B. physalus*, as to admit the little-finger no further than the distal joint. No auricular sign presents outwardly whatever, though one case of "pinna" similar to those described by Howes in *Phocaena* (1879, p. 468; pl. 29, figs. 1-3) presents in the right opening of one *Ziphius*<sup>1</sup>, which does not protrude so far as his illustrations (fig. 2). But this structure is not a pinna in its exact literal sense because it is shown microscopically to be a cord of the deciduous epithelium of the auditory meatus, being degenerated in the center. It is doubtful if this is of identical nature with Howes' or not for he wrote that he had "failed to discover aught else than a few fatty connective tissue fibres".

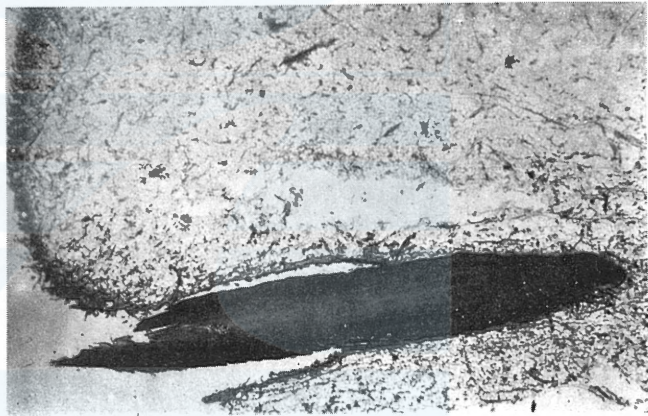


Fig. 2. Pinna-like cord of *Ziphius* protruding from the external aperture ( $\times 8$ ).

Whereas, other lines are read of a foetal *Beluga* as the "pinna" appears to spring from the integument forming the posterior lip of the aperture rather than altogether behind it. This description seems not to exclude the possibility of the deciduous epithelium, while on one hand, it reveals that Howes established the terminology in its original meaning, viz., auricle. Be this structure of *Ziphius* identical with the pinnae of Howes or not, it is of some significance that sometimes the external ear hole of odontoceti happens to be stuffed in this way.

1) This specimen, which came to my study by courtesy of Prof. Ogawa, was caught by a tunny-boat and delivered to him at the fish-market of Tokyo in 1949.

## 2. External Auditory Meatus:

### a. Closure of the Meatus:

It has been well known, as is the case with the external opening, that the external auditory meatus is both in odontoceti and mystacoceti to be extremely vestigial. It is vestigial not only in dimensions but also it is striking that it happens in some whales that the meatus is closed and interrupted during its course. The first reported species in this direction is *Megaptera* by Lillie in 1915. In regard to this problem, I stated suspiciously in my former paper (1948, p. 24) that Lillie (1910) and Hinoura (1938) had overlooked the discontinuance of the meatus, and that Kellogg (1928, p. 204; fig. 24) had seemingly been the only one before me, who was correct in this description. But after my later bibliographic references, I have to correct this because Lillie *en personne*, five years later of his first overlooking in *Balaenoptera*, noticed the perfect closure of the meatus correctly in *Megaptera* (1915, pp. 104-05) and this seems to be original. It is also read in that paper that Burfield and Erik Hamilton noticed the similar closure in *Balaenoptera* (species unknown), but that Carte and Macalister (1867, p. 252) were of opposite opinion in *B. acuto-rostrata*. And for the latter animal, Lillie leaves some question as the closure is easy to overlook, although he states that it may be so in that species. The condition seems same with Hinoura who worked also on the same whale. Also Boas (1912) worked on *B. rostrata* and mentioned that the meatus is continuous but becomes suddenly very narrow under the blubber after presenting the first expansion in the cutis, which expands further noticeably into a large sac right under the blubber. Hanke (1914, p. 492) interpreted this narrowing as was caused by the presence of an unusual cartilage which Boas mentioned.

Concerning the disputes I can agree Lillie, and with stronger presumption I expect the closed meatus throughout the entire family of balaenopteridae to say the least. This is because I added myself in 1950 at Akkeshi, Hokkaido, to the previously reported *B. physalus* (Yamada, 1948, p. 24), a male *B. borealis* of 35-foot length, whose meatus was closed up for an interval of about 19 cm., the lateral portion being 7 cm. and the medial 28 cm., and also because the structure is likewise in *B. musculus* though I have failed to make measurements. The meatus of *Balaena mysticetus* was figured by Gray (1889, p. 301) and recorded as open, but the possibility of the similar closed area is not hereby excluded because the deeper portion has escaped the examination and the lumen of the meatus really goes extremely narrow at the bottom of the blubber. No record of rhachianectidae whales has been known to me.



In odontocete whales, on the other hand, any closure of the meatus has never been learned, and it has been widely known that it stretches continuously from the external opening to the tympanic membrane. This has been the settled belief of all authors, but recently a question has been raised by Clarke (1948, p. 979) who established that the meatus of *Physeter* was a short blind sac which penetrated from the external aperture a distance no deeper than the blubber thickness, and which lost altogether the organic connection with the middle ear. This is with no wonder superficial and erroneous as will be revealed later in the following paragraph, but it was good of Clarke that he noticed this because the meatus seems really to end blindly after a little further penetration than his establishment, before it reaches the tympanic membrane.

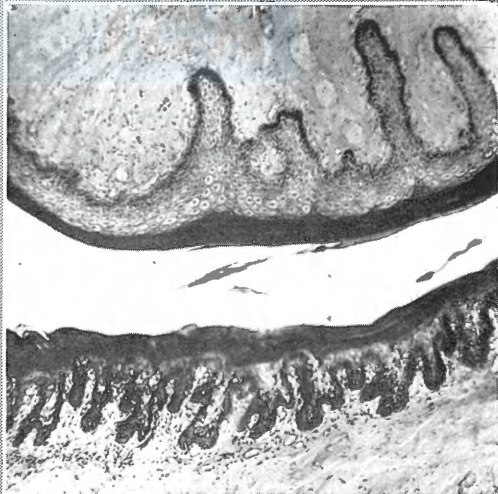
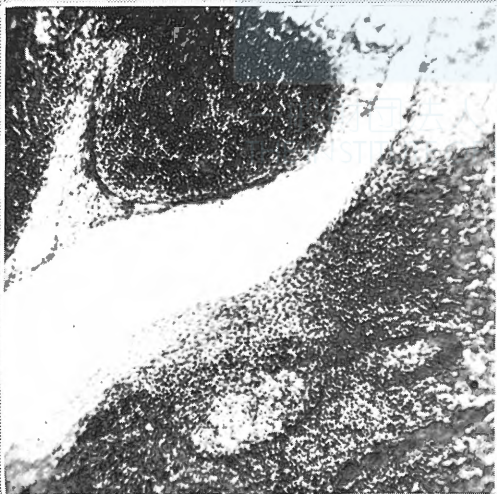
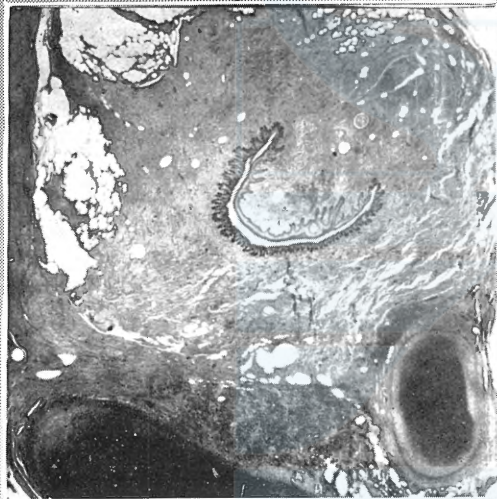
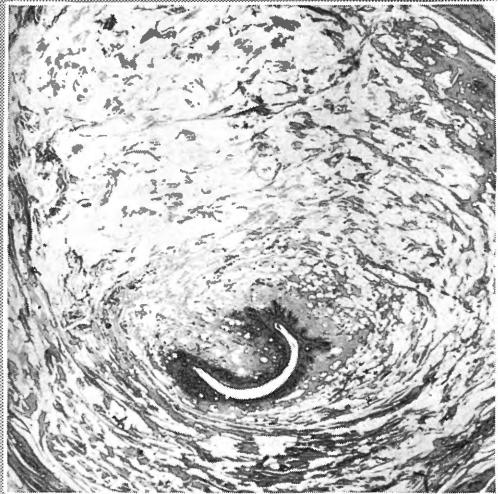
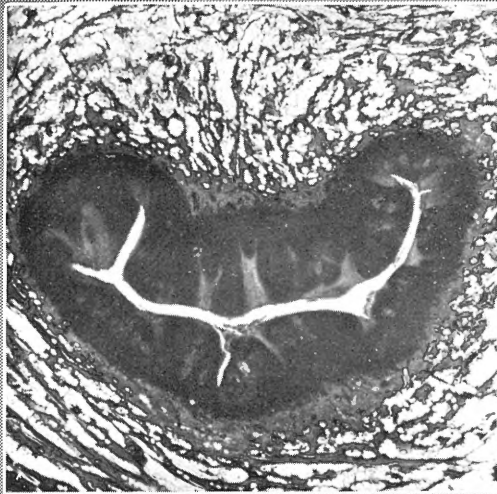
b. General Peculiarities of the Meatus:

**Berardius** (fig. 3): The meatus of *Berardius* measures about 16 cm. in length from the external aperture to the tympanic membrane. In frontal section of the head, the course marks somewhat S-shaped slight curve, turning ventrad beneath the squamosal region of the skull after penetrating the blubber, this being seemingly common to all species of cetacea. In the course of the blubber, however, the meatus presents certain complication which seems to be a new knowledge by far. Within the blubber and through the underlying layer, the meatus becomes sheathed by the peculiar fibro-adipose tissue which gradually grows thicker until 2 cm. in diameter just under the blubber. In this sheath, the meatal lumen, which is first round in section, expands gradually but flattened until its maximum breadth at a distance of about 6 cm. from the aperture as seen in the table below. The meatus shifts at

Table of dimensions of a slit-expansion of *Berardius* in mm.

Distance from the external aperture	18	37	58	75	90
Diameter* or width of the meatus	2.3*	3.5	8.0	2.5	2.0*

the same time to the ventral part of the sheath and the lumen becomes crescentic, being convex ventrad. After the meatus runs 7 cm., the meatal slit gradually diminishes the width and loses its crescentic form, possessing again the round narrowness slightly larger than the first. The peri-meatal sheath of the fibro-adipose tissue is histologically composed of the collagenous fibers mainly in circular direction and the well marked adipose tissue among them. It comes into notice that around



the sheath some of the auricular muscles insert, which is not touched here at all because the wider treatment is necessary with the superficial cutaneous musculature known as the panniculus carnosus as well as its innervation.

It seems also new and interesting here that the meatal epithelium is, in the region of the crescentric expansion, transformed into a peculiar lymphoid organ similar to the tonsils. Many crypts and the lymphoid infiltrations of the epithelium are well marked, although the so-called germinal centers are not typically clear. This lymphoid organ goes weaker as the expansion diminishes, and at the bottom of the blubber layer, where the sheath is thickest, it appears no more. The lumen is again crescentric, being coated by the stratified squamous epithelium, under which one or two, large or small infiltrations by the lymph follicles can usually be seen in each section. The meatal epithelium is, in the land mammals, the continuation of the exterior integument. It is naturally understood, therefore, that the basement cells of the epithelium are marked by a lot of pigment granules in *Berardius*. It is also characteristic to the epithelium as the continuation of cutis that it is beset by the well developed papillae throughout, which are noticed simultaneously by the abundant blood capillaries. However, when the lymphoid organ as well as the follicles are brought into consideration, the meatal epithelium is of mucous nature rather than a cutis. As the meatus rolls further inward and merges underneath the skull the sheath becomes slender and loses the concentric structure, where two or three rudimentary cartilages covers the meatus from below. The cartilages are of irregular form but usually club-shaped.

So far as the crescentric portion of the meatus goes from the end part of the sheath through the cartilaginous portion, there are distributed, in the sub-epithelial tissue, a large number of sensory nerve endings. These endings are distributed most frequently in an interval of 2-3 cm. where the meatus goes under the skull. Microscopically, these endings occur most frequently under the convex epithelium, less frequently on the opposite concave side and few sideways. The facing epithelia differ strikingly: the concave epithelium is thin and beset with numerous but

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Fig. 3. External auditory meatus of *Berardius*. *Top left*- Slit-expansion with the sub-epithelial lymphoid organ ( $\times 8$ ); *top right*- Fibro-adipose sheath sectioned at its maximum development ( $\times 5$ ); *middle left*- Deeper portion with cartilage and abundant sensory corpuscles ( $\times 7$ ); *middle right*- Trumpet-like expansion ( $\times 7$ ); *bottom left*- Lymphoid organ in section *top left*, note the lymphoid infiltration of the epithelium ( $\times 90$ ); *bottom right*- Facing epithelia in section *middle left* ( $\times 90$ ).

similarly high papillae than the convex one where it is thicker and presents less papillae which are naturally broader and taller. The famous trumpet-like medial expansion presents also in this species, being filled up with gray paste-like substance which seems homologous with the ear-wax of mystacoceti. No hairs are present in the meatus throughout, and accordingly no sebaceous glands nor any sign of the ceruminous glands exist. These may support the mucous nature of the meatal epithelium in addition to the lymphatic peculiarities mentioned before. Consequently, the paste-like substance and the plug of ear wax as well as the pinna-like formation protruding from the external aperture seem equally to be produced by the meatal epithelia and not the products of glands.

The meatus of *Ziphius* is different because no expansion nor tonsil-like lymphatic apparatus presents, but is otherwise similar to *Berardius*, nerve endings being also present.

**Physeter** (fig. 4): The meatus of *Physeter* measures approximately 60–65 cm. in cases of 35–40 feet body length. It is striking here that the meatus, after penetrating the blubber thickness, diminishes to a microscopic dimension of 160–170 $\mu$  at a distance of about 10 cm. from the external aperture. It is unfortunate for researchers that this area is cut up when the blubber is removed. This seems to have caused the failure of Clarke that the meatus is a short blind sac which stays within the blubber layer, but I can understand his condition sympathetically because intensely careful examination is needed, which is pretty hard to expect on the operating deck of a factory ship. To make the matters worse, sperm whales lie perfectly sideways because of the gigantic spermaceti organ, and to the consequence, one of the apertures stays underneath and the other at top, both being difficult to examine in the natural state. However, the meatus is really a fine cord not absolutely hard to pick up with naked eyesight for its oblique course of S-shape, descending toward the under side of the squamosal region through the layer of loose connective tissue under the blubber, thereby running by the rudimental auricular cartilage. This continuous cord of the meatus is further prepared from the surrounding tissues along the meatal furrow of the squamosal bone, in which, however, I could not demonstrate any lumen. Though I could not mark the spot where the meatus comes to a blind end, it seems very much probable that it is practically obliterated as Clarke wrote suspiciously (1948, p. 980).

Within the blubber, the peri-meatal lymphoid organ develops far stronger than *Berardius*, measuring more than 2 cm. in diameter. It

happens thus that the external aperture, in spite of its obscure appearance, can be probed with a finger which is pitted into the lumen for the weaker resistance of the lymphoid organ. The organ stretches as far deep as 10 cm. from the aperture, and hereby it is peculiar that it is divided into lobules by the continuous septula of the capsule of connective tissue. The crypts are deep, the infiltrations are commonly

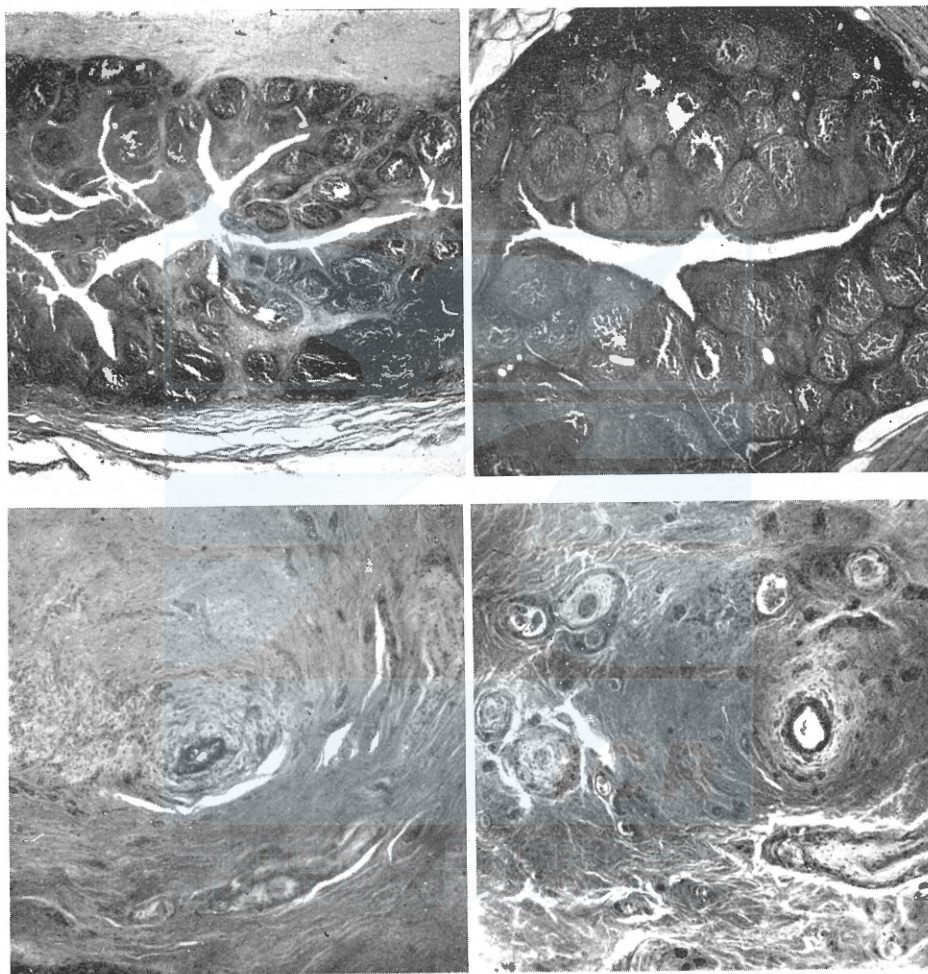


Fig. 4. External auditory meatus of *Phylseter*. *Upper row*- Sub-epithelial lymphoid organ ( $\times 5$  and  $7$ ). In the *left* section, the meatus is artificially flattened; *bottom row*- Almost obliterated meatus ( $\times 90$ ). Note the sensory corpuscles. In the *left* section, the meatus is coiled up and sectioned obliquely, the stretching sub-epithelial layer is shown to the left with blood capillaries.

shown and a large number of germ centers are present.

The organ seemingly corresponds with the blind sac of Clarke as he wrote, "the sac has somewhat thickened unpigmented walls wherein muscular tissue may be developed: internally, these walls are thrown into transverse folds". It may be homologized that the unpigmented walls of Clarke are of the lymphoid organ, the muscular tissue being questionable but reasonably supposed to have been expected by the pinkish tint of the fresh lobules, and the transverse folds are the lobular arrangements divided by the crypts. The priority of this establishment is naturally delivered to Clarke but it is important to note that he was too hasty to make it public without necessary examinations. Really many disputes in our field seem to have brought the confusions in this way.

Surrounding the lymphoid organ, the sensory nerve endings appear in the capsule of connective tissue. But it is in the deeper portion of the meatus where the lymphoid organ no longer appears that the endings are remarkable both in number and dimensions; at the distance of 15 cm. from the external aperture, the endings are most abundant and well developed, where the meatal lumen diminishes its caliber to 60-70 $\mu$  and the lining epithelium becomes quite thin, being beset still by the blood capillaries.

*Kogia* has the similar meatal peculiarities: total length 6.5 cm., of which 2 cm. is blubber portion and the lymphoid area ranges as deep as 4 cm. from the external aperture with the maximum breadth of 0.4 cm. toward the end of the blubber thickness, accordingly that portion penetrates twice further inward than the blubber; the trumpet-like expansion measures 0.9 cm. of the most interior part of the meatus. In the remaining portion, the meatus seems to be obliterated as in *Physeter* but this is not conclusively mentioned for the histologic examinations are remained. Therefore, the nerve endings are not yet known though it is quite possible to expect them.

Concerning other species of delphinidae as well as balaenopteridae, I have nothing particular to mention here for the important problem has been treated in details in the first paragraph (a) of this chapter.

### c. The Meatus as the Independent Sensory Organ:

The sensory nerve endings, presenting abundantly around the auditory meatus in the sub-epithelial layer, are the laminated corpuscles. Some of these of *Berardius* at a distance of about 15 cm. from the external aperture are illustrated in fig. 5 after reconstruction. They are very much elongated with some occasional convolutions, each being supplied

presumably by a single myelinated nerve fiber.

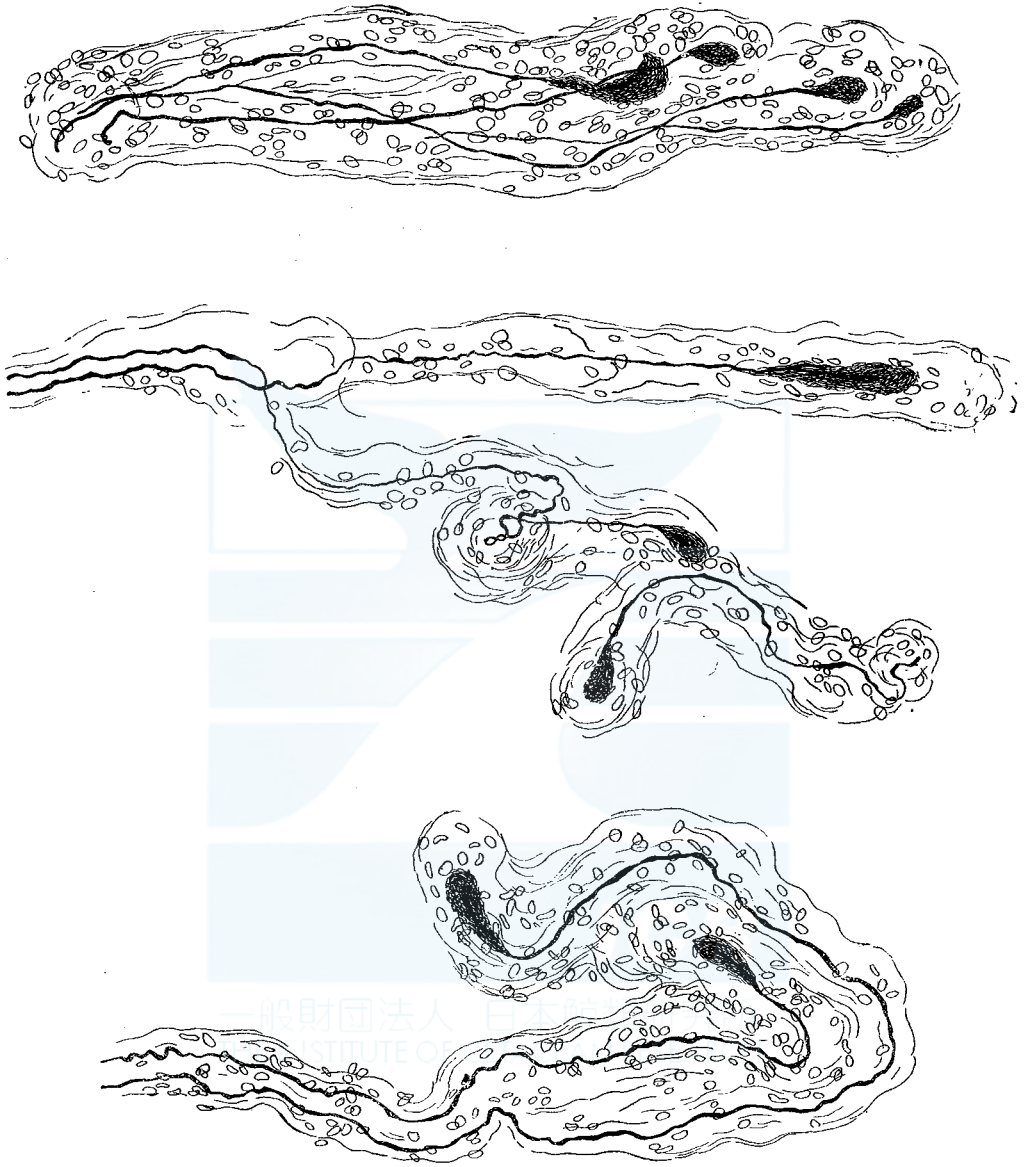


Fig. 5. Peri-meatal sensory corpuscles of *Berardius* (ca.  $\times 230$ ).

Recently some similar sensory corpuscles have been known from the oral cavity including the lips of *Balaenoptera*, described as the nearest ones to the so-called Golgi-Mazzoni's corpuscles, being unlike, however,

in the respects, namely the surprisingly elongated and convoluted characters (Ogawa & Shida, 1950, pp. 8-9). The corpuscles now in question resemble to a great extent to those now referred to, but not a single case of termination of the axon has been learned, which is one of the characters of the Golgi-Mazzoni's corpuscles (Boeke, 1934, p. 867). Nor any branching of the corpuscles themselves has been shown. Every termination of the axons is dilated into an elliptical knob with a network of fine fibrils.

The endings of other species are also the similar laminated corpuscles (fig. 6). It is of interest that the lateral portion of the meatus in *Balaenoptera physalus* has also similar endings though scanty in number but well marked. They measure in *Physeter* 60-110 $\mu$  and in *Balaenoptera* 30-15 $\mu$  in breadth.

To consider of these sensory nerve endings, the meatus of cetacea may well be attributed with a hitherto unknown sensory function which I expect to be the pressure gauge<sup>1</sup> under water. In regard to these considerations, the manner of distribution of the corpuscles in *Berardius* is of special significance. As mentioned before, the corpuscles are distributed mainly within a rather limited area where the meatus merges underneath the skull, marking a slight curve. From the topographical relations of the meatus chiefly to the solid tissues of the head, it may be conclusively said that the meatus is compressed most remarkably at this region by the immense water pressure against the skull, when the stress caused lengthwise in the meatal cord itself by the same outside pressure seems also to bring some similar effects simultaneously. In this way, the facing walls of the crescentric meatus are regarded to be squeezed against each other, and the deeper the whales dive, the stronger this occurs. It may also be the answering characters that the elongated corpuscles lie mostly lengthwise along the meatal lumen, being particularly abundant under the convex side of the epithelium. These parallel relations of the corpuscles as well as their seemingly most effective distribution similar to *Berardius* are popular in *Physeter* and *Balaenoptera* too. Finally, the enormous development of the corpuscles in those species as *Physeter* and *Berardius*, famous excellent divers<sup>2</sup> in the cetacean order, assures me, on the other hand, of the present functional prospect concerning the new sensory rôle of the auditory meatus.

In conclusion, the auditory meatus of cetacea, which is so vestigial

1) Lillie (1910) wrote a certain possibility of a pressure gauge to the protruded tympanic membrane of *Balaenoptera*, but his reasons were not clearly mentioned.

2) It has been recorded that a 45-foot sperm whale dived as deep as 3,240 feet where the animal was strangled to death by a submarine cable (Kellogg, 1940).



and retired from its original function, often undertakes probably a new one as an independent sensory organ secondarily specialized. Accordingly, the auditory meatus is in cetacea really unstable in its ontogenetic fortune, for the upper branchial cleft of the early embryonic stages has remained so, otherwise as an open meatus through which the sound waves are conveyed to the tympanic membrane.

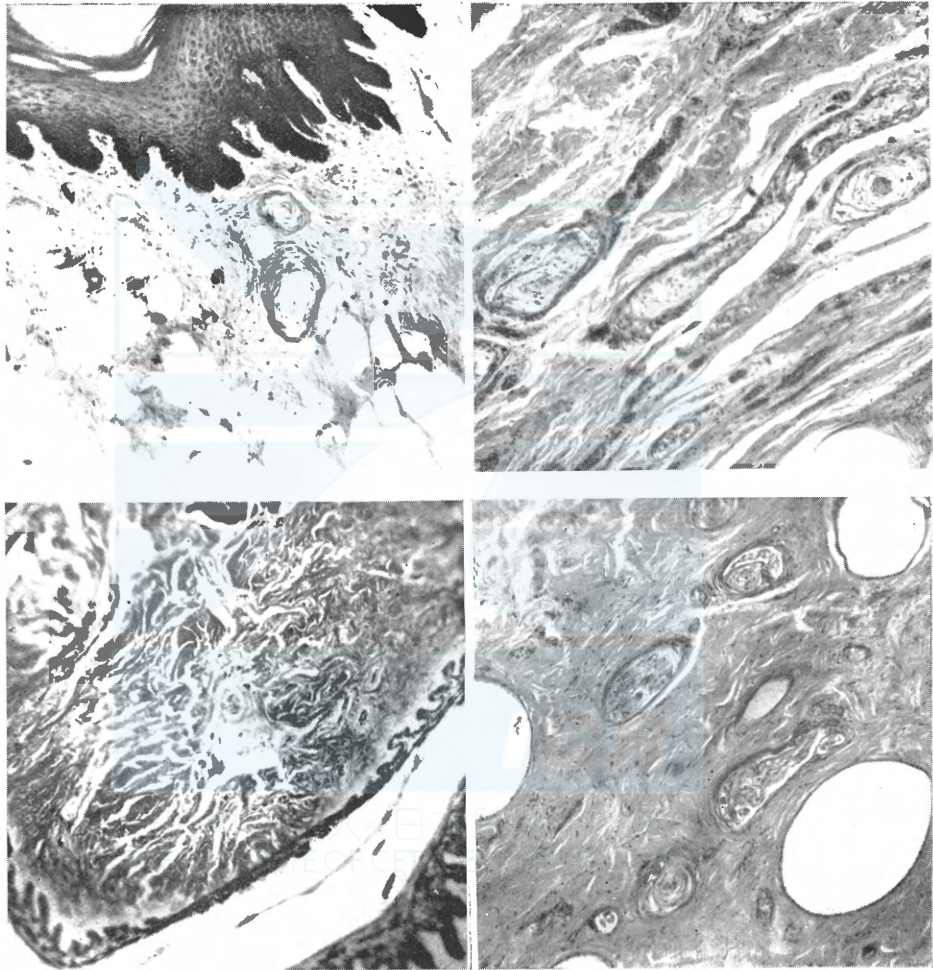


Fig. 6. Peri-meatal sensory corpuscles ( $\times 90$ ). *Upper left- Balaenoptera physalus*, the deep portion of the lateral meatus; *upper right- Physeter*, in the capsule of the lymphoid organ; *bottom left- Ziphius* (Bielschowsky's staining); *bottom right- Berardius*.

## Chapter 2 Middle Ear

### 1. The Tympano-Periotic Bone :

#### Introductory Remarks :

The tympano-periotic bone of cetacea is of special interest for its peculiar morphology and of the great importance in the entire organ of hearing, since the labyrinthic organ is embedded within the periotic, and this, together with the tympanic bulla, confirms the tympanic cavity. The tympanic bone is shaped bullar not unlikely as the many terrestrial mammals but in every way cetacean. By "cetacean", however, I mean two different ways as odontocete and mystacocete; and the periotic bone also can be classified likewise into two. Needless to say, the bone differs more or less in form and dimensions according to the taxonomic genera and families in each suborder. Among them, some have been variously described by the previous authors, yet it seems to me some further treatments of synthetic nature are here necessary throughout the whole order.

In general, I cannot emphasize too much that the cetacean tympano-periotic bone is extraordinarily so compact and so dense like the enamel substance of the mammalian teeth that the bone can be sawed with great difficulty and fortitude; whereas other bones are mostly spongy and impregnated with much oil. In a sense, another nomenclature "petrosal" sounds superb to express the structure, though the term concerns the periotic bone exclusively. The bone is naturally known also by name of "cetolith". Now it is easy to understand the geologic-oceanographic or palaeontologic knowledge (Zittel, 1891-93, p. 162; Bennett, 1931, p. 38) that the isolated tympanic as well as the periotic bones are found in almost all strata yielding cetacean remains, and have been dredged from the floor of the ocean because the bone remains intact long after every trace of the remainder of the whale body has disappeared.

The bone tissue is, in the meantime, pretty fragile, particularly in thin portions. This is clearly noticed on the sawing and chiseling opportunities. One rare case of *Balaenoptera borealis* who was harpooned on the head and came to my experience in 1950 at Akkeshi, Hokkaido was interesting because the tympanic bones were crushed into pieces. In my opinion this phenomenon may throw a side light to the solution of the tympanic function.

#### a. Family Delphinidae (hereto figs. 7, 8) :

The two components of the tympano-periotic bone are ankylosed each other, so each is not natural if treated separately. But here they will

be treated so for the sake of convenience.

**Globicephalus:** The tympanic bone of *Globicephalus* is divided into the bulla and the posterior mastoid process. The bulla presents a semi-cylindrical form slightly compressed in vertical direction, with its long axis pointing rostro-mesad, broad posteriorly and becoming narrower anteriorly. The lateral border is irregular and thin; whereas the medial is rolled over and massive, which is named by Kellogg (1928) as the involucrum. Toward the posterior extremity of the bulla, the two borders are united altogether, thus forming the neck which is continuous to the mastoid process. This process is the processus petrosus ossis tympanici

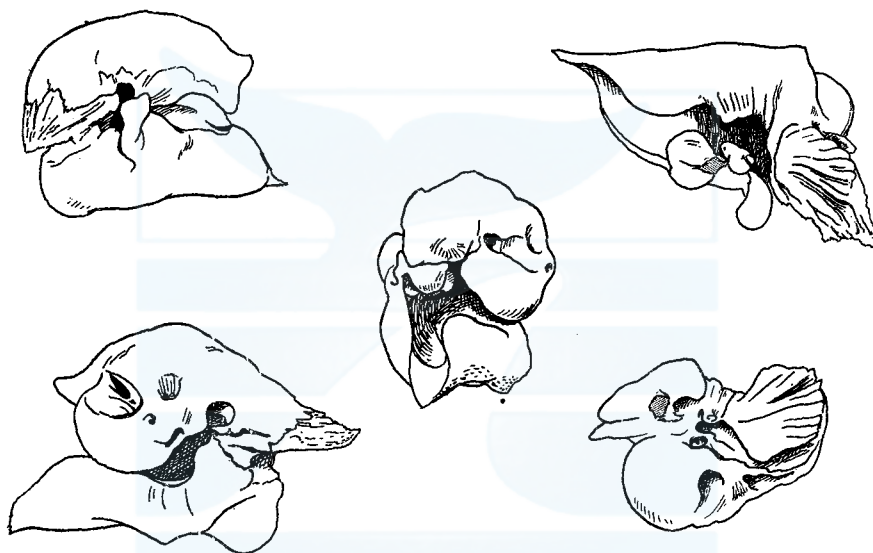


Fig. 7. Tympano-periotic bone of *Globicephalus* (7/8 natural size). Complete bone of right side to the left, dislocated left bone to the right.

of Denker (1902) and is called by Schulte and Kernan (1917; 1918-19) as the tympano-mastoid. The process projects horizontally in the lateral direction slightly backward. On the upper side of the process, at its proximal portion, there is a facet, with which the tympanic bone syndesmoses with the periotic. This joint-facet is rhomb-shaped, the short diagonal being located antero-posteriorly and the long one transversely. The facet is usually indented by several ridges which radiate from the anterior angle toward the posterior sides. The ridges are outstanding especially on the lateral half of the facet and concentrate after refraction on its posterior margin toward the tip of the process, while the medial half presents the ridges less markedly, being absent anteriorly.

The thin lateral border of the tympanic bulla draws a line convex outward, of which the apical half remains free, the margin rolling inward in a manner of concha. Meanwhile, the proximal half is ankylosed with the tegmental process of the periotic bone. The ankylosis hereof, however, is somewhat complicated by the pea-sized tubercle, figured and marked *P* by Denker as the process for the bony connection with the tympanic bone (1902, tab. 14, figs. 2, 3), which evidently corresponds to the processus tubarius of Boenninghaus and the accessory ossicle of Kellogg, and which I would call hereafter as the tubal tubercle after Boenninghaus' interpretation. On the outer surface of this portion, a marked groove presents in the longitudinal direction, which borders the tubercle from the bulla, and where the lateral border is extremely thin and fragile (fig. 27). Corresponding to the outside groove, the wall protrudes inward in a wavy way. The union between the tubercle and the tegmental process of the periotic is characteristic, namely the two bone portions are seemingly squeezed each other and comes into close contact but are ankylosed only in a limited area (half-toned in fig. 7). Laterally, a bow-shaped fissure presents bordering these two portions, while entally the tubercle is bordered continuously by the same fissure which fades out finally in the posterior side, for the tubercle is here ankylosed with the periotic. This ankylosis is not lamellated but thick, still the union is as fragile as that between the tubal tubercle and the bullar border.

Toward the posterior end of the lateral border, a prominent process juts out upward and outward. The process is somewhat S-shaped, known after Beauregard as the sigmoid process. The upper border of the sigmoid process comes into close contact with the corresponding dam-shaped eminence which protrudes at the base of the tegmental process of the periotic. The hind surface of the sigmoid process and that of the facing eminence of the periotic thus altogether make the anterior border of the large aperture, *apertura tympanica* of Denker. The neck of the mastoid process of the tympanic borders posteriorly the aperture. In other words, the aperture is practically a deep incisure in the bullar lateral border, between the sigmoid process and the mastoid process, and it is only partly that the periotic borders the aperture in the upper part. The tympanic aperture is divided by the isthmus between the sigmoid process and the facing crest of the mastoid process almost completely in a sand-glass form into two minor apertures, the upper and the lower. The lower aperture is the osseous part of the external auditory meatus and is the genuine tympanic aperture. The upper part, to the contrary,

is peculiar to odontoceti and is named by Beaugard as the ductus petro-tympanicus and by Boenninghaus as the hiatus epitympanicus. At the bottom of the tympanic aperture the conical process juts out upward into the aperture. This is the processus conicus posterior of Beaugard and Denker, and the processus medius bullae of Boenninghaus. Both sigmoid process and the conicus process are hollow inside and the margins are similarly rolled inward.

Anterior to the sigmoid process, a minute incisure is present on the margin of the bullar lateral border. The incisure borders a triangular opening<sup>1</sup> in the perfect tympano-periotic combination, the tegmental process of the periotic making the upper side. Along the hind side of the triangle, the malleus is rigidly fused with the bulla, and through the opening the caput mallei can be seen. The opening is located in the bottom of a deep recess, of which the anterior portion continues with the longitudinal groove mentioned above between the tubal tubercle and the bulla. The tegmental process of the periotic and the tubal tubercle in front border the recess from upper side, the bullar lateral expansion in front of the sigmoid process borders it from below, and the sigmoid process from behind. This recess should be noted because it attracted special attention of Boenninghaus as will be discussed in the following chapter as the "sound-funnel" or "Schalltrichter".

The under side of the bulla is shield-shaped pointing with its bottom rostro-mesad. The surface is slightly concave lengthwise and convex crosswise. Of the two side angles of the shield, the lateral is the sigmoid process and the conicus process, while the medial is the hindermost prominent corner of the vertically compressed involucrum. At top of the shield swells a globular prominence mesad, this being hollow inside where it is the posterior end of the tympanic cavity. Between these bilateral prominences a distinctly deep furrow presents on the surface. The bullar shield is smooth on the lateral surface, while medially the surface is rough throughout, affording insertion of the thick fibrous layer.

The upper surface of the medial involucrum presents an impression posteriorly, which becomes gradually deeper as it approaches the neck of the mastoid process. The deepest position of the impression forms a furrow which traverses the involucrum, the site corresponds to the hind corner of the involucrum, namely the medial side angle of the bullar shield in simile. The impression, as well as the furrow, are apparently caused by the passage and expansion of the cavernous body with nerves and blood vessels into the tympanic cavity through the tympano-periotic

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1) For the interpretation of this opening, see page 58.

fissure between the involucrum and the spheric portion of the periotic. The upper side of the involucrum, in the region of the impression, expands inward a minor limbus-like rolling over the bullar depression, this and the mesad prominent flattened corner of the involucrum suggest that some dynamic invasion, probably by the resistance of the cavernous body, has attacked the involucrum strongly on the spot. Between the thin lateral border and the massive medial involucrum lies the remarkable and longitudinal deep bullar depression which forms the bottom of the tympanic cavity and provides the bulla with a semi-cylindrical form.

The periotic bone consists of three portions, viz., the labyrinthic or cochlear portion, spheric in shape, and the anterior, pro-otic or tegmental process, and the posterior or mastoid process. The mastoid process is the processus tympanicus ossis petrosi of Denker, or can be called as the opisthotic process to introduce Lillie's nomenclature (1910). Whereas Schulte divides the bone into two portions, the cochlear<sup>1</sup> and the vestibular (1917, p. 396).

On the lower surface of the mastoid process presents the rhombic facet which articulates with that of the tympanic in syndesmosis, where the furrows make the facet wavy corresponding to the ridges on the tympanic facet as referred to before. These ridges and furrows seem to tight the articulation, and in many cases this articulation cannot be freed without destroying some of these structures. Anterior to the facet, the epitympanic recess presents a depression, in which mesad the fenestra vestibuli opens, and closely laterad to the window lies the tympanic opening of the facial nerve canal, continuing backward to an S-shaped sulcus on the under surface through the isthmus between the cochlear portion and the mastoid process, where the medial edge of the articulation facet and the lamellated process of the cochlear portion face against each other flooring the isthmus incompletely, until it appears on the medial side of the mastoid process just above the facet's hinder edge. The sulcus then makes a turn laterad and downward around the medial corner of the tympanic mastoid process, leaving a short, sometimes faint depression on its hinder margin.

Within the epitympanic recess, closely behind the posterior end of the fenestra vestibuli, another groove lies medially parallel to the facial nerve sulcus separated from it by a ridge. The groove lodges the stapedia muscle and goes further backward and somewhat mesad and upward, becoming free from the named muscle and affords the communication

1) Though the division is originally described of *Kogia*, it comprehends also other odontoceti.

of the tympanic cavity with the posterior pneumatic sinus. The groove goes along with the facial nerve sulcus through the isthmus mentioned above. Laterad to the epitympanic recess, the hiatus epitympanicus of Boeninghaus traverses a furrow between the articulation facet and the dam-shaped transverse eminence of the tegmental process which is in contact with the upper border of the sigmoid process. The furrow of the hiatus borders the epitympanic recess laterally, descending lower than the ceiling-level of the recess. At the ental border of the furrow, a minute ledge expands mesad, on which the short crus of the incus articulates.

The tegmental process is prolonged before the posterior articulation and the hiatus epitympanicus, being bordered posteriorly by the transverse eminence provided on it with a smooth contact surface facing to the sigmoid process of the tympanic. Slightly in front and mesad of this contact surface, a small oval depression is noted facing inward and downward, which lodges the caput mallei in it, so can be called malleolar fossa. Further distal under surface of the tegmental process presents two slight concavities both lengthwise, of which the lateral closely contacts with the tubal tubercle, and toward the proximal end of it, the process is ankylosed with the tubercle, the union stretching partly over the medial concavity. The apical end of the tegmental process is bicuspid, the lateral cuspis, pointing rostrad and slightly downward, is regarded to be equivalent to the proper apex, while the medial turns upward like a hook. The tegmental process roofs the tympanic cavity above the bullar depression.

The cochlear portion protrudes downward in a spheric and dome-like form facing against the upper side of the tympanic involucrum. The promontory presents toward the hind border of the portion, mesad to the fenestra vestibuli. On the posterior surface of the dome, opens backward the fenestra cochleae, the contour, however, being somewhat heart-shaped instead of being round.

On the upper side of the periotic, two processes, tegmental and the mastoid, present lengthwise a continuous S-shaped smooth surface, convex and inclined laterad, and the cochlear portion presents a semicircular border attached mesad to the long S-shaped combination of two processes, facing obliquely mesad and upward. The arcade borders a deep fossa in it, the fundus of the internal auditory meatus. The fossa is piriform because the upper portion of the fundus slips off forward and the facial nerve canal is located apart from the remaining foramina (fig. 12). The poor transverse crest divides the posterior portion of the fundus up and

down. The upper foramen is the superior area vestibularis. In the lower portion, the tractus spiralis presents anteriorly, the inferior area vestibularis posteriorly, including the foramen singulare in it. On the border of the cochlear arcade, the infundibule-shaped vestibular aquaeduct opens at the posterior extremity, and at a short distance mesad to it, the minute and oblong cochlear aquaeduct opens.

Finally, some remarks concerning the entire tympano-periotic *in toto*. The tympanic cavity, bordered by the epitympanic recess and the tegmental process of the periotic above and by the bullar depression below, opens rostrad through an aperture which is named by Boenninghaus as the orificium tympanicum of the Eustachian tube. The orifice is bordered above by the tubal tubercle, the tegmental process and the cochlear portion of the periotic, and the bottom being incised between the conch-like free portion of the lateral border and the medial involucrum of the tympanic bulla. The orifice communicates medially backward with the tympano-periotic fissure between the involucrum and the cochlear portion. On the posterior side of the bone, a minute foramen must be mentioned for the chorda tympani nerve. The foramen presents near the medial border of the posterior side of the neck of the mastoid process. The foramen perforates the proximal portion of the involucrum rostrad and upward and presents its interior opening on the ental surface of the involucrum.

The tympanic and the periotic are ankylosed by the thin medial border of the bulla with the tegmental process of the periotic anteriorly and articulates by the posterior facets in syndesmosis. Beyond these, the two components are nowhere in contact but the sigmoid process and the facing periotic eminence, elsewhere they are separated from each other by fissure of varying widths. The peculiar topography of these unions of the tympano-periotic bone is important in relation with the massive and heavy involucral border of the bulla which remains free. I would like to stress the dynamic correlation likely to occur within these structures, in particular that between the involucrum and the thin and fragile union (fig. 27).

Another important remark is that the mastoid process varies in dimensions according to species of delphinidae family, namely it stretches in general shorter than *Globicephalus* in lesser dolphins and porpoises as *Prodelphinus*, *Steno*, *Tursiops*, *Grampus* and *Neomeris* examined by me. I am of prediction that the killer whale, *Orcinus* may have more prolonged mastoid process than *Globicephalus*, and feel sorry, in this respect, to have missed the species. Hyrtl (1845, tab. 9, fig. 10) figured the



tympanic bulla of *Delphinus gladiator*, but the mastoid process is unfortunately lacking. Meanwhile it interests me in this connection that another species of *Globicephalus* from Ayukawa, probably *G. scammonii*, has a longer process than *sieboldii* species from Taiji (fig. 8).

I am afraid the above description of the tympano-periotic of *Globicephalus* might be redundant because the family has been most popularly treated by the previous authors. I dared this, however, in order to make it easy to put the bones of various species into better comparison. Within the delphinidae family no remarkable difference presents, but the dimensions and the length of the mastoid process just mentioned seem to be a matter of importance. But to mention any among them,



Fig. 8. Developmental series of the mastoid process of the tympanic bone in delphinidae family. From left to right: *Grampus*, *Globicephalus sieboldii*, *G.* sp. (probably *G. scammonii*). Cf. further fig. 17.

the tympanic bone of *Tursiops* as well as *Prodelphinus*, and probably that of other dolphin species, presents an elliptical foramen perforating the hind wall of the neck of the mastoid process transversely; and secondly the fundus of the internal auditory meatus is distorted and elongated much more than *Globicephalus*, so the foramina line up in the more strongly distorted comma-shaped fossa with more faint sign of the transverse crest (fig. 12). This latter relation, altogether with some remarks mentioned before, may indicate that some external force has influenced the morphology of the bone during development. Practically, the bone of delphinidae shows in common a compression more or less mainly in vertical direction which does not present in other families.

b. Family Ziphiidae :

**Berardius** (hereto fig. 9):

The tympano-periotic bone of *Berardius* is much larger than *Globicephalus* and other delphinids just described, length of the bulla and

the periotic measuring about 6 cm. and 7 cm. respectively. The bulla is more roundish in all directions as compared with that of delphinidae. The under side of the bulla is similarly shield-shaped as delphinids but generally more roundish, even the rostral extremity being round and not pointed. The surface is convex both lengthwise and crosswise though the convexity in longitudinal direction curves less strongly. The transverse convexity is almost perfectly semicircular, provided with no sign of the vertical compression. The globular prominence at top of the shield, namely at the hindermost corner of the bulla, is comparatively larger, and between this and the other medial corner, viz., the posterior end of the involucrum, the furrow is shallower than delphinidae. The sigmoid process bends backward and does not disturb the lateral borderline sideways so strongly as in delphinidae. The margin of the sigmoid process is crowned with an obtuse angle which is situated closely laterad to the less prominent conicus process; whereas that of delphinidae is bordered by a gentle arc-line. In front of the sigmoid process, the lateral border of the bulla is traversed by a striking sulcus seemingly folded-over rostrad by the basement of the process. This sulcus is characteristic to the present family as was so illustrated of the various species by True (1910, pl. 35). The anterior bony union of the tympano-periotic in front of the sigmoid process is less lamellated and relatively thicker and shorter than delphinids, still being extremely fragile. The lateral border more rostrad to the union is strongly rolled inward in a concha and closely contacts with the tegmental process of the periotic within its marked longitudinal impression throughout. The involucrum is slender in its anterior half, while posteriorly it develops extraordinarily thick and continues with the neck of the mastoid process. On the outer, posterior surface of the neck, perforations often occur, where the tympano-hyal cartilage is connected and the wall around being quite thin. This is probably equivalent to the already related striking fenestration in some dolphins. The posterior articulation facets are shaped like a parallelogram rather than a romb and provided with no particular structures as ridges upon them. The facets are rather gentle, being convex with the tympanic and concave with the periotic. The mastoid process of the tympanic markedly expands laterad, backward and downward. Toward the extremity, the process grows irregularly broad and thick. The upper surface of the process is rugged and is sutured with the skull in a notch bordering the squamosal and the exo-occipital bones.

The periotic bone is not far apart from delphinidae family, though the general morphology is characteristic and it is not difficult to identify

the family. The comparatively large and pointed tegmental process is quadriangular in crosswise section, being upperly broader. The mastoid

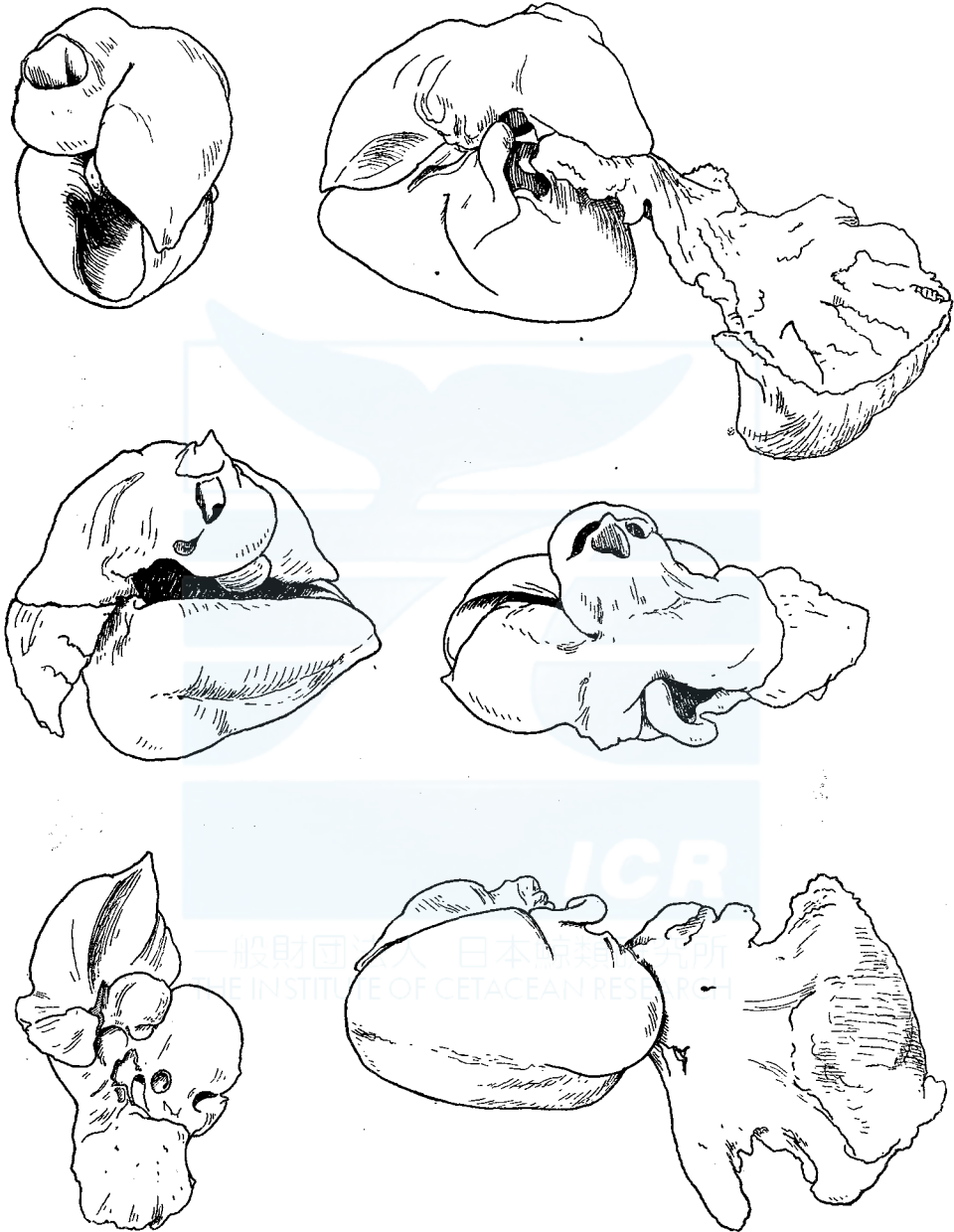


Fig. 9. Left side tympano-periotic bone and right periotic of *Berardius* (ca. 4/5 natural size).

process is bordered from the anterior portions by a slightly prolonged neck than in delphinids. Accordingly, the bone is comparatively long or slender as a whole and the cochlear portion stays in a relatively small scale. Boundaries of the three portions are thus distinct, constricted behind and deeply incised in front. On the lower surface of the bone, scarcely nothing is remarked other than delphinids but the tubal tubercle. This tubercle is located sequestered in the tympanic cavity due to the tegmental prolongation. The tubercle is practically one part of the periotic fused more firmly than in delphinids.

On the upper surface of the bone, the elliptical porus acusticus internus perforates the spheric portion, situated obliquely from the posterior bottom toward the anterior top. The fundus of the meatus presents more distinct transverse crest than delphinids, and the facial nerve canal stays closer to the remaining foramina. No foramen singulare appears



Fig. 10. Periotic bone of *Ziphius*  
(Natural size).

independent as is the case with delphinids. The vestibular aquaeduct broadens the infundibular lumen in a triangular pyramidal shape behind the internal auditory meatus, bordered from it by a thin lamellated but prominent wall. Mesad and backward to the vestibular aquaeduct, opens the cochlear aquaeduct in comparatively larger dimensions than in delphinids.

The tympano-periotic bone of *Ziphius* (fig. 10) is much the same with *Berardius* though smaller in scale, so it seems needless to add detailed descriptions concerning it. In general, the bone seems to be somewhat thicker and more stumpy than *Berardius*.

#### c. Family Physteridae:

*Physeter* and *Kogia* represent the third family, the last of the odontocete suborder. However, the intergeneric differences shown in the tympano-periotic bone are pretty noticeable, so each genus will be described here separately.

#### *Physeter* (hereto fig. 11):

The tympano-periotic bone of *Physeter* is the largest among all odontocete species examined by me. But the bone of *Orca* apparently exceeds that of *Physeter* as described by Flower (1867, p. 321) and as figures of *Delphinus gladiator* by Hyrtl demonstrate (1845, tab. 9, figs. 8, 10).

In my opinion, however, this is merely outwardly so, the bone of *Physeter* being essentially not inferior because it lacks the prolonged anterior portions whatever. Anyway, the bone is remarkable for its small size in comparison with the entire skull as noted by Flower.

The tympanic bulla is semi-cylindrical in the most literal sense of the word, namely it is not pointed nor tapers rostrad. Above all, the anterior portion of the bulla in front of the sigmoid process, to say the least, is literally cylindrical, amputated somewhat obliquely mesad at the anterior margin. Along this unusual margin, the lateral border ends in a conch-like in-rolling, and the medial one in a stump. The central bottom border between these two borders slightly caves in backward, this occurring in no other odontocete species previously mentioned. The sigmoid process juts out laterad prominently, and practically is of remarkable size and crowned with a corner almost in right angle at the bottom of it. The tympanic aperture is much elongated, apparently due to the vertical expansion of this sigmoid process. The posterior portion of the bulla behind the sigmoid process presents a comparatively confused appearance, still the structures do not differ much apart from two other families. There the bilateral prominences present, being bordered by a shallow groove between them. The medial one is massive and the posterior corner of the involucrum; whereas the lateral is hollow inside and evidently equivalent to those described as globular of the formerly mentioned families. The lateral surface of this hollow expansion is, however, shortened so remarkably that it continues directly with the lower margin of the tympanic aperture. The margin expands laterad between the two processes, the sigmoid and the mastoid, presenting a fossa which faces downward. Such a relation does never occur in other families and accordingly characteristic to this species alone. Because of this external concavity, the conicus process is naturally lacking. And besides, the lower margin of the tympanic aperture is so lamellated into a thin plate that here perforations sometimes occur. It is also characteristic that the lateral portion of the bulla expands also in front of the sigmoid process less markedly, corresponding to the shortening tendency as seen strongly behind the sigmoid process. To the consequence, the so-called "sound-funnel" of Boenninghaus is less developed than others. The medial half of the bullar under surface is rough throughout as in other families but much more complicated. The bilateral prominences, above all, present a marked tuberosity or tuberosity-crest transversely, which affords the fibrous connection to the bulla more firmly. From the posterior lateral corner of the upper side of the bulla,

the mastoid process projects, which is peculiarly composed of a large number of distinct thin plates, commonly held together at the attachment, and radiates laterad, backward and downward. The process interdigitates with the squamosal and the exo-occipital bones so firmly

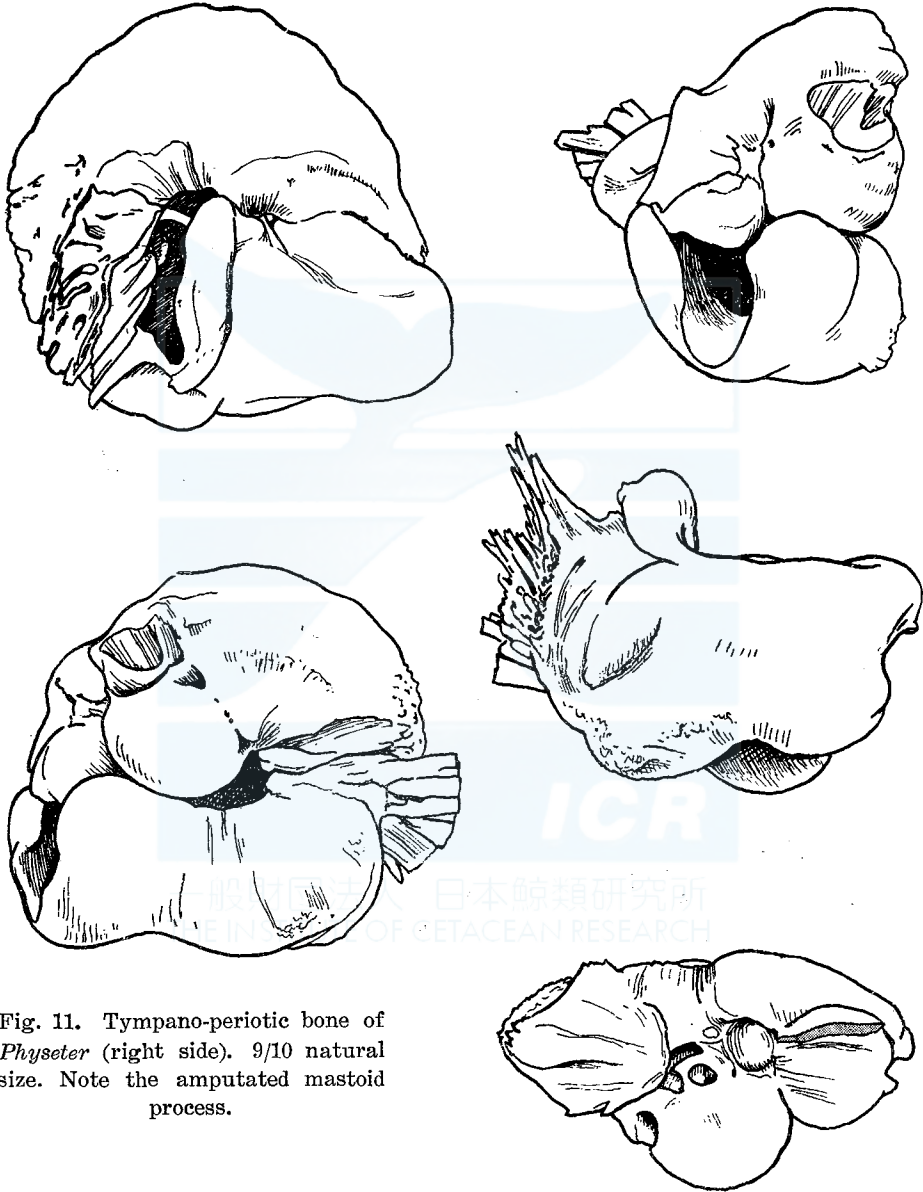


Fig. 11. Tympano-periotic bone of *Physeter* (right side). 9/10 natural size. Note the amputated mastoid process.

each other that the tympano-periotic cannot be separated from the skull without destroying this connection of the mastoid process. These conditions have been correctly described by Flower alone so far as known to me (1867, p. 321), who simultaneously pointed out imperfect figures of the bone by Camper and Owen, in which the process is broken off (footnote, same page).

The lateral view of the periotic is shaped like a helmet, of which the anterior peak corresponds to the tegmental process and the posterior to the mastoid process. It is peculiar too that the mastoid process of the periotic stretches its pointed extremity downward over the same process of the tympanic, both sides of the process being provided with rough tuberosities toward its margins continuing sideward with the complicated upper side of the mastoid process of the tympanic. The syndesmotic articulation facet of the periotic is diamond-shaped though in some cases often irregular, but its curvature is somewhat like a saddle, namely concave lengthwise and rather convex crosswise, presenting a central longitudinal crest which divides the surface into two oblique side slopes. Otherwise the articulation facets of the periotic as well as the tympanic present not prominent signs of the ridges and corresponding negatives which radiate backward from the anterior corner of the diamond. In other words, the long crest just mentioned may be interpreted as an extreme one of these ridges. Along the furrow of the epitympanic hiatus, several striations traverse the bone in a way which likely to associate us with some filed artifacts but in reality not. The medial border of this epitympanic furrow marks a crest which stretches between the mastoid process posteriorly and the posterior rim of the malleolar impression anteriorly. The crest is well developed but is equivalent to the ledge described in *Globicephalus* because an oval facet for the articulation with the short crus of the incus presents on its under side. In contrast to the previous families, this facet is characteristic for its slight elevation instead of impression. It is of some interest, in this relation, that a serial development is noticed from a thin osseous ledge to the thick crest as traced through *Globicephalus*, *Berardius* and *Physeter*, each representing other members of its own family with it. The epitympanic recess is relatively deeper and narrower as compared with the former families. Above all, the sulci lodging the facial nerve and the stapedial muscle are of remarkable depth, but the ridge between them develops less than other families, and the posterior boundary of the fenestra vestibuli borders sharply these sulci at their confluence. In front of the fenestra as well as the facial nerve canal opening, a round

impression presents, the malleolar impression which lodges the caput mallei in it. Anterior to this impression, a large tubal tubercle presents between the cochlear sphere and the tegmental process, being fused at its posterior upper part with these portions, elsewhere the tubercle is bordered from them by fissures but in close contact. This contact relation of the tubal tubercle to the cochlear sphere does not present in delphinidae family. The tegmental process, that is, the anterior peak of the helmet in simile, is pointed and turns steeply downward, but is extremely so short that the upper side of the periotic continues directly with the rostral margin of the bulla at its in-rolled lateral border across a fine fissure. It happens quite peculiarly, to the consequence, that the tubal tubercle as well as the cochlear portion present almost in a vertical plane together with the tegmental process and the bullar rostral margin.

The internal auditory meatus is free from those distortions as seen previously and is really round in contour. The foramina presenting in the fundus are as described before, but the vestibular aquaeduct, though less developed in caliber but similarly infundibularly shaped, is involved within the meatus. Serial distortions of the internal meatal foramina can be shown in the similar order of family-series, as is the case with the ledge-to-crest series of the articulation of the periotic with the short crus of the incus, as *Prodelphinus*, *Globicephalus*, *Berardius* and *Physeter* (fig. 12). The cochlear aquaeduct, which is minute in comparison with other families, presents closely posterior to the internal auditory meatus.



Fig. 12. Serial distortions of the internal auditory meatus (right side). From left to right: *Prodelphinus*, *Globicephalus*, *Berardius*, *Physeter*.

The anterior bony union of the tympano-periotic components is again lamellated and relatively broad, measuring about 1.5 mm. in thickness and not less than 15 mm. in breadth. The union is continuous with the lateral border of the tubal tubercle and is fused, as in the previous cases but in broader extent, with the tegmental process posteriorly. Another remark with the physeterian tympano-periotic *in toto* is the contact relation of the cochlear portion to the bullar anterior involucreum



in the tympano-periotic fissure. This is practically almost contact and a sheet of paper is hardly inserted through it, still this is not so strictly contact, for the facing massive bones can be swayed against each other by the opponent fingers of a hand, though slightly yet to a visible and sensible extent. These contact surfaces usually present impressions which border the tympano-periotic fissure.

**Kogia** (hereto fig. 13) :

The tympano-periotic bone of *Kogia* is the smallest of all species examined by me, to exclude its enormous mastoid process, and probably so throughout the whole order. The bulla and the periotic are of almost equal size, measuring 2.6–2.8 cm. in length. Therefore, the bone is remarkable for its small size both relatively and absolutely.

Schulte (1917, pp. 394–398) described the bone into fine details and few is added here, but descriptions should be arranged in order to make coincide with the foregoing ones, particularly in regard to the terminology including the terms of direction. Schulte mentioned that the long axis of the bulla was nearly transverse, and consequently two borders are described as rostral and caudal respectively. The fact is, however, that the axis is pointing rostro-mesad, though stronger than other species, so the customary terms are seemingly preferable in the present paper.

The bullar semi-cylinder of *Kogia* can be expressed to be crushed or sharply folded into the usual two borders along a longitudinal crest. In spite that the bulla is pointed at the rostral extremity of this crest, the whole border of the rostral margin resembles that of *Physeter*. The lateral border of the bulla shows a transverse expansion along its rostral margin but the general contour of this side is shaped like an irregular parallelogram. The surface is rather flat but slightly convex crosswise, being marked by three elevations. The first presents on the rostral expansion of the parallelogram which is constricted a little distance behind the margin. The sigmoid process is greatly developed and massive, and really a tubercle of rather peculiar form like comma. The process is turned forward, probably due to the remarkable thickness, and consequently the "sound-funnel" of Boeninghaus appears deeper. The tympanic aperture is very narrow and shaped like a sand-glass in which the hiatus epitympanicus is broader, whereas the lower genuine aperture is like a slit which stretches backward in an acute incisure along the neck of the mastoid process. The conicus process is obscure or lacking<sup>1</sup>

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1) More or less strong process of the tympanic aperture may occasionally present between the lower margin of this aperture and the posterior side of the sigmoid process, when the conicus process becomes less obscure.

and the lower margin of the tympanic aperture expands laterad only faintly but in the manner of *Physeter*. The posterior portion of the bulla behind the sigmoid process presents a wider elevation which is the posterior one of the three related elevations. This portion is homologized as the globular hollow prominence of others and borders the posterior side of the parallelogram, of the lateral border of the bulla.

The involucrem is comparatively very massive, being broad posteriorly and gradually tapering rostrad. The tendency of in-rolling of the bullar borders is generally so remarkable that the whole border, with exception of the lateral border, strongly rolls. The posterior end of the involucrem forms a thick prominence. This has been described of the foregoing species as the medial one of the bilateral prominences of similar size, but in *Kogia* it is smaller in comparison with the lateral hollow one. The bullar depression inside between the two borders is very narrow and somewhat complicated.

The neck of the mastoid process is very much shortened and strongly strangulated. The process is enormously expanded in a shape of a fan laterad, backward and downward; above all the downward expansion rolls further forward so as to cover the bullar hind border from below. The articulation facet presents proximally on the upper surface of the process as is in other cases. The surface is smooth and slightly concave lengthwise. Its form is a rhomb with rounded angles. From the two posterior sides of this articulation facet, radiate ridges, around score in number, within an approximate angular expansion of  $85^\circ$  laterad and backward. Somewhat similar ridges can also be seen in a deep and narrow depression between the bullar posterior border and the forward and downward expansion of the process on the lower side of it. These structures suggest us of the widely radiating platal formation of the same process of *Physeter*, which is seemingly embedded this time wholly in the routine spongy bone tissue. Toward the border of the mastoid process, the upper surface of it, which is proximally provided with the just mentioned ridges, suddenly becomes elevated along the margin, the surface of this elevation faces obliquely laterad and syndesmoses in a notch of the squamoso-occipital border with the skull.

The periotic bone of *Kogia* is of peculiar shape, but resembles that of *Physeter* greatly, and it is in a sense practically a miniature of the latter. The periotic bone of *Physeter* bows deeply downward in a helmet-like manner as mentioned before; whereas that of *Kogia* is flattened and angulated in tubercles. To enumerate these tubercles, they are: two on the cochlear portion of which the major one protrudes out of the spheric

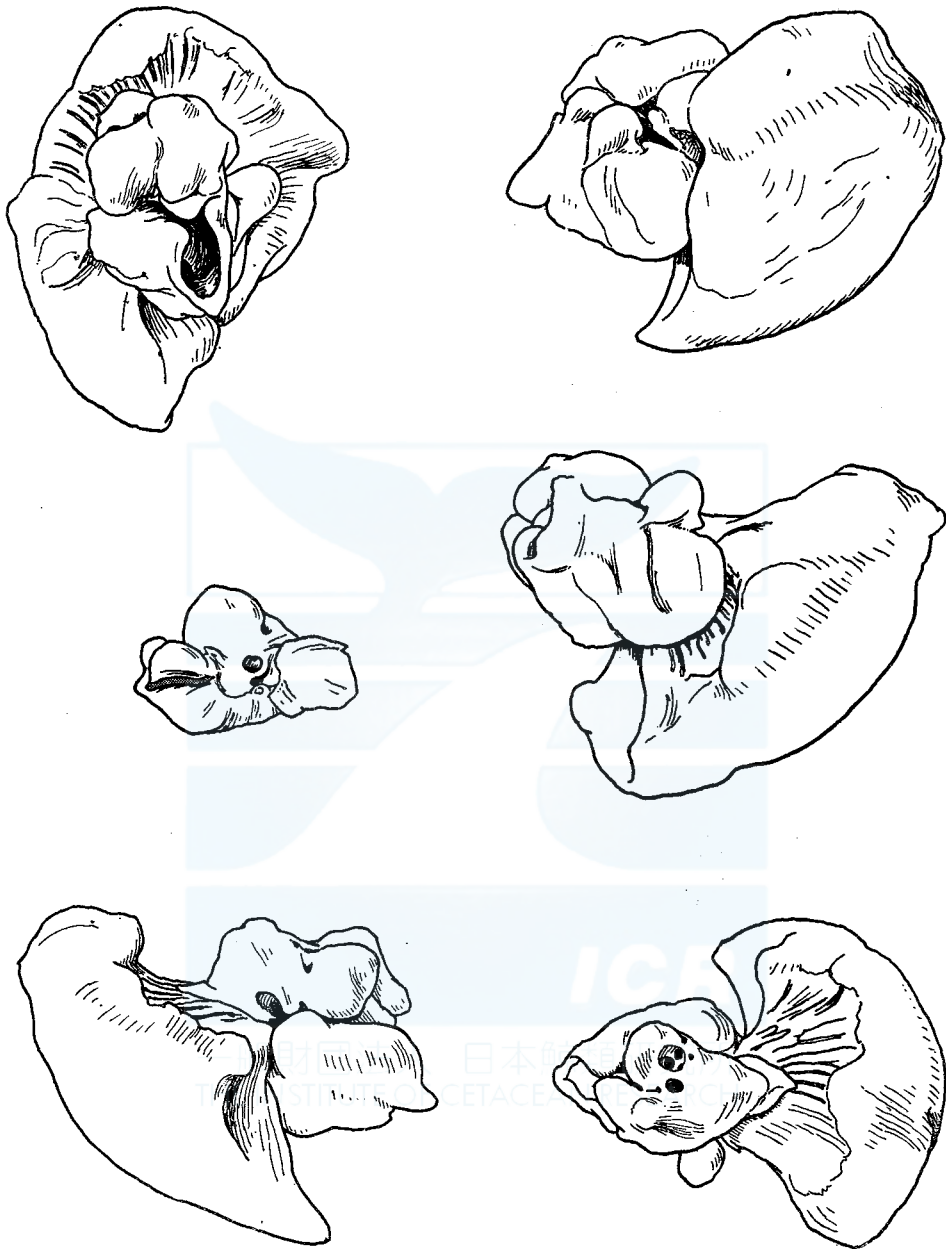


Fig. 13. Tympano-periotic bone of *Kogia*. Complete left side bone and dislocated right side periotic (*middle left*), somewhat larger than the natural size. Ankylosis artificially fractured is shown in half-tone as in other figures.

surface mesad, while the minor one upward in front of the internal auditory meatus; the tegmental process presents another one on its upper side at the symmetric position against the last mentioned one across the fissure which borders the tegmental process and the cochlear portion; the anterior extremity of the tegmental process presents another major one which protrudes mesad at a short distance medial to the proper apex; posteriorly the backward slope of the upper surface presents a remarkable prominence, which being prominent in longitudinal direction and so seems to be equivalent to the long crest of *Physeter* along its mastoid process; finally a prominent tubercle on the lateral border which is equivalent to the transverse dam-shaped eminence at the base of the tegmental process of other species. Here the contact is imperfect between the sigmoid process and this last tubercle. The anterior union between the bullar lateral border and the tegmental process or the tubal tubercle is quite similar to that of *Physeter*. The internal auditory meatus is bordered less distinctly and the facial canal as well as the vestibular aquaeduct open separately from the proper meatus.

d. Family Balaenopteridae :

**Balaenoptera** (hereto fig. 14) :

The tympano-periotic bone of *Balaenoptera* has been thoroughly described since Dwight (1872) by many authors including myself. The bone is enormous in size and weight as compared with odontoceti, still remarkably small in comparison with the huge head of the animal. The proportion differs greatly according to species. The tympanic bullae measure in length 13.1 cm. in *borealis*, 13.4–13.7 cm. in *physalus*, and 13.7–15.7 cm. in *musculus* species; and in greatest breadth 9.3 cm. in the first, 10.1 cm. in the second, and 9.8–11.2 cm. in the last species. Thus, it is noticed that the dimensional difference of the bulla remains comparatively little in spite of the remarkable difference of the body length, and consequently length of the head according to species.

The bulla of *B. physalus* is rather renal and of cowrie-shell form. It appears too like a man's profil facing laterad, in which the facial contour is figured by the irregular lateral border. From anterior to posterior, marked formations are: largest convex elevation appearing like forehead; then a transverse furrow becoming shallower downward, this looks like eye; about halfway of the border-line, the sigmoid process juts out laterad like nose; and continuing closely downward to this process, another elevation looks like cheek; behind the sigmoid process, the border protrudes laterad like mouth; and finally the posterior corner is prominent like chin. The lateral mouth-like protrusion of the border behind the

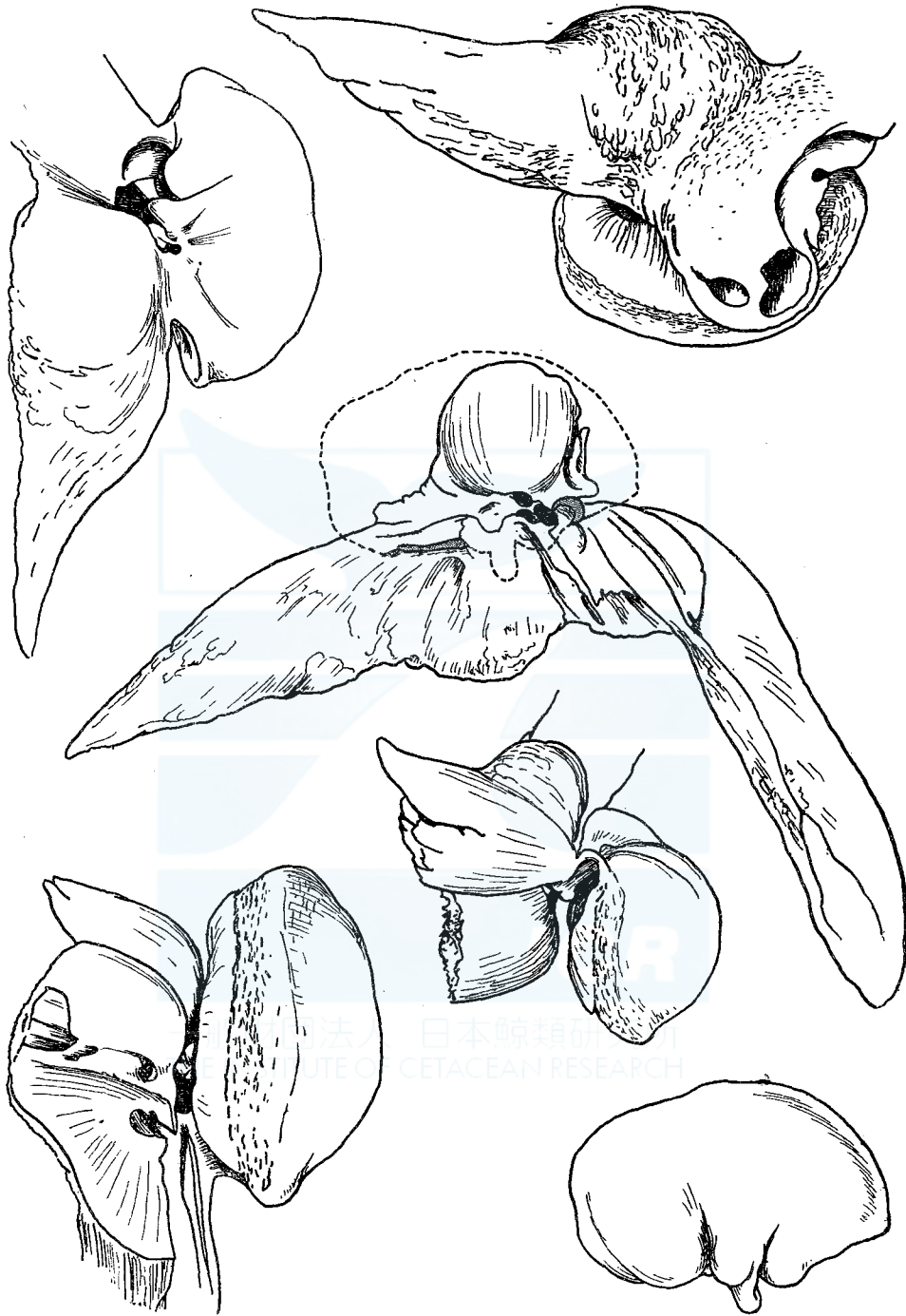


Fig. 14. Tympano-periotic bone of *Balaenoptera physalus* (ca.  $1/3$  natural size).

sigmoid process may be homologized as the conicus process which commonly presents in odontoceti with an exception of physeteridae, the margin rolling likewise inward. The sigmoid process stays about 5 mm. apart from the periotic, where the process in odontoceti comes into contact with the transverse eminence at the base of the tegmental process. The tympanic aperture, therefore, communicates with the triangular opening anterior to the sigmoid process, which is, in odontoceti, mostly<sup>1</sup> independent as previously described.

The medial border is an enormously developed involucrum like odontoceti but far heavier, broad posteriorly becoming narrower anteriorly. On the upper side of the involucrum, two distinct areas are present. The lateral area, facing upward to the tympanic cavity, is broader and smooth, traversed by faint wrinkles of which only a few are well marked. This area is somewhat but sharply elevated than the medial area which is narrower than the lateral and extraordinarily coarse and rugged with tuberosities, affording strong insertion of thick fibrous layer to the bulla. The anterior portion of the involucral border turns gradually laterad until it is continuous with the lateral border in the end. It is characteristic to *Balaenoptera* that the bulla is anteriorly thus closed. While at the posterior extremity, the two borders are united above the hindermost portion of the bullar depression like odontoceti, and the posterior pedicular union fuses the bulla here to the periotic. This posterior pedicle is thin but is curved just like the neck-portion of the mastoid process of the odontocete tympanic. This pedicle is peculiar too with the anterior one to the present genus. The anterior pedicle is obviously homologous to the anterior union as described of odontoceti and is broad but as thin. It should be emphasized here that no articulation presents in *Balaenoptera* between the tympanic and the periotic, which presents in all odontoceti.

The periotic bone is divided as well into three marked portions as the anterior pro-otic or tegmental process, the cochlear portion and the opisthotic or mastoid process. The general peculiarity of the bone is the surprisingly prolonged or extended development of the mastoid process which is wedged between the squamosal and the exo-occipital bones of the skull. The posterior pedicle is situated at the base of this mastoid process, where the process turns strongly laterad. The pedicle has a fossa concave laterad in its curvature, which is visible through the

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1) The sigmoid process of *Kogia* usually does not touch the tegmental process. To the consequence, the triangular opening, which is now a slit, communicates with the tympanic aperture like *Balaenoptera*. See p. 36.

tympanic aperture. The epitympanic recess is rather a deep sinus which caves in sharply and markedly between the posterior pedicle and the cochlear portion, presenting its oblong aperture to the tympanic cavity. The recess stretches backward in a narrow sulcus along the medial border of the posterior pedicle and finally opens in the posterior side of the bone. This sulcus is bordered downward by a slit-like fissure as is the case with *Globicephalus*, of which I mentioned as isthmus because of its more incomplete formation. No saying, the facial nerve canal and the fenestra vestibuli open at the bottom of the recess, and the backward stretching sulcus lodges the stapedial muscle as well as the facial nerve in it. No malleolar impression presents but the well preserved meatal furrow traverses the under side of the bone, bordering the tympanic aperture in its ceiling. The contour of the tympanic aperture is not sand-glass shaped like odontoceti, because any marked portion like the epitympanic hiatus of odontoceti does not develop at all in the aperture above the tympanic membrane.

The tegmental process is somewhat pyramidal and tapers rostrad, slightly curving laterad. At the base of this process, a remarkably large tubercle protrudes laterad, which does not touch the sigmoid process as mentioned before, though this tubercle resembles the dam-shaped transverse eminence of odontoceti. The highly lamellated anterior pedicle fuses the basement of this process with the lateral border of the bulla. The tubal tubercle is utterly obscure.

The cochlear portion expands mesad from the confluence of other two processes, and is marked by a spheric dome-shaped eminence corresponding to the interior labyrinth. The lateral part of this dome slopes backward and its free margin borders sharply a remarkably large recess which presents on the posterior side of this portion lodging in it a considerably large mass of cartilaginous structure between this and the exoccipital bones. The fenestra cochleae opens in the posterior slope of the dome. The internal auditory meatus is composed solely of the nervous foramina, others being excluded outside the meatal formation. The vestibular and the cochlear aqueducts present backward in this given order and the facial nerve canal anterior to the meatus. Concerning the upper side of the periotic bone, no particular mentioning seems necessary but the rugged and coarse nature throughout, which resembles somewhat the rocky mountain side.

The above description seems to be comprehensive of other species of *Balaenoptera* for the differences among them are quite slight. The bone of *musculus* species is most strongly bulit, while that of *borealis*

less strongly, in both of which the tegmental process does not taper so sharply as in *physalus* (fig. 15). It can be added finally that *Magaptera* as well as *Balaena* seem to resemble *Balaenoptera* in outline as are illustrated by Hyrtl (1845, tab. 3, figs. 1, 2) and Hinoura (1943, fig. 12).

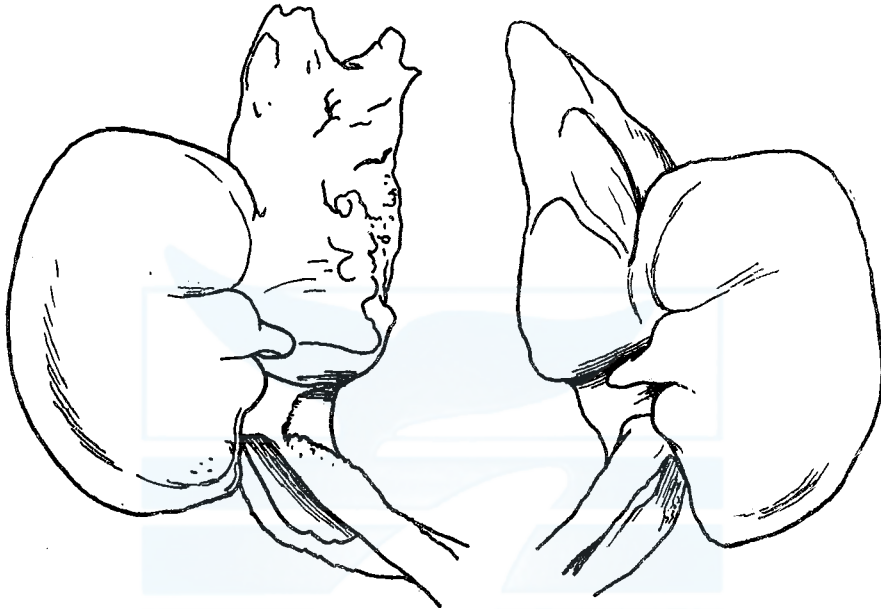


Fig. 15. Tympano-periotic bone of other balaenopterids. *Left*- Left side of *B. musculus*; *right*- Right side of *B. borealis*.

## 2. Relations of the Tympano-Periotic Bone to the Skull :

In earlier stages of development, the tympano-periotic bone of cetacea remains in a relatively large territory within the cranial basis like other mammals. But the further the development goes, the less becomes its relative size, and finally it happens that the bone is forced out of the cranial basis, this occurring particularly stronger in odontoceti than mystacoceti.

This procedure can be traced in *Globicephalus* as follows:—In the cranial basis of a foetal *Globicephalus* shortly prior to the birth, a major foramen concerned to the tympano-periotic bone is bordered by the ali-sphenoid, the basi- and exo-occipital and the parietal bones (fig. 16, top). After birth this foramen becomes strangulated in its anterior portion into a form of sand-glass by the approaching development of the ali-sphenoid, basi-occipital as well as the parietal (center). The foramen is thus divided finally into separate foramina by the completion of approach



(bottom). The tympano-periotic bone is now perfectly excluded out of the formation of the cranial basis, and consequently the eighth nerve comes out of the brain case penetrating the cranial basis through the posterior foramen with other nerves, VII and IX-XI; whereas the anterior one is now the foramen ovale. As the animal grows further, the oto-cranial flange around the foramen develops taller, and accordingly the tympano-periotic bone is forced to shift with it further downward for the mastoid process is connected with the flange in the squamoso-occipital notch. In the meantime, the contraction of the foramen goes parallel and the one time foramen becomes at last a perfect canal. The condition resembles that of the development of the visual organ to a certain extent because of the surprising prolongation of the nerve. The periotic bone, which is first connected directly to the meninges along the margin of the internal auditory aperture, now becomes an organ which stays perfectly outside the brain case. It is noteworthy that the unfinished state remains in some smaller species. In *Neomeris*, for example, the foramen stays still undivided and the periotic bone keeps the direct connection with the meninges

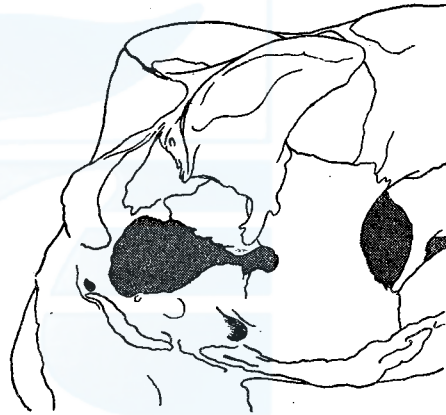
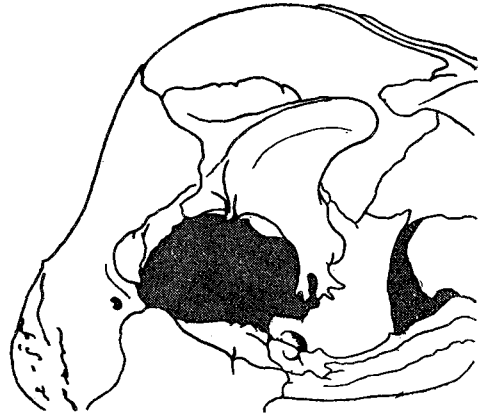


Fig. 16. Development of the cranial basis of *Globicephalus*.

through which the brain is visible when the tympanic cavity is opened. It seems also likewise in *Phocaena* judging from the descriptions of Boenninghaus. The connection between the tympano-periotic bone and the oto-cranial flange with the mastoid process of the former in the squamoso-occipital notch of the latter is of connective tissue as Boenninghaus described correctly (1904. p. 226). This connection naturally becomes un-united after maceration but is quite important as will be revealed by putting it into comparison with other families. This will be proved to be a specialized form of highest extreme.

For this comparison, any species will do good if it is of other families than delphinidae because those species have a more developed mastoid process as has been described before, and the process really connects the tympano-periotic bone far stronger to the skull in the same notch of the oto-cranial flange (figs. 24, 25). However, some species presents only loose connection which becomes usually ununited after maceration, while others more tight connection for its syndesmosing characteristics. Here it should be reminded that certain species of *Globicephalus* has a longer mastoid process which shows a probable intermediate form between the extreme delphinidae and the remaining other species (figs. 8, 17). Hyrtl's remark concerning *Delphinus gangeticus* of its wedging process (1845, pp. 34-35) seems, in this connection, most likely to be a stronger case of this kind, but unfortunately no detailed descriptions are given, which are needed here for comparison<sup>1</sup>. Mystacocete species has a more markedly developed mastoid process which is of similar relation to the skull, in which the connection is far stronger. Only one remark seems enough here to note that the process of mystacoceti is peculiarly of periotic and not of tympanic (fig. 17).

The second connection of the tympano-periotic bone to the skull is seen anteriorly between the tegmental process of the periotic and the so-called falciform process of Beaugard of the squamosal bone. The latter process remains falciform in delphinidae but develops thicker in ziphiidae as well as *Physeter* into a club-shaped or digitiform process (figs. 16, 24). The process extends downward over the upper side of the tegmental process, and is closely related in this way to the periotic bone and holds this securely under it by a strong connective tissue. Curiously this process as well as the fibrous connection thereof are lacking in *Kogia* alone (fig. 25). Similar relation to connect the tympano-periotic bone to the skull other than the mastoid process is found also in *Balaenoptera* in a different way as was already mentioned and dia-

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1) The process is said to be of periotic. Confer further p. 64.

grammatically illustrated in my former paper (1948, p. 28, fig. 1 b). To supply or to correct that, the tegmental process of the periotic, being coated and continuing with a thick cord of connective tissue, penetrates the lateral border of a large fossa, wherein the tympano-periotic bone as well as the sinus system lodge, in the rostral direction to the exterior periost which lines the infratemporal fossa through a canal bordered by the pterygoid and the squamosal bones (fig. 18). The periost now in question is directly continuous with that of the mandibular fossa where it develops surprisingly well in order to tight the mandibular articulation which lacks any joint cavity or disk whatever. This second connection of *Balaenoptera* seems to strain the organ strongly to the skull and most likely to be the similar connection though it occurs peculiarly in a different form in comparison with odontoceti.

Beside the above men-

Fig. 17. Various development of the mastoid process. From top to bottom: *Grampus*, *Berardius*, *Physeter* (ventral view), *Kogia*, *Balaenoptera*. Periotic component is marked by toning. Cf. fig. 8.



tioned two major connections, the formation of the sesamoid ossicles are peculiarly learned in some species. The most striking development of these bones is shown in *Balaenoptera* and has been already mentioned in my former paper (1948, p. 29, fig. 1 a). They are large and small and irregularly shaped and scores in number and distributed within the layer of connective tissue between the upper side of the periotic and the facing surface of the skull, abundant chiefly in the cochlear area

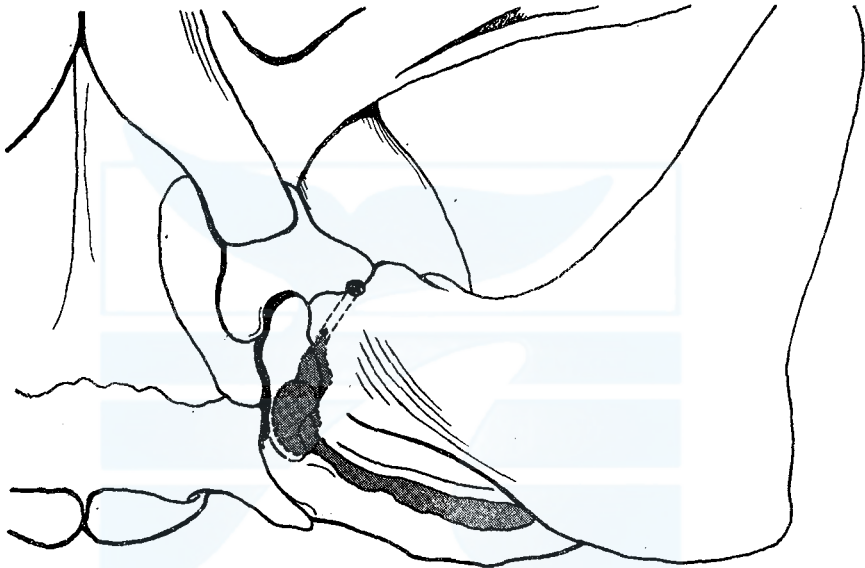


Fig. 18. Cranial basis of *Balaenoptera physalus* (based on the skeleton in possession of the Zoo of Osaka). Tympano-periotic bone in half tone.

but also in the proximal part of the tegmental process. The extremely rugged surface all over the upper side of this area of the periotic bone is now fully understandable as the closely related feature to this remarkable structure. The sesamoid ossicles present also in *Physeter* likewise in the same layer lining the contact surface of the periotic to the skull, and in ziphiidae too some really appear in occasions, particularly in aged individuals, though much weaker in development.

Considering these peculiarities throughout the entire order with the structure of the tympano-periotic bone altogether, it seems that the organ is planned after one major principle, probably that the tympano-periotic functions as a vibrating organ as a whole. This will be discussed in the following chapter in details over again, but it seems of much significance and interest of morphology that so many characters coincide

well each other, partly however, in developmental series, among different species, despite the genera, families and suborder.

### 3. Tympanic Cavity :

#### a. Tympanic Ossicles :

The tympanic ossicles are peculiar both in odontoceti and mystacoceti for their stumpy and thick development as well as the ankylosed relation of the malleus to the lateral border of the tympanic bulla. Above all, this ankylosis has been disputable whether it is of the manubrium mallei or the anterior process of Folius. The dispute, however, now seems to be settled to the latter as mentioned by Boenninghaus (1904) and Lillie (1910). I myself stand on this side too because of the mode of attachment of the tympanic membrane to the malleus. The tympanic ossicles do not differ in their general formation from the usual mammalian principle (Hyrtil, 1845; Doran, 1879), but they are in every way cetacean, of which some inter-subordinal differences should be mentioned.

The malleus of odontoceti (fig. 19) has generally a proportionally large caput which presents a large articulation surface with the incus in its posterior part of the upper side. This surface is divided sharply into two facets bordered nearly by a right angle, both being slightly



Fig. 19. Right side malleus of (from left to right) *Globicephalus*, *Berardius*, *Physeter*, *Kogia*, *Balaenoptera (physalus)* (twice natural size).

convex, of which the upper vertical one is much broader. The incudo-mallear articulation is a compound articulation because the facets are so sharply marked from each other and no movements can be expected. The anterior part of the upper side of the caput lies in the already mentioned mallear depression of the periotic bone, being closely related to it. The manubrium is reduced to a minute process or tubercle and is connected with the triangular ligament of Beauregard to the tympanic

membrane. The tympanic membrane is in odontoceti concave, while in mystacoceti curiously protruded like a finger-sac laterad, in both cases the membrane is pretty thick and obviously cannot vibrate. The vibrating possibility of the tympanic membrane can be excluded also by the closure or practical obliteration of the external auditory meatus. The membrane, which receives sound waves through the external auditory meatus no more, now becomes vestigial and seemingly thickened. In both cases the membrane is forced remarkably laterad and between its internal surface and the malleus the triangular ligament has been well known (figs. 22, 23). This ligament is in odontoceti literally triangular and arises from the lower margin of the membrane stretching rostro-mesad toward the manubrium within the tympanic cavity. The ligament is, on the other hand in mystacoceti, rather a strong cord and arises from the upper interior surface of the protruded tympanic membrane. From these relations, the manubrium is always identified with more or less difficulty. But this has escaped curiously from the researchers' notice in the past including Cuvier as well as Beaugard, until Denker who described this tubercle as the "Falz" although he did not regard it as the manubrium (1902, p. 435). In my examination, the manubrium always presents, though in both species of physeteridae and in *Berardius* it is utterly rudimental and hardly identified. The neck portion, collum is pretty well preserved in delphinidae because of its marked development of the muscular process, while in other species this portion is obscure or quite lacking. At any rate, the muscular process affording the insertion for the tensor tympani muscle usually presents at the anterior end of the malleus. This is a minute process in *Berardius* and in *Physeter*, but in *Kogia* it is an utterly minute recess instead, and in other delphinids the similar recess can be seen at top of the muscular process. The malleus of *Balaenoptera* is much larger but does not differ so strikingly from odontoceti that particular treatments seem unnecessary but to point out that the ossicle has more developed manubrium and the muscular process and is flattened as a whole antero-posteriorly and that the bone has some comparable common appearance to delphinidae. The synostotically ankylosed anterior process of malleus is rigid and easily broken by a slight force. The process is directed laterad as has been well illustrated by Boenninghaus (1904, p. 264). This seems to have been caused by the forced transfer of the bullar border laterad together with the tympanic membrane.

The incus of odontoceti (fig. 20) is usually stumpy and short, being divided into the corpus and two crura, the long and the short ones. The

corpus presents the articulation surface with the malleus, which faces laterad and is divided by a transverse crest into two concave facets corresponding to those of the malleus. From the corpus two crura extend backward and laterad. The former is the long crus and the latter the short one. The short crus is directed sideward, but in *Berardius* whose bone is medium sized, it is really longer than the long crus though much more slender. In *Globicephalus*, whose bone is minute, both crura are of almost of similar length, yet the short crus is usually more slender than the long one, and it seems only in *Physeter* that the short crus stays in every way short but comparatively thick, in this species the ossicle being largest of all odontoceti. The incus of *Kogia* is somewhat smaller than *Globicephalus* as well as *Grampus* and slightly bigger than *Prodelphinus*, but it is really a miniature of *Physeter*, being more strongly compressed in its long axis. In both species of physeteridae, the short crus curves peculiarly more mesad than other families. The short crus



Fig. 20. Right side incus of (from left to right) *Globicephalus*, *Berardius*, *Physeter*, *Kogia*, *Balaenoptera (physalus)* (twice natural size). Note the short crus of odontoceti with an articulation facet on its end.

presents on its free end an oblong and minute characteristic facet upward for the articulation with the already mentioned facet of the periotic bone (cf. pp. 23, 31). In this respect, Boenninghaus is obviously erroneous because he described that the short crus was for the connection with the tympanic bulla (1904, p. 268), on which some comments will be repeated in the next chapter. The long crus turns near its end suddenly upward and there is another lenticular articulation facet as minute and of similar shape as that of the short crus. The facet articulates the incus with the head of the stapes.

The incus of *Balaenoptera* is less stumpy but is exceedingly larger than odontoceti, and probably the largest in the entire mammalian class. The short crus is now reduced to a minute and pointed process, accordingly it lacks the facet whatever as seen in odontoceti. In the meantime, the long crus curves upward and its end is provided with a renal or

lenticular articulation facet which connects the incus with the stapes.

It is summarized, to the consequence, that the incus of odontoceti is strikingly different from *Balaenoptera* not only in its size but also in one more important respect, that is, the peculiar prolonged development of the short crus, and the articulation facet on its free end. This articulation is very much interesting not only morphologically but also to the functional side because some important mechanical rôle such as fulcrum in the ossicular movements can presumably attributed to it. I believe therefore, that this structure stands strongly on the affirmative side concerning the also disputable function of the tympanic ossicles.

The stapes also, is in odontoceti, short and stumpy in general (fig. 21). This tendency is most striking in *Physeter*, of which the two crura are so thick that no intercrural spatium can be seen, but instead, small depressions indicate the position of the spatium on both sides of the ossicle. The most striking stapes is of *Kogia*. Kernan (1918, p. 266) referred to the ossicle of a foetal *Kogia* as it is not fenestrated; while he illustrated the ossicle with a dimple which indicates the fenestra (fig. 16 of his paper). But in adult kogiids, not a slightest sign of dimple nor crura can be seen and the bone is practically an extremely thick stump. In delphinidae the crura are well developed but the ossicle



Fig. 21. Right side stapes of (from left to right) *Globicephalus*, *Berardius*, *Physeter*, *Kogia*, *Balaenoptera (physalus)* (twice natural size).

is here thinner than the foregoing species, and the minute spatium still exists inter-crurally. But some of delphinidae species may present obliteration of the spatium since Denker described such case of *Phocaena* (1902, p. 436). Of the same species, however, Boenninghaus is opposite because the spatium still remains as a minute opening (1904, p. 269). Therefore, considering either of the case of *Kogia* together with the remark of Kernan, or of *Monodon* and other species by Rapp (1837), Hyrtl (1845) and Doran (1879), obliteration may occur as the individuals grow older. While, *Berardius* seems to be exceptional in this respect because I have never experienced any obliteration, and the spatium is as narrow but usually exists. In this species, the stapes is far taller than other odontocete families and the crura are distinct. The stapes



of *Ziphius* is similarly tall but the spatium is usually closed. The capitulum has a minute tuberosity facing backward on the upper end of the posterior crus, which affords the insertion of the stapedial muscle. And at top of the capitulum, a minute elliptical articulation facet presents downward usually in a more or less twisted direction mesad, and consequently approaching the transverse direction to the body axis more or less. The basis of the stapes is comparatively well developed in odontoceti, in a form renal or elliptical. The basis presents a sharply prominent annular margin toward the labyrinthic vestibule, which causes a more or less strong concavity of the basal surface. This concavity occurs most strikingly in ziphiidae. Due to the prominent annular margin, the basis is encircled by an edge of certain depth in a cylindrical way, and to the consequence, the basis lodges relatively deep in the fenestra vestibuli. This margin is incised characteristically in its posterior lateral part, apparently related to the ampulae of the two semicircular ducts of the labyrinth, viz., the lateral and the superior (fig. 26).

The stapes of *Balaenoptera* is some several times larger than odontoceti and seems to be the biggest among mammals like the other two ossicles. The bone is still typically cetacean because of its thick and stumpy development and of the minute intercrural foramen.<sup>1</sup> It is relatively tall, and in this respect, comparable to those of ziphiidae. But distinct differences of this bone from other odontoceti are the comparatively more slender crura but the larger spatium and capitulum as well as the not concave basal surface. The surface is flat throughout with only slight elevations. Therefore, it is rather convex though slightly, being conclusively opposite against odontoceti. But it should be kept in mind that the basal surface of *Balaena* is concave according to Hyrtl (1845, p. 72).

Some disputes have been known concerning the connection of the stapedial basis with the border of the fenestra vestibuli. This is a problem whether an oto-sclerosis occurs in cetacea or not. Hyrtl who discovered the synostosed stapes of *Monodon* and some other delphinidae species, mentioned that the stapes is rather broken and thus comes out of the window and not slips out, whereupon Denker is a denier (1902, p. 436). Boeninghaus revealed that the annular connection is of synchondrotic nature like other articulations within the ossicular chain but that synostosis can occur in occasions (1904, pp. 271-272). I myself regard that synostosis may occur, but the fact is that such cases seem

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1) A thin bone plate is stretched between the crura. The intercrural foramen is a fenestration of this bone plate.

hardly to happen so far as learned by me. I can mention, therefore, that the stapes is easily broken leaving its part of the basis in the fenestra, but this seems greatly due to the peculiarly deep and close fitting of the stapes in the fenestra for the sharply prominent margin of the stapedia basis as has been just described. I stress further in this connection that much care and attention are needed to pull the stapes out of the fenestra vestibuli without destroying its basis, for this is quite easily broken when some other dimensional force is given than the lengthwise one.

b. Tympanic Cavity with Pneumatic Sinus.

The tympanic cavity is both in odontoceti and mystacoceti rather a limited room of some complexity, expanding between the tympanic bulla and the periotic, ental depression of the former bordering the bottom and the epitympanic recess of the latter the ceiling. The cavity expands in odontoceti through the tympano-periotic fissure, and the hiatus epitympanicus as well as the anterior aperture, i. e., the orificium tympanicum of the Eustachian tube of Boenninghaus, with large and small expansions known commonly by name of the pneumatic sinus. From the lateral tympanic membrane, the tympanic ossicles stretch continuously mesad across the cavity to the fenestra vestibuli. Beside these, the peculiar cavernous body, the corpus cavernosum tympanicum develops well in odontoceti within the cavity. This cavernous body arises with a broad origin from the medial mucous layer lining the lateral wall of the striking crest of the basi-occipital bone, which extends downward and borders the middle ear medially, and stretches into the tympanic cavity through the tympano-periotic fissure. Therefore, this is a mucous fold of the middle ear, in which the cavernous structure is well developed. Posteriorly the body presents a chord-like free margin, in which run some branches of the ninth nerve of relatively large caliber supplying the tympanic plexus with blood vessels rostrad (cf. p. 21). Anteriorly the body gradually diminishes continuing through the tympanic orifice of the Eustachian tube with the medial mucous wall of the middle ear without any distinct demarcation. Both species of ziphiidae have most striking development of this structure which presents less strongly in delphinidae and least in physeteridae (fig. 22). Histological examinations prove that this structure is really the cavernous body, wherein nerve bundles of the tympanic plexus can be shown running strongly undulated. From these observations, it is most likely that the cavernous body can be distended so remarkably as to fill up the entire tympanic cavity as

demonstrated after intravascular injection by Boenninghaus (Denker, 1902. p. 439). But the relation of the cavernous body to the fenestra cochleae seems important to note because Boenninghaus described that this window was usually stuffed or covered by the cavernous body, and consequently he attributed to this structure a special and important rôle (1904, pp. 274, 286) to which I will refer afterward and deny it though such tendency often presents in delphinidae species to a certain extent. The cavernous body is so well developed that it can be examined easily and correctly if the bottom of the bulla is properly fenestrated or removed.

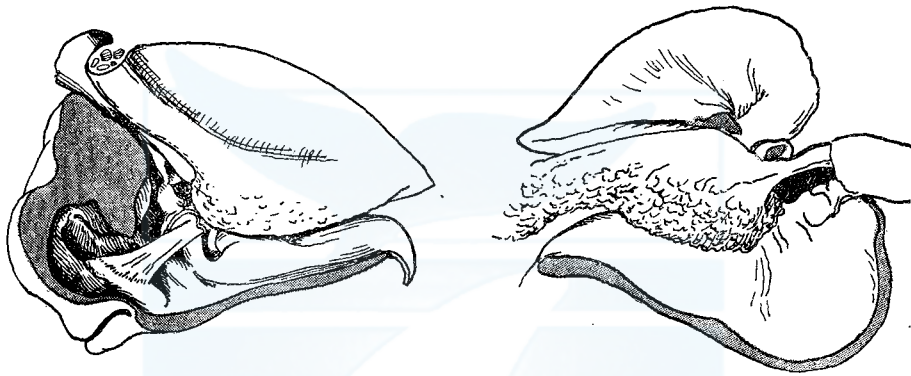


Fig. 22. Left side cavernous body of *Globicephalus* (left) and *Berardius* (right). In *Globicephalus* the triangular ligament and the chorda tympani nerve are illustrated.

But the tensor tympani muscle seems problematic in odontoceti because its existence has been quite disputable. For instance, Hyrtl (*Monodon*, *Delphinus*), Boenninghaus (*Phocaena*), Kernan (*Tursiops*) and Kellogg (*Monodon*) are affirmative authors; whereas Cuvier (*Phocaena*), Beauregard (*Delphinus*), Denker (*Phocaena*) and Kernan (*Kogia*) are deniers. Here it is noticed as curious that concerning the same species some workers stand opposite against each other. Such a dispute may bring a speculative decision by itself that this muscle really exists. And really this decision is correct.

The tensor tympani muscle of odontoceti arises from the medial side of the tubal tubercle and runs backward ending in a fine cord of tendon which is inserted into the muscular process, tubercle or recess of the malleus already described. The muscle is naturally minute and really rudimental throughout and in occasions it may go more or less degenerated. But every time I examined the fibers under microscope during

dissection, striations were clearly certified on its fibers. I have made this examination not for an intention to establish degenerations but to certify the scanty fibers of unknown nature if they are really muscular or not, which come into sight after preparing the cavernous body off from the tubal tubercle, and which are quite uncertain to identify. Probably this deep position of the muscle under the cavernous body, connected firmly to the tubercle, may have been the reason of the overlooking, but the tendon can usually be observed with less difficulty (fig. 23). The most recommendable way to ascertain the existence of the

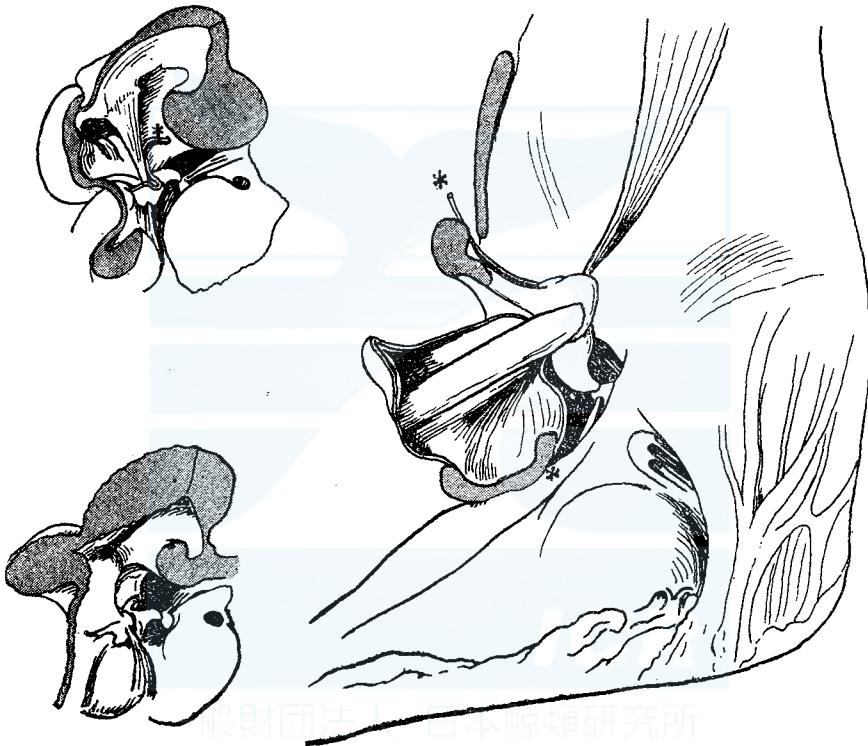


Fig. 23. Tympanic muscles. *Left top*- Left side of *Globicephalus*; *left bottom*- Left side of *Kogia*; *right*- *Balaenoptera*, right side. Chorda tympani nerve is illustrated in *Globicephalus* and *Balaenoptera* marked \*.

muscle is simply done by confirming the minute muscular process, tubercles or recess which presents on the anterior surface of the malleus. This is recommended because no preserving of material nor careful preparation is necessary and the macerated bones are good enough. These topographical peculiarities of the tensor tympani muscle reveal well that the interpretation as well as the terminology of Boenninghaus of the

processus tubarius and the orificium tympanicum of the Eustachian tube are quite proper and correct. While in mystacoceti no disputes have been known against the existence of the muscle which is strongly and aponeurotically degenerated. This reason may be that the muscle can be easily identified submucously, though it is much more vestigial than odontoceti.

The stapedial muscle is, in the meantime, pretty well preserved both in odontoceti and mystacoceti. The muscle arises in both cases from the already mentioned sulcus in the epitympanic recess and runs rostrad ending in a similar tendon like the tensor tympani muscle and is inserted into the minute elliptical tuberosity at the capitulum stapedis. It may be generally surmised that this muscle still functions (fig. 23).

It must be added with some significance that the tympanic cavity is very often, and in cases almost perfectly, filled with a striking glomerular mass of nematodes, which is sometimes partly forced out of the tympanic cavity into some attaching sinuses. One case of *Neomeris* was quite extreme in this respect, but less extreme parasites are seemingly common to *Grampus* and *Globicephalus* to say the least. These parasites have been well known since Rapp (1837). In one individual of *Kogia*, I observed a large number of distoma.

From the tympanic orifice of the Eustachian tube of Boenninghaus and from the tympano-periotic fissure as well as the hiatus epitympanicus, the tympanic cavity of odontoceti communicates with the pneumatic sinus system. To mention them with exception of delphinidae family, they are commonly four in number (figs. 24, 25), of which the pterygoid sinus is greatest. This sinus may well be interpreted as an expansion of the proximal part of the Eustachian tube according to the relation of the tensor tympani muscle mentioned before. The sinus expands enormously in the as big pterygoid fossa of the pterygoid bone. The mucous layer of this sinus is well marked for the trabecular framework as seen commonly throughout the surface. In its medial wall, the mucous layer presents under it a striking vascular plexus which is characterized by a strong framework affording apparently an enormous distension of the wall. This submucous framework attains its fullest development at the rostral corner of the sinus. Under the lateral wall, the pterygoid muscles lie submucously, being covered by the surprising adipose body from outside, which fills up laterally the mandibular hiatus and stretches on one hand further backward until it comes contact to the lateral under side of the bulla, where to the bottom of the so-called "sound-funnel" of Boenninghaus the adipose body has some particular connection by the concentrating but scanty connective tissue fibers with the periost

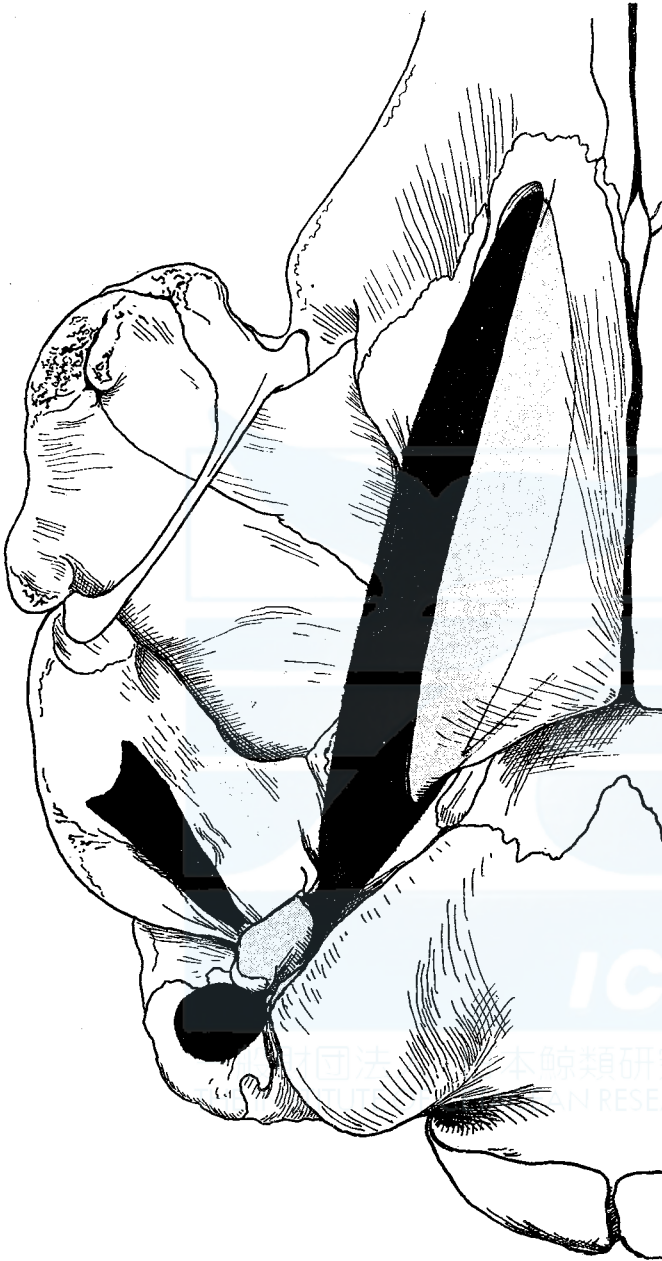


Fig. 24. Diagrammatic distribution of the pneumatic sinus in *Berardius*, based on the specimen in possession of the Dept. of Anat., Univ. of Tokyo (about 1/16 natural size), the otic region is reconstructed. Note the falciform process of the squamosal bone, which lacks in *Kogia* (fig. 25).

thereof. From these topographical relations between the mandibular adipose body and the lateral wall of the pterygoid sinus, I guess that the movements of the lower jaws may effect strongly upon the distension of the pterygoid sinus. The Eustachian tube begins in front of the tympanic orifice at the proximal lower part of the medial wall of this sinus and ascends through a marked incisure of the pterygoid bone and opens into the nasal passage. At the pterygoid entry of the tube, the mucous layer presents a plica which presumably functions as a valve not to force out the enclosed air under high pressure when the animal dives to depths.

Other sinuses are minor and not so peculiar as the pterygoid one but in a different way in their mural structures,

and naturally seem not to afford so much dilating possibility like that with exception of the epitympanic one. They have commonly the trabecular connections across the lumen between the facing walls, strongly in particular in corners. The epitympanic sinus, which is probably analogous with the sinus moyen of Beaugard, expands laterad under the zygomatic process of the squamosal bone in close contact with its surface. The sinus is situated above the mandibular articulation and accordingly may be put in expansion and compression by the mandibular movements. The sinus is continuous with the tympanic cavity through the hiatus epitympanicus which opens directly above the tympanic membrane in the tympanic aperture. The peri-

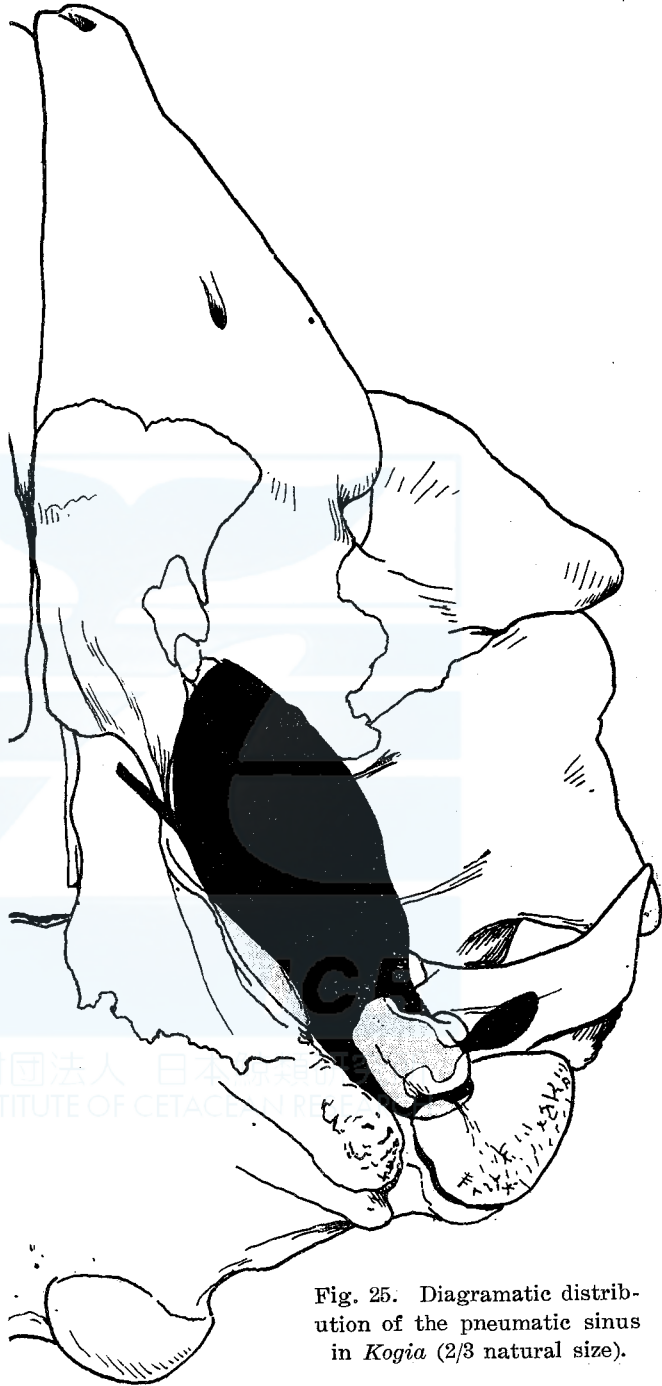


Fig. 25. Diagrammatic distribution of the pneumatic sinus in *Kogia* (2/3 natural size).

petrosal sinus<sup>1</sup> is communicated with the tympanic cavity through the tympano-periotic fissure. The sinus is expanded upward surrounding the cochlear portion of the periotic bone so irregularly with abundant trabecular connections across its lumen. This sinus is peculiar to odontoceti and of some historical meaning because the view of the acoustically isolated tympano-periotic organ or labyrinth seems to have been originated from its unusual expansion. The posterior sinus expands in an oval form under the mastoid process of the tympanic bone, and continues with the tympanic cavity through the posterior portion of the tympano-periotic fissure around the medial side of the neck of the mastoid process. The ground layer of this sinus is characteristically cartilaginous because the tympano-hyal cartilage is here flattened into a similar-shaped plate and is continuous with the posterior surface of the neck of the tympanic mastoid process. The sinus is similar to the epitympanic one but differs strikingly from it by this underlying cartilage. The lumen is flattened too and the facing mucous walls are so close that they are usually connected by the trabeculae. The sinus system of delphinidae, particularly the pterygoid sinus, is specialized much more and presents some further expansions as the maxillar, frontal and temporal other than the above mentioning as has been fully demonstrated by Boenninghaus (1904).

The tympanic cavity of mystacoceti is more simple because so well developed cavernous body as seen in odontoceti is lacking whatever. But the mucous layer lining the ceiling of the cavity is rugged complexly with various folds and vesicular formations as described in my former paper (1948, p. 26). Therefore, it is now conclusively mentioned that the tympanic cavity of mystacoceti has no structure so perfectly fill it up like the cavernous body of odontoceti does, but only slightly. The tympanic orifice of the Eustachian tube is not so well marked as in odontoceti nor the tubal tubercle. This tubercle seems to have been united with the tegmental process because the tensor tympani muscle arises from the furrow between the process and the cochlear sphere. The pneumatic sinus system is weaker in development but of some peculiarity of mystacoceti itself. The pterygoid sinus of *Balaenoptera* expands greatly, but relatively in less dimensions in comparison with odontoceti, within the pterygoid fossa which stays rather isolated from the exterior of the sinus, being perfectly covered behind the pterygoid process by the enormously thick layer of connective tissue together with the bulla and other sinuses from below. Thus the sinus seems in *Balaenoptera* free from the mandibular movements and differs from odontoceti con-

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1) The peribullar sinus of Boenninghaus is involved here.



siderably. However, the sinus is capable of distension pretty well because its wall is beset with the cavernous tissue with vascular network which is developed peculiarly in it. The peribullar sinus communicates with the tympanic cavity, and also with the pterygoid sinus anteriorly. It does not occur that the sinus expands so far upward around the periotic bone as in odontoceti. Posteriorly the tympanic cavity as well as the peribullar sinus expand laterad into a blind sac stretching around the medial side of the posterior pedicle, so this may be called as the posterior sinus for its relation with the tympanic cavity similar to odontoceti. On the upper wall of this sinus the vesicular formations and the vascular trabeculae similar to those of the tympanic cavity usually hang.

As has been described before and in my former paper too (1948, p. 25), the otic region is separated and protected in *Balaenoptera* by the thick layer of connective tissue. This has been also mentioned in *Megaptera* by Lillie (1915, p. 106). Lillie divides this layer into the interior yellow elastic and the exterior spongy tissues, and notices furthermore between the bulla and these layers another fatty tissue. The structure is the same in *Balaenoptera* but such a demarcation seems not always proper nor necessary in this genus because the development of the spongy tissue varies and is not constant. This layer, which borders downward upon the pharyngeal cavity, is continuous on the other hand laterally with the strong fibrous connection of the mandibular articulation. The layer connects interiorly the medial border of the bulla very firmly to the basi-occipital bone, thus bordering the floor of the peribullar pneumatic sinus. But between the under side of the bulla and this layer the connection is quite loose but fatty as apparently called by Lillie accordingly. Similar fibrous connection presents commonly in odontoceti too and is called by Boenninghaus as the "Bindegewebsplatte der Bulla", who stressed simultaneously the firm connection between the medial border of the bulla and the cranial basis by this tissue (1904, pp. 229-230). Now it is well and fully understood that the medial side of the bullar under surface is strongly coarse without exception. Whereas the lateral side of the bulla is smooth and the connection becomes suddenly loose. The already mentioned adipose body of the mandibule in odontoceti extends so far as this region. While, mystacoceti has no such adipose body for the mandibular hiatus is not specially deformed. However, the similar tissue structures are seen in the impression in front of the sigmoid process, which is in odontoceti the "sound-funnel" of Boenninghaus.

The chorda tympani nerve is another very interesting problem in the present field, but I have not perfectly succeeded to examine it. In

*Globicephalus* the nerve really exists (fig. 23) and the minute perforation is observed in the caput mallei (fig. 19) as described by Boenninghaus (1904, p. 267) closely in front of the articulation surface. But I could not ascertain the penetrating relation of the nerve through it probably because of the condition of the material. In ziphiidae as well as physteridae, the nerve did not come under my notice, nor the malleus is perforated. It should be noted in this connection that the perforation does not appear in *Grampus* too. Boenninghaus remarked simultaneously that such a perforation occurs characteristically in odontoceti alone, though some insectivores have the nerves which do penetrate the anterior process of the malleus (Hyrtl, Doran). However, a pinniped, *Lobodon carcinophagus* Gray of the Antarctic<sup>1</sup>, is interesting because it has so resembled malleus that it is hardly distinguishable from delphinidae, wherein the perforation really presents at the exactly same spot of the caput. Therefore, this species may well be expected to present the similar relation of the chorda tympani nerve. While in *Balaenoptera*, there is the nerve but no malleus perforation can be seen. At any rate, I am of opinion that the triangular opening in front of the sigmoid process between the tympano-periotic components, which is in *Balaenoptera* communicated with the tympanic aperture over the margin of the sigmoid process, may afford the pathway to the nerve, therefore it may well be interpreted as the Huguier's canal in the human anatomy. In reality the strange but common structure of the concentrating scanty fibers of the mandibular adipose body toward the bottom of the "sound-funnel" of Boenninghaus appears to have some meaning, and further the outwardly curious extension of the adipose body as far as the bottom of this recess seems to be understood if the just mentioned interpretation be allowed, to the establishment of which I should go further.

### Chapter 3 How the Organ Functions

#### 1. Introductory Review :

As stressed by the previous authors, and as described in the present work, the external auditory meatus of whales cannot be allowed to transmit any sound waves through it to the tympanic membrane or to some apparatus of conduction within the middle ear. The external auditory meatus is extremely vestigial, being closed up during its course (mystacoceti) or toward the medial extremity (physteridae), or being

1) I had an opportunity to examine this animal during my last whaling trip by favor of Maj. J. A. Crombie of the U. S. Army, an Allied observer on board the ship, who hunted seals several times.

so narrow that there exists no lumen of some significance (delphinidae and ziphiidae). The tympanic membrane which is so thick or curiously protruded and the indirect connection of the malleus with the membrane but ankylosed relation with the tympanic bulla hardly expect the vibrating possibilities of the membrane nor those of the malleus.

Denker (1902, pp. 433-434) demonstrated, through Bezold's experiment in *Phocaena*, that the vibrations of the tympanic membrane could never be transmitted into the tympanic ossicles. But other authors had tried, before Denker, to conclude the transmitting pathway to take over that of the normal mammalian principle. In this direction, Camper (1762) alone was exceptional, who was of opinion that sperm whale could hear by way of the external auditory meatus and the tympanic membrane. In the meantime, Buchanan (1828) considered whales to hear through the Eustachian tube. Buchanan's view, however, was later protested by Claudius (1858) because the nares open only intermittently at times of breathing, and usually stay closed under water. Denker did not forget to note further that usually loud noises are unfavorably accompanied by every breathing. Meanwhile, Boenninghaus (1904, p. 287) accepted Buchanan with a proviso that it might happen momentarily when the animal swallows, otherwise the tube remains closed even when the nasal passages open to the air.

Obviously, these views are wholly erroneous after our present knowledge because they argued from a premise that whales would hear the air-borne sounds and not the water-borne ones. Anyway such a premise have been regarded improbable by the later authors.

Claudius (1858) stated that vibrations borne in the water and accepted by the entire head, put the air in the pneumatic sinus of the middle ear into strong resonance, which is transmitted into the labyrinth by way of the chain of ossicles or the secondary tympanic membrane in the fenestra cochleae. It is important here that the acoustic isolation of the entire tympano-periotic organ from the skull is noticed first by Claudius. Later Denker (1902, pp. 444-445) agreed this view in outline, being apart from Claudius in one respect that he was suspicious about the vibrating possibility of the triangular ligament which was allowed by Claudius.

Boenninghaus comes next in 1904. After careful and detailed work on harbor porpoise, he concluded a new theory that the sounds are accepted with the formerly related "sound-funnel" (Schalltrichter) which is said to function as a substitute of the absent auricle, and the sounds, after reaching its bottom, namely the anterior process of the malleus, are transmitted by the ossicular chain into the vestibule. According to

him, the conduction through the chain is molecular and the stumpy and compact comparatively large ossicles developing rather progressively should favor the conduction through that chain. He stressed too, like Claudius and Denker, the acoustic isolation of the labyrinth and that the isolation is essential to shut out the energetic interference by the strong vibration of the whole skull. He added further that the partial connection between the tympanic and the periotic restrains the conduction from the bulla to the cochlea to a least extent: the peculiar fusion of the two components within the tympano-periotic organ is thus involved in the category of the labyrinthic isolation. He was of opinion that first by the isolation fine hearing comes possible to whales. He pre-cautiously enumerated further possible interferences and mentioned how each is removed. Boenninghaus seems to have dealt with the sinuous problem with much considerations because he accepted that the air-filled cells are quite easily and strongly resonated under water—these were very much annoying structures to his Schalltrichter theory. Hereupon the thick mucous layer with the developed vascular network and the cavernous tissue within the tympanic cavity as well as the sinus system remove the interference, and the fenestra cochleae is protected by the cavernous body from the invasion of the resonating air in the sinus. Next those possible interferences come into question in relation to the conduction through the ossicular chain, which might be caused by the tympanic membrane through the triangular ligament and by the tympanic bulla through the short crus of the incus (pp. 283–284). The latter is particularly un-understandable because the crus has no connection with the bulla but with the periotic, of which Boenninghaus was obviously incorrect. It is a matter of much importance here to note that the so-called “sound-funnel” of Boenninghaus did not occupy Denker’s attention, and to the contrary that the pneumatic sinus which was regarded indispensable as resonator by Denker, was neglected by Boenninghaus being attributed by the different hydro-static function. In spite of the detailed and earnest-minded work with circumspect considerations, the view of Boenninghaus could not exceed delphinidae and was really so hard to understand that soon later a serious confusion was brought into our field.

In a book published in 1912, Abel (p. 458) quoted Boenninghaus by mistake or after his own modifications that the sounds, penetrating the soft parts to the tympanic bulla, are hold of by this apparatus and further transmitted upon the tympanic membrane and into the ossicular chain to the fenestra vestibuli. Concerning the mystacocete organ of hearing, Abel considered the mastoid process of the periotic to function

not only as a fulcrum but also as a propagating apparatus. Boenninghaus must have seemed awkward to Abel who was apparently of intention to synthesize the cetacean organ of hearing as a whole in one definite principle or in a series of modifications.

Two years before Abel, Lillie (1910, p. 781) published his view, on treating of mystacocete whales, *Balaenoptera musculus* and *B. sibbaldii*, as whales probably receive sound vibrations by means of vibrating bony surfaces because the tympanic bula is a relatively dense and heavy sounding-box and could easily be set into vibration. It is noteworthy that Lillie did never refer to the so-called isolation of the organ of mystacoceti whatever, and that his view is practically similar to Abel's. Further Hanke (1914, pp. 522-523) concluded that *Balaenoptera* indicates an adaptation attained in a different way from odontoceti<sup>1</sup>, because the tympano-periotic bone is not forced aside out of the formation of the cranial basis as is the case with odontoceti, but is supported firmly with the skull with two processes. Concerning the odontocete organ, he gives in entirely to the view of the acoustic isolation of the tympano-periotic which he confirmed himself of some dolphins in reference—*Delphinus delphis* and *Tursiops tursio* (p. 488).

Matthes (1912) had good reasons, in this connection, in criticizing Abel severely. He, as a devoted supporter of Boenninghaus, denounced Abel, particularly in two points. One was Abel's mistake that the tympanic membrane, which had been excluded once by Boenninghaus out of the conduction system, was brought into it again. Another point was the mastoid process of mystacoceti as the fulcrum as well as the propagating apparatus because this Abel's view practically violated the precept of Boenninghaus that the labyrinth was acoustically isolated.

In the meantime, Kernan reported in 1918 (p. 267) of a foetal *Kogia* and emphasized concerning the present question as, "it is important to recall that the os tympanum and the periotic are nowhere in contact with the other bones of the skull and that they are surrounded by numerous cells capable of distention with air. So it seems necessary to suppose that sound waves must reach the internal ear through a cushion of air immediately related to the periotic, though not necessarily that contained in the tympanum alone". Kernan seems to have been influenced at that time more than necessary by Denker of the question of isolation. But Boenninghaus seems not to have influenced Kernan because strangely to this German author few had made references and his name being never

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1) His intention was to make mystacoceti clear, in concert with Boenninghaus, but the material was limited in foetuses.

given in Kernan's paper too. I cannot understand at all concerning this, how and why Kernan came to consider this way, since Schulte described (1917, p. 394) the well developed tympano-mastoid which fits between the squamosal, the exo-occipital and the oto-cranial flange of the basi-occipital, presenting its broad base in the lateral surface of the skull.

Kernan wrote, however, one year later in the *Laryngoscope* (1919, p. 512), without correcting his previous view of isolation, that the tympano-mastoid, "an outgrowth of one of the bones related to the organ of hearing, should be noted, as it had in all probability much to do with the ability to hear". This is because the process "appears largely on the surface of the skull in a notch between the squamosal and exooccipital". He concluded that (p. 520) "sounds are evidently transmitted to the cochlea through the solid tissues of the head. The possibility of this is increased because in both forms<sup>1</sup> the auditory bones themselves present on the surface of the skull a considerable bony process. In both, moreover, the periotic and tympanic are but loosely connected to the other bones of the skull. Thus they can receive only such sound waves as impinge directly on themselves. Since the malleus is firmly fused to the tympanic it would share the vibrations of that bone, transmitting them through the other ossicles to the oval window".

Finally Kellogg (1928, p. 204) wrote that "whales have acquired an organ of hearing in which resonance must play an important part", and that "water-borne sound vibrations transmitted to the air contained in the tympanic bulla cause it to function as a sounding box, and its vibrations reach the cochlea by way of the ossicular chain and the vestibule". And further Kellogg noticed (p. 206): "the porpoises, dolphins, sperm whales, beaked whales and their relatives all have the ear bones attached to the skull by the ligaments".

These are the outline of the past disputes concerning the question how the organ functions. Now that any experiment is almost impossible, I would not like to advance my own view if it would practically add one more dispute toward the confused problem. The mentioned situation of the problem, however on one hand, urges me to do it because it sounds to me quite unfavorable to leave the confused disputes to the future as they are at present. The experiments will become possible in time and surely the cetacean organ of hearing will forward some suggestions to the science of hearing sense, in particular to the physiology, above all, to that of the bone conduction of sounds because the organ is in every way mammalian in principles and the seemingly different structures are

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1) Odontoceti and mystacoceti.

nothing but the wonderful re-modelling, that is to say, consequences of adaptation to life in the water.

The views of the previous authors can be summarized and classified as follows:— a) Classic views of Camper and Buchanan who regard the function similar or not far apart from that of the land dwellers. These are so simple and lacks the sound foot-steps on the morphological data that they will be set outside of the present considerations. b) Schalltrichter theory of Boenninghaus is peculiar, being supported by Matthes and Hanke, but not by others, at least originally not. c) Resonance theory with which Claudius, Denker, later Kernan (1918) and Kellogg took part. They are mostly of opinion except Kellogg that the air in the pneumatic sinus is brought into resonance which is transmitted to the cochlea by way of the fenestra vestibuli, though Kernan does not states clearly so. According to Kellogg, the resonating air in the sinus makes the bulla a resonating sounding box, the vibrations herein being transmitted to the vestibular window by way of the ossicular chain. d) The so-called osteo-tympanic conduction such as Lillie, Abel and Kernan (1919).

## 2. General Accounts on the Question of Acoustic Isolation :

The first of the matters which my criticisms would deal with hereafter is the question of the acoustic isolation of the labyrinth or the tympano-periotic organ from the skull. This is most important because every branch of further discussions in the entire problem gets influenced in essentials by this matter. As is obvious through the foregoing pages, some authors have clung to this view of isolation. It is important here that most of those authors participated almost exclusively in the family delphinidae. It is true that the tympano-periotic organ of delphinidae is connected with the remaining skull only by fibrous tissues including the meninges; consequently the bone becomes isolated after maceration. It is true also that delphinids are convenient material due to their small size, but it cannot be exaggerated that one should be fully shy and careful to discuss the whole order according to the results obtained from dolphins or porpoises. It seems to me very much instructive that nobody has ever advanced practically such theory as the isolation of the hearing organ in mystacoceti.

At any rate, the tympano-periotic bone of whales is connected to the skull by the mastoid process of either periotic or tympanic as described in the previous chapter in details—with concessive exception of delphinidae family to admit the so-called isolation. The shape of the mastoid process as well as the size and manners of attachment to the skull are naturally

different specifically and individually. According to my experience, the tympano-periotic bone of family ziphiidae and *Kogia*, whose mastoid process develops well, becomes often separated after maceration; this seems usual in *Kogia* or likely to occur when the animal stays immature. Concerning these cases, do the exponents of isolation theory insist the bone to be still isolated because the connection is of merely fibrous? This may sound as my pin-prick trick, but I do believe the principle is the same both in delphinidae and other families. If the connection in delphinids would be interpreted as isolated acoustically, whole order must have the hearing organ acoustically isolated though usually weaker in scale. The so-called acoustic isolation is wholly un-understandable.

Hyrtl (1845, pp. 34-35) remarked *Delphinus gangeticus* as exceptional in this respect since its periotic is provided with a process which wedges the bone between the squamosal and the occipital. I do not know that fresh-water dolphin has the process of either the periotic like mystacoceti, or the tympanic like ziphiidae and physeteridae, but this remark of Hyrtl is quite suggestive toward the present dispute. It is important that a single exception has been known against the isolation theory whether the process is really of periotic or tympanic. How can the fact be explained that within a family all have the tympano-periotic organ acoustically isolated but one—*Platanista*?

### 3. Concerning the Schalltrichter Theory of Boenninghaus :

As referred to before, Boenninghaus was right in description of the fibrous connection of the tympano-periotic to the skull, still he interpreted it like other connections, no particular meaning being ascribed to it. This is, in my opinion, because he participated solely in *Phocaena* and some other species of delphinidae. He concluded (1904, p. 281) the acoustic isolation of the labyrinth, by putting special weight in the lack of direct connection of the tympano-periotic to the skull and in the partial separation of the tympanic and the periotic components, plus in the peculiar topography that the periotic stays perfectly apart outside the cranial basis. Such an isolation was essential to Boenninghaus, because it was indispensable to exclude the bone-conduction which might interfere with the normal vibrations of his own, transmitted through the Schalltrichter and the ossicular chain to the fenestra vestibuli. If single case of *Platanista* or some other family would have come to his reference work simultaneously, he would have changed his conclusion of the acoustic isolation into some other form.

The situation of Boenninghaus is thus understood, but it is my undis-



solved question if the view of isolation has been derived from many imperfect descriptions including Hyrtl's, in which the mastoid process of the tympanic is broken entirely off. It seems to me, in this connection, that Kellogg (1928, p. 206) was such a case, as he wrote all members of odontocete suborder to lack those connections which are in reality well developed in ziphiidae and physeteridae to say the least.

With the end of a discussion about the acoustic isolation, the theory of Boenninghaus receives the most fundamental head-lines of the criticisms. But the *Schalltrichter* overlaid by the soft parts seems so strange to attribute to it a function to concentrate sounds, as was practically misunderstood by Abel. According to Boenninghaus, the sounds reach the bottom of the *Trichter* after penetrating the soft parts over it, but it is almost impossible to accept his view that the sounds selectively put the malleus alone into direct vibration on its anterior process at the bottom of the *Trichter*. The simultaneous vibration of the bulla to which the malleus is ankylosed is, in his opinion, damped by the soft parts covering directly its surface. How can the vibration of the malleus alone be undamped in spite of its rigid connection with the bulla?

#### 4. Concerning the Resonance Theory :

This theory also argues the problem on assumption of the isolated organ as is the case with the *Schalltrichter* theory, consequently it does not comprehend mystacocete organ in it, may it sound probable in odontoceti. This is really easier to accept and the sound is received by the solid tissues of the head and further puts the air in the pneumatic sinus system including the tympanic cavity into resonance. This resonance was a serious problem to Boenninghaus who interpreted that the cavernous body as well as the thick mucous layer of the middle ear function as an eliminator of the annoying resonance from interference. For the propagation of the resonance into the cochlea, seemingly possible paths are the fenestra cochleae, particularly the secondary tympanic membrane stretched in the window, and the ossicular chain.

The physiology of the secondary tympanic membrane is usually learned as to set the cochlear liquid into vibration by its countervibration in response to the movements of the stapedial basis. But the relation is different in cetacea of which the stapes is synchondrosed in the fenestra vestibuli and no movements of the basis are accepted to occur against the cochlear liquid but the molecular vibrations. This relation seems inconvenient to the resonance theory, may the secondary tympanic membrane do vibrate. Now that the stapes is so firmly secured in the window,

it seems hard to find out the counter-vibrator of the secondary tympanic membrane elsewhere of the two aquaeducts of the internal ear. Of these aquaeducts, the vestibular or endolymphatic duct is better suited to the rôle due to its topographical relations, but the duct is so slender and seems really impossible to meet such a function (fig. 26). While the cochlear or perilymphatic aquaeduct is usually developed much better and the vibration may well be caused in the cochlea by the combined movements of the secondary tympanic membrane and the liquid in the aquaeduct. But the liquid vibration thereby apparently does not cover the most important part of the organ—the organ of Corti, hence it is far from the expected function.

Boenninghaus (1904, p. 286) denies the conduction of the resonating vibration of the air in the pneumatic sinus system into the cochlea through the fenestra cochleae because the window is clogged by the cavernous

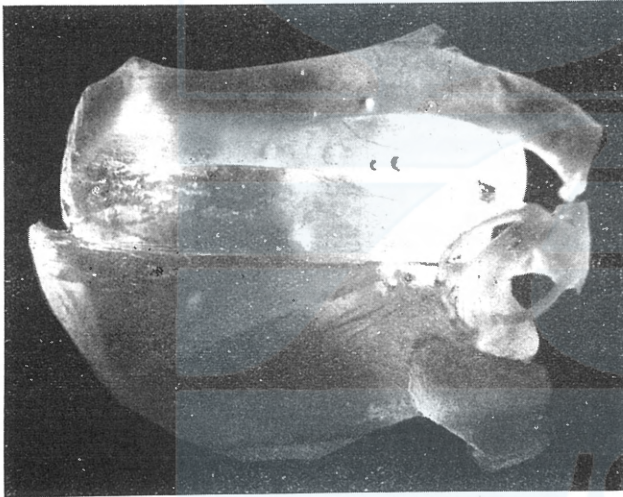


Fig. 26. Cast of the labyrinth of *Berardius* (right side) to illustrate the topographical relations as well as the dimensions of the cochlear and vestibular aquaeducts (ca.  $\times 3.3$ ).

body. I mention that the window is not always clogged entirely by the cavernous body nor overlaid by the thickened mucous layer. Nay, to the contrary, it seems favorable to the resonance theory when the window is only imperfectly covered.

Denker was reasonable to advance his resonance theory because he overlooked the existence of the tensor tympani muscle which

remains in a perfect form though small or quite vestigial. The case of Denker may be judged therefore as he has put no value to the ossicles. Laying the difficult-to-find tensor tympani muscle aside, always perfect stapedial muscle suggests that the tympanic ossicles stay not functionless. For what purpose does the stapedial muscle outlive the ossicles if they became really functionless? If Denker had noticed these muscles and thought as far as the ossicles, he would have never risked to put these structures out of his considerations.

Naturally Kellogg is different, who believes the existence of the

tensor tympani muscle and the function of the ossicles. He is of opinion that the ossicles really transmit the vibration of the tympanic bulla caused by the resonated air in the middle ear. But these are the theories based on the isolated tympano-periotic organ from the skull, to which I cannot yield.

#### 5. Concerning the Osteo-Tympanic Conduction :

The last views of Lillie (1910), Abel (1912) as well as Kernan (1919) belong to the category of the so-called osteo-tympanic conduction and seems really to outlive the foregoing theories. However, the fact has been against my expectation that this view has a few supporters, and to make the matters worse, that even the concerned authors themselves gave only insufficient remarks which seem like one kind of mere ideas. This view is noted since it has been originally advanced from the side of mystacoceti, and odontoceti has been later introduced into this by Kernan. The outline goes in the following way. The sound vibrations are first received by the solid tissues of the head directly from the water, then transmitted through the mastoid process into the tympano-periotic organ. The malleus which is rigidly fused to the bulla transmits the vibration of it further to the fenestra vestibuli.

Lillie seems to have advanced the view with little confidence because he referred five years after his first publication to some other possibilities (1915, pp. 107-108), either that the sound vibration could be transmitted to the elastic lids of the external nares, being further transmitted into the tympanic cavity through the Eustachian tube, or that it could be conducted from the alae of the external nares to the bullae. At that time, the tympanic bulla should act as a sounding-box which is connected to the fenestra vestibuli by the chain of ossicles. The former view appears similar to that of Kellogg which has been just commented in the last paragraph. Whereas the latter is different considerably from his original view (1910) in which it was the bony surface that received the vibrations from the water.

Abel's view concerning mystacoceti is exactly of this category but he never succeeded to bring any satisfactory solution into our field to involve the odontocete suborder, as has already been quoted in review by myself.

Finally Kernan is curious indeed and hardly understood because in 1918 he advanced once the resonance theory in *Kogia*, but became suddenly converted one year later to another not typical view of the present category. May it be allowed, he became then too bold to mention that the

tympano-periotic bone presents a *considerable* bony process on the surface of the skull both in odontoceti and mystacoceti. In my opinion he has made more successful and presumable approach than anyone else did, but his view does not explain delphinidae, in which any *considerable* process of the tympano-periotic organ does never exist, which appears largely on the surface of the skull. Therefore, delphinids seem to lack those portions whatever on which sounds might directly impinge. Moreover to make the matters worse, nobody of this category in general has mentioned how the tympanic bulla could be regarded as a sounding box and how significant the auxiliary structures were.

My anatomical remarks mentioned hereafter in review as well as the functional considerations will make this view more probable than the previous theories, being less in troubles. The tympanic bulla is of very striking relation to the periotic bone. The connection is extremely so fragile between these components that they can be easily broken and separated by a slight force as is well learned during treatments both in odontoceti and mystacoceti. In odontoceti the connection is made by the anterior synostosed union and the posterior syndesmosed articulation; while in mystacoceti by two thin pedicles, the anterior and the posterior. In *Physeter*, whose anterior union is comparatively strong, the bulla can be swayed against the periotic by hand to an extent visible and sensible. This experiment can be safely tried because the bullar involucrum is in so close relation to the cochlear portion of the periotic that these two portions come into contact before the union goes broken. While in *Balaenoptera* the bulla is very often dislocated by the inevitable shocks in sawing operation of the huge skull by the steam-driven bone-saw into cubes as big as convenient to handle. One extreme and unusual case was already related of a sei whale in the beginning of the second chapter, whose bullae were not only dislocated but crushed into pieces by the harpooned shock on the head.

From these experiences I have come to a belief that the tympano-periotic bone of cetacea is specially planned according to some important dynamic principle. This dynamic is apparently that of a seismographic principle. When the solid tissues of the head receive the sound vibrations from the water, the entire tympano-periotic organ may be put under seismic influences, when the proportionally heavy involucral border of the bulla acts as a weight of pendulum because that border lies medially exactly at the pendulous remote position to the lateral thin and fragile union or unions (fig. 27). The separated relation of the bulla to the bordering crest of the basi-occipital bone is thus well understood. Accord-

ing to this dynamic the malleus stays relatively still in the vibration, and the seismographic amplitudes are caused between the malleus and the periotic bone. These amplitudes are transmitted by the remaining ossicles to the fenestra vestibuli, when in odontoceti the short crus of the incus seemingly functions as a fulcrum of more effective conduction by its articulated connection with the periotic bone. It is for this reason that I believe the significance of the tympanic muscles in the not unusual physiology though the tensor tympani muscle is often more vestigial.

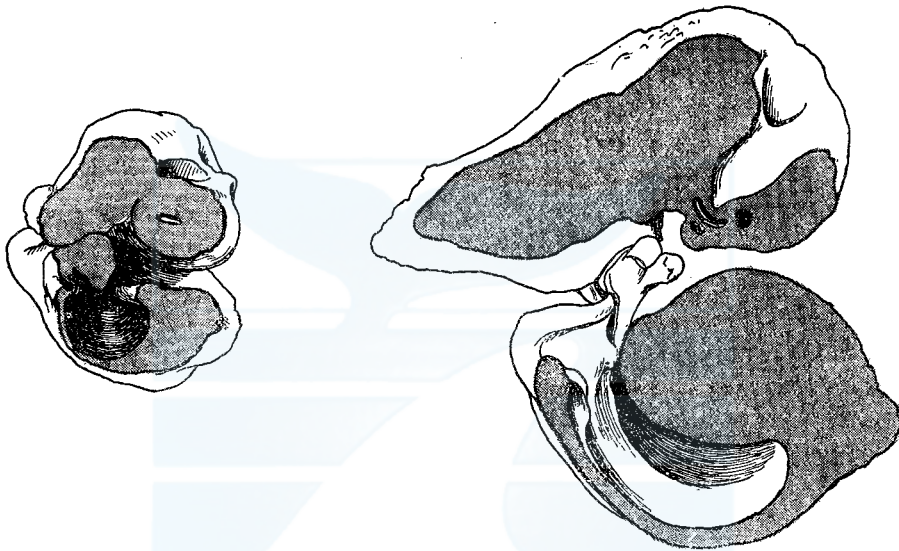


Fig. 27. Transverse section of the tympano-periotic bone (right side).  
Left- *Globicephalus*; right- *Balaenoptera*.

The specially stressed characteristic connections of the tympano-periotic bone with the skull most probably amplify the vibrations of this entire complication of bone components, the "tympano-periotic organ" as a seismometer. In these connections the tympano-periotic organ is without doubt isolated from the skull, strongly in particular in odontoceti, but the isolation is *never acoustic* because the propagating connection is indispensable, which is wonderfully achieved by the mastoid process between this organ and the skull. Really the neck of the mastoid process is quite easily broken and by some authors described as it is; while the falciform process of the squamosal bone in odontoceti as well as the pro-otic fibrous cord straining the tegmental process to the infratemporal periost in mystacoceti similarly protect the entire organ from excessive vibration. Delphinidae species can never be exceptional but is a specialized case of

the same principle.

I can enumerate further some concerning auxiliary peculiarities by which the organ can be set in good and noiseless vibrations as: the well developed peripetrosal pneumatic sinus of odontoceti, the remarkable formation of the sesamoid ossicles between this organ and the cranial basis in *Balaenoptera* together with some larger odontocete species, and the cartilaginous buffer body behind the cochlear portion of the periotic bone in *Balaenoptera*. The entire pneumatic sinus system may be one of these auxiliary structures. The function of the sinus system has been variously surmised by the foregoing authors, namely Denker (1902), Boenninghaus (1904) and Hanke (1914) mentioned the sinus to make the submergence of the head or its sustentation above the water surface easy by regulating the head weight. Kernan (1918) did likewise, but he added another one to afford additional surface for the absorption of oxygen by the blood. Kellogg (1928) explained the sinus to regulate the pressure of the entire pneumatic cavity of the middle ear.

I myself agree with Kellogg because the sinus system develops far better in odontoceti for its deeper submergence, than mystacoceti both in dimensions<sup>1</sup> and in its mural structures, including the cavernous body, probably in order to regulate the pressure of air inside the sinus system in wider range. I would like to point out with some stress that the largest pterygoid sinus is in odontoceti generally covered by the enormous mandibular adipose body, and the particularly close topographical relations of the epitympanic sinus to the mandibular articulation because, as has been mentioned in the last chapter, these relations seemingly indicate that the entire sinus system is strongly influenced by the movements of the lower jaw. These may not be positively related to the auditory function but it may be indirectly significant to that that the pressure of air in the sinus is seemingly raised temporarily when the animal opens the mouth for feeding under water, when the pterygoid opening of the Eustachian tube becomes closed by the mucous valve to prevent the interior air from leaking out. Thus the sinus system resists against the enormous pressure of the water, still it seems to happen that some amount of water soaks into the sinus because the interior of the sinus is often found foaming and because really one little fish as well as krills have come to my examination in the sinus, the former in one *Physeter* and the latter in some cases

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1) Though I did never try to gauge the pneumatic sinus system of either suborder, it is apparent that odontoceti greatly exceeds mystacoceti in proportion.

2) I am not entirely confident of these discussions of the sinus problem because these observations could be abnormal cases.

of *Balaenoptera physalus*<sup>2</sup>. Meanwhile, the air of the middle ear cavity might be resonated as is insisted so in the resonance theory but I cannot take it as essential to the auditory function of cetacea because the already mentioned cases of the glomerular parasites often fills up every corner of the tympanic cavity in some odontoceti, when the resonance can never be transmitted into the cochlea but the conduction of sound waves through the ossicular chain is not bothered at all.

The remarkable difference of the organ of hearing between odontoceti and mystacoceti lie, in the structure of the labyrinth, particularly in the arrangement of the cochlear spirals and in the development of the secondary lamina spiralis of Hyrtl. The surprising development of the secondary lamina in odontoceti has been repeatedly learned by many authors since Hyrtl (1845). Above all, Kolmer (1908) revealed that this extreme case occurs only in odontoceti. Whereas, concerning the first mentioned difference, no remarks have been known to me. It occurs in odontoceti that any apical portion of the cochlear canal never lies above the more basal portions and this is also peculiar to this suborder (fig. 28).

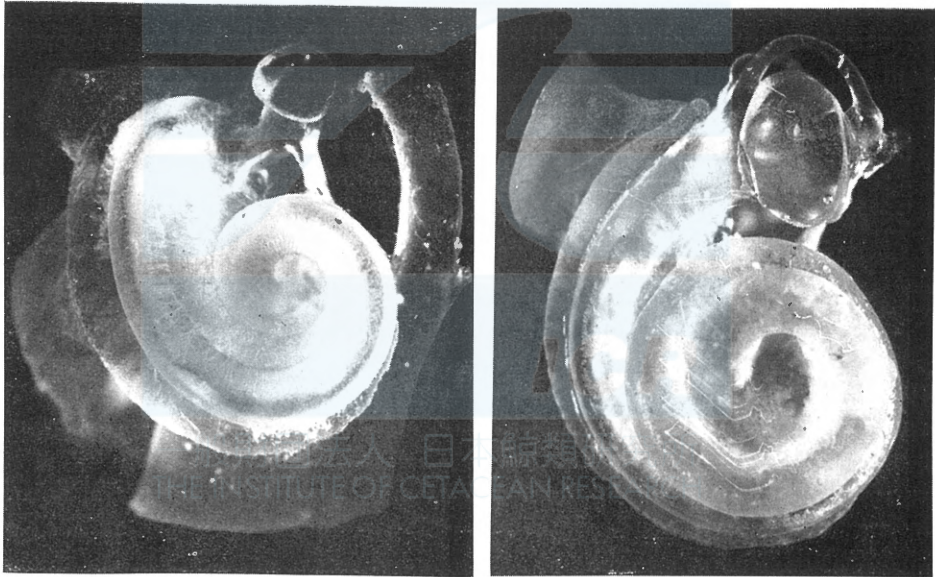


Fig. 28. Cast of the labyrinth (right side). *Left- Berardius* (ca.  $\times 3$ ); *right- Balaenoptera* (ca.  $\times 2.5$ ), showing the different coiling manners of the cochlear canal.

Here is a minor experiment of myself concerning *Berardius* which will contribute a little morphological datum toward the cetacean audiogram. Owing to this last mentioned characteristic of the odontocete cochlea, the

macerated bones can be operated along the full cochlear length with dental lathe and various points. This procedure must be carried out, however, with finest care because the delicate bony laminae as well as the modiolus are quite easily broken or vanish by the slightest touch of the rotating points. When the preparation is finished successfully, the spiral laminae both primary and secondary appear in the canal, opposing against each other so closely across the lengthwise spiral slit which gradually broadens toward the apical end. According to the histology, the width of the spiral slit seems well to be regarded almost equal to that of the actual basilar membrane. The increasing widths of this spiral slit can now be measured (fig. 29)<sup>1</sup>. In *Berardius* this slit increases the width very gradually in its basal portion and stretches as far as ca. 8/10 length of the whole canal.

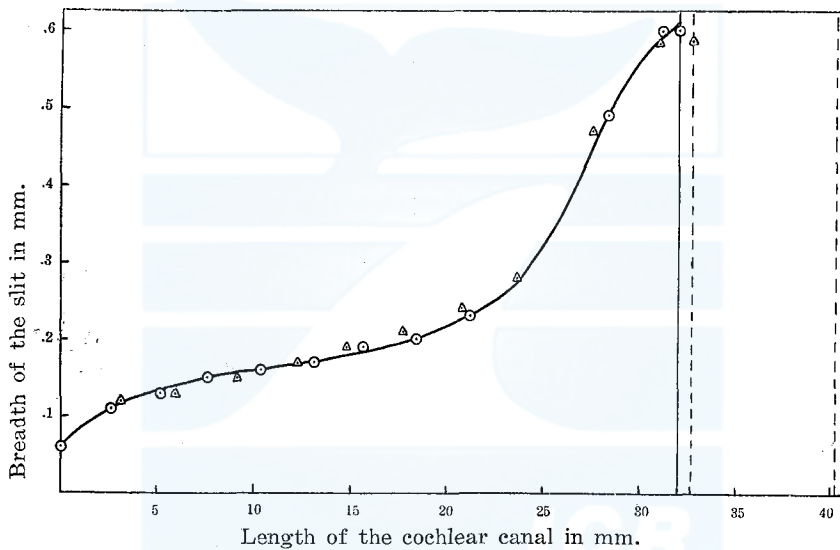


Fig. 29. Increasing curve of breadth of the spiral slit in *Berardius*. The curve shows *case 1.* (left cochlea) which is illustrated to coincide well with *case 2.* (right cochlea of another animal) marked by *triangles* and *perforated lines*. The curve naturally does not exceed the range of the secondary spiral lamina, the region being limited at 79% (*case 1.*) and 82% (*case 2.*) of the entire length of the cochlear canal which measures 40.6 mm. and 40.1 mm. respectively.

<sup>1</sup>1) After the grinding procedure, the spiral slit is marked with Indian ink at regular intervals along the margin of the primary lamina. Then possibly high photographic enlargement (usually around 40×) is made, on which the measurements are based as follows: First, measure the widths of the spiral slit at previously marked spots directly under microscope; secondly calculate the mean magnification of the photograph according to widths, actual and printed; thirdly measure the marked intervals on the photograph and; finally divide them by the calculated magnification; from these quotations desired intervals can be approximately reckoned.



According to Kolmer (1908) the basilar membrane of *Phocaena* measures  $50\mu$  at the basal end,  $100\mu$  at the middle height and  $270\mu$  at the apical end in breadth. Therefore the membrane expands more than five times. In the meantime, it seems different in *Berardius* because the breadth of the spiral slit increases not less than ten times within the range of the secondary spiral lamina. It would be premature to compare the differences between *Phocaena* and *Berardius* in this way, between the actual membrane and the bony slit, but the present increasing curve of the slit shows something about the actual widths of the basilar membrane, which Kolmer did not make clear. In this respect, Guild has been the only one worker who originated the prominent graphic reconstruction method (1927). According to his data, the basilar membrane of guinea pig increases its width not in an uniform inclination, the rates of change being actually greatest in the basal portion, becoming less and finally decreasing as it approaches the apical end (tabs. 1 and 2 of his paper). Therefore, *Berardius* is quite contrary to guinea pig to say the least, and after consideration of this curve I have come to a belief that the audiogram of *Berardius* is utterly different from our common knowledge of the terrestrial mammals, in other words, that this whale must hear the high tones, possibly super-sonics, in particularly fine distinction. This is probably similar in other odontoceti and with less probability in mystacoceti. I feel gratified in this direction that recently this possibility has been proved through observations of dolphins by Kullenburg and Fraser in succession (1947)<sup>1</sup>.

According to them (Kullenburg, p. 648; Fraser, p. 759) dolphins squeak in high tones which I myself also experienced at Taiji of blackfish when they are hauled ashore and killed by fishers. Further Fraser noticed some possible signs of super-sonics emitted by dolphins. Another experience of his own is interesting that dolphins with no doubt hear the super-sonics because a school of *Delphinus delphis* suddenly dashed away at great speed instantly when the ship's super-sonic echo-sounding machine was switched on.

The water-borne sounds can be reasonably expected to be the most effective and significant stimulus to their life in the water, since the speed of sounds under water is said as fast as 1,450 m./sec. and about 4.4 times faster than in the air, and moreover, since the vibration becomes

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1) A postscript: W. N. Kellogg and R. Kohler of the Oceanographic Institute, Florida State University, reported quite recently the first experiment of this nature of some captive *Tursiops* at the Marine Studios, and their results are really of special interest and make me confident of the present work very strongly. Pertaining to the particulars, confer the original paper in the Science, vol. 116, no. 3010 (Sept. 5, 1952).

damped far less in the water than in the air, and these high tones are extraordinary in energy because of their immense frequency of vibration. So it seems to be hypothetically expected that whales not only communicate each other by means of some sounds but also navigate safely by the supersonic soundings even at night and search their food by the sounds emitted by those creatures.

#### 6. Notes on Archaeoceti :

Finally it is of much interest of morphology to bring archaeoceti into the present considerations in order to throw a light upon the evolution which the living whales have undergone. Kellogg (1928, p. 202) wrote in this direction that the initial stages in the transformation of the hearing organ of whales are unknown, because the earliest known zeuglodonts have the osseous portions of this organ as highly developed as any of the living whales. This summarized conclusion of Kellogg excites a question how *any* whales out of the two living suborders are put into comparison with zeuglodonts, because he regards that these suborders are different, namely odontoceti lacks the osseous connection between the tympano-periotic bone and the skull; whereas mystacocete tympano-periotic is wedged by the mastoid process of it between the squamosal and the exo-occipital bones.

According to Pompeckj (1922), the periotic bone of zeuglodonts seems to be ankylosed to the lateral inner side of the skull by the processus superior, and the periotic takes part in the formation of the brain case by the whole medial or cerebral surface. The figured skull of the oldest known archaeoceti, *Protocetus atavus* (Fraas, 1904) from middle-eocene Egypt is also worthy of reference toward the present question. Both sides tympanic bullae present in the cranial basis, oblong or renal in shape, long axis lying almost parallel to that of the skull. The tympano-periotic bone of this fossil cetacea is obviously not outside of the cranial basis as seen in the living cetaceans especially in odontoceti. The borders of the bulla are in contact everywhere with the adjacent bones of the skull, and no room can be seen as to suggest any possible pneumatic sinus. Frankly speaking, the osseous portions of *Protocetus* appear not to differ remarkably from our knowledge of land mammals, and rather resemble mystacoceti than odontoceti. It may well be emphasized as remarkable in cetacea that both bullae have remained up to the present in the fossilizing procedure, and this shows more clearly than anything else that the bullae are most likely connected with the periotic bone or with the skull far more firmly than mystacoceti and, no saying, than odontoceti. If *Protocetus* possessed the similar bullae fused by thin unions with the periotic bone,

those remained bullae should be said quite miraculous.

Since I have no means to examine any zeuglodonts whatever, it may not be qualified to pick up fossil cetaceans here, but these bibliographic references go so far as to make me expect that archaeoceti will show some earlier stages of the transformation, in spite of the pessimistic remarks by Dr. Kellogg.

### Summary

The organ of hearing was studied in ten genera of cetacea, with special reference to the problems of lasting disputes. The observations and discussions are summarized as follows.

The external auditory meatus is closed in mystacoceti in wider specific range than has been established before. The obliteration seemingly occurs also in physeteridae. At any rate the meatus is extremely vestigial, with which the past contributions coincide well. However it is of special new interest both anatomically and cetologically that the vestigial meatus can be regarded as the independent sensory organ, probably the pressure gauge, for the abundant distribution of the laminal sensory corpuscles in the sub-epithelial tissues. These corpuscles are well marked particularly in odontoceti but also mystacoceti presents some (cap. I).

The tympano-periotic bone is different between two suborders to some extent but in general principle the structure resembles well each other. The bone is composed of two components, the tympanic bulla and the periotic bone. The bulla is semi-cylindrical (odontoceti) or of cowie-shell form (mystacoceti) and is in both forms delicately connected at its lateral border with the periotic bone. In odontoceti the connection is the anterior synostotic union and the posterior syndesmototic articulation; while in mystacoceti the bulla is connected by two thin bone pedicles. In both cases the connection, which is quite fragile, sustains the entire bulla of which the dense and heavy involucral border is located medially at the most remote position from the union (cap. II).

The mastoid process, which is in odontoceti of tympanic, and in mystacoceti of periotic, expands laterad in more or less dimensions. The process is in odontoceti usually flattened and broad, but in mystacoceti thick and stout, long and club-shaped. In either case the process obviously acts as a fulcrum of the entire tympano-periotic bone in connecting it with the remaining skull. The odontocete mastoid process is sutured in the squamoso-occipital notch of the oto-cranial flange of the skull from below; while that of mystacoceti is wedged firmly between the same bones of the skull. The connection seems more tight in larger species, and really

in delphinidae the process is quite short. One particular case of odontoceti is *Physeter* whose mastoid process is composed of thin plates which sustain the entire bone by interdigitation (cap. II-1).

The main portion of the tympano-periotic bone becomes forced out of the formation of the cranial basis during development, and is, in the final state, more or less separated or isolated from the cranial basis. This isolation is stronger in odontoceti and only partly in mystacoceti. But however strong the isolation may be, it is not acoustical as insisted so by many authors in the past. It seems just outwardly so in delphinidae whose mastoid process is extremely shortened (cap. II-2).

Concerning the further relations of the tympano-periotic bone to the skull, both suborders seem similar or to have some structures in common. The falciform process of the squamosal bone of odontoceti is closely connected with the upper side of the tegmental process of the periotic with one exception of *Kogia* to which the process is lacking. While in mystacoceti, the tegmental process of the periotic is strained to the infratemporal periot outside the otic region by a strong fibrous cord through a canal bordered by the pterygoid and the exo-occipital bones (cap. II-2).

These two peculiarities differ greatly from each other morphologically but functionally seem similar. The peculiar sesamoid ossicles sometimes develop between the periotic and the under side of the skull. They are most abundant and well marked in *Balaenoptera*, while less ossicles occur also in some larger odontoceti (cap. II-2).

In the tympanic cavity of odontoceti the cavernous body is well marked expanding through the tympano-periotic fissure into the cavity. In *Balaenoptera* instead, various folds and vesicular formations of the mucous layer are present. The tympanic ossicles are generally short and stumpy, of which the malleus is ankylosed to the bullar lateral border by its rigid anterior process. The incus of odontoceti is different from mystacoceti for its longer crus breve. This unusually long crus breve articulates with the periotic bone. The tympanic muscles never lack in any form examined by me (cap. II-3).

The pneumatic sinus system develops well but far stronger in odontoceti. The sinuses are in odontoceti usually four in number, of which the pterygoid is the largest and most peculiar in its trabeculated mural structure; an interpretation may be well understood that this sinus is the expanded proximal portion of the Eustachian tube, to this interpretation some structures of the tympano-periotic bone are affirmative. The pterygoid sinus is greatest also in mystacoceti and can be similarly interpreted. Other sinuses expand more posteriorly and communicates with the tympanic

cavity through the tympano-periotic fissure, but in odontoceti the epitympanic sinus is peculiar for its communication through the epitympanic hiatus. The peripetrosal sinus of odontoceti is also peculiar corresponding to the downward isolation of the tympano-periotic bone. Naturally this sinus does not exist in *Balaenoptera* and stays as the peribullar sinus (cap. II-3).

The entire otic region including the sinus system is covered in odontoceti by the adipose body of the mandibule from lateral side and by the fibrous layer from under side; while in mystacoceti the fibrous layer develops dominantly and this region seems really isolated by that enormous layer of fibrous tissue. The sinus system seems to be closely related to the mandibular movements in odontoceti (cap. II-3).

From these observations I believe that the tympano-periotic bone is in both suborders a dynamic unit of seismographic principle. The heavy involucrum is the weight of pendulum, when the malleus stays relatively still and this resulting amplitudes between the malleus and the periotic, which are conducted further into the labyrinth through the ossicular chain (cap. III-5).

The past disputes concerning the function are classified as: a) classic view, b) resonance theory, c) *Schalltrichter* theory and d) osteo-tympanic bone conduction. The first view is wholly erroneous because substitute path was searched for to transmit the air-borne sounds to the tympanic membrane. The second and third theories have many troubles because they thought the tympano-periotic bone to be acoustically isolated. Obviously the view of myself mentioned in this paper belongs to the last one. But nobody has advanced detailed considerations how the peculiar structures of the tympano-periotic organ are surmised to function (cap. III-1~5).

Finally one minor experiment in *Berardius* shows something about the audiogram of cetacea. That is, the basilar membrane is indirectly revealed to increase its breadth very slowly in the basal part of the cochlea, which seems quite contrary to the guinea pig. Thus here is an important belief that this whale must hear high tones, possibly supersonics, in particularly fine distinction (cap. III-5).

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From the Department of Anatomy (Director: Prof. Ryoji Ura), School of Medicine,  
University of Okayama, 164 Oka, Okayama-shi, Japan