OSSEOUS LABYRINTH OF CETACEA

MUNESATO YAMADA* AND FUMIHIKO YOSHIZAKI*

Since as early as the eighteenth century, the cetacean labyrinth has been referred to by the pioneers of comparative anatomy including Cuvier, Monro and v. Baer. But it was not until 1789 that Monro and Comparetti discovered the disproportionately minute semicircular canals, apparently one of the most important peculiarities in the cetacean ear. However, the author who first took out the cetacean labyrinth by means of cast preparation was probably Rapp (1837), and this monograph was followed by a fascinating one by Hyrtl (1845) which also dealt with a number of cetacean species. Gray (1907–08) was another who ingeniously prepared and described the membranous labyrinth of vertebrate animals also including some cetaceans.

The present investigation was attempted with the initial intention of affording fundamental data and knowledge towards a histological research proposed by the senior author (Yamada). His impression is that the previous records do not help the intended purpose. This applies not only to the cetacean labyrinth alone but to general labyrinthine anatomy including man and the so-called experimental animals. This is because the criteria of the measurements, for instance, are not always clear, and also because something else had to be contrived in order to present its morphology as such. The present paper was first read in 1957, and incidentally, it became more than a mere presentation of the cetacean varieties. This work has become a starting point so that in fact some novel data and propositions have been developed with the aim to standardize the sectioning and indexing of the human labyrinth (Yamada, 1959).

MATERIAL AND METHOD

Material of the present investigation consists of sixteen species from fourteen genera representing the two suborders of Cetacea as follows:

Mystacoceti or Whalebone whales	1 *Balaenoptera* (three species); 2 *Megaptera*; 3 *Eubalaena*;
Odontoceti or Toothed whales	4 *Physeter*; 5 *Kogia*; 6 *Berardius*; 7 *Ziphius*; 8 *Globicephala*; 9 *Grampus*; 10 *Feresa*; 11 *Lagenorhynchus*; 12 *Delphinus*; 13 *Prodelphinus*; 14 *Neomeris*.

---

* Department of Anatomy, Okayama University Medical School.

Labyrinths of each of the above species were cast in a small number of specimens but in many cases in one example only. The findings on these casts were supplemented in some instances by the direct method, in which direct access was made to the labyrinthine interior by grinding the bone with dental engine or lathe. Such a small number is obviously far from sufficient in order to discuss the specific characteristics, but altogether they accumulate a good sum of findings so that the cetacean labyrinth may be considered as a whole.

One each specimen of *Delphinus* and *Lagenorhynchus* perioticum came from Prof. Ogawa's collection, and *Megaptera* came from the Antarctica by courtesy of Mr. G. Tandai. The authors acknowledge their great indebtedness to the above donators.

Cast specimens were made by use of acrylic resin in a way not very unlike the dental routine. After complete maceration and rinsing, the whole or part of the perioticum, depending on the size, is embedded in an investment flask within gypsum plaster. Plaster should be made in separable strata of base, so that the bottom seizes the bone capsule and the upper negative can be detached. As the resin paste is made to permeate into the labyrinthine lumen through the openings, such as two each of fenestrae and aquaeducts and the internal acoustic meatus, these openings should be so placed as to line up and open in the demarcation of the two plaster bases.

After these preliminary procedures, a proper amount of resin paste is squeezed into the umen by pressure of a screw press. The plaster bases tightly encapsulate the bone and thus prevent the raw resin from leaking out when the flask is pressed. However, this moulding technique is a matter of considerable difficulty. This is followed then by polymerization as indicated, and the cast is taken out. To remove the petrous tissue of the perioticum, 5% nitric acid is applied. Ordinary alkali solution has no effect, especially in the case of Odontoceti perioticum. As the semicircular canals are generally so minute, cast of these by alloy either of Wood or Lipowitz hardly survives such decalcification, although alloy is really wonderful material for casting purposes.

However, resin cast is easy to examine, and this advantage may be enhanced when the transparent resin is used, because it renders, for instance, the lamina spiralis well visible if they remain encapsulated within the cast specimen. Another advantage of the transparent resin may be well appreciated in the stereographs (Pls. I–III).

Measurement was made exclusively under microscope or according to microscopical drawing of low magnification. By such drawing, the method of which is to be briefly described, perfect parallel-ray-projection is attained. A specimen is observed under microscope and is traced along its contour by an intersection of a crossline plate, or preferably a net micrometre plate, which is incorporated within the micrometre eyepiece. Now that the intersection is fixed this is attained by shifting the specimen horizontally with the mechanical stage. The contour is thus plotted on graph paper as loci of nonius readings of the mechanical stage at a convenient magnification, for example 10× or 20×. The most important advantage of this method is that the drawing is rendered absolutely free from any optical distorsion or perspective. This is because all the points are read on one definite axis within the optical system. The use of verniers limits the errors within the order of one tenth of a millimetre. Besides, no danger of destroying the specimen by touch is incurred, which is otherwise by no means avoidable.

Measurement of the cochlear canal length was made according to a map, which is composed of a sequence of subdivided drawings. In order that each successive portion to be drawn may be placed horizontally under microscope, a special holder was designed in the ball-and-socket principle. Any portion of the specimen may in this way be evenly focused by an adequate tilting of the holder. A small amount of modelling compound used for dental purposes has proved suitable for fixing a specimen onto the holder.

Photography was made in all instances with a Leica, screwed on an arm vertically adjustable, and 135 *mm* objective at a fixed bellows extension 1:1. For stereo-photography (Pls. I–III), a special semicylindrical holder was designed in order to rotate the specimen. A couple of photographs taken before and after an adequate angle of rotation make a stereo. The specimen was water-immersed.

SIZE AND GENERAL NOTE

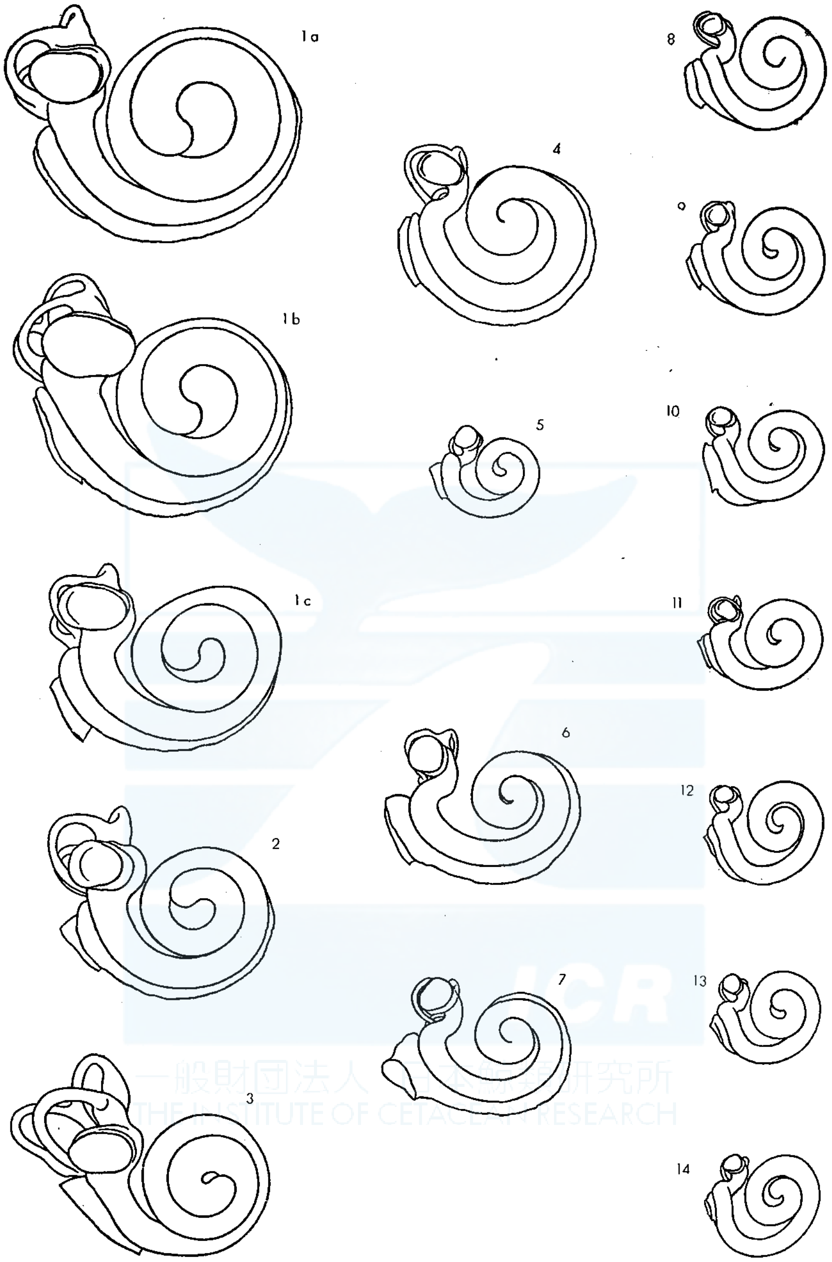
Text-fig. 1 illustrates the labyrinths of all the species examined at uniform 1.5× magnification. It is self-explanatory, and therefore no figures are given, for a common measuring criterion is rather difficult to set up. At any rate, the size of labyrinth corresponds roughly, except in the case of Physeteridae, with the body length of the species concerned. For instance, that of *Balaenoptera musculus*, the greatest creature which ever lived on earth, is the biggest, whereas *Kogia* possesses the smallest one. Thus a special remark may be made that the two genera belonging to Physeteridae possess labyrinths of reduced size in comparison with the body length.

Remarkable cetacean peculiarities are generally seen. The flat type of cochlea is observed to have a rather small number of turns. The whorl pattern is unusually robust and loose, and the vestibule and semicircular canals are disproportionately minute. Closer examination and comparison reveal however, that a rough division may be made according to the taxonomic position of each whale species. As regards the whorl pattern of the cochlea, for instance, they may be divided in four categories as: 1) Balaenidae, 2) Balaenopteridae, 3) Physeteridae-Ziphiidae and 4) Delphinidae. The labyrinth of *Eubalaena* (Balaenidae) is so different and non-cetacean that for the sake of convenience and emphasis the species will be discussed as a separate matter at the end.

COCHLEA

The number of cochlear turns has been a main topic of interest in labyrinthine morphology, and it more or less exceeds two in Mystacoceti, with an exception of *Eubalaena*, in which it is two and a half. In Odontoceti on the other hand, it is slightly below two. The authors do not intend to enter into more details because they are not inclined to ascribe to the number of turns such a significance as has commonly long been attributed to them. This is because the criteria are again not easy to set up. The authors are inclined rather to put the matter in the hands of those who are interested in the question, and actually they can find out as they wish from the diagrams of Text-fig. 1.

As a matter of fact, whorl radius decreases as the cochlear canal goes from the vestibular extremity up towards the apex. The rate of



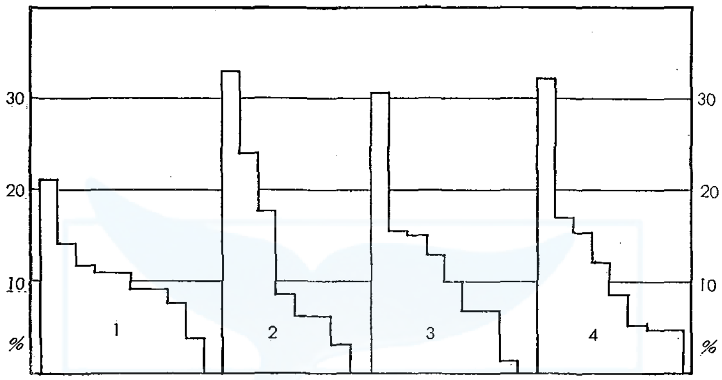
Text-fig. 1. Cast specimens of cetacean labyrinths (1.5 ×). The modiolus of cochlea is situated upright in all the drawings so that the number of turns of each may be estimated according to the reader's criteria. 1-a. *Balaenoptera musculus*; 1-b. *B. physalus*; 1-c. *B. borealis*; 2. *Megaptera*; 3. *Eubalaena*; 4. *Physeter*; 5. *Kogia*; 6. *Berardius*; 7. *Ziphius*; 8. *Globicephala*; 9. *Grampus*; 10. *Feresa*; 11. *Lagenorhynchus*; 12. *Delphinus*; 13. *Prodelphinus*; 14. *Neomeris*.

such decrease is different from one species to another, namely it is gradual in Mystacoceti and more abrupt in Odontoceti. In Mystacoceti, the apical whorl covers a part of the more basal portion in a way similar to many terrestrial mammals. In its apical aspect, however, Mystacoceti is characteristic. Here a considerable space is unoccupied, embraced by an arc of apical whorl in a form not unlike a large comma, so that whole of the canalicular system within the upper modiolus is exposed as cast. In Odontoceti, on the other hand, neither of these peculiarities occurs. There is no portion of the cochlear canal covered by the other. The portion at the apex coils so tightly that the whorl radius progressively decreases, and in the result there is no space as in the one observed in Mystacoceti. However, space is seen towards the widely expanded base, particularly within the first quadrant of the cochlea. In short, the cochlear pattern of Cetacea is, with the exception of *Eubalaena*, loose in two ways. That of Balaenopteridae is loose on the apex, and that of Odontoceti in the basal portion or in the beginning.

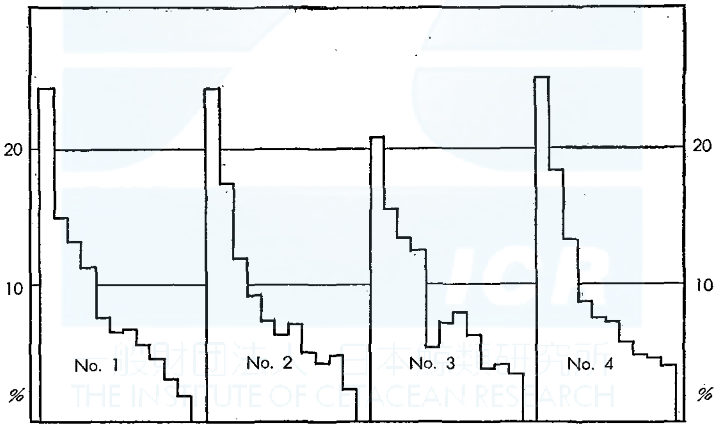
The rate of ascent of the cochlear canal is also different according to species. Delphinidae is among others very unique particularly in the first quadrant of *Neomeris* as is shown in Plate-fig. 10. In addition to the peculiarity as observed in its apical aspect (Text-fig. 1, *14*) that this portion of the cochlea considerably swerves out towards the bottom, left of the reader, it does undulate also up over the round window and down further, and up again. The dètour over the round window is seen in many mammalian cochleae, although it is very conspicuous in Cetacea and especially in Delphinidae. It should be noted that the portion that swerves abruptly inclines from above the round window. The canal also inclines even sideways. It seems natural therefore that the cochlear canal is conspicuously elongated within the first quadrant.

In order to put the matter in a more objective light, the cochlear canal was sectioned by an optical method up into quadrants, and the length of each was measured. The result (Text-fig. 2) reflects clearly, as was expected in advance, the nature of whorl pattern. For instance, the first quadrant of Odontoceti cochlea well exceeds 30% of the total length. Graph of *Physeter* is a regular one, and well represents its regular vorticose pattern. That of Balaenopteridae does not differ greatly from the more common mammalian pattern belonging to the higher type of cochlea. In other words, there are three categories of quadrant graphs, as Balaenopteridae, *Physeter* and Delphinidae. Those of *Kogia* and Ziphiidae do not differ from Delphinidae, and may be included herein.

For a reference purpose, the human cochlea was sectioned in a similar way (Text-fig. 3). It is noticed, in this higher type of cochlea, that occasional irregularities occur in the graphs. The authors are of the opinion, however, that this is due rather to the deviation involved in the measuring procedure than to the actual differences among individuals. It is apparently because the section of cochlea in quadrants involves some arbitrary factors, especially pertaining to the uprightness of the modiolus. In other words, if the modiolus is slightly tilted, the length of some or all quadrants as measured may deviate more or less.



Text-fig. 2. Graphs of quadrant-length of the cochlear canal.
1. *Balaenoptera (musc.)*; 2. *Physeter*; 3. *Kogia*; 4. *Globicephala*.



Text-fig. 3. Graphs of quadrant-length of the human cochlear canal. Occasional irregularity may not necessarily be the result of individual variation, but probably measuring artefact which is not avoided in the case of higher type of cochlea.

Because of these experiences the authors propose not to put too much weight on the number of turns, especially in a way that according to the sequence of turns a particular locus of the cochlea is mentioned.

In view of the enormous variety of the cochlear pattern ranging from Monotremata to Rodentia, the authors should like to remind the reader of the fact that the cochlea is really nothing but a blind canal system. Its number of turns may be the result of the ultimate length of the canal itself and the space available to invest the organ. Chronological relationships during development in between various tissue components may also influence its final vorticose pattern. The authors thus believe that a particular locus in the cochlea should be indexed by its distance from the vestibular extremity in percentage of the total length. This applies to all kinds of cochlea alike, and is not a question of cetacean ear alone. The senior author actually has published recently some data on its practical application to the human labyrinth (Yamada, 1959).

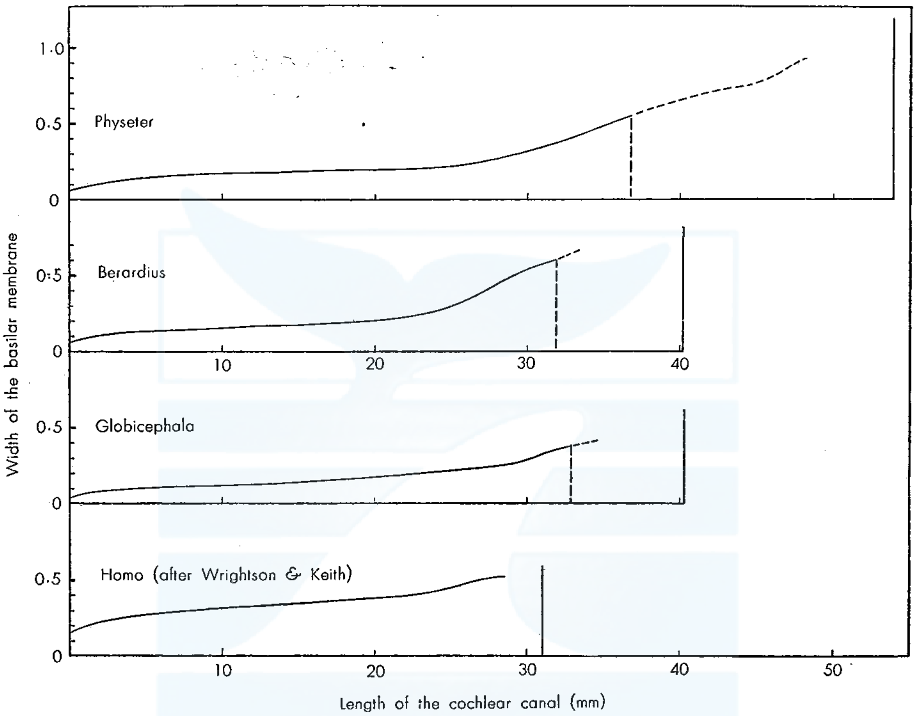
It is observed finally in the apical aspect that the scala tympani is characteristically spacious and exceeds the scala vestibuli in the basal portion of larger cochleae. This is observed in Mystacoceti, except *Eubalaena*, and in Odontoceti representatives such as *Physeter*, *Berardius* and *Ziphius*. There is a noteworthy contrast between the surfaces of the two scalae. That is to say, the scala tympani is rough, whereas the scala vestibuli is smooth. Besides, on the surface of the latter in Odontoceti, stand out radial markings for cochlearis propria arteries.

LAMINA SPIRALIS SECUNDARIA

A trial to estimate the basilar membrane was made by the senior author on macerated material of *Berardius* (Yamada, 1953, Fig. 29). This was possible because the secondary lamina spiralis of *Berardius* develops well in a way that it is situated in the bottom of ligamentum spirale, and therefore, this supports the whole ligamentum, in the range of basal 80% of the cochlear canal, almost to the attachment of the basilar membrane. Therefore, the spiral slit, where it comes out in macerated specimen between the two bony laminae, reasonably corresponds with the actual expansion of the basilar membrane. Later investigation has revealed that this structure is commonly seen in Odontoceti. The width of spiral slit, in other words the width of the basilar membrane itself, increases as it transits towards the apex of the cochlear canal. Width increase of the basilar membrane is a fact very well known in all mammalian cochlea, but there is a peculiarity which may be ascribed to Odontoceti.

Text-fig. 4 shows some examples of such transition as compared with a curve of human basilar membrane after Wrightson and Keith (Fletcher, 1939). Although this is presented according to a histological investigation, these may be compared with each other, and it is noticed that in

Odontoceti nearly half of the canal length is occupied by a very gradual increase of the width, generally in a range of 0.1–0.2 *mm*. This is not the case with the human cochlea, nor with an instance of *Balaenoptera physalus* examined. This slow increase and striking development of the secondary lamina spiralis in Odontoceti may be regarded altogether as morphological evidence supporting our increasing knowledge of the cetacean hearing capabilities, namely that these whales can hear a wider range of frequencies and especially high pitches of sound including ultrasonics (e.g. Kollogg, 1953).



Text-fig. 4. Rate of the width increase of the basilar membrane in Odontoceti representatives, as estimated from the slit between the two spiral laminae. Upper limit of the secondary lamina is also shown (perforated lines), which is 68% for *Physeter*, 79–82% for *Berardius*, and 81% for *Globicephala*. Note over-all similarity of the three, each representing its own family. Curve of human basilar membrane after Wrightson and Keith is for reference. Similar data for Mystacoceti is obtained in too small a range because of the far weaker development of the secondary lamina. Curve of 15% range of *Balaenoptera physalus* falls on that of man. From the macerated specimen no further information is available.

The spiral laminae are delicate but they may be well preserved in some instances as Plate-figs. 4 and 6 show, where they are observed satisfactorily well through the transparent cast material. In many instances however, they are broken and the débris are scattered and give to the cast an ugly appearance (Plate-figs. 7–10).

In Mystacoceti, however, the secondary lamina spiralis is definitely weaker. Reysenbach de Haan (1957) wrote as though there was certain controversy about Mystacoceti cochlea in this particular respect. According to him, similar development of the secondary lamina is seen also in some rodents and Chiroptera, and he expected the same to occur in Mystacoceti also. However, the difference between the two cetacean suborders in this respect is in actual fact definite as stereographs of *Balaenoptera* and *Megaptera* (Plate-figs. 1–2) show it clearly. In one example of *Balaenoptera physalus*, the secondary lamina is to be seen in a much shorter region of no more than 40% of the total length, and the slit measures 0.19 *mm* in width at the vestibular extremity. So far as the basal approximate 15% is concerned, where the slit is expected to coincide with the actual basilar membrane, the width increases in a similar curve like the one of human membrane after Wrightson and Keith (Text-fig. 4).

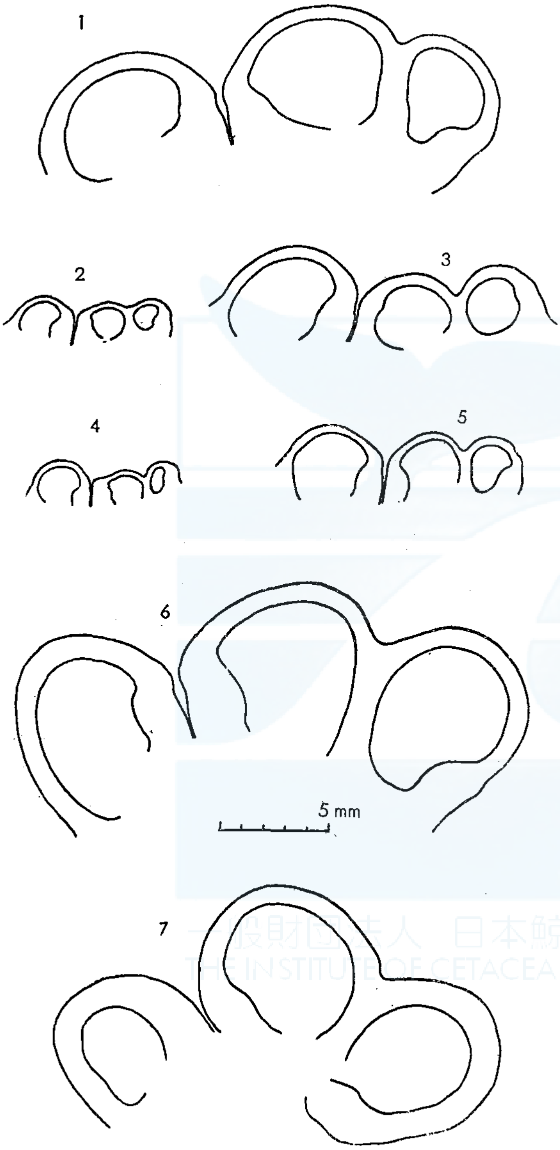
SEMICIRCULAR CANALS

Text-fig. 5 shows some examples of semicircular canals presented in a form comparable with those of the human labyrinth. The canal system is a three-dimensional structure, and it is consequently difficult to illustrate. Text-fig. 5 is, in that sense, a new type of illustration, in which crus simplex of the lateral or horizontal canal is dislocated at the base and the whole canal system is arbitrarily expanded in a single plane. An important advantage of this is probably appreciated that the three canals are put into a better comparison both in form and dimension. It is again self-explanatory to a certain extent.

The size differs roughly in accordance with the body length, and *Neomeris* is the smallest of all. However, dimensions of the ampullae as well as the span of each canal are not exactly proportionate. In other words, in smaller canals the height of arch becomes progressively less and the ampullae relatively greater. It is observed, in histological sections and whole preparations of the membranous labyrinth, that the osseous canals do not directly reflect the actual calibre of the membranous ductus within them. Thus the membranous ductus is relatively thicker in smaller canals.

But the most conspicuous respect of the semicircular canal system of Cetacea is the dimensional relationship of the three. It is noticed generally that the posterior canal is, with the exception of *Eubalaena*, the smallest of the three. In Odontoceti, this is more conspicuous and the lateral canal is, in good contrast with the posterior, the greatest. The superior or anterior canal is the intermediate. This is really striking because in many of the land mammals, either anterior or posterior canal is the greatest, whilst the lateral is always the smallest.

It may be too early to mention from this finding that the horizontal movement either of the head and neck or the entire body is of the most important functional significance in cetaceans. But the authors' impression is that such muscular control as is called upon by the vestibular reflex, originating among others in the lateral canal, may be a unique one which the cetaceans have learned in the long course of evolution to be important in the life under water. Such control might be needed the more in Odontoceti which is generally supposed to be more alert and active.

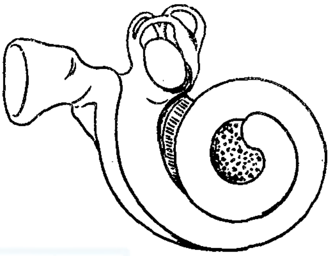


Text-fig. 5. Semicircular canals, arbitrarily expanded. In all the drawings the canals are from left to right: lateral, anterior and posterior. 1. *Balaenoptera* (*musculus*); 2. *Kogia*; 3. *Physeter*; 4. *Neomeris*; 5. *Ziphius*; 6. *Eubalaena*; 7 Man (for reference).

EUBALAENA GLACIALIS; A STRIKING EXCEPTION

Finally special mention should be made of the right whale, *Eubalaena glacialis*. The labyrinth of '*Balaena*' has been described and illustrated only once by Hyrtl (1845) as reproduced in

Text-fig. 6. His illustration was also reproduced in Bolk's *Handbuch der vergleichenden Anatomie* by de Burlet (1934). Gray (1907) was another who mentioned the labyrinth of '*Balaena australis*', but no illustration was given because his specimen of the membranous labyrinth was far from perfect due to the putrefactive changes. However, his comment seems worthy of quotation: "From what could be seen the labyrinth differed from that of the porpoise only in size".



Text-fig. 6. *Balaena mysticetus*, only one illustration of this sort given by Hyrtl (Natural size reproduction after Fig. 7 in Taf. IX). Obviously the species is not genuinely identified.

The present authors themselves, and probably all those who were interested in the topic alike, could hardly suspect the genuineness of these previous findings. Consequently, it has long been a widely accepted view that there exists such a general uniformity which may be called "cetacean" as was mentioned previously. It was only recently, however, when two specimens of *Eubalaena* were captured in the Japanese waters for a scientific survey (e.g. Omura, 1957) and when the authors were blessed with the opportunity of examining these animals that the labyrinth of right whale was first known, against the common belief, as an extraordinary exception.

Cast specimen is illustrated stereographically (Plate-fig. 3), and one may at first sight notice this. The cochlea is of rather pointed high type in two and a half turns which coil tightly. The semicircular canal system is not diminished. Moreover the conspicuous relationship, noticed in the size of the semicircular canals generally, is not apparent in the right whale. Any significant difference is not noticed in the dimension of the three canals. In actual fact it is rather terrestrial, and strikingly "non-cetacean". It is obvious therefore that the right whale of neither Hyrtl nor Gray was genuinely identified.

The authors are not in the position to raise a speculation as to the reason of diminished vestibular organ of the cetaceans, but it seems worth while to pay attention to a recent paleo-biological statement by Edinger (1955). According to her, the cerebellum develops in early cetaceans better than the cerebrum, vestibular nerve being dominant to the acoustic. Such interrelationship apparently has been reversed during the course of evolution as the function demands. In view of the fact that the unveiled findings on the right whale have something in common with Edinger's statement, it may well be mentioned that the right whale is, at any rate, probably a species which still retains to a marked degree such primitive status as the early fore-runners had once possessed. This whale is, in that sense, a "Living Fossil" in the cetacean evolution. The authors naturally look forward to the possibility of examining a fossil labyrinth. Gray whale (*Rhachianectes*) may be another species that should be investigated.

One more mention may be made in this connexion of a recent communication by Aoki (1957). A high school boy, who is diagnosed as cerebellar ataxia, is incidentally an excellent swimmer but strongly ataxic when he tries to stand and walk. It is suggested in the résumé that the cerebellar innervation of muscular tonus is under-developed and that the tonus itself becomes unnecessary to such an extent, when the subject is in the water, as up to the amount of floating force which reduces his body weight considerably. Although nothing is known about the vestibular system of the patient, neither in the central nervous system nor in the labyrinth itself, this may eventually be a representation of the actual transition that happened in the cetacean history.

The posture is, in Cetacea, no longer balanced on the limbs as in the land animals. The authors have become rather inclined therefore, to believe that the noticeable alteration of the balancing in Cetacea might be responsible for the diminution of the semicircular canals. No doubt, however, much evidence should be extensively collected, probably also in the central nervous system, before anything more definite can be said. Previous views on this problem will be discussed when such opportunity arises.

SUMMARY

With the aim of obtaining fundamental data for subsequent histological investigation, labyrinths of 16 species of Cetacea were investigated, mainly on cast specimens. New findings and remarks are summarised as follows.

1) As regards the dimension of the labyrinth, Physeteridae representatives (*Physeter* and *Kogia*) are relatively small in comparison with the body length. Otherwise the dimension diverses roughly according to the specific body length.

2) Vorticose pattern of the cochlea is different according to the taxonomy. In Mystacoceti the vortex is open on the apex, and in Odontoceti, especially in Delphinidae, the cochlear canal of the first quadrant region swerves in a unique way away from the modiolus. In the consequence of such détour, the first quadrant is strikingly long. The length exceeds 30% of the total length.

3) Since the cochlear pattern differs considerably according to species, a proposition is made to adopt widely an "index method" in order to indicate a particular locus of the cochlea. In place of the more popular method, in which the sequence of turns is mentioned, the proposed method puts the special weight on the distance of each locus from the vestibular extremity in percentage of the total length. This is not so difficult a matter as might be expected, and it has been found to be practical. This applies not only to Cetacea, but to all mammals including man and experimental animals.

4) A unique peculiarity of Odontoceti is that the secondary lamina spiralis develops up to as far as 68–82% of the cochlear canal. There is evidence that the slit between this and the primary lamina spiralis coincides, within this range, with the actual basilar membrane. In the first 50% range, the basilar membrane increases its width at an extremely slow rate, generally between 0.1–0.2 *mm*. This is probably related to the high frequency hearing capability of those animals. In Mystacoceti, the secondary lamina spiralis is far less noticeable. In one example of *Balaenoptera physalus*, the slit between the two laminae is estimated to coincide only in the first 15% range with the basilar membrane. Width increase in this range is as in human membrane.

5) As regards the semicircular canals, which as unanimously agreed are extraordinarily diminished, the size of each is in a reverse relationship in contrast to many, if not all, terrestrial mammals. The lateral is the greatest and the posterior the smallest, especially in Odontoceti.

6) *Eubalaena* presents a serious exception, in which none of the known cetacean peculiarities are to be found. Cochlea is of high type, closely coiled in two and a half turns. Semicircular canals are well preserved, and the general impression is strikingly "non-cetacean". This is an absolutely new finding. In view of paleontological transition between the equilibrial and acoustic nervous components (Edinger, 1955), *Eubalaena* may well be called as a "Living Fossil" in the cetacean descent.

The authors are grateful to Professor H. Outi for his encouragement and helpful criticism. Miss D. E. L. Brown kindly read the script and made corrections.

REFERENCES

AOKI, S. (1958). One case of equilibrial ataxia (Japanese Résumé). *Jibi Rinsyo*, 51(1): 9.

BURLET, H. M. DE (1934). Die Innere Ohrsphäre. *Bolks Handb. d. vergl. Anat.*, 2(2): 1293–1380.

EDINGER, T. (1955). Hearing and smell in cetacean history. *Monatschr. f. Psych. u.*

Neurol., 129: 37-58.

FLETCHER, H. (1939). Speech and Hearing. New York (Nostrand), p. 117, Fig. 64.

GRAY, A. A. (1908). The labyrinth of animals. London (Churchill), vol. 2: 22-34 (Cetacea and Sirenia).

HYRTL, J. (1845). Vergleichend-anatomische Untersuchungen über das innere Gehörorgan des Menschen und der Säugethiere. Prag (Ehrlich): 91-130 (Labyrinth), Taf. IX.

KELLOGG, W. N. (1953). Ultrasonic hearing in the porpoise, *Tursiops truncatus*. *J. comp. and physiol. Psych.*, 46: 446-450.

MONRO and COMPARETTI (1789). Observationes anatomicae de aure interna. Patavii: 156 (cited from Rapp).

OMURA, H. (1958). North Pacific Right Whale. *Sci. Repts. Whales Res. Inst.* (Tokyo), 13: 1-52.

RAPP, W. (1837). Die Cetaceen, zoologisch-anatomisch dargestellt. Stuttgart and Tübingen (Cotta): 98-104 (Gehörorgan).

REYSENBACH DE HAAN, F. W. (1957). Hearing in whales. *Acta Oto-Laryngol.*, Suppl. 134: 1-114.

YAMADA, M. (1953). Contribution to the anatomy of the organ of hearing of whales. *Sci. Repts. Whales Res. Inst.* (Tokyo), 8: 1-79.

——— (1959). Basic data for the standard sectioning of the human ear labyrinth (Japanese Text). *Kagaku*, 29(7): 363-364.

YAMADA, M. and YOSHIZAKI, F. (1957). On the osseous labyrinth of cetacea (Japanese Résumé). *Acta. Anat. Jap.* (*Proc. Soc. Anat. Jap.*), 32: 44.

EXPLANATION OF PLATES

Specimens are generally so placed that as good as possible comprehension of the structure may be attained, hence there is no uniformity as to the direction like that of Text-fig. 1. Specimens are water-immersed. As regards the method of photography see 'Material and Method'.

PLATE I

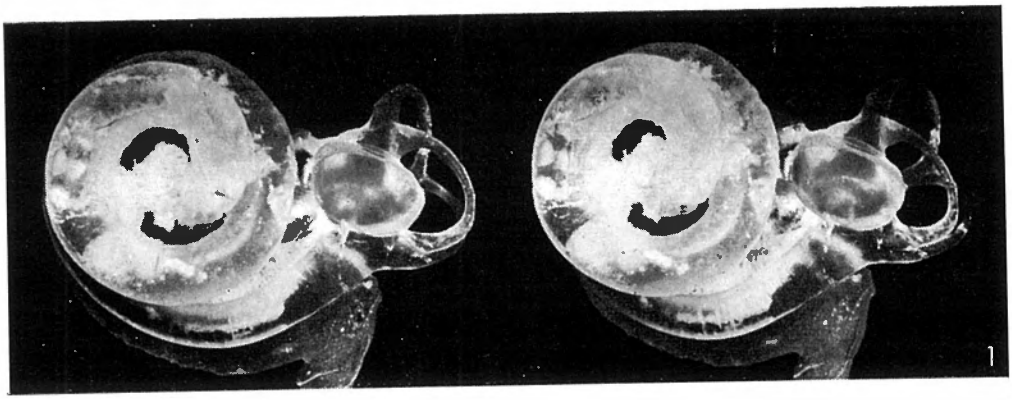
Fig. 1. *Balaenoptera musculus* (left). 2.0×
Fig. 2. *Megaptera nodosa* (right). 2.6×
Fig. 3. *Eubalaena glacialis* (right). 2.6×

PLATE II

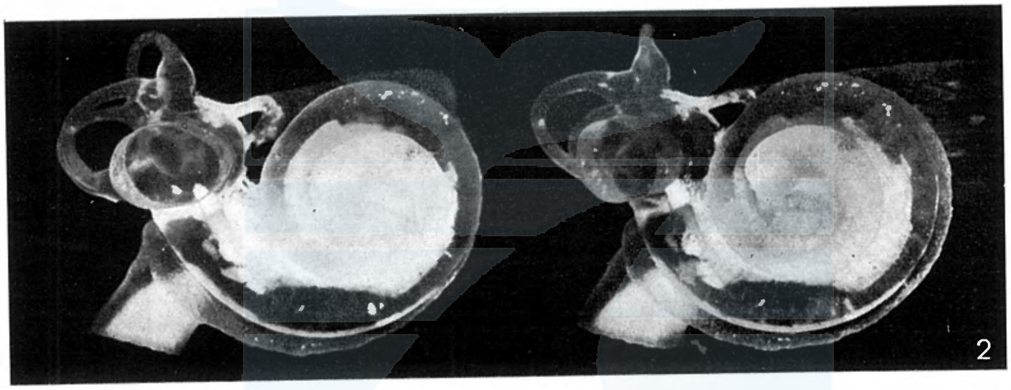
Fig. 4. *Physeter catodon* (right). 2.6×
Fig. 5. *Kogia breviceps* (right). 4.6×
Fig. 6. *Berardius bairdii* (right). 3.0×

PLATE III

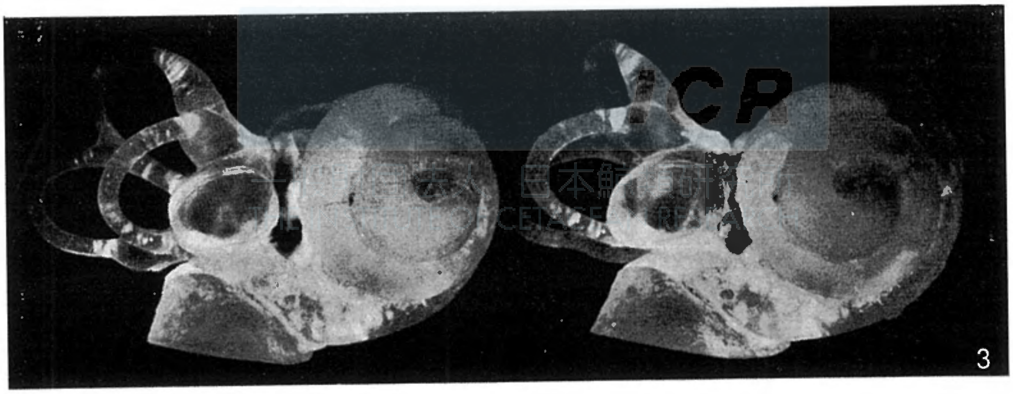
Fig. 7. *Globicephala melaena* (right). 3.2×
Fig. 8. *Delphinus delphis* (right). 3.8×
Fig. 9. *Neomeris phocaenoides* (right). 4.3×
Fig. 10. *Neomeris phocaenoides.* 4.7× The same specimen as Fig. 9 is seen from the side. Note the strong détour and undulation of the cochlear canal in the first quadrant region.



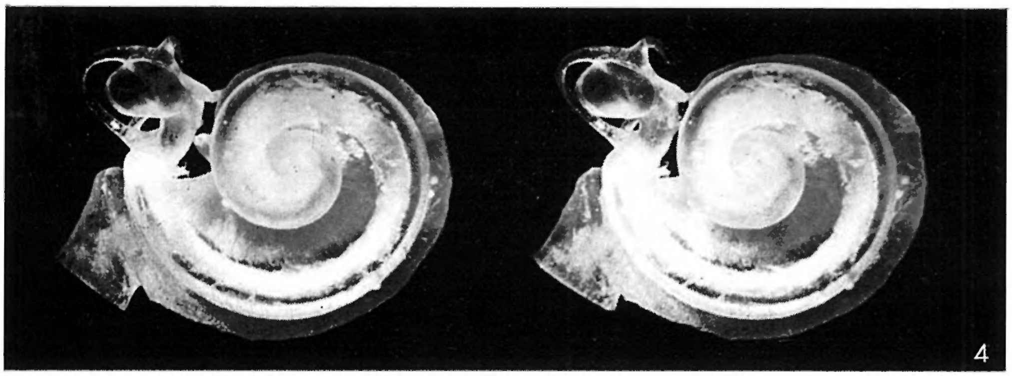
1

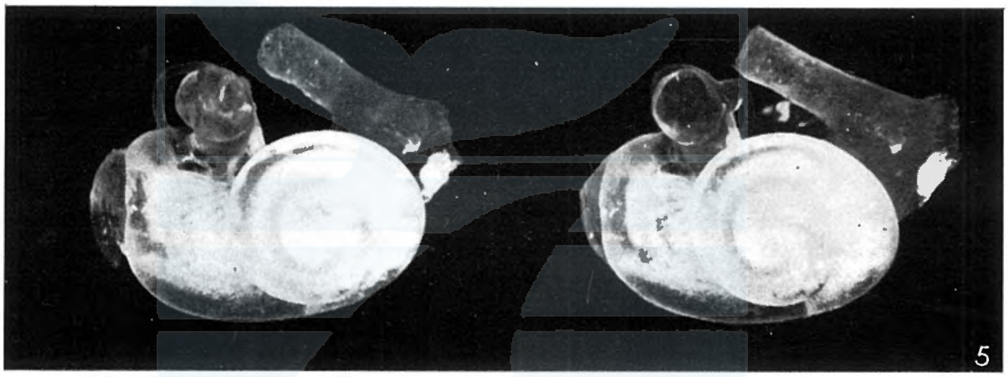


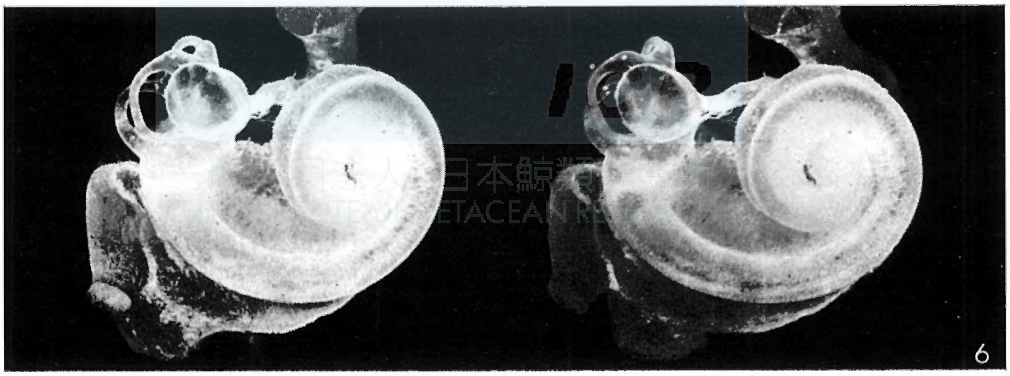
2

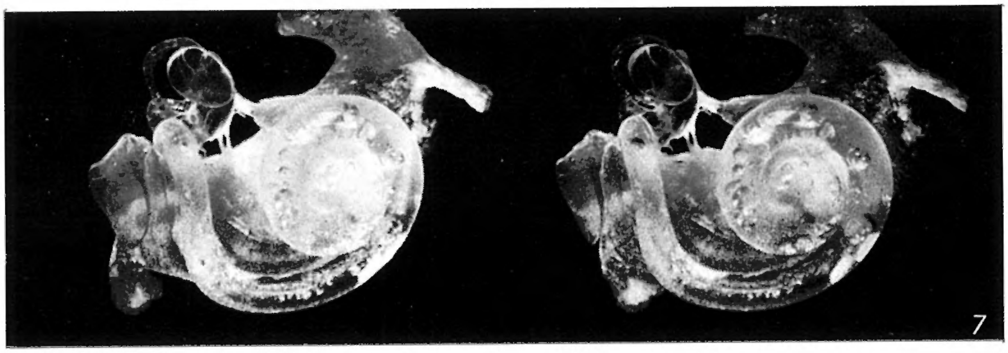


3

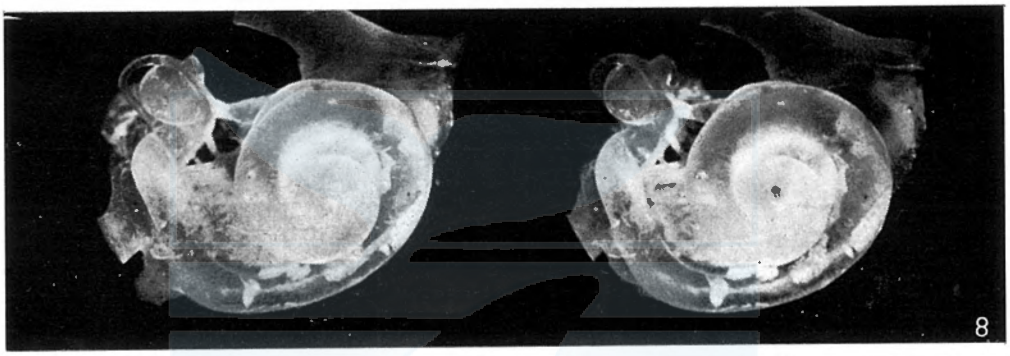

4


5

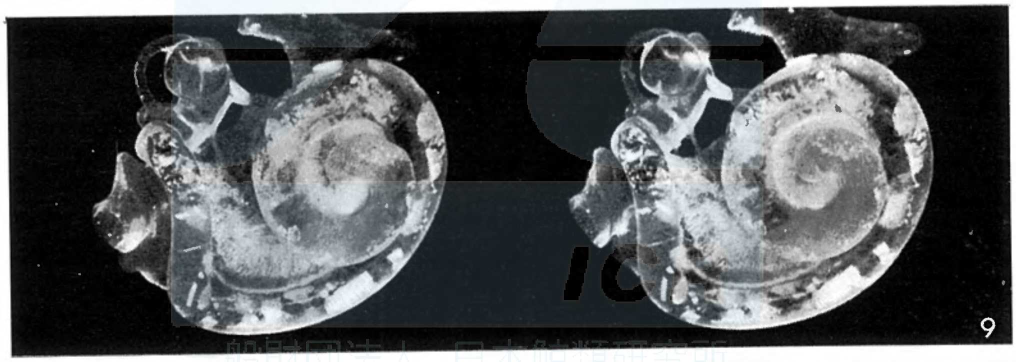

6



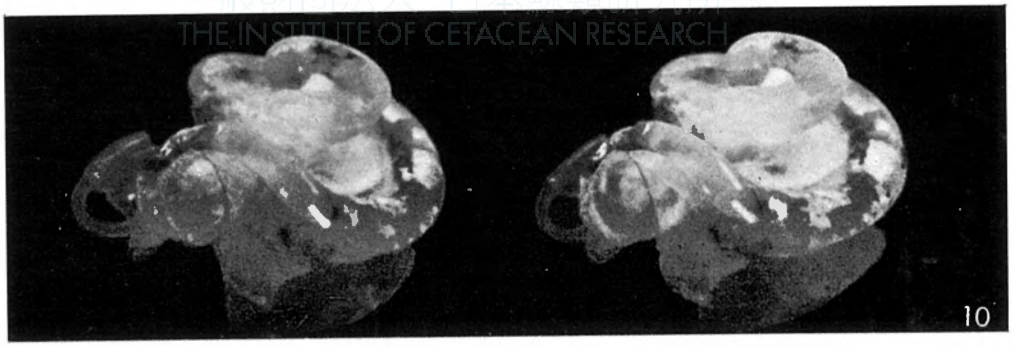
7



8



9



10