# SYSTEMATIC CONSIDERATION OF RECENT TOOTHED WHALES BASED ON THE MORPHOLOGY OF TYMPANO-PERIOTIC BONE

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ABSTRACT

The tympano-periotic bones of recent Odontoceti have attained wide variety of morphological peculiarities. The individual and sexual variations, and the bilateral asymmetry of this part are considered to be small. Though it is possible to identify most of Odontoceti species based on the morphology of tympano-periotic bones, it is usually difficult to do the Delphininae species. Considering the several series of specialization observed in various characteristics of tympano-periotic bone, its process of evolution and the phylogenetic relationships of Odontoceti species are discussed.

CONTENTS



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## INTRODUCTION

Though the taxonomical or morphological study of tympano-periotic bone have been made on some fossil species (Kellogg, 1931, 1955, 1957, 1965) or on recent species (Yamada, 1953) and the morphological variety is reported, the systematics of the toothed whales have been based mainly on the skeletal and external characteristics and less importance was put on the morphology of tympano-periotic bone. However, as the tympano-periotic bones of toothed whales are considered to have established a special adaptation for the underwater acoustics and have attained various morphological peculiarities, the morphology of this part seems to be useful in the taxonomy of Odontoceti.

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The present study intends to re-examine the systematics of toothed whales based on the morphology of the tympano-periotic bones, and to throw some light upon the classification of toothed whales. The knowledge on the morphology and individual variation of tympano-periotic bone, obtained in this study, will offer some key to identify the species or genus by means of tympano-periotic bone.

## MATERIALS AND METHOD

The materials used in this study are shown in Table 2, which comprise 313 individuals in 30 genera. They are mostly composed of the specimens collected by me or prof. M. Nishiwaki of the Ocean Research Institute, and are kept in the Ocean Research Institute, University of Tokyo. Other than these specimens, some were kindly offered by various persons and institutes shown in Table 1.

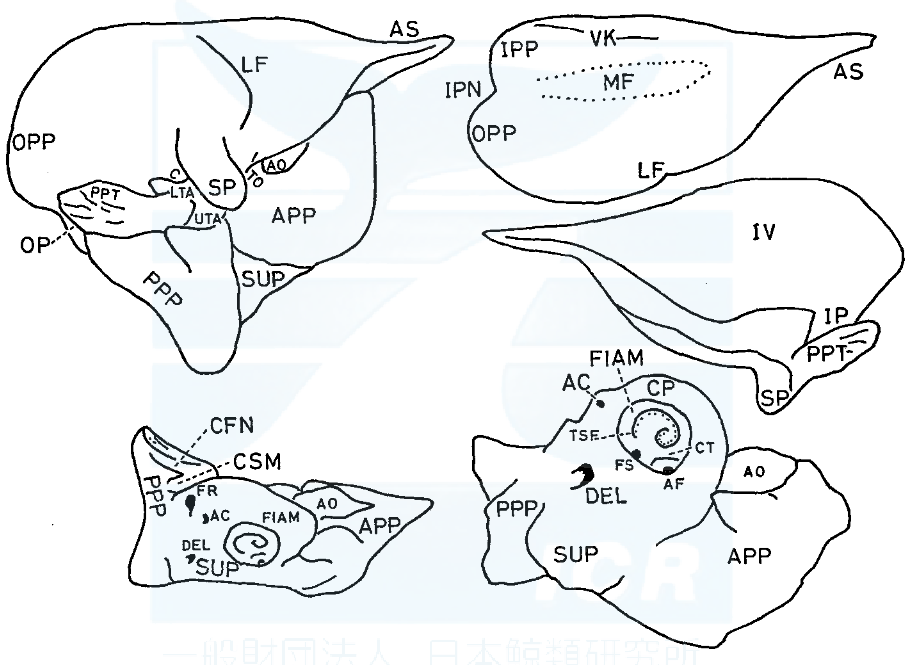


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Fig. 1. Tympano-periotic bone of *Platanista gangetica*, showing the morphological terms used in this report. AC, Aperture of aquaeductus cochleae. AF, Internal aperture of aquaeductus Fallopii. AO, Accessory ossicle. APP, Anterior process of periotic. AS, Anterior spine. C, Conical process. CP, Cochlear portion. CFN, Canal for facial nerve. CSM, Canal for stapedial muscle. CT, Crista transversa. DEL, Aperture of ductus endolymphaticus. EF, Elliptical foramen (see Fig. 2). FIAM, Fundus of internal auditory meatus. FR, Foramen rotunda. FS, Foramen singulare. IP, Inner pedicle. IPN, Interprominential notch. IPP, Inner posterior prominence. IV, Involucrum. LF, Lateral furrow. LTA, Lower tympanic aperture. MF, Median furrow. OP, Outer pedicle. OPP, Outer posterior prominence. PPP, Posterior process of periotic. PPT, Posterior process of tympanic bulla. SP, Sigmoid process. SUP, Superior process. TO, Triangular opening. TSF, Tractus spiralis foraminosus. UTA, Upper tympanic aperture. VK, Ventral keel.

TABLE 1. LIST OF INSTITUTES AND PERSONS, WITH ABBREVIATIONS, WHO OFFERED THEIR SPECIMENS FOR THE PRESENT STUDY

| | |
|---|---|
| AMNH | American Museum of Natural History, New York C. USA, R. G. Van Gelder |
| AWM | Ayukawa Whale Museum, Ayukawa Japan, N. Kimura |
| CLH | Carl L. Hubbs, Scripps Inst. Oceanography, Univ. of Calif., San Diego USA |
| CNHM | Chicago Natural History Museum, Chicago USA, J. C. Moore |
| DWR | Dale W. Rice, Fish and Wildlife Service, Seattle USA |
| EML | Enoshima Marineland, Enoshima Japan, M. Nakajima |
| HCY | Hung-cha Yang, Taiwan Fisheries Res. Inst., Formasa. |
| NSM | National Science Museum, Tokyo Japan, Y. Imaizumi |
| LACM | Los Angeles County Museum of Natural History, Los Angeles USA, D. K. Caldwell |
| MVZ | Museum of Vertebrate Zoology, Univ. of Calif., Berkeley USA, S. B. Benson |
| NUF | Faculty of Fisheries, Nagasaki Univ., Nagasaki Japan, K. Mizue |
| NUMS | Faculty of Medical Science, Nagasaki Univ., Nagasaki Japan, K. Mizue |
| SDNHM | Natural History Museum, San Diego USA, R. D. Mason |
| TK | Ocean Research Inst. Univ. of Tokyo, Tokyo Japan, M. Nishiwaki and T. Kasuya |
| TWM | Taiji Whale Museum, Taiji Japan, T. Higashi |
| USNM | United States National Museum, Washington D. C. USA, C. O. Handley |
| WAW | Marineland of the Pacific, Los Angeles USA, W. A. Walker |
| ZSI | Zoological Survey of India, Calcutta India, D. K. Ghosal |

TABLE 2. LIST OF MATERIALS USED IN THIS STUDY

| No. | Species | Number of individuals |
|---|---|---|
| 1 | *Platanista gangetica* | 5 from the Brahmaputra (4TK and 1ZSI specimens) |
| | | 2 from India (USNM 172409, 23459) |
| 2 | *Inia geoffrensis* | 5 from the Amazon (LACM19588, 19589, 19590, USNM239667, 45982) |
| 3 | *Lipotes vexillifer* | 1 from Tunting Lake (AMNH57333) |
| 4 | *Pontoporia blainvillei* | 1(USNM 49494) |
| 5 | *Neophocaena phocaenoides* | 16 from Japan (14NUMS and 2TK specimens) |
| | | 1 from China (USNM 240862) |
| | | 2 no locality (AMNH57332, USNM239990) |
| 6 | *Phocoena ph. vomerina* | 3 from the North Pacific (MVZ21509, 97900, USNM274588) |
| 7 | *Phocoena ph. phocoena* | 3 from the North Atlantic (AMNH21514, TK84, USNM36591) |
| 8 | *Phocoena sinus* | 1 from California Bay (SDNHM20688) |
| 9 | *Phocoenoides dalli* | 6 from Japan (6 TK specimens) |
| 10 | *Phocoenoides truei* | 6 from Japan (6 TK specimens) |
| 11 | *Delphinus bairdi* | 5 from California (DWR988, TK150, SDNHM 20140, 21204, 21209) |
| | | 1 from Formosa (TK255) |
| 12 | *Delphinus delphis* | 2 from the Atlantic (USNM21525, 1 TK specimen) |
| 13 | *Lagenorhynchus obliquidens* | 11 from north east Japan (TK sepcimens) |
| | | 3 from California (DWR3768, LACM F355, USNM21218) |
| 14 | *Lagenorhynchus acutus* | 3 from the west Atlantic (USNM14229, 14265, 20960) |
| 15 | *Lagenorhynchus albirostris* | 3 from the west Atlantic (AMNH143520, CNHM 30522, TK87) |
| 16 | *Lagenorhynchus obscurus* | 1 from New Zealand (AMNH34935) |
| 17 | *Lagenorhynchus australis* | 1 from Chiloe I., Chile (CHNHM22248) |
| 18 | *Steno bredanensis* | 7 from Japan (TK specimens) |
| 19 | *Lissodelphis borealis* | 3 from Japan (TK205, 257, 258) |
| | | 3 from the north east Pacific (DWR1965–2, 1965–3, USNM270981) |
| 20 | *Stenella caeruleoalba* | 15 from Japan (TK specimens) |
| 21 | *Stenella styx* | 1 from the Atlantic (TK specimen) |

TABLE 2. (continued)

| | | |
|---|---|---|
| 22 | (?) *Stenella roseiventris* (Hawaiian spinner dolphin) | 4 from Japan (NUF specimens) 2 from Hawaii (DWR1194, TK50) |
| 23 | (?) *Stenella longirostris* (Eastern Pacific spinner dolphin) | 2 from the east Pacific (SNHM21199, WAW52) |
| 24 | *Stenella attenuata* | 7 from Japan (TK specimens) |
| 24a | *Stenella graffmani* | 3 from the east Pacific (DWR1965-1, SENHM 20637, WAW44) |
| 24b | *Stenella plagiodon* | 3 from the north Atlantic (AMNH38206, 63779, USNM292070) |
| 25 | *Tursiops truncatus* | 43 from Japan (19 EML specimens, 24 TK specimens) |
| 25a | *Tursiops truncatus* | 3 from the west Atlantic (MVZ23705, 23708, USNM16504) |
| 26 | *Tursiops gilli* | 2 from California (SDNHM20143, 20144) |
| 27 | *Cephalorhynchus* spp. | 1 from Forkland (USNM252568), 1 from Chile (USNM 21167) |
| 28 | *Sotalia* spp. | 1 from the Amazon (AMNH94169, *S. fluviatilis*) 1 (CNHM34907, *S. guianensis*) |
| 29 | *Sousa teuszii* | 1 from Senegal (TK260) |
| 30 | *Pseudorca crassidens* | 2 from the north Atlantic (USNM11320, 218360) 2 from the north Pacific (TK specimens) |
| 31 | *Orcinus orca* | 5 from the north Pacific (DWR832, 986, 2TK specimens, TWM specimen), 2 no locality (LACM781, USNM219326) |
| 32 | *Peponocephala electra* | 6 from Japan (TK specimens) |
| 33 | *Feresa attenuata* | 7 from Japan (TK specimens) |
| 34 | *Globicephala melaena* | 4 from the north Atlantic (AMNH180143, USNM14044, 20457, 1TK specimen) |
| 35 | *Globicephala macrorhyncha* | 26 from Japan (TK specimens) |
| 36 | *Grampus griseus* | 11 from Japan (8EML specimens, 3 TK specimens) 1 from the Atlantic (USNM22446) |
| 37 | *Orcaella brevirostris* | 1 from Borneo (USNM199743), 1 no locality (ZSI274) |
| 38 | *Delphinapterus leucas* | 4 (AMNH180017, SDNHM20046, USNM7536, 215015) |
| 39 | *Monodon monoceros* | 4 (AMNH63987, 73318, SDNHM7096, USNM267960) |
| 40 | *Berardius bairdi* | 5 from the north Pacific (LACM1964, MVZ125602, TK299, 300, USNM49727) |
| 41 | *Berardius arnouxi* | 1 from New Zealand (USNM21511) |
| 42 | *Hyperoodon ampullatus* | 1 from Norway (USNM14449) |
| 43 | *Mesoplodon stejnegeri* | 7 specimens (AMNH185311, 143829, MVZ130250, TK97, 365, USNM143132, 286826) |
| 44 | *Mesoplodon densirostris* | 4 specimens (AMNH139931, 69579, TK256, HCY specimen) |
| 45 | *Mesoplodon ginkgodens* | 2 specimens (NSM specimen, HCY specimen) |
| 46 | *Mesoplodon europaeus* | 3 specimens AMNH121894, 90051, USNM306302) |
| 47 | *Mesoplodon carlhubbsi* | 2 specimens (AWM specimen, USNM274591) |
| 48 | *Mesoplodon mirus* | 1 specimen (AMNH174293) |
| 49 | *Ziphius cavirostris* | 6 from the north Pacific (MVZ129645, SDNHM 19558, USNM 20993, 3TK specimens), 1 no locality (USNM21975) |
| 50 | *Kogia breviceps* | 5 specimens (CHL specimen, LACM RLB145, TK244, SDNHM 20139, SDNHM—) |
| 51 | *Kogia simus* | 5 specimens (LACM RLB240. TK47, 49, TK specimen, USNM 22015) |
| 52 | *Physeter catodon* | 8 specimens (3 NUMS specimens, TK301, 302, 303, 304, USNM 49488) |

The materials are usually grouped into the species, but in some cases into smaller units considering the locality. In the genera as *Cephalorhynchus* and *Sotalia*, where only few samples are obtained and the taxonomy is not fully established, the samples are dealt combining into the genus.

The measurement and general observation were made on 21 points shown in Fig. 2 and Table 3. The measurements are usually made on a straight line connecting the two points to nearest 1/10 mm, with a caliper of 1/20 mm accuracy, and if available on both sides. In the calculation of the mean value and other statistical analysis of the measurements, measurements of one side were randomly selected. But in the analyses of *Growth and bilateral symmetry* and of the largest and smallest range of the measurement, all the available measurements were included.

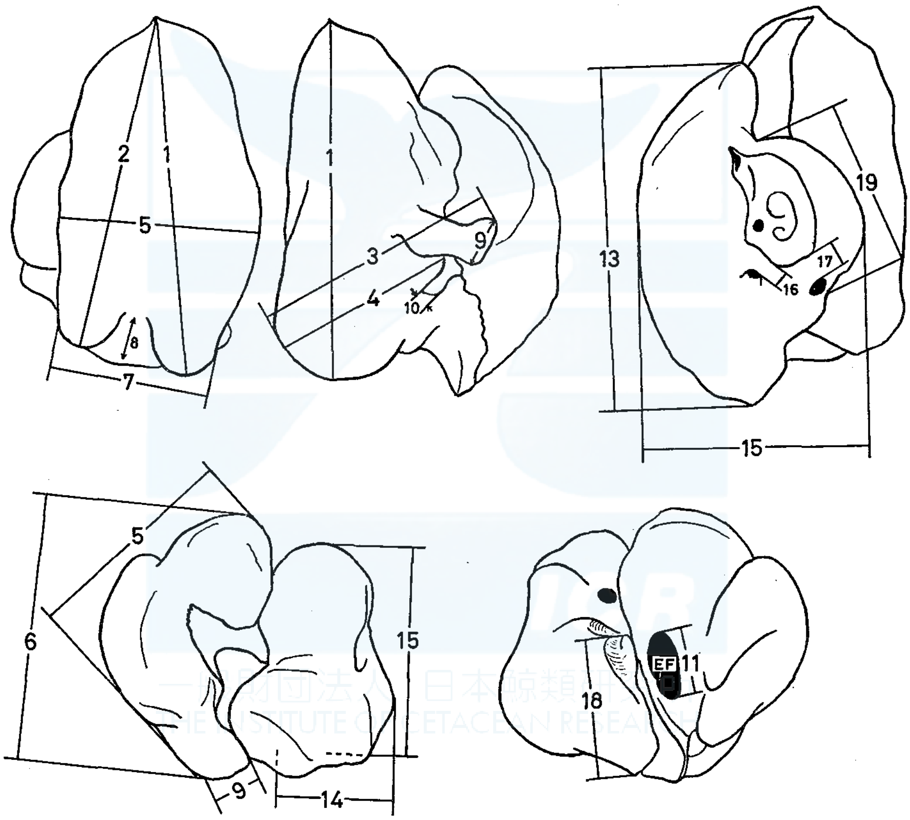


Fig. 2. Measurements used in this report, for the explanation see Table 3. The contour of the tympano-periotic bone is based on that of *Stenella*. For EF see Fig. 1.

The anatomical terms are conformed mainly to Kellogg (1936) and partly to Yamada (1953), but some terms are newly introduced in this report. All of these terms are shown in Figs. 1 and 2.

TABLE 3. POINTS OF MEASUREMENTS AND OF OTHER GENERAL OBSERVATIONS

Tympanic bulla

1. Standard length of tympanic bulla, distance from anterior tip to posterior end of outer posterior prominence
2. Distance from anterior tip to posterior end of inner posterior prominence
3. Distance from postero-ventral tip of outer posterior prominence to tip of sigmoid process
4. Distance from postero-ventral tip of outer posterior prominence to tip of conical process
5. Width of tympanic bulla at the level of the sigmoid process
6. Height of tympanic bulla, from tip of sigmoid process to ventral keel
7. Width across inner and outer posterior prominences
8. Greatest depth of interprominential notch
9. Width of upper border of sigmoid process
10. Width of the posterior branch of lower tympanic aperture
11. Presence of elliptical foramen. If present, its greatest diameter
12. The thicker side between outer and inner posterior prominences

Periotic

13. Standard length of periotic, from tip of anterior process to posterior end of posterior process, measured on a straight line parallel with cerebral border
14. Thickness of superior process at the level of upper tympanic aperture
15. Width of periotic across cochlear portion and superior process, at the level of upper tympanic aperture
16. Least distance between the margins of fundus of internal auditory meatus and of aperture of ductus endolymphaticus
17. Least distance between the margins of fundus of internal auditory meatus and of aperture of aquaeductus cochleae
18. Length of the articular facet of the posterior process of periotic for the posterior process of tympanic bulla
19. Antero-posterior diameter of cochlear portion
20. Presence of sutural connection between the posterior processes of tympanic bulla and of periotic
21. Presence of the sutural connection between posterior process of tympanic bulla and squamosal
22. Length of periotic shown by the percentage of length of tympanic bulla

## GROWTH AND BILATERAL SYMMETRY

### *Bilateral symmetry*

The bilateral comparizon of tympano-periotic bones was made on 6 species of Delphinoidea, *Neophocaena phocaenoides*, *Stenella caeruleoalba*, *Lagenorhynchus obliquidens*, *Tursiops truncatus* (from the coast of Japan), and *Grampus griseus*, on the standard length (measurement nos. 1 and 13) and on the other measurements shown by the percentage of the standard length.

On each particular points, mean of the remainder of the right value minus the left were calculated, then the significance of its deviation from 0 was examined with t table. This result shows that most of the observed bilateral asymmetry is not significant. But as shown in Table 4, the bilateral deviation in some measurements is so large that can be expected with the probability less than 2% and is suggested to be significant. But if the deviation between the mean values of both sides are examined, neglecting the individuals, there can be expected no significant bilateral asymmetry. This is because the bilateral asymmetry in each individuals is smaller comparing with the individual variation. As the result it is concluded that, in spite of the possibility of bilateral asymmetry on some part of the tympano-periotic bone, it will not lead to the erroneous result to neglect it and to select randomly the right or left side in the calculation.

TABLE 4. SOME MEASUREMENTS OF TYMPANO-PERIOTIC BONES WHERE BILATERAL ASYMMETRY IS EXPECTED. FOR MEASUREMENT NO. SEE TABLE 3.

| Species | No. of the measurement | Sample size | Range of measurement | Mean of the right minus left | Probability |
|---|---|---|---|---|---|
| *N. phocaenoides* | 3 | 11 | 74.8–83.2 | −0.773 | 0.02–0.01 |
| *N. phocaenoides* | 8 | 14 | 10.4–17.8 | −0.564 | 0.01> |
| *S. caeruleoalba* | 10 | 7 | 2.2– 5.8 | 0.421 | 0.02–0.01 |
| *T. truncatus* | 13 | 37 | 31.7–37.8 | −0.908 | 0.02–0.01 |
| *Gl. macrorhyncha* | 3 | 23 | 57.1–73.6 | −2.165 | 0.02–0.01 |
| *Gr. griseus* | 17 | 4 | 46.8–58.6 | 1.150 | 0.02–0.01 |

*Growth of tympano-periotic bone*

To obtain a general feature of the growth of tympano-periotic bone of toothed whales, the growth of tympano-periotic bone accompanied with the growth of the animal and its relative growth were studied on 4 species of Delphinoidea, or *Globicephala macrorhyncha*, *Tursiops truncatus*, and *Neophocaena phocaenoides*. In Figs. 3–57, if available, the measurements of the both sides are plotted.

Generally speaking the standard length of tympanic bulla slightly increases in parallel with the growth of the animal, but that of periotic shows almost no increase. The proportional dimensions of tympano-periotic bone show rather wide individual variation. As observed in these figures, the sexual difference is not expected.

*Globicephala macrorhyncha*

Tympano-periotic bones from 26 individuals are used here, among which the sex and body length are known on 23 individuals.

The tympanic bulla of this species has conspicuous anterior spine, ventral keel, and posterior process. These characters seem to be formed soon after birth. As shown in Pl. XXVII the anterior margin of the tympanic bulla of adult individual has a plate-like anterior spine. The corresponding part of two newborn calves of 138 cm (♂) and 141 cm (♂) in body length is smooth and has no anterior spine. But the spine is formed on a juvenile female of 203 cm in body length. In the two newborn calves, the ventral keel is not developed, but retains only a granulated structure. But this granulated area is changed, in the 203 cm female, into a usual ventral keel observed in the adult. The shape of the posterior process of the newborn calves is short, and round and resembles that of adult *Phocoenidae*. But it develops longer, in the 203 cm female, and attains the form of a long spongy process directing postero-laterally.

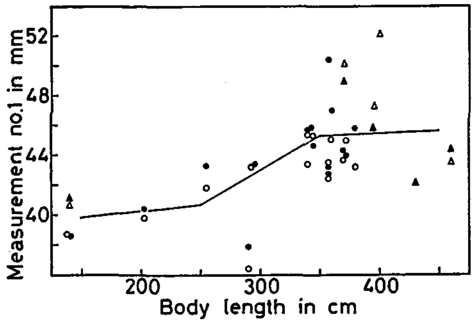


Fig. 3. *Globicephala macrorhyncha.* Relation between body length and length of tympanic bulla (measurement no. 1). Triangle indicates male, circle female. In both sexes closed mark indicates the left side, and open the right.

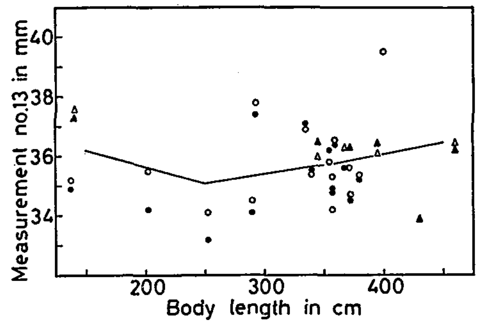


Fig. 4. *G. macrorhyncha.* Relation between body length and length of periotic (measurement no. 13). For marks see Fig. 3.

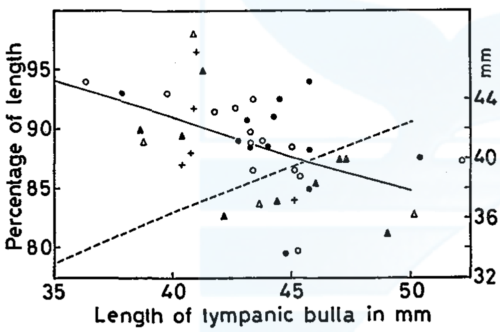


Fig. 5. *G. macrorhyncha.* Measurement no. 2 Anterior tip of tympanic bulla to inner posterior prominence. Cross mark indicates the sex unknown, solid line average percentage, and dotted line the length re-calculated from the average percentage. For other marks see Fig. 3.

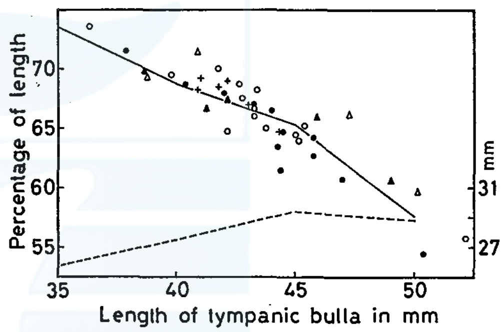


Fig. 6. *G. macrorhyncha.* Measurement no. 3 Tip of sigmoid process to outer posterior prominence. For marks see Fig. 5.

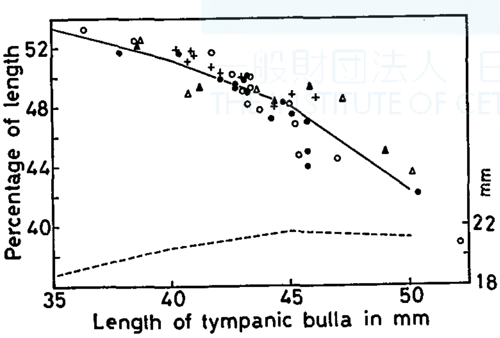


Fig. 7. *G. macrorhyncha.* Measurement no. 4 Tip of conical process to outer posterior prominence. For marks see Fig. 5.

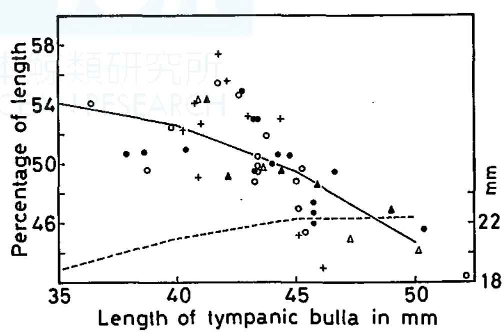


Fig. 8. *G. macrorhyncha.* Measurement no. 5 Width of tympanic bulla. For marks see Fig. 5.

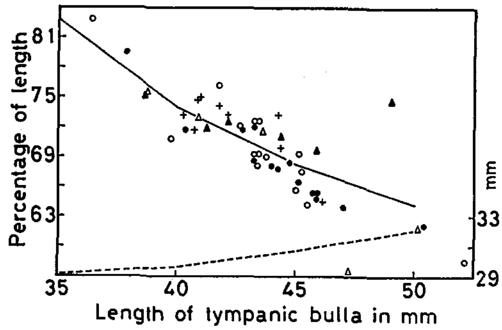


Fig. 9. *G. macrorhyncha.* Measurement no. 6 Height of tympanic bulla. For marks see Fig. 5.

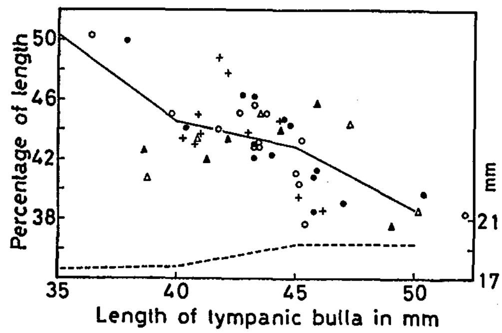


Fig. 10. *G. macrorhyncha.* Measurement no. 7 Width across posterior prominences. For marks see Fig. 5.

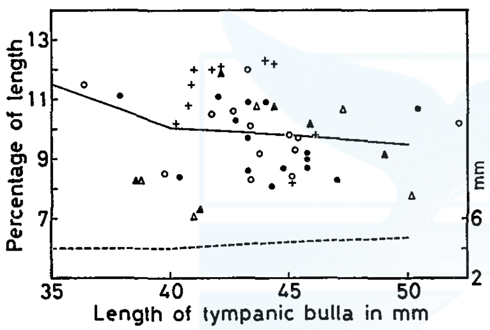


Fig. 11. *G. macrorhyncha.* Measurement no. 8 Depth of interprominential notch. For marks see Fig. 5.

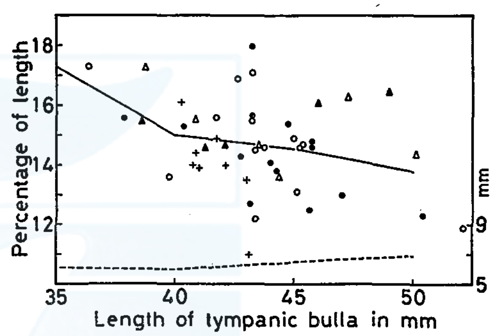


Fig. 12. *G. macrorhyncha.* Measurement no. 9 Width of upper border of sigmoid process. For marks see Fig. 5.

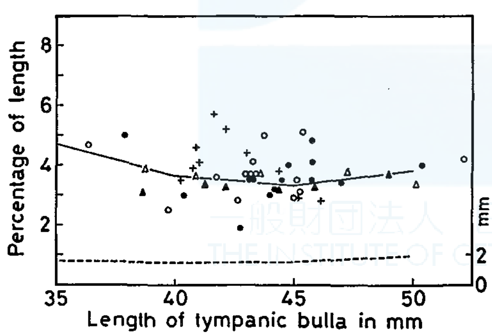


Fig. 13. *G. macrorhyncha.* Measurement no. 10 Width of posterior branch of lower tympanic aperture. For marks see Fig. 5.

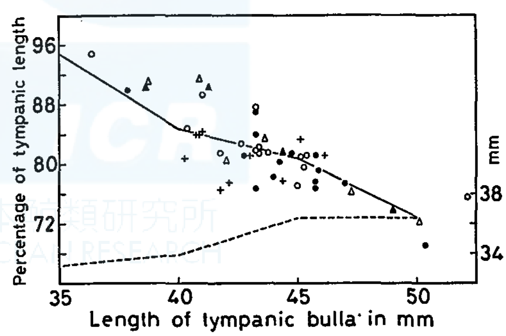


Fig. 14. *G. macrorhyncha.* Measurement no. 13 Length of periotic shown in percentage of measurement no. 1. For maeks see Fig. 5.

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On the periotic, the needle-shaped processes on the dorsal surface of superior process and around the fundus of internal auditory meatus are one of the characteristic features of this species. This structur is considered to be formed in the latter

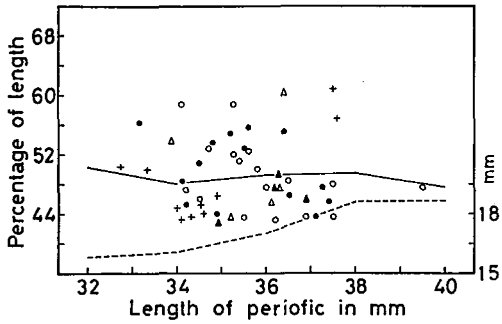


Fig. 15. *G. macrorhyncha.* Measurement no. 14 Thickness of periotic. For marks see Fig. 5.

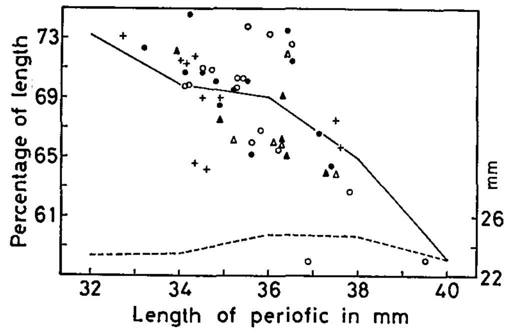


Fig. 16. *G. macrorhyncha.* Measurement no. 15 Width of periotic. For marks see Fig. 5.

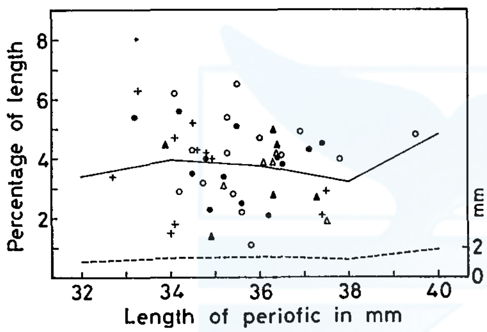


Fig. 17. *G. macrorhyncha.* Measurement no. 16 Fundus of internal auditory meatus to ductus endolymphaticus. For marks see Fig. 5.

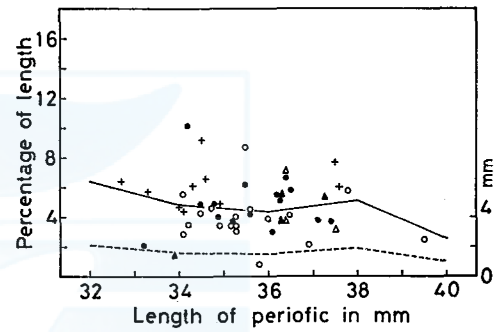


Fig. 18. *G. macrorhyncha.* Measurement no. 17 Fundus of internal auditory meatus to aquaeductus cochleae. For marks see Fig. 5.

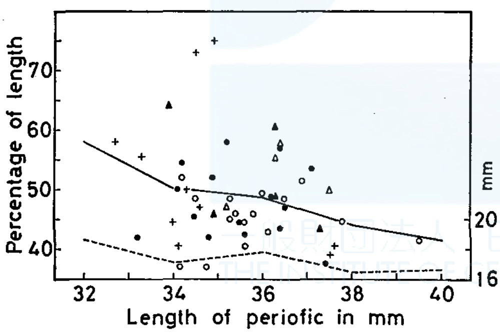


Fig. 19. *G. macrorhyncha.* Measurement no. 18 Length of facet on posterior process of periotic. For marks see Fig. 5.

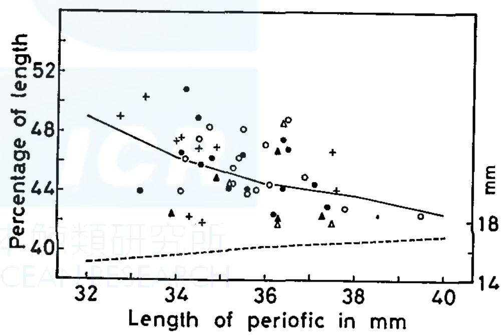


Fig. 20. *G. macrorhyncha.* Measurement no. 19 Diameter of cochlear portion. For marks see Fig. 5.

part of the growth, as this is observed, in the females, on the animal more than 350 cm in body length.

The relations between body length and length of tympano-periotic bone are shown in Figs. 3 and 4, and those between the lengths of tympano-periotic bone

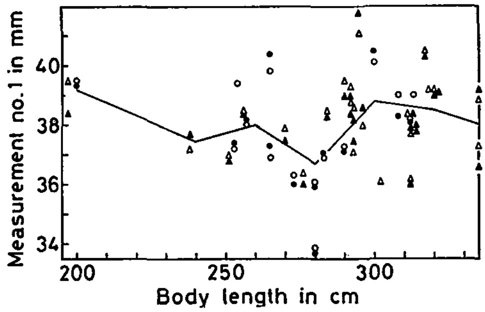


Fig. 21. *Tursiops truncatus*. Relation between body length and length of tympanic bulla (measurement no. 1). For marks see Fig. 3.

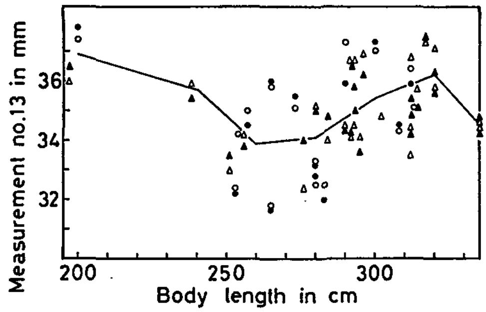


Fig. 22. *T. truncatus*. Relation between body length and length of periotic (measurement no. 13). For marks see Fig. 3.

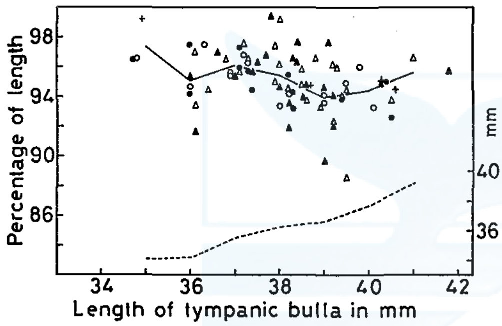


Fig. 23. *T. truncatus*. Measurement no. 2 Anterior tip of tympanic bulla to inner posterior prominence. For marks see Fig. 5.

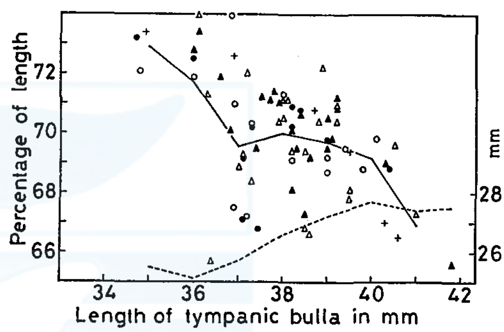


Fig. 24. *T. truncatus*. Measurement no. 3 Tip of sigmoid process to outer posterior prominence. For marks see Fig. 5.

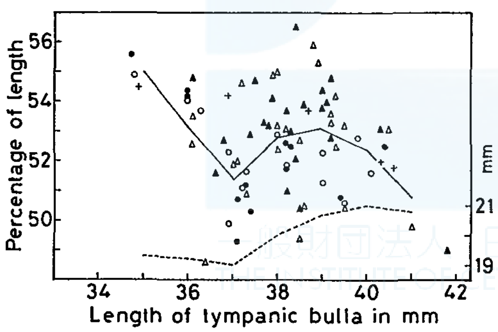


Fig. 25. *T. truncatus*. Measurement no. 4 Tip of conical process to outer posterior prominence. For marks see Fig. 5.

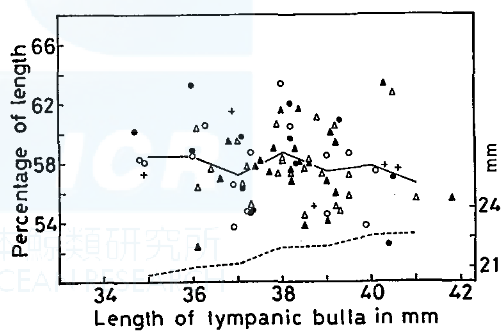


Fig. 26. *T. truncatus*. Measurement no. 5 Width of tympanic bulla. For marks see Fig. 5.

and their proportional dimensions are shown in Figs. 5–20 and Table 5. Though the length of periotic bone does not increase after the birth, that of tympanic bulla increases about 6 mm in the adult than the new born animal. As the result, the ratio of the periotic bone to the tympanic bulla decreases with the growth of the animal.

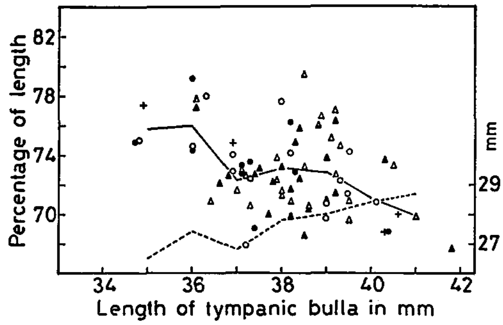


Fig. 27. *T. truncatus*. Measurement no. 6 Height of tympanic bulla. For marks see Fig. 5.

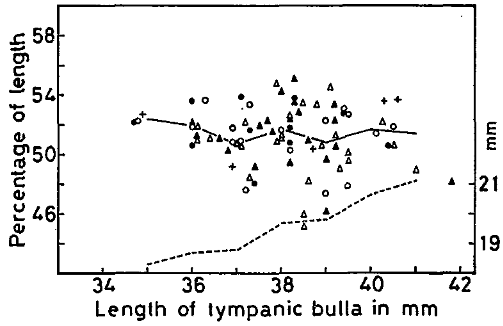


Fig. 28. *T. truncatus*. Measurement no. 7 Width across posterior prominences. For marks see Fig. 5.

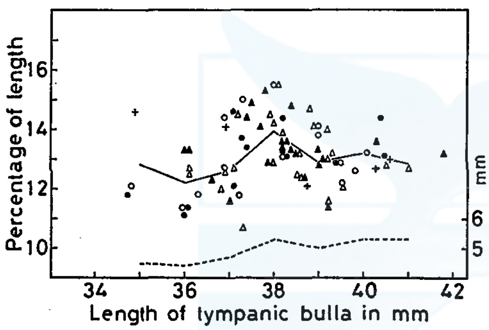


Fig. 29. *T. truncatus*. Measurement no. 8 Depth of interprominential notch. For marks see Fig. 5.

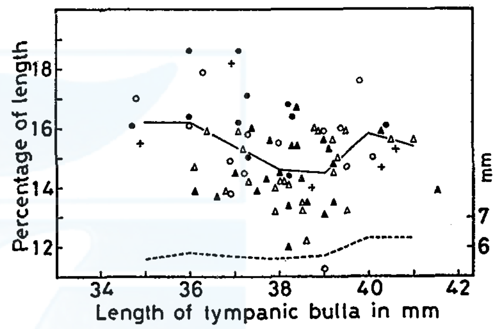


Fig. 30. *T. truncatus*. Measurement no. 9 Width of upper border of sigmoid process. For marks see Fig. 5.

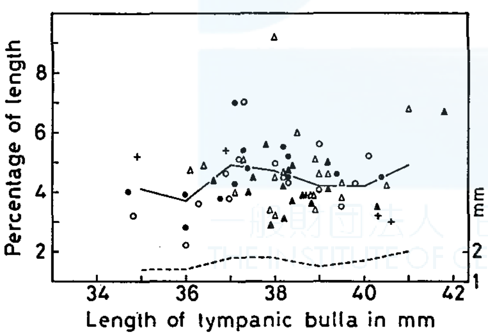


Fig. 31. *T. truncatus*. Measurement no. 10 Width of posterior branch of lower tympanic aperture. For maeks see Fig. 5.

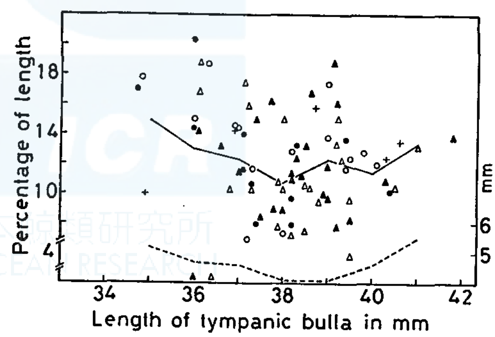


Fig. 32. *T. truncatus*. Measurement no. 11 Length of elliptical foramen. For marks see Fig. 5.

### *Tursiops truncatus*

The tympano-periotic bones of 43 individuals caught in the Pacific coast of Japan are used here. Among them the body length and sex are known on 38 in-

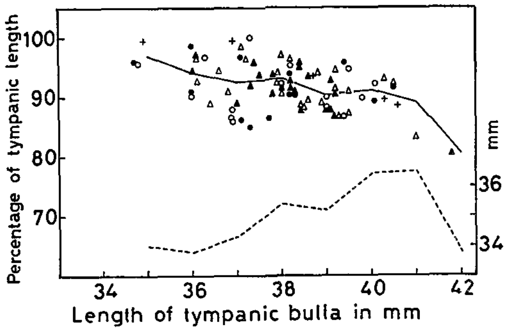


Fig. 33. *T. truncatus.* Measurement no. 13 Length of periotic shown in percentage of measurement no. 1. For marks see Fig. 5.

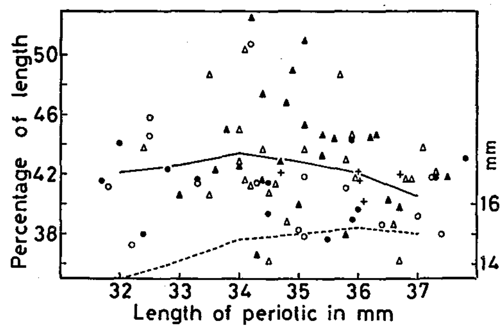


Fig. 34. *T. truncatus.* Measurement no. 14 Thickness of periotic. For marks see Fig. 5.

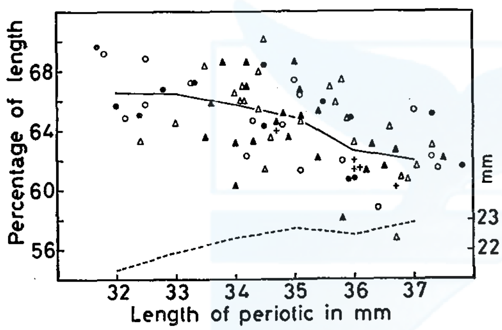


Fig. 35. *T. truncatus.* Measurement no. 15 Width of periotic. For marks see Fig. 5.

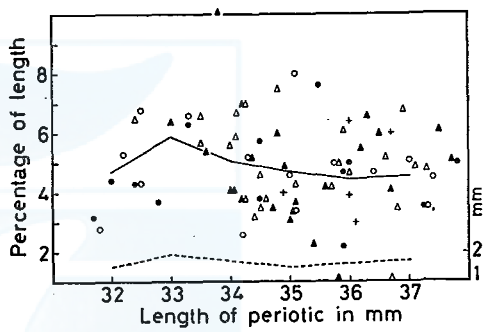


Fig. 36. *T. truncatus.* Measurement no. 16 Fundus of internal auditory meatus to ductus endolymphaticus. For marks see Fig. 5.

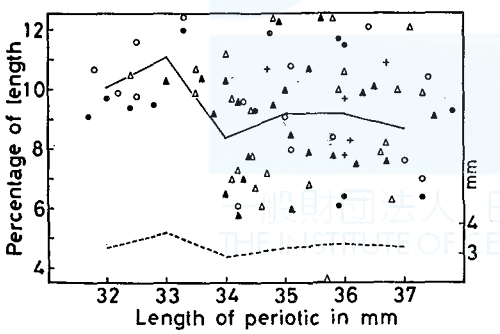


Fig. 37. *T. truncatus.* Measurement no. 17 Fundus of internal auditory meatus to aquaeductus cochleae. For marks see Fig. 5.

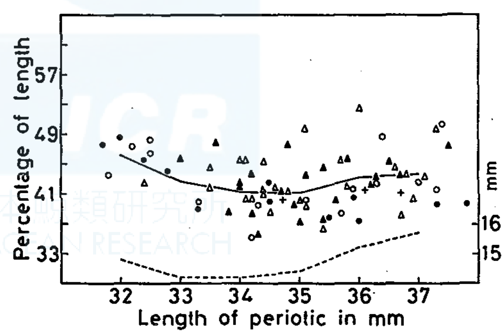


Fig. 38. *T. truncatus.* Measurement no. 18 Length of facet on posterior process of periotic. For marks see Fig. 5.

dividuals. Though the morphological feature of tympano-periotic bone of this species is the typical of Delphininae, it resembles that of *Globicephala* in the presence of needle-shaped processes on the superior process of periotic of the adult, and in the developed ventral keel of tympanic bulla.

The relation between body length and length of tympano-periotic bone are shown in Figs. 21 and 22. There is observed almost no increase of the length of tympanic bulla accompanied with the growth of the animal. This is different from the case of *Globicephala*, and will be related with the weak development of anterior spine in *Tursiops*.

The average length of periotic shows the increase of only about 2 mm in the body length range between 250 cm and 320 cm. But this growth is considered to be negligible in the latter discussion. The ratio of periotic length to the length of tympanic bulla slightly decreases with the increase of the latter (Fig. 33).

As shown in Figs. 23–39 and Table 5, the proportional dimensions of tympano-periotic bone are stable in most of measurements. But in the measurements nos.

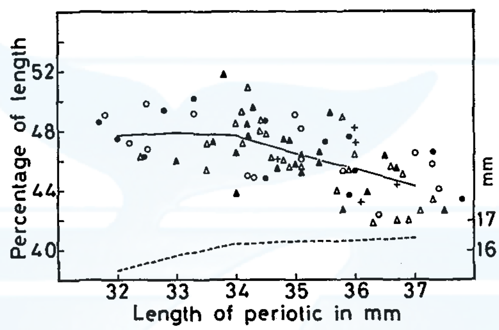


Fig. 39. *T. truncatus*. Measurement no. 19 Diameter of cochlear portion. For marks see Fig. 5.

TABLE 5. CHANGE OF THE PROPORTION OF TYMPANO-PERIOTIC BONES, WITH THE INCREASE OF TYMPANO-PERIOTIC OR BODY LENGTH. A INDICATES INCREASING TENDENCY, B STEADY, C DECREASING.

| Measurements | *G. macrorchyncha* | *T. truncatus* | *N. phocaenoides* |
|---|---|---|---|
| 1 | A | B | A |
| 2 | C | B | A |
| 3 | C | C | A or B |
| 4 | C | B or C | A or B |
| 5 | C | B | A or B |
| 6 | C | C | B or A |
| 7 | C | B | A or B |
| 8 | B | B | A or B |
| 9 | C or B | B | B |
| 10 | B | B | C or B |
| 11 | B | B | B |
| 13 | B | B | B |
| 14 | B | B | C |
| 15 | C | C | C or B |
| 16 | B | B | B |
| 17 | B | B | B |
| 18 | C | B | A |
| 19 | C | B or C | B |
| 22 | C | C | C |

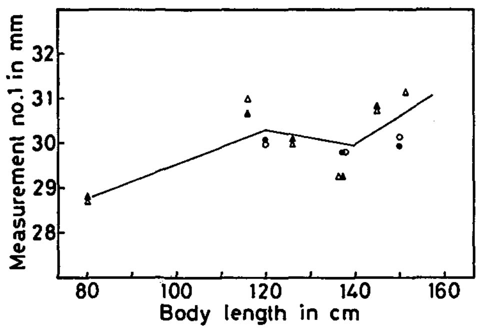


Fig. 40. *Neophocaena phocaenoides*. Relation between body length and length of tympanic bulla (measurement no. 1). For marks see Fig. 3.

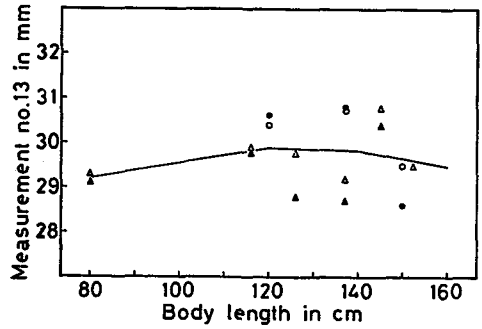


Fig. 41. *N. phocaenoides*. Relation between body length and length of periotic (measurement no. 13). For marks see Fig. 3.

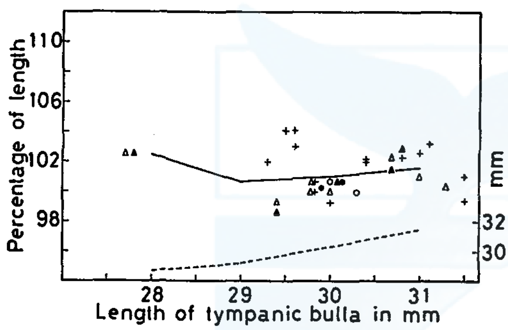


Fig. 42. *N. phocaenoides*. Measurement no. 2 Anterior tip of tympanic to inner posterior prominence. For marks see Fig. 5.

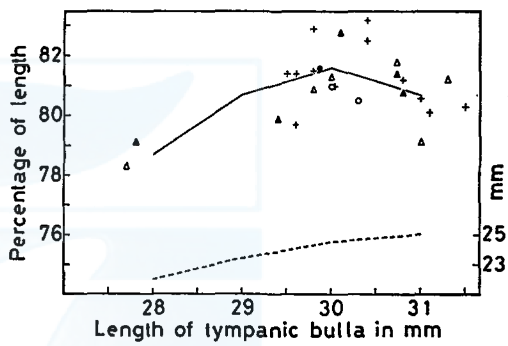


Fig. 43. *N. phocaenoides*. Measurement no. 3 Tip of sigmoid process to outer posterior prominence. For marks Fig. 5.

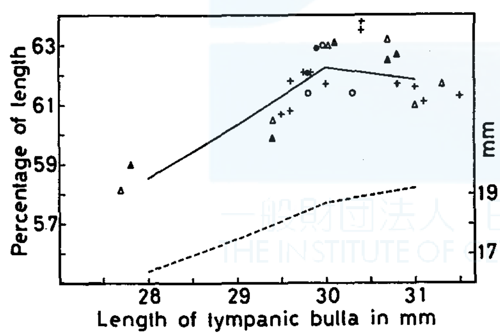


Fig. 44. *N. phocaenoides*. Measurement no. 4 Tip of conical process to outer posterior prominence. For marks see Fig. 5.

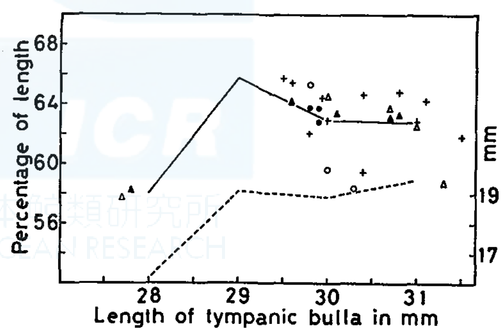


Fig. 45. *N. phocaenoides*. Measurement no. 5 Width of tympanic bulla. For marks see Fig. 5.

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3, 4, 6, 15, and 19, the ratio decreases with the increase of the length of tympanic bulla or that of periotic. This will indicate that the growth of inner posterior prominence and cochlear portion is not parallel with the increase of standard length.

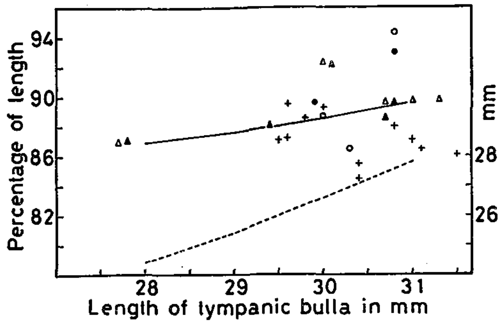


Fig. 46. *N. phocaenoides*. Measurement no. 6 Height of tympanic bulla. For marks see Fig. 5.

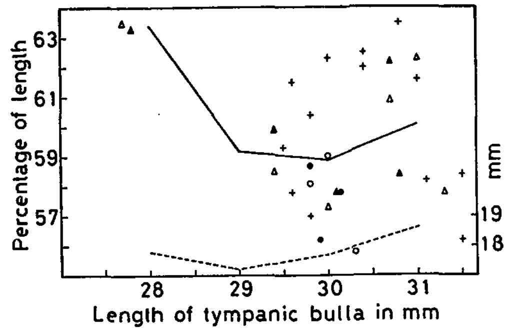


Fig. 47. *N. phocaenoides*. Measurement no. 7 Width across posterior prominences. For marks see Fig. 5.

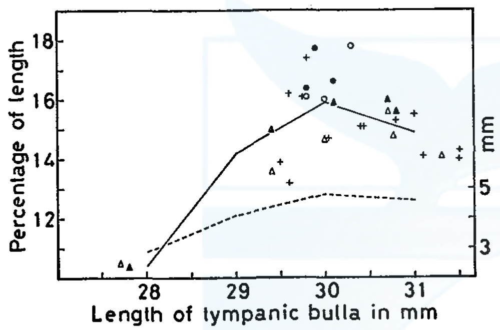


Fig. 48. *N. phocaenoides*. Measurement no. 8 Depth of interprominential notch. For marks see Fig. 5.

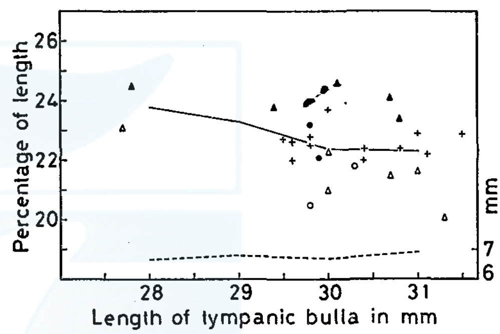


Fig. 49. *N. phocaenoides*. Measurement no. 9 Width of upper border of sigmoid process. For marks see Fig. 5.

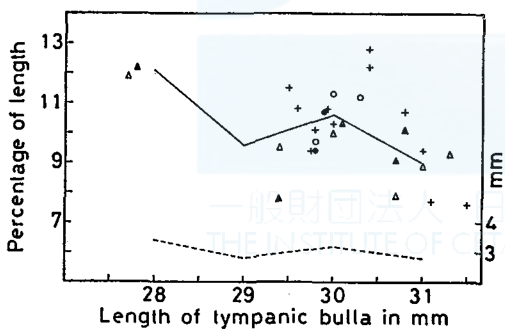


Fig. 50. *N. phocaenoides*. Measurement no. 10 Width of posterior branch of lower tympanic aperture. For marks see Fig. 5.

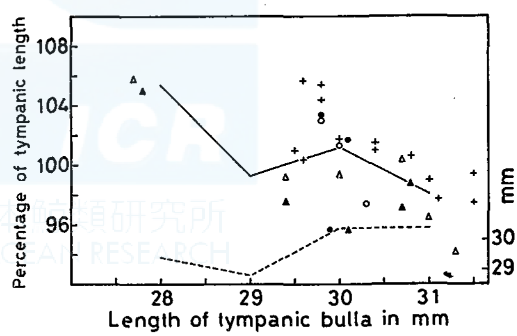


Fig. 51. *N. phocaenoides*. Measurement no. 13 Length of periotic shown in percentage of measurement no. 1. For marks see Fig. 5.

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*Neophocaena phocaenoides*

The tympano-periotic bone of this species shows the typical features of that of Phocoenidae. In this chapter samples from 19 individuals, including 16 from the

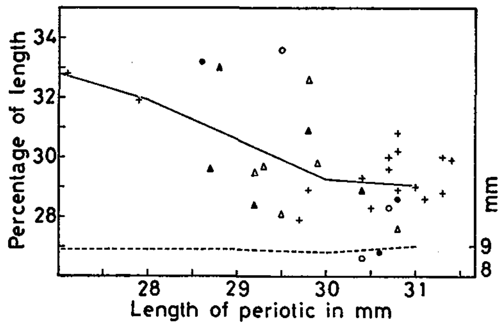


Fig. 52. *N. phocaenoides*. Measurement no. 14 Thickness of periotic. For marks see Fig. 5.

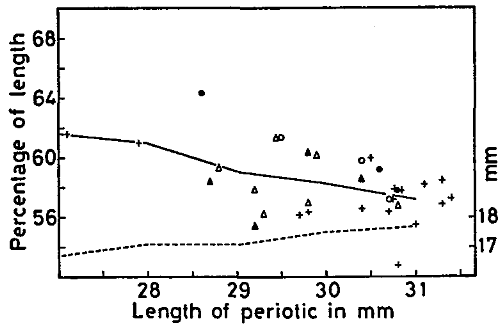


Fig. 53. *N. phocaenoides*. Measurement no. 15 Width of periotic. For marks see Fig. 5.

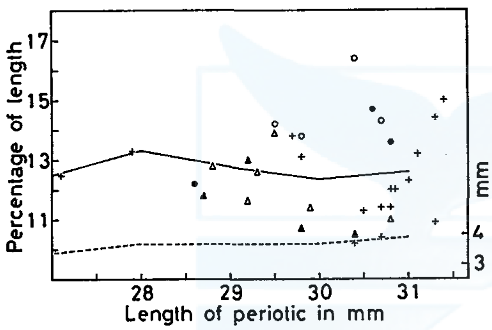


Fig. 54. *N. phocaenoides*. Measurement no. 16 Fundus of internal auditory meatus to ductus endolymphaticus. For marks see Fig. 5.

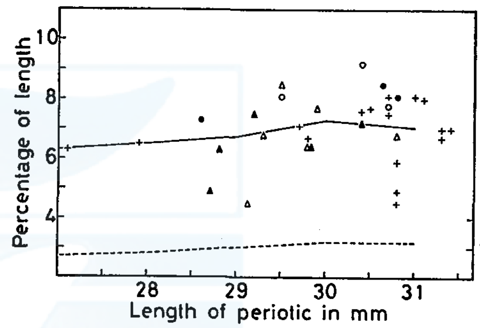


Fig. 55. *N. phocaenoides*. Measurement no. 17 Fundus of internal auditory meatus to aquaeductus cochleae. For marks see Fig. 5.

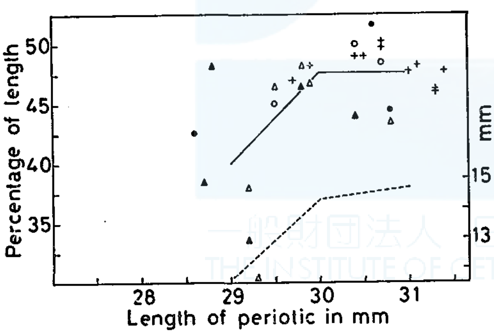


Fig. 56. *N. phocaenoides*. Measurement no. 18 Length of facet on posterior process of periotic. For marks see Fig. 5.

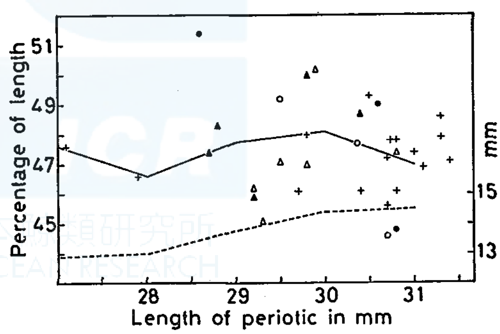


Fig. 57. *N. phocaenoides*. Measurement no. 19 Diameter of cochlear portion. For marks see Fig. 5.

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adjacent waters of Japan, are used.

As shown in Fig. 40, there is observed slight increase in the length of tympanic bulla accompanied with the growth of the animal. The increase is about 2 mm when the body length increases from 80 cm to 150 cm. The length of periotic bone seems not to increase after birth (Fig. 41). As the result the ratio of the periotic length to the tympanic length decreases with the increase of the latter (Fig. 51).

The relative growth of tympano-periotic bone is shown in Figs. 42–57 and Table 5. The proportional dimensions of the tympanic bulla are increasing or stable in relation to the length of tympanic bulla. The posterior branch of lower tympanic aperture (measurement no. 10), which is large in this species, decreases the relative width in the larger tympanic bulla (Fig. 50). The thickness of periotic bone (measurement no. 14) is nearly constant (Fig. 52). The length of the facet on posterior process of periotic is proportionally large in the larger periotic (Fig. 56). This seems to be related with the fact that, in this species, the posterior process of periotic is directed toward posterior direction, and the length of periotic is directly influenced by this process.

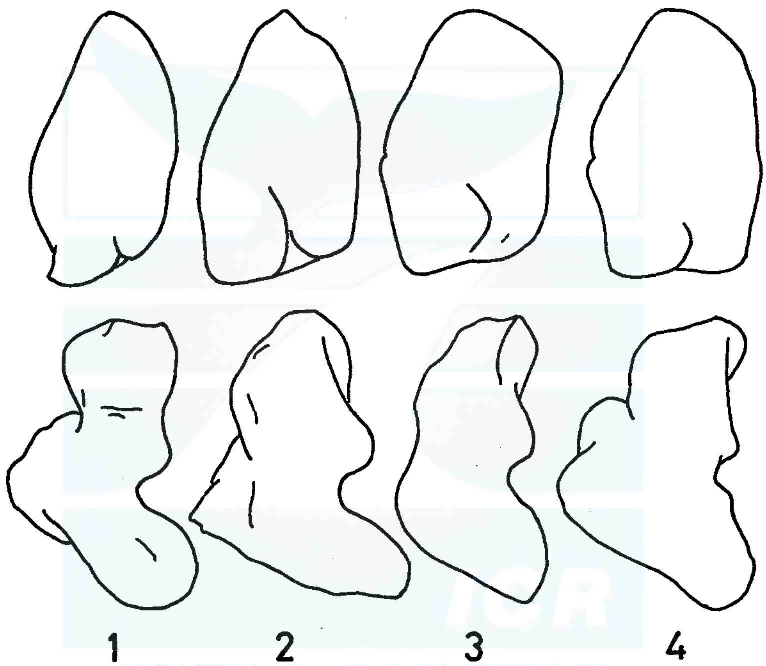


Fig. 58. Contour of ventral view of tympanic bulla and of lateral view of periotic. 1, *Ziphius cavirostris*. 2, *Berardius bairdi*. 3, *Hyperoodon ampullatus*. 4, *Mesoplodon ginkgodens*.

## MORPHOLOGY OF TYMPANO-PERIOTIC BONE

It is intended, in this chapter, to show the diagnostic characteristics of the tympano-periotic bones of each species and taxa. The taxa used here is based on the classification considered from the morphology of tympano-periotic bone (Table 15).

The discussions on these morphological characteristics from the evolutional point of view, or on the interrelationships of each taxa is made in the latter chapter.

*Physeteroidea*

The most conspicuous feature of the tympano-periotic bones of this superfamily is observed on the posterior process of tympanic bulla. It has large laminated or spongy element elongated and expanded distally, which is wedged between exoccipital and squamosal. Posterior process of periotic is usually sutured, not so firmly, to the base of posterior process of tympanic bulla. Main part of accessory ossicle is moved toward the tympanic cavity from the position between lateral wall of tympanic bulla and anterior process of periotic.

Sigmoid process is square or globular and large in size, cochlear portion inclines anteriorly.

*Ziphiidae*

In the members of this family, the anterior part of the ventral wall of tympanic bulla is cylindrical and is lacking in anterior spine. Involucrum is shorter than the lateral wall. Both posterior prominences are thick and short. Deep lateral furrow is prominent on the lateral wall of tympanic bulla. Sigmoid process is square and rather thin, and its lateral border is twisted posteriorly. Elliptical foramen is present.

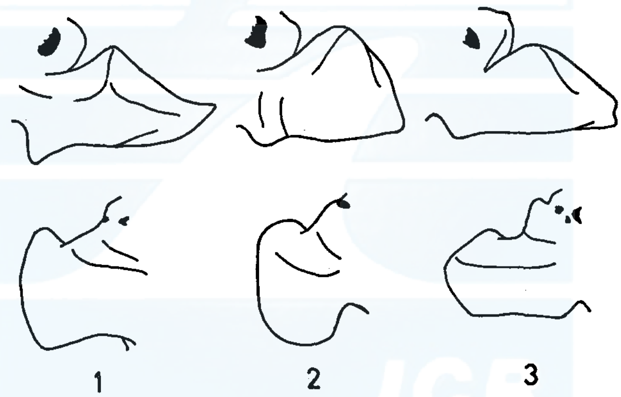


Fig. 59. Contour of the lateral view of anterior process of periotic (top), and of the dorsal view of posterior process of periotic. 1, *Berardius bairdi*. 2, *Ziphius cavirostris*. 3, *Mesoplodon ginkgodens*.

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On the periotic, anterior process, superior process, and posterior process are arranged, when seen from the dorsal, nearly on a straight line and the three parts are clearly distinguished. Anterior process is shaped of triangular pyramid and has a wide contact with the dorsal border of the lateral wall of tympanic bulla. The posterior process is short, and flat at the distal end. Its facet for the posterior process of tympanic bulla is almost smooth. Fundus of internal auditory meatus is usually slender. Tractus spiralis foraminosus is separated by a developed septum from the area containing foramen singulare and aperture of aquaeductus Fallopii. There are two cases in the opening of foramen singulare, in one case it opens near aquaeductus Fallopii (*Ziphius, Berardius, Hyperoodon*), and in the other case it openes near tractus spiralis foraminosus (*Mesoplodon stejnegeri*). The dorsal area of superior process between fundus of internal auditory meatus and aperture of ductus endolymphaticus is highly protruded. Accessory ossicle is, different from that of *Physeter*, small and does not entirely cover the anterior part of dorsal opening of tympanic cavity.

1. *Ziphius cavirostris* (Pl. II)

As shown in Table 6, the size of tympano-periotic bone of this species is intermediate of *Mesoplodon* and *Berardius*.

The tympanic bulla is more flat and its ventral wall is narrower than those of *Berardius*. The rugose area on the ventral surface of tympanic bulla starts from interprominential notch and reaches the anterior margin of the bulla. The posterior prominences, especially the inner, are small and interprominential notch is rudimental. There is formed a wedge-shaped protuberence at the postero-lateral tip of outer posterior prominence (Fig. 58). The posterior branch of lower tympanic aperture is narrower in this species than in *Berardius bairdi* and *Mesoplodon* spp. (Table 6).

TABLE 6. MEASUREMENTS OF TYMPANIC BULLA OF ZIPHIOID SPECIES.

| Species | | *Ziphius cavirostris* | *Berardius bairdi* | *Mesoplodon stejnegeri* | *Mesoplodon ginkgodens* |
|---|---|---|---|---|---|
| Sample size | | 7 | 6 | 7 | 2 |
| 1. Standard length (mm) | | 51.8–59.7 | 63.1–70.4 | 46.9–49.0 | 39.8–44.1 |
| 5. Width (%), | range | 52.1–64.9 | 57.1–67.7 | 67.0–70.2 | 69.0–70.4 |
| | mean | 61.3 | 64.5 | 67.1 | 69.7 |
| 7. W. across post. prom. (%) | range | 38.6–50.2 | 52.6–57.0 | 48.2–55.8 | 51.0–64.6 |
| | mean | 41.6 | 54.5 | 50.8 | 57.8 |
| 10. W. post. branch of LTA (%), | range | 3.8– 4.0 | 9.1– 9.6 | 7.6–13.0 | 6.6 |
| | mean | 3.9 | 9.3 | 8.2 | — |

TABLE 7. MEASUREMENTS OF PERIOTIC OF ZIPHIOID SPECIES (mm)

| Species | | *Ziphius cavirostris* | *Berardius bairdi* | *Mesoplodon stejnegeri* | *Mesoplodon ginkgodens* |
|---|---|---|---|---|---|
| Sample size | | 7 | 6 | 4 | 2 |
| 13. Standard length | | 54.0–62.4 | 66.9–75.8 | 44.3–50.9 | 41.0–42.3 |
| 14. Thickness, | range | 22.3–27.0 | 29.0–38.1 | 16.4–18.3 | 20.4–20.6 |
| | mean | 24.0 | 32.9 | 17.8 | 20.5 |
| 15. Width, | range | 29.5–34.1 | 34.7–37.2 | 26.9–29.1 | 22.3–23.1 |
| | mean | 31.7 | 36.4 | 27.7 | 22.7 |

Though the periotic resembles that of *Berardius bairdi*, it is distinguished by the short and round anterior process and shorter posterior process (Fig. 59). There is sometimes observed a transverse groove on the lateral surface of the base of anterior process. But this occurs on some periotic bones of other Ziphioid species.

2. *Berardius bairdi* (Pl. III)

The tympano-periotic bones of this species is the largest in this family (Table 6). The anterior part of the ventral wall of tympanic bulla is narrow and triangular (Fig. 58). Both inner and outer posterior prominences swell well as in the case of *Mesoplodon*.

Periotic is characteristic, other than the size, in the long and slender anterior process, wider upper tympanic aperture, and slender and long posterior process.

On *Berardius arnouxi* (Pl. IV), only one sample from New Zealand was observed. It was indistinguishable from *B. bairdi*.

3. *Hyperoodon ampullatus* (Pl. IV)

The length of tympano-periotic bone is nearly same with that of *Ziphius cavirostris*. The tympanic bulla is cylindrical and the contour of anterior portion of the ventral wall is not triangular, which condition is different from the case of *Berardius bairdi*. Anterior margin of the ventral wall of tympanic bulla concaves slightly. Though outer posterior prominence is thick, interprominential notch is shallow as in the case of *Ziphius cavirostris* (Fig. 58).

On the periotic, anterior process is shorter than *Berardius* but not so round as *Ziphius* and *Mesoplodon*. The opening of fundus of internal auditory meatus is round and the margin of the openning provides a circular keel. The upper tympanic aperture is wide but shallow (Fig. 58).

4. *Mesoplodon*

The tympanic bulla of this genus is characterized by the thick posterior prominences and deep interprominential notch as those of *Berardius*, the flatness of the bulla, wide posterior branch of the lower tympanic aperture which is different from that of *Ziphius*, and square-shaped ventral view of tympanic bulla. Posterior process of tympanic bulla is shorter and thicker than that of *Berardius*.

The surface of the periotic is smooth and the contour is roundish in general. Anterior process is rather hemispherical than triangular pyramidal. Posterior process is slender and not so strongly fan-shaped as *Ziphius*. Upper tympanic aperture is smaller than those of other Ziphioid species. The size of tympano-periotic bone is small.

*Mesoplodon stejnegeri* (Pl. IV). The ranges of the length of tympanic bulla and periotic of seven individuals are between 46.9 mm and 49.0 mm, and 44.3 mm and 50.9 mm respectively. These values are smaller than those of *Berardius bairdi* or *Ziphius cavirostris*.

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On the tympanic bulla the both posterior prominences and interprominential notch develop well. The anterior extension of the latter opens on the lateral wall of tympanic bulla encircling the anterior base of globular outer posterior prominence. Ventral keel, originating at the anterior base of inner posterior prominence and passing the inner side of the center of the ventral wall of tympanic bulla, reaches to the anterior end of involucrum. The rugose area on the ventral wall occupies wide area between ventral keel and the lateral border of ventral wall (Fig. 60).

On the periotic, anterior process is slightly flat hemispherical with a small conical protuberence on the anterior tip. Posterior process of periotic is slender than that of *M. densirostris*, *M. carlhabbsi*, and *M. europaeus*. Though there is a deep furrow on the lateral surface of superior process, connecting the upper tympanic aperture and base of cochlear portion, this is observed also on other *Mesoplodon* species. The protuberence on the superior process is not developed. The canal for stapedial muscle is shallow.

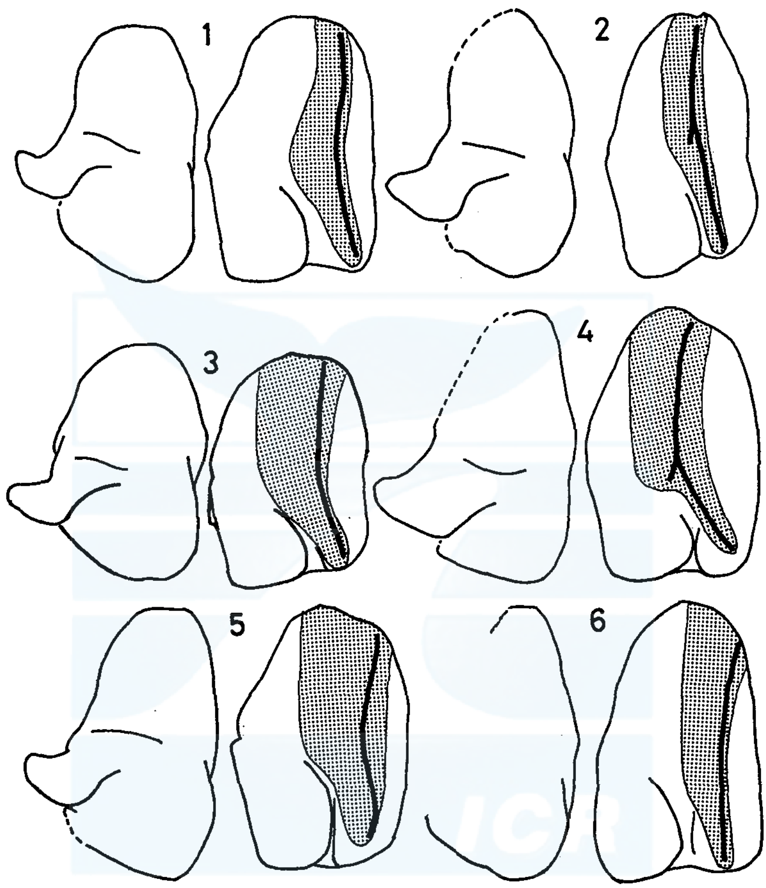


Fig. 60. Contour of the ventral and lateral aspect of tympanic bulla of *Mesoplodon*. Black line and dotted area indicate ventral keel and rugose area surrounding it. 1, *Mesoplodon europaeus*. 2, *M. densirostris*. 3, *M. mirus*. 4, *M. ginkgodens*. 5, *M. stejnegeri*. 6, *M. carlhubbsi*.

*Mesoplodon densirostris* (Pl. V). 4 tympanic bullae and 1 periotic were studied. Their size is slightly larger than those of other *Mesoplodon* species.

The ventral keel situates on the center, and the smooth area in the involucrum side is wide, which feature is different from that of *M. stejnegeri*. As the inner posterior prominence is thin, the interprominential notch situates at the inner side. Interprominential notch is shallow.

The dorsal surface of periotic is smooth, and the lateral contour is arc shaped. There is no furrow on the bases of anterior and posterior processes nor upper area of upper tympanic aperture. The canal for stapedial muscle forms a deep crescent furrow. Anterior process is of trigonal pyramid, and has a small conical protuberence on the anterior tip. Cochlear portion is flat, and pentagonal.

*Mesoplodon europaeus* (Pl. V). Tympanic bullae of 3 individuals and periotic of an individual were studied. Their sizes are smaller than those of other species of this genus.

The tympanic bulla resembles that of *M. stejnegeri* in the situation of ventral keel, and in the globular and protruding outer posterior prominence, but differs from it in the thin inner posterior prominence which is similar to that of *M. densirostris*.

The most conspicuous feature of the periotic is the presence of a cylindrical protuberence on the dorsal surface of superior process (Pl. V). Though the similar structure is also observed on *M. ginkgodens*, *M. europaeus* can be distinguished from it by the shallower canal for stapedial muscle and the shape of cochlear portion in which the anterior and posterior margin is not in parallel. There is a vertical furrow on the superior process near upper tympanic aperture.

*Mesoplodon ginkgodens* (Pl. VI). Tympano-periotic bones from two individuals were studied. Its size is nearly same with that of *M. europaeus*. The flatness of tympanic bulla is weaker than any species of *Mesoplodon* mentioned before. Outer posterior prominence is very low and its apex is flat and oval in the contour. Inner posterior prominence is higher but thinner than the outer. Prominent ventral keel situates at the center of ventral wall of tympanic bulla and reaches the anterior tip of the bulla. The area inside of ventral keel is occupied by a wide smooth area continuing to involucrum as in the case of *M. densirostris*. The rugose area is restricted in the narrow part between ventral keel and lateral wall of tympanic bulla (Fig. 60). The anterior part of interprominential notch is not smoothly connected to the lateral wall.

Periotic resembles to that of *M. europaeus*. The base for stapedial muscle seems to be wide and shallow as in the case of *Ziphius cavirostris*, but in *M. europaeus* it forms a narrow furrow encircling the cochlear portion different from *M. ginkgodens*. Cochlear portion is approximately square.

*Mesoplodon mirus* (Pl. III). Only one tympanic bulla was observed. The ventral keel situates at the inner side of the center of ventral wall of the bulla as in the case of *M. stejnegeri* and *M. europaeus*, but is characteristic in the strong elevation at the anterior part of the keel. The smooth area inside of the ventral keel is wide (Fig. 60). Outer posterior prominence is thick and high. Inner posterior prominence is small.

*Mesoplodon carlhabbsi* (Pl. VI). The size of tympano-periotic bone is nearly similar to that of *M. stejnegeri*. On the tympanic bulla, the posterior prominences especially the outer develops well. Interprominential notch is wide and smoothly continues to the slope of lateral wall of tympanic bulla. Ventral keel continues from the base of inner posterior prominence to the point near the anterior border of the bulla. It situates at the inner side of the center of ventral wall, and its highest point at the middle of tympanic bulla. The smooth area on the inner side of ventral keel is narrow (Fig. 60).

When seen from the cerebral side of periotic, the front border of anterior process, lateral border of superior process, and posterior border of posterior process cross in a right angle (Pl. VI Fig. 15). Anterior process is large and conical with the apex on the cerebral side. Though there is a slight protuberence on the superior process near the fundus of internal auditory meatus, it is not so conspicuous as that of *M. europaeus* or *M. ginkgodens*. The cochlear portion, which contour is round, has a wide fossa at the mesial side of the opening of fundus of internal auditory meatus. The furrow of the base for stapedial muscle is wide and deep. The furrow on the lateral surface of superior process is shallow.

*Physeteridae*

This family includes only one species *Physeter catodon*. The tympano-periotic bone of this species was precisely described by Yamada (1953). Several important diagnostic features of the ear bones of *Physeter catodon* (Pl. VII) are described below in comparison with other Physeteroidea species.

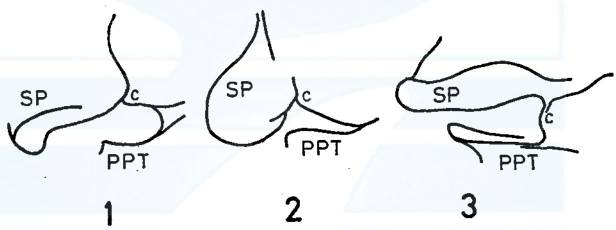


Fig. 61. Schematic figure of the lower tympanic aperture of Physeteroidea. C, Conical process. SP, Sigmoid process. PPT, Posterior process of tympanic bulla. 1, Ziphiidae. 2, Kogiidae. 3, Physeteridae.

The tympano-periotic bone of *Physeter catodon* is massive and the largest in Physeteroidea. On the tympanic bulla, in spite of the strong development of involucrum and inner posterior prominence, outer posterior prominence and interprominential notch are greatly reduced. As the result of this modification, outer and inner posterior prominences and lateral border of sigmoid process situate nearly on one plane (Pl. VII Fig. 5). Though the sigmoid process is thin and square as in the case of Ziphiidae, the width is larger than the length. Its lateral margin is not twisted posteriorly. Conical process and posterior branch of lower tympanic aperture are almost disappeared (Fig. 61). Accessory ossicle is large and roofs the anterior part of tympanic cavity. Posterior process of tympanic bulla is long and composed of thin laminated plates. In one example, a tympanic bulla of 59.3 mm in standard length had the posterior process of 175 mm in length (Pl. VII Fig. 11). The facet for the connection between posterior process of tympanic bulla and that of periotic has vague keels and grooves, and not so smooth as Ziphiidae and Kogiidae. The tympanic bulla of *Physeter* differs in these features from those of Ziphiidae and Kogiidae, but it resembles to that of Kogiidae in the U shaped anterior openning of tympanic bulla, swallen involucrum and its " 3 " shaped dorsal margin, absence of lateral furrow, and in the closed elliptical foramen.

The superior process of periotic is massive, and continuous in structure with anterior and posterior processes. Anterior process is shaped of a curved slender rod. Posterior process is cylindrical and tapered distally, which is connected to superior process at a right angle and bent to downward. The posterior surface of posterior process of periotic is rugose suggesting a sutural connection with squamosal. Aquaeductus Fallopii, foramen singulare, ductus endolymphaticus, and tractus spiralis foraminosus opens in one openning of fundus of interal auditory meatus (Pl. VII Fig. 9).

*Kogiidae*

This family is composed of two species in one genus *Kogia*. The diagnostic features of the ear bones are as follows.

The size of tympanic bulla is one of the smallest among the toothed whales. The smaller size is only found in *Pontoporia blainvillei*. The ventral wall of tympanic bulla is flat and crosses with the lateral wall at a right angle, and there is observed no lateral compression of tympanic bulla nor deformation of posterior prominences.

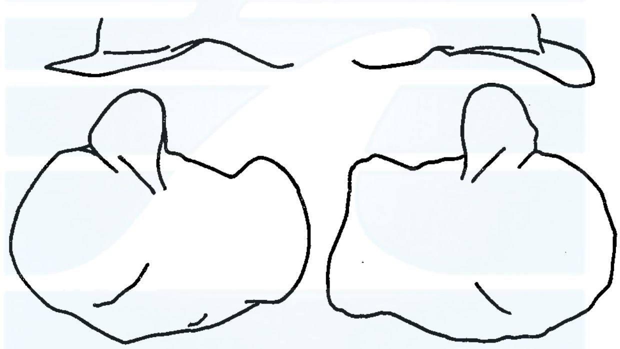

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Fig. 62. Schematic figure showing the difference of antero-lateral border of tympanic bulla, and of upper tympanic aperture between *Kogia breviceps* (1), and K. simus (2). Anterior direction is at the center.

Inner and outer posterior prominences developes well, and the latter protrudes posteriorly and the former postero-mesial direction at nearly a right angle with the latter. Interprominential notch opens only posteriorly, and does not extend on the ventral wall of tympanic bulla. As sigmoid process is not twisted, the anterior surface is exactly directed toward antero-posterior axis of tympanic bulla. The tip of sigmoid process is spheric. The distal portion of posterior process of tympanic bulla is funnel shaped. The facets for the connection between the two posterior processes are smooth.

The anterior process of periotic is flat and rectangular with the concaved margins, which is different from other Physeteroidea species. On the thick superior process, thin plate-like posterior process extends posteriory. Aquaeductus Fallopii and ductus endolymphaticus opens outside of the opening of fundus of internal auditory meatus inside of which foramen singulare opens.

*Kogia simus* and *K. breviceps* (Pl. VIII)

Though the ear bones of the two species is quite similar, they can be distinguished by several characteristics. On the tympanic bulla, the anterior margin of the lateral wall is concaved in *K. simus* but is convex in *K. breviceps*. In this respect the ear bone reported by Yamada (1953, Fig. 13) is classified into *K. simus*. On the tympanic bulla of 3 *K. simus*, conical process is hidden inside of the sigmoid process and cannot be observed from outside. But on one example of *K. breviceps* it is observed from outer side. This will probably be a specific difference. The upper tympanic aperture is large in *K. breviceps* and small in *K. simus* (Fig. 62).

*Platanistoidea*

This superfamily includes the three families, Platanistidae, Iniidae, and Pontoporiidae. There are found some common features in the morphology of their ear bones as mentioned below. On the tympanic bulla, the swollen base of outer posterior prominence, the existance of median and lateral furrow, no lateral compression, and thick and square sigmoid process are common in Platanistoidea. On the periotic, the opening of fundus of internal ausitory meatus is characteristic in the roundness. The posterior processes of both tympanic bulla and periotic are very small in size and the latter is bent downward.

TABLE 8. MEASUREMENTS OF TYMPANO-PERIOTIC BONES OF PLATANISTOIDEA, SHOWN IN MM OR PERCENTAGE OF THE STANDARD LENGTH.

| Species | *P. gangetica* | *I. geoffrensis* | *L. vexillifer* | *P. blainvillei* |
|---|---|---|---|---|
| Sample size | 7 | 5 | 1 | 1 |
| 1. Length of tympanic bulla (mm) | 47.1-63-5 | 38·2-45.6 | 47.1 | 24.3 |
| 5. Width of tympanic bulla (%) | 44.3-54.4 | 60.3-70.3 | 51.7 | 61.3 |
| 6. Height of tympanic bulla (%) | 61.3-74.8 | 74.0-81.4 | 58.0 | 83.0 |
| 13. Length of periotic (mm) | 33.4-42.3 | 25.7-30.4 | 52.0 | 20.0 |
| 14. Thichness of periotic (%) | 23.9-35.9 | 41.6-58.3 | 26.9 | 47.5 |
| 15. Width of periotic (%) | 55.3-66.5 | 79.6-90.0 | 46.2 | 81.0 |
| 19. Diameter of cochlear portion (%) | 38.3-44.8 | 54.3-68.5 | 37.5 | 68.0 |
| —. FIAM, Width/Length | 0.79-1.33 | 0.40-0.60 | 0.88 | 0.37 |

*Platanistidae*

This family includes only one species *Platanista gangetica*. The most conspicuous feature of the ear bone of this species is in the relation to the skull (see page 48).

The anterior part of tympanic bulla is cylindrical and smoothly changes into anterior spine, which length increases with the growth of animal. There is formed small irregular needle-shaped processes in the median furrow, and gives the base of ligament connecting the tympanic bulla and basioccipital. The lateral wall is highly convex. The width of tympanic bulla is smaller than that of *Inia geoffrensis* (Table 8). This is related with the shape of involucrum. Sigmoid process, which situates at a right angle to the long axis of the bulla, is large in both thickness and width. Lateral furrow is weaker than that of *Inia*. The elliptical foramen opens, but the shape is irregular. The facet for the posterior process of periotic has weak longitudinal grooves and ridges.

Though the periotic is larger than that of *Inia geoffrensis*, cochlear portion is smaller than it in both thickness and diameter. The apex of cochlear portion touches the involucrum. Round opening of fundus of internal auditory meatus is surrounded by a circular keel. The apertures of aquaeductus Fallopii and foramen sigulare open at a close distance in the opening of fundus of internal auditory meatus. Anterior process is slender and curves along cochlear portion. At the dolsal base of anterior process there is usually a small pillar shaped process directing toward cochlear portion (Pl. IX Figs. 8–10). As there is usually attached one or two ossicles on the anterior process, the shape of this part varies between individuals (Pl. IX Figs. 12–13). Accessory ossicle touches the anterior base of cochlear portion. Superior process is thin and is clearly separated by the grooves from the anterior and posterior processes. The antero-dorsal corner of the posterior process of periotic forms a nodular protuberence. A small rod shaped downward protuberence is on the posterior wall of upper tympanic aperture (Pl. IV Fig. 7), this structure strengthens the mechanical connection between posterior process of periotic and squamosal.

*Iniidae*

This family includes two genera *Inia* and *Lipotes*. One of the two features of tympano-periotic bones distinguishing this family from other Platanistoidea is that the posterior processes of tympanic bulla and of periotic are not sutured to the skull. And the other is the relatively strong sutural connection between both posterior processes. The former structure is also observed in *Pontoporia blainvillei*, and the latter in *Platanista gangetica* but the suture is stronger in *Inia* and *Lipotes*. Lateral margin of sigmoid process is strongly convexed posteriorly. Elliptical foramen opens.

1. *Inia geoffrensis* (Pl. X)

The ear bones of this species is smaller than those of *Platanista* and *Lipotes*. As the involucrum expands to the inside, the width of tympanic bulla is large. Lateral furrow is prominent. Median furrow is nallow and shallow, and situates at slightly outer side of the center of tympanic bulla. The size of two posterior prominences are nearly same, which is different from the case of *Lipotes*. The short posterior process of tympanic bulla extends posteriorly. Its length is from 20.8% to 24.8% of the length of bulla.

On the periotic, the anterior and posterior processes are smaller in comparison with the size of cochlear portion, as in the case of *Pontoporia blainvillei*.



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Anterior process is square and short, but small process sometimes attaches on the tip. The thickness (measurement no. 14) and breadth (no. 15) of periotic is larger than the corresponding values of *Lipotes* and *Platanista* (Table 8). The opening of fundus of internal auditory meatus is usually round.

2. *Lipotes vexillifer* (Pl. X)

The length of tympanic bulla of this species is intermediate of *Inia* and *Platanista*, but that of periotic is larger than any of the two genera.

As involucrum of tympanic bulla does not expand to the inner side, the width of tympanic bulla is smaller than that of *Inia* but resembles to that of *Platanista* (Table 8). The anterior part of tympanic bulla is conical and posseses no anterior spine. Median furrow reaches to a shallow hollow near the anterior end of the bulla. Outer posterior prominence is large and spherical, but the innerposterior prominence is thin. Ventral keel is low and narrow, and curves to the outer side at the middle of the length. The diameter of cochlear portion is 19.2 mm, which is nearly same with that of *Inia* and larger than *Platanista*. But its ratio to periotic length is far smaller than both of them. The opening of fundus of internal auditory meatus is nearly round (14.5 mm $\times$13.5 mm) as in the case of *Platanista*. Anterior process of periotic can be clearly distinguished from superior process, and its slender tip extends along the supero-lateral border of tympanic bulla. This feature is similar to *Platanista* rather than *Inia*. Posterior process of periotic is also distinguished from superior process as in the case of anterior process.

*Pontoporiidae*

This family includes only one species *Pontoporia blainvillei* (Pl. IX). Most conspicuous feature of this family is the almost smooth articular facets on both posterior processes, but more perfect smoothness is found in Phocoenidae. Following descriptions on the ear bones are for this species.

The tympano-periotic bone of this species is the smallest among the observed Odontoceti. The ventral view of tympanic bulla is convexed laterally. Anterior spine is absent. Median furrow developes well and is in parallel with the concaved involucrum. Both posterior prominences are slightly large and nearly in same size. It is a characteristic feature of this species that the lateral wall between base of outer posterior prominence and the lateral furrow greatly swells. Lateral furrow is inconspicuous. Sigmoid process is square in the anterior view and its thickness is large. Elliptical foramen is closed. The posterior branch of lower tympanic aperture (measurement no. 10) is larger than any other species of Platanistoidea. The posterior process of tympanic bulla and the tip of posterior process of periotic is directed to the posterior.

The anterior process of periotic is short and pointed. The posterior and anterior processes are continuous with superior process, which is similar to *Inia* and different from *Platanista* and *Lipotes*. Cochlear portion is proportionally large as in the case of *Inia*. This seems to have a relation with the shorter anterior and posterior processes. The openings of aquaeductus cochleae and ductus endolymphaticus are widely separated from the opening of fundus of internal auditory meatus.

*Delphinoidea*

In this superfamily, the posterior process of tympanic bulla is relatively large, and not sutured with the skull. Sigmoid process is small and thin, and L-shaped in the lateral view. Lateral furrow is almost completely disappeared. Outer posterior prominence is round or flat, and projects postero-ventrally. Interprominential notch is deep. Elliptical foramen is closed in some species.

On the periotic, the anterior, posterior, and superior processes are continuous. Accessory ossicle lies between anterior process and lateral wall of tympanic bulla, separating the two parts. Anterior process is thick and square. Anterior margin of cochlear portion does not touch the anterior process.

This superfamily includes Delphinapteridae, Phocoenidae, Delphinidae, and Monodontidae.

*Delphinapteridae*

This family includes *Delphinapterus leucas* and *Orcaella brevirostris*. The common features of tympano-periotic bones are as follows.

The outer and inner posterior prominences are developed well, and the width across these prominences is large. The posterior branch of lower tympanic aperture opens wide as in the case of Pontoporiidae and Phocoenidae. Elliptical foramen is

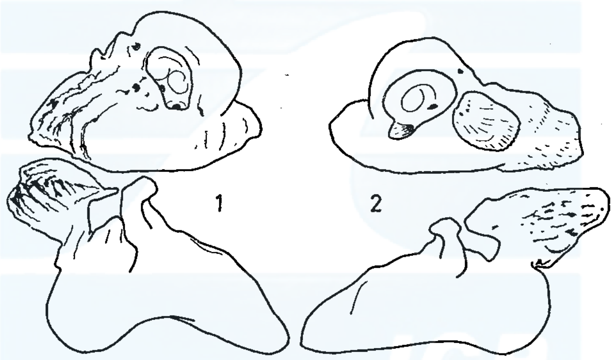


Fig. 63. Schematic figure of tympanic bulla and periotic of *Delphinapterus leucas* (1) and *Orcaella brevirostris* (2).

TABLE 9. WIDTH OF TYMPANIC BULLA SHOWN IN PERCENTAGE OF THE LENGTH, IN *ORCAELLA*, *DELPHINAPTERUS*, AND *MONODON*.

| Species | *O. brevirostris* | *D. leucas* | *M. monoceros* |
|---|---|---|---|
| Sample size | 2 | 4 | 4 |
| Range of the width | 52.0–57.5 | 58.0–59.0 | 37.5–41.4 |
| Mean | 54.8 | 58.9 | 39.6 |

closed. Bilateral compression of tympanic bulla is not occurred (Table 9, Fig. 63). The posterior processes of tympanic bulla and of periotic are large and extend straightly to the posterior direction. The suture between both posterior processes is rigid by the existence of deep ridges and grooves.

1. *Delphinapterus leucas* (Pl. XI)

The anterior margin of tympanic bulla is lacking of anterior spine, and round in the contour. Because of the low ventral keel and highly projected outer posterior prominence, the ventral contour of tympanic bulla is saddle shaped when seen from the lateral side. Involucrum is strongly projecting to inner side. The tip of posterior process of tympanic bulla is highly thickened.

The posterior process of periotic is thick and wide at the base, but thin at the tip to form a wedge shape. On the dorsal surface of the posterior process there are irregular grooves (Fig. 63). Periotic of this species is sutured by this structure to the squamosal (Pl. I Fig. 8, and Kleinenberg *et al* 1964). Superior process is thick and have a flat elevation higher than the opening of the fundus of internal auditory meatus. The opening of the fundus of internal auditory meatus is surrounded by a circular crest. The opening of aquaeductus Fallopii is separated from foramen singulare and tractus spiralis foraminosus by a developed crista transversa.

2. *Orcaella brevirostris* (Pl. XI)

The tympano-periotic bone of this species is nearly similar in size to that of *Delphinapterus leucas*.

When seen from the lateral side the ventral contour of tympanic bulla is flat, which is greatly different from *D. leucas*. The low ventral keel reaches slightly beyond the midpoint of tympanic bulla. Shallow median furrow is formed along the ventral keel. The outer posterior prominence, which is flat in *D. leucas*, is cylindrical in this species. The projection of involucrum to the inner side is observed on ZSI 274 in a same form as *D. leucas*, but weaker on USMN 199743. The posterior process of tympanic bulla is larger than that of *D. leucas* in both thickness and length, and possesses a large part of spongy structure.

The posterior process of periotic is also large and have a spongy structure. The USNM specimen had larger posterior process than the ZSI specimen. Probably this will be related with the age of the animal. Opening of ductus endolymphaticus is surrounded by a large shallow funnel shaped area. Superior process is slender than that of *D. leucas*.

*Phocoenidae*

The diagnostic features of the tympano-periotic bones of this family are in the direction of the posterior processes and in the smooth facets for the connection between both posterior processes. The former is similar to Delphinapteridae, but the latter differs from it. The posterior process of tympanic bulla is large, but that of the periotic is smaller and shaped of a rod. The both posterior processes have no spongy structure (Fig. 64).

Other characteristics common in the tympanic bulla of this family are observed in the developed posterior prominences, deep interprominential notch, wide posterior branch of lower tympanic aperture, existence of a vague median furrow reaching nearly anterior part of the bulla, absence of anterior spine, elevated anterior end of the ventral wall, closed elliptical foramen, and in the absence of lateral compression of tympanic bulla. But most of these characteristics are common to Delphinapteridae.

The characteristic features of the periotic of this family are the linear arrangement of anterior, superior, and posterior processes, the triangular shape of cochlear portion, and low crista transversa. The lengths of tympano-periotic bones are small and approximately in the range between 27 mm and 34 mm.

1. *Neophocaena phocaenoides* (Pl. XII)

The outer posterior prominence is cylindrical and far thicker than the inner posterior prominence. The posterior process of tympanic bulla is thick and spindle-shaped in lateral view. Ventral keel is high as in the case of *Phocoenoides*. Posterior process of periotic is shaped of a slender rod with the pointed tip (Fig. 64).

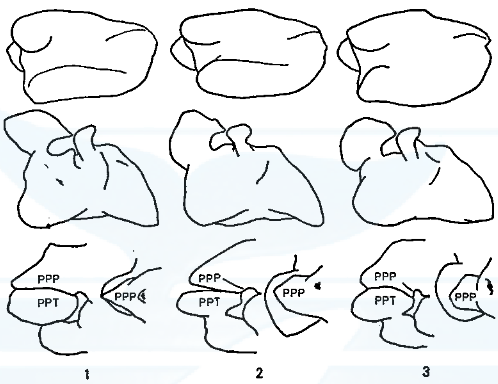


Fig. 64. Schematic figure of tympano-periotic bones of Phocoenidae, ventral (top) and lateral view (middle) of tympanic bulla, and lateral and dorsal views of posterior processes (bollom). PPP, Posterior process of periotic. PPT, Posterior process of tympanic bulla. 1, *Neophocaena phocaenoides*. 2, *Phocoenoides* spp. 3, *Phocoena phocoena*.

TABLE 10. RANGE OF THE MEASUREMENTS OF TYMPANO-PERIOTIC BONES OF PHOCOENIDAE, SHOWN BY THE PERCENTAGE OF THE STANDARD LENGTH.

| Species | *N. phocaenoides* | *P. phocoena* | *Phocoenoides* spp. |
|---|---|---|---|
| Sample size | 19 | 6 | 12 |
| Tympanic bulla | | | |
| 2. Tip to inner post. prom. | 98.7–108.0 | 89.3–97.9 | 89.2–97.2 |
| 6. Height | 81.5– 94.3 | 75.2–87.3 | 67.9–82.5 |
| Periotic | | | |
| 14. Thickness | 26.6– 33.6 | 32.6–39.0 | 35.8–39.4 |
| 19. Diameter of cochlear portion | 45.1– 51.4 | 38.9–44.6 | 37.5–43.5 |

This species differs from other two genera of Phocoenidae in the following measurements, or the distance from anterior tip of tympanic bulla to posterior end of inner posterior prominence (measurement no. 2), height of the bulla (no. 6), thickness of periotic (no. 14), and diameter of cochlear portion (no. 19) (Tables 10 and 16).

2. *Phocoena phocoena* (Pl. XII)

The outer posterior prominence of the tympanic bulla is flat as in the case of



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*Phocoenoides*. Ventral keel is low and most inconspicuous among the three genera of Phocoenidae. The central area of the ventral wall of tympanic bulla is flat and is not concaved as that of *Neophocaena* and *Phocoenoides*. The posterior process of tympanic bulla is similar to that of *Phocoenoides*. The tip of posterior process of periotic is robust as in the case of *Phocoenoides*, but it differs in the existance of a weak constriction at the base.

The observation of each 3 specimens of *Ph. phocoena phocoena* and *Ph. phocoena vomerina* could not find the difference between the two subspecies. One tympano-periotic bone of *Ph. sinus* did not show any difference from *Ph. phocoena*.

3. *Phocoenoides* (Pl. XIII)

The shape of outer posterior prominence and of posterior process of tympanic bulla differs from that of *Neophocaena* but resembles to *Phocoena*. The presence of the high ventral keel and the deep concavity at the middle area of ventral wall of the bulla differs from *Phocoena*. Though the periotic of *Phocoenoides* resembles to that of *Phocoena*, it may be distinguished by the shape of the posterior process (Fig. 64).

There is found no morphological difference between the tympano-periotic bone of *Ph. dalli* and that of *Ph. truei*.

*Delphinidae*

One of the characteristic features of this family is found in the posterior processes of tympanic bulla and of periotic. The posterior processes project laterally or postero-laterally, and their connection forms the suture with the longitudinal grooves and ridges on the facets. But these features are observed also in Monodontidae. Other characteristics of this family are the larger or equal thickness of outer posterior prominence in comparison with that of the inner, the narrow posterior branch of lower tympanic aperture, the low crista transversa, and aquaeductus Fallopii openning in the same base with tractus spiralis foraminosus.

The presence of elliptical foramen, median furrow, and of anterior spine, height of ventral keel, and strength of lateral compression of tympanic bulla show wide variation between taxa.

This family is divided, in this study, into 4 subfamilies or Sotaliinae, Delphininae, Orcininae, and Globicephalinae.

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*Sotaliinae*

The characteristics of the tympanic bulla of this subfamily are the presence of median furrow (*Sotalia* and *Sousa*) or similar longitudinal furrow (*Cephalorhynchus*), swallen outer posterior prominence, weak ventral keel, usually closed elliptical foramen, no lateral compression of the bulla, and absence of anterior spine.

On the periotic, there is no common characteristics except the slenderness of the superior process.

1. *Sotalia* spp. (Pl. XV)

Only two specimens from a *S. guianensis* and a *S. fluviatilis* are measured. The size of ear bone is nearly same with that of *Stenella* or *Delphinus*.

The anterior margin of ventral wall of tympanic bulla is nearly symmetrical and oval-shaped. Shallow median furrow, starting from the wide interprominential notch, reaches near the anterior end of tympanic bulla. The rugose area on the ventral surface of tympanic bulla is restricted to the inner side of median furrow. Ventral keel is not so developed as *Tursiops* and *Stenella*. The inner posterior prominence is short and its tip does not project posteriorly beyond its posterior base. This condition is not observed in *Sousa* and *Cephalorhynchus*. As the outer posterior prominence, especially its anterior base swells well, the highest point is at the point corresponding to the base of sigmoid process when seen from the lateral side. The periotic is characteristic in the two longitudinal keels on the superior process (Fig.

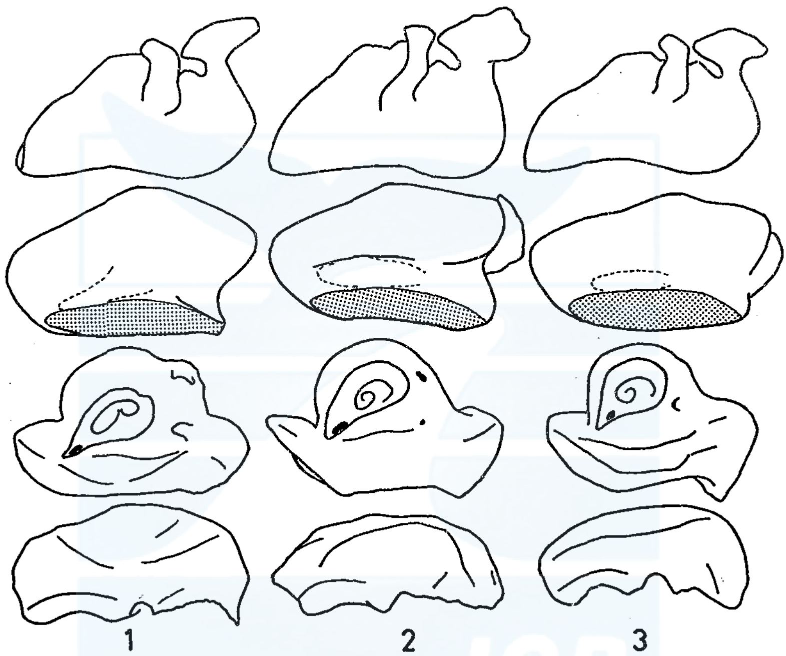


Fig. 65. Schematic figure of tympano-periotic bones of Sotaliinae. Dotted area indicates ventral keel, and the dotted line Median furrow or similar structure. 1, *Cephalorhynchus*. 2, *Sousa*. 3, *Sotalia*.

TABLE 11. RANGE OF THE MEASUREMENT OF TYMPANO-PERIOTIC BONES OF SOTALIINAE, SHOWN BY THE PERCENTAGE OF THE STANDARD LENGTH.

| Species | *Sotalia* spp. | *Sousa t.* | *Cephalorhynchus* spp. |
|---|---|---|---|
| Sample size | 2 | 1 | 2 |
| Tympanic bulla | | | |
| 2. Tip to inner prost. prom. | 91.3–91.4 | 97.4 | 89.2–90.9 |
| 5. Width | 56.2–57.3 | 57.3 | 57.2–58.2 |
| 7. Width across post. prominences | 48.6–49.4 | 54.1 | 44.6–46.4 |
| 10. Width of post. branch of LTA | 5.4 | 7.3 | 4.0 |
| Periotic | | | |
| 17. Aquaeductus cochleae to FIAM | 5.7– 6.8 | 5.4 | 17.9 |

65). According to the observation on several *Sotalia* specimen in Museo de Zoologia de la Univ. de Sao Paulo, the opening of elliptical foramen is not rare.

There was observed no significant difference between *S. guianensis* and *S. fluviatilis*.

2. *Sousa teuszii* (Pl. XIV)

Only one specimen from Senegal was studied. The size of ear bone is slightly larger than that of *Sotalia*. The form of the anterior tip of tympanic bulla is, different from *Sotalia* and *Cephalorhynchus*, asymetric and outer margin projects laterally. There is a clear median furrow along the outer base of low ventral keel. Its width is largest at the middle of tympanic bulla. The lateral border of median furrow is bounded by a weak keel. The tip of inner posterior prominence projects posteriorly beyond the base. The width across posterior prominences (measurement no. 7) is slightly larger than the other species of this subfamily (Table 11). Posterior process of tympanic bulla is square.

The superior process of periotic is slender and divided into lateral and dorsal planes by a longitudinal keel (Fig. 65). The opening of fundus of internal auditory meatus is slender and separated from the triangular hollow surrounding the opening of ductus endolymphaticus by a keel on its lateral margin.

3. *Cephalorhynchus* spp. (Pl. XIV)

Only two individuals were studied. The size of ear bone is nearly same with that of *Stenella*.

Anterior margin of the ventral wall of tympanic bulla is oval. The ventral wall is elevated at the anterior part. The inner posterior prominence is thin and the tip projects beyond the posterior base. Interprominential notch opens wide. The median furrow like structure extend to the anterior margin of the bulla, but it opens to the lateral wall of the bulla at its middle. The inner margin of involucrum is straight. Posterior process is square.

The superior process of periotic has no prominent keel observed in *Sousa* and *Sotalia*. The distance between aquaeductus cochleae and the opening of fundus of internal auditory meatus is markedly large (Table 11). Opening of fundus of internal auditory meatus is surrounded by irregular small processes.

*Delphininae*

Wide variation is observed in the morphology of tympanic bulla among the members of this subfamily. The lengths of tympanic bulla and of periotic are found between 28.0 mm and 41.5 mm, and 25.4 mm and 37.8 mm respectively. On the tympanic bulla of this subfamily the bilateral compression is not occurred, elliptical foramen is open, median furrow is absent, and inner posterior prominence projects posteriorly beyond the base. The shape of ventral keel of tympanic bulla can be used as the diagnostic characteristics of the genera. It is highest in *Tursiops* and varies in the order of *Tursiops*, *Stenella*, *Lissodelphis*, *Delphinus*, *Lagenorhynchus*, and *Steno*. A low hemispheric prominence is present on the ventral wall of tympanic bulla near the anterior end of involucrum (Fig. 66).

1. *Tursiops truncatus* in the Japanese waters (Pl. XVI)

The taxonomical position of *Tursiops* in the coastal waters of Japan is not fixed yet. In this paper the name *T. truncatus* is tentatively applied for it after Ogawa (1938) and Rice and Scheffer (1968).

The ear bones of this species are the largest in the Delphininae. Ventral keel develops high and reaches to the anterior margin of the bulla. Interprominential notch is deep, and opens on the lateral wall of tympanic bulla in front of outer posterior prominence. The both posterior prominences are nearly equal in the thickness. In the ventral aspect of tympanic bulla the anterior margin is oval and symmetrical (Fig. 66).

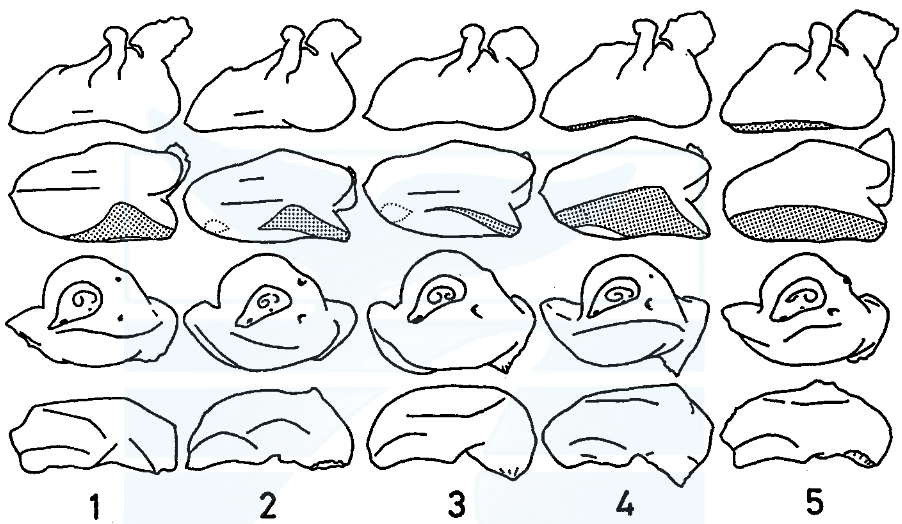


Fig. 66. Schematic figure of tympano-periotic bones of Delphininae. Dotted area indicates ventral keel, and dotted line the hemispheric protuberance. 1, *Steno*. 2, *Lagenorhynchus*. 3, *Delphinus*. 4, *Lissodelphis*. 5, *Tursiops*.

On the periotic, it is characteristic that the posterior margin of the posterior process is smoothly bent to the lateral direction. In other species of this subfamily this part usually forms a clear angle. Fundus of internal auditory meatus opens at the same level with superior process, where small needle-shaped processes are usually formed in the adult individual.

*T. gill* from the eastern Pacific and *T. truncatus* from the north Atlantic could not be distinguished from *Tursiops* in the Japanese waters.

2. *Stenella caeruleoalba* (Pl. XVII)

Though ventral keel is high and straight as in the case of *Tursiops*, the tympano-periotic bone of this species are far smaller. The inner posterior prominence is thinner than the outer, and the ventral view of the anterior margin of tympanic bulla is not oval but possesses a short semicylindrical anterior spine. The antero-lateral part of ventral wall of tympanic bulla slopes laterally, and shows a slight flattening of the bulla.

On the periotic of *Stenella*, the posterior process, anterior process, superior process, and the opening of fundus of internal auditory meatus show wide individual variation, and the identification of the species in this genus is difficult. But the presence of an angle on the border between the dorsal and the posterior margins of posterior process, of a flat area on the superior process which are present also in some Globicephalinae may be used as one of the characteristics of *Stenella*.

One tympano-periotic bone of presumably young *Stenella styx* from the north Atlantic was indistinguishable from that of young *Stenella caeruleoalba*.

(?) *Stenella roseiventris* (Pl. XIX). This means the Hawaiian spinner dolphin. The ventral keel of tympanic bulla is slightly lower than that of *S. caeruleoalba*, and scatters a irregular tubercles on it. Ventral keel is convexed to outer side. Its

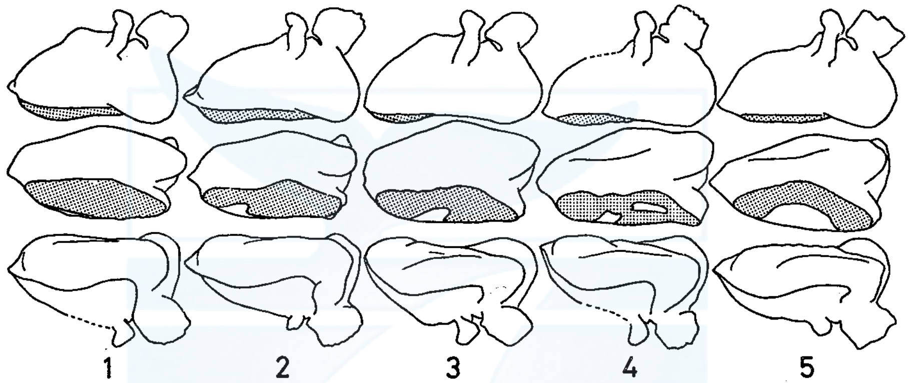


Fig. 67. Schematic figure showing the variation of ventral keel in *Stenella*. Dotted area indicates ventral keel. 1 is observed in *S. caeruleoalba*, 2 in *S. attenuata* and *S. caeruleoalba*, 3 in *S. graffmani*. 4 in *S. longirostris*, 5 in *S. roseiventris*. In the last three species, sample is scarce to find the range of individual variation.

inside slopes to the involucrum (Fig. 67). Though this convexity is also observed on *Delphinus* and *S. longirostris*, the length and width of ventral keel differ between *Delphinus* and *Stenella* (Fig. 66). The swelling at the anterior end of ventral keel is of long oval in the contour. The ventral view of the anterior margin of tympanic bulla is of slender triangle with the anterior spine at slightly outer part (Fig. 67). This species and *S. longirostris* show a common feature in the presence of a low keel on the outer border of ventral surface of tympanic bulla.

(?) *Stenella longirostris* (Pl. XIX). This means the eastern Pacific spinner dolphin, only two specimens are used here. Though the general feature of ventral keel resembles that of *S. roseiventris*, its height is smaller and nearly same with that of *Lissodelphis*. The hemispheric swelling at the anterior end of ventral keel was round in the contour and higher than the ventral keel.

The flat area on the dorsal surface of superior process seems to be larger than that of *S. roseiventris*, but it may be in the range of individual variation.

*Stenella attenuata* (Pl. XVII). This is the spotted dolphins in the Pacific coast of Japan. I hope to reserve the conclusion on the validity of several species of spotted dolphins in the genus *Stenella*. The tympanic bulla and periotic bone of this species resemble those of *S. caeruleoalba*, and the discrimination of tympano-periotic bone of the two species is difficult. The ventral keel is conspicuously high. The round prominence at the anterior end of ventral keel is flat and inseparable from ventral keel.

*Stenella graffmani* (Pl. XVIII) This species indicates the spotted dolphin distributing in the eastern Pacific. The tympanic bulla of this species closely resembles that of *S. attenuata*. But the ventral keel seems to be slightly lower than that of *S. attenuata* or of *S. caeruleoalba* (Fig. 67). The thickness of periotic (measurement no. 14) is slightly smaller in this species than *S. attenuata* and *S. caeruleoalba*, but further confirmation will be necessary.

*Stenella plagiodon* This includes the spotted dolphin in the Atlantic. The tympano-periotic bone resembles that of *S. caeruleoalba* and of other species of spotted dolphins in the Pacific.

3. *Lissodelphis borealis* (Pl. XX)

The size of tympano-periotic bone is similar to that of *Stenella*. On the surface of ventral keel of tympanic bulla distributes a longitudinal fine reticular grooves. Though the ventral keel is long and wide, its height is smaller than that of *Stenella* spp. (Fig. 66). The hemispheric prominence at the anterior end of ventral keel continues to low ventral keel. Inner posterior prominence is thinner than that of *Stenella*, *Delphinus*, and *Tursiops*, and its tip is pointed.

The periotic is characteristic in the flatness of the area surrounded by the posterior margin of the opening of fundus of internal auditory meatus, aperture of ductus endolymphaticus, and aperture of aquaeductus cochleae. The base for the stapedial muscle is concaved, and the aquaeductus cochleae opens on the same plane with the opening of fundus of internal auditory meatus. The last feature is observed also on *Steno*, but in other delphininae species it opens near the posterior wall of cochlear portion (Pl. XX Figs. 4 and 10, and Text Fig. 66). Anterior process is square and slender.

4. *Delphinus bairdi* (Pl. XX)

Banks and Brownell (1969) distinguished the Common dolphin in the eastern Pacific into two species of *D. bairdi* and *D. delphis*, and showed the difference of the habitat. According to my unpublished data, each one specimen from Formosa and Kyushu in southern Japan have the feature of skull coinciding to *D. bairdi*. Probably this *D. bairdi* distributes widely in the warmer warters in the North Pacific. Present specimens includes this Formosa specimen. The Kyushu specimen was used for reference.

The size of tympano-periotic bone is same with that of *Stenella*. The ventral keel of tympanic bulla is so low as that of *Lissodelphis* and inconspicuous especially in the anterior part, where only slender low keel continues to the base of the round hemispheric protuberence at the antero-mesial corner of tympanic bulla (Fig. 66). The inner area of this ventral keel, where fine tubercles are scattered, is wide and slopes to the involucrum. In the ventral view, the anterior border is more acute at the mesial side than the lateral side. The interprominential notch is wider than *Stenella* and *Lissodelphis*, and the bottom is U shaped. A vague longitudinal keel is present along the middle line of ventral wall of tympanic bulla.

The aquaeductus cochleae opens on the posterior wall of cochlear portion as in the case of *Stenella*.

*Delphinus delphis* (Pl. XXI). The thickness of sigmoid process seems slightly larger in this species than in the *D. bairdi*. Similar difference is also observed in the width of the head of sigmoid process (Table 12). Other features are same with *D. bairdi*.

TABLE 12. RANGE OF THE MEASUREMENT NO. 9, WIDTH OF UPPER BORDER OF SIGMOID PROCESS, IN *DELPHINUS*.

| Species | *D. bairdi* | *D. delphis* |
|---|---|---|
| Sample size | 6 | 2 |
| Range in mm | 4.1– 5.0 | 4.8– 5.7 |
| Range in % of standard length | 13.2–15.2 | 14.0–17.0 |
| Mean in% | 14.4 | 16.0 |

TABLE 13. RANGE OF THE MEASUREMENT NO. 7, WIDTH OF TYMPANIC BULLA ACROSS POSTERIOR PROMINENCES, IN *LAGENORHYNCHUS*

| Specie | Sample size | Range in mm | Range in % of standard length | Mean in % |
|---|---|---|---|---|
| *L. obliquidens* | 14 | 14.2–17.7 | 42.0–49.4 | 45.5 |
| *L. acutus* | 3 | 16.0–16.5 | 48.0–49.6 | 49.0 |
| *L. albirostris* | 3 | 20.1–20.5 | 54.2–56.0 | 54.9 |
| *L. obscurus* | 1 | 16.5 | 49.2 | 49.2 |
| *L. australis* | 1 | 15.5 | 47.4 | 47.4 |

5. *Lagenorhynchus obliquidens* (Pl. XXI)

The length of tympano-periotic bone is intermediate of *Tursiops* and *Delphinus*. The height and width of the ventral keel of tympanic bulla exceed those of *Delphinus*, but it fades at or slightly beyond the middle of tympanic bulla. Two vague longitudinal keels are on the ventral surface of the bulla as in the case of *Steno bredanensis* (Figs. 66 and 68). In the ventral view of tympanic bulla the anterior margin is round and has inconspicuous anterior spine which situates slightly outer side. The dorsal contour of the periotic is of arc, this feature is common to all species of *Lagenorhynchus* (Pl. XXI Figs. 15 and 16).

*Lagenorhynchus acutus* (Pl. XXII). A smooth area in the mesial side of ventral keel is wide in this species (Pl. XXII Fig. 1). In the ventral view, the anterior margin of the bulla is triangular and has an anterior spine.

*Lagenorhynchus albirostris* (Pl. XXIII). Tympano-periotic bone of this species is slightly larger than that of *L. obliquidens*.

As the both posterior prominences of tympanic bulla are thick and their tips diverge, the width across the posterior prominences (measurement no. 7) is large (Table 13). Sigmoid process is peculiar in the posteriorly convexed lateral margin

(Fig. 68). The ventral view of anterior part of tympanic bulla is strongly asymmetric.

In the lateral view of periotic, the contour of anterior process, superior process, and posterior process shapes of a arc. Though this feature is common in all Lagenorhynchi species, it is most conspicuous in this species.

*Lagenorhynchus obsculus* and *L. australis* (Pl. XXII). Observation is based on only each one specimen. Though the anterior margin of the ventral view of tympanic bulla is symmetric in both species, the former differs in the presence of a short anterior spine from the latter, in which it is round lacking in the anterior spine. The sigmoid process is thicker in *L. australis* than in *L. obsculus* (Fig. 68).

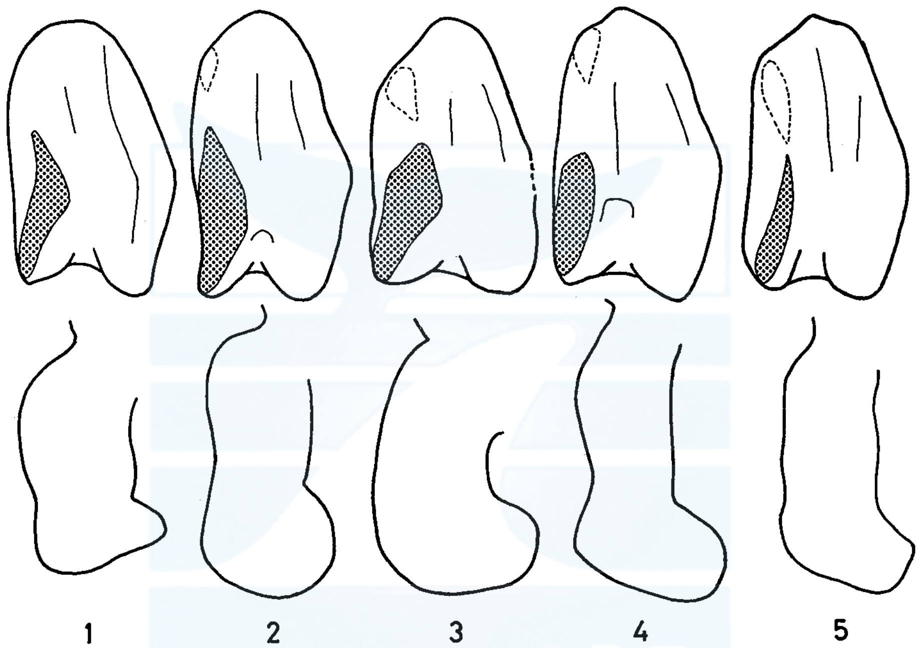


Fig. 68. Schematic figure of the ventral view of tympanic bulla and of lateral view of sigmoid process of *Lagenorhynchus*. 1, *L. australis*. 2, *L. obliquidens*. 3, *L. albirostris*. 4, *L. obscurus*. 5, *L. acutus*. For the dotted area and dotted line see Fig. 66.

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In *L. obsculus*, the interprominential notch is closed at the anterior base of posterior prominences. Though the similar structure is also often observed in *L. obliquidens*, it is more conspicuous in *L. obsculus*.

6. *Steno bredanensis* (Pl. XXIII)

The size of tympano-periotic bone is nearly same with that of *Tursiops*. The ventral keel is developed both in the length and height, but it never reaches to the anterior tip (Fig. 66). The anterior half of ventral wall is cylindrical and presents a deep groove at the antero-lateral border of ventral keel. The ventral view of anterior margin of tympanic bulla is round lacking in the anterior spine. There are observed two low longitudinal keels on the ventral wall of tympanic bulla, as in the case of *Lagenorhynchus*.

The dorsal and posterior surfaces of posterior process of periotic cross at a right angle. On the cochlear portion, the area posterior of the opening of fundus of internal auditory meatus is flat and wide. The aquaeductus cochleae opens in this plane as in the case of *Lissodelphis borealis* (Fig. 66).

*Orcininae*

The tympanic bulla of this group is characteristic in the large size, atrophied ventral keel, no bilaternal compression, and cylindrical anterior portion. Inner posterior prominence is long. Anterior spine is absent.

1. *Pseudorca crassidens* (Pl. XXIV)

The lengths of the tympanic bulla and periotic are in the range between 47.7 mm and 50.5 mm, and 42.8 mm and 49.0 mm respectively. The tympanic bulla of this size with no trace of bilateral compression is found only in this species.

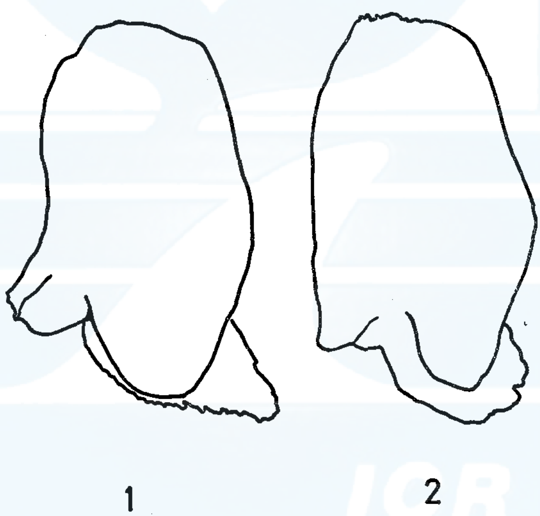


Fig. 69. Contour of the ventral view of tympanic bulla of *Orcinus orca* (1) and that of *Pseudorca crassidens* (2).

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The ventral keel is slightly observed in the posterior half of the bulla. On the inner part of anterior margin of the bulla, there are sometimes observed short needle-shaped processes. The direction of posterior prominences is parallel or slightly converging distally (Fig. 69). Interprominential notch is wide and U-shaped. Though the elliptical foramen was present on all the 4 specimens, some were nearly closing.

The anterior process of periotic is straight and narrow. On the dorsal surface of superior process there is a long longitudinal keel. The area lateral of this keel forms a wide flat area.

2. *Orcinus orca* (Pls. XXIV and XXV)

The tympano-periotic bone of this species is the largest among the recent Odontoceti. On the tympanic bulla, ventral keel is entirely disappeared and the ventral surface is rugose with many scattered tubercles. The inner posterior prominence is smaller than the outer, and the two prominences diverge posteriorly at the angle of about 45°. The bottom of interprominential notch is narrow and V-shaped. Elliptical foramen is completely closed.

On the periotic bone, the superior and anterior processes are massive. In comparizon with other parts of periotic, cochlear portion is small and its diameter (measurement no. 19) is only from 31.8% to 38.6% of the standard length of periotic. Superior process protrudes higher than the opening of fundus of internal auditory meatus, and on its dorsal surface short needle-shaped processes are present.

*Globicephalinae*

The tympanic bulla of this subfamily is strongly flattened laterally. As the result, the lateral and ventral walls cross at a shallow angle, and the distinction of the two parts is not clear. The ventral keel develops well. The inner posterior prominence is short, and its posterior tip does not project posteriorly beyond the base. Anterior process develops in various degree. The frequency of the individuals where elliptical foramen opens varies among the genera. The posterior branch of lower tympanic aperture is narrow.

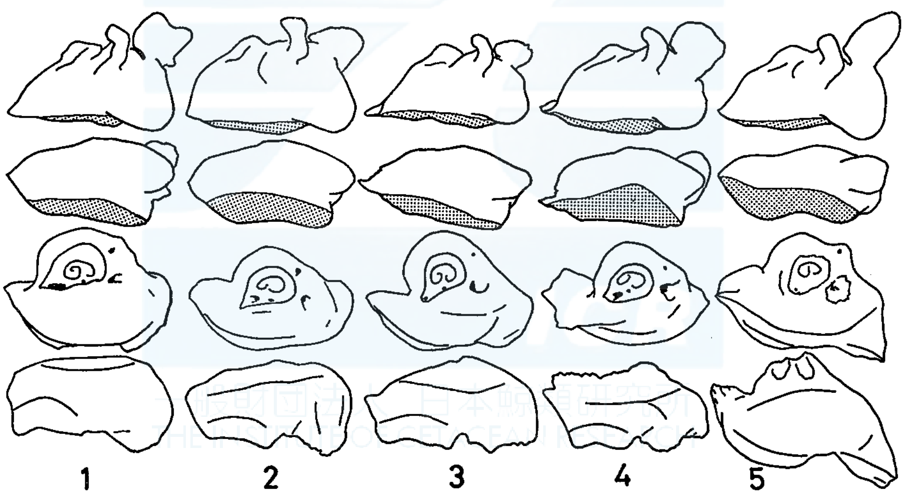


Fig. 70. Schematic figure of tympano-periotic bones of Globicephalinae and *Monodon*. For the dotted area see Fig. 66. 1, *Peponocephala electra*. 2, *Feresa attenuata*. 3, *Globicephala macrorhyncha*. 4, *Grampus griseus*. 5, *Monodon monoceros*.

Usually there is a plateau-like flat area on the dorsal surface of superior process of periotic. In some cases needle-shaped processes are formed on this plateau.

The lengths of tympanic bulla and periotic were observed in the range from 34.0 mm to 52.1 mm and from 30.8 mm to 45.2 mm respectively.

1. *Peponocephala electra* (Pl. XXV)

The lateral compression of tympanic bulla is developed less strongly than other Globicephalinae species (Table 17, Fig. 75). Elliptical foramen of tympanic bulla was present on all 6 individuals studied. The outer slope of ventral keel does not smoothly continue to the ventral surface of tympanic bulla, which condition is different from *Feresa*. The mesial contour of involucrum is straight.

The plateau on the dorsal surface of superior process is wide (Fig. 70), but in lesser degree than *Grampus*. No needle-shaped process is formed on the superior process.

2. *Feresa attenuata* (Pl. XXVI)

The tympano-periotic bone is larger in this species than *Peponocephala*. As the mesial border of involucrum concaves and the outer posterior prominence is directed to postero-mesial direction, the general contour of the ventral view of tympanic bulla convexes externally (Pl. XXVI Fig. 4). The involucrum is short. Anterior spine is short and situates at the center of the bulla. The anterior part of the lateral wall is wide (Fig. 70, top). Similar feature is seen on the tympanic bulla of *Grampus*. The lateral slope of ventral keel smoothly merges into the ventral surface of the bulla. Elliptical foramen was open on the 2 among 7 individuals studied.

The characteristic features of periotic are in the relatively smaller cochlear portion, narrow but thick anterior process, and in the straight contour of the dorsal surface of anterior process and superior process (Fig. 70). The dorsal plane of superior process, on which no needle-shaped process is formed, is not clearly separated from the lateral surface.

3. *Globicephala macrorhyncha* (Pl. XXVII)

On the tympanic bulla of this species, the anterior spine situates slightly at the inner side, and its length increases with the growth of animal. Inner posterior prominence is shorter than the former two species. The lateral view of outer posterior prominence is more stumpy in *Globicephala* and *Grampus* than the former two globicephalids. The height of ventral keel is lower at the middle of the length. The outer slope of the ventral keel is not continuous to the ventral surface of tympanic bulla. As the anterior part of the lateral wall of tympanic bulla is narrow, its lateral view is triangular. Elliptical foramen was present, among 26 animals studied, on only one adult male of 431 cm in body length. The presence of this foramen is considered to be individual variation.

When seen from the lateral side, the dorsal contour of anterior, superior, and posterior process of periotic is round. Anterior process is thin. Superior process is not wide. Needle-shaped processes are sometimes formed on the dorsal surface of superior process.

The ear bone of *Globicephala melaena* (Pl. XXVII) was not distinguished from that of *G. macrorhyncha*.

4. *Grampus griseus* (Pl. XXVI)

The tympanic bulla is characteristic, as *G. macrorhyncha*, in the strong flatness, short inner posterior prominence, and stumpy outer posterior prominence. But it differs from *G. macrorhyncha* in anteriorly expanded anterior border of lateral wall of tympanic bulla, and the shape of ventral keel. In *Grampus* the ventral keel is not low at the middle but shows the same height from the posterior end to the anterior. But its height and width show wide individual variation. The outer slope of ventral keel is not continuous to the ventral surface of the bulla. Anterior spine is on the anterior end of involucrum, but is lacking in rare case. Elliptical foramen was found on one among 12 individual.

Periotic is massive. A conspicuous semicircular plateau project on the dorsal surface of superior process. But on some individual, crowded needle-shaped processes conceal this plateau. Anterior process of periotic is short (Fig. 70).

*Monodontidae*

This family includes only one species *Monodon monoceros.* The following description is for it (Pl. XVIII).

The tympano-periotic bone is larger than those of Globicephalinae. The tympanic bulla is strongly flattened. Its width is only from 37.5% to 41.4% of the tympanic length (Table 17, Fig. 75). Ventral keel is high and sigmoidal. Involucrum strongly increases the thickness near the anterior end. Inner posterior prominence is thin and very short. Outer posterior prominence is long. Elliptical foramen was closed on all observed specimens. Anterior spine is short. The width of the posterior branch of lower tympanic aperture is wider than those of Globicephalinae (Table 14).

TABLE 14. RANGE AND MEAN OF THE MEASUREMENTS OF TYMPANO-PERIOTIC BONES IN SOME DELPHINOIDEA SPECIES, SHOWN BY THE PERCENTAGE OF THE STANDARD IENGTH.

| Species | Measurement No. 10 | Measurement No. 18 | Sample size |
|---|---|---|---|
| *Monodon monoceros* | 5.2– 9.7, 7.5 | 51.3–68.4, 63.3 | 4 |
| *Globicephala macrorhyncha* | 2.5– 5.7, 3.8 | 37.0–74.8, 48.5 | 26 |
| *Tursiops truncatus* | 2.2– 9.2, 4.5 | 35.1–52.8, 43.0 | 43 |
| *Phocaenoides* spp. | 7.7–12.6, 9.7 | 37.9–44.4, 40.7 | 12 |
| *Delphinapterus leucas* | 10.1–11.8, 10.8 | 44.4–53.0, 48.9 | 3 |

Measurement no. 10: Width of posterior branch of lower tympanic aperture.
Measurement no. 18: Length of the facet on posterior process of periotic.

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On the periotic, the opening of fundus of internal auditory meatus is surrounded by the thick needle-shaped processes. Crista transversa is inconspicuous. The contour of the opening of fundus of internal auditory meatus shows wide individual variation, but it is usually round.

The long posterior processes of tympanic bulla and of periotic are firmly sutured and project laterally. Their lengths are nearly same.

## BIOMETRICAL BETWEEN-SPECIES SIMILARITY OF TYMPANO-PERIOTIC BONES

The between-species similarity indices of tympano-periotic bones were calculated from the 18 measurements and 4 morphological characteristics shown in Table 3. As this is not to study the taxonomy of individuals but the systematic relationships of species, species are used for the unit of discussion. As shown in Figs. 71 and 72, the 29 species were compared. The numbers of individuals in one species are between 4 and 43 with the average of 9.1 individuals (Table 2).

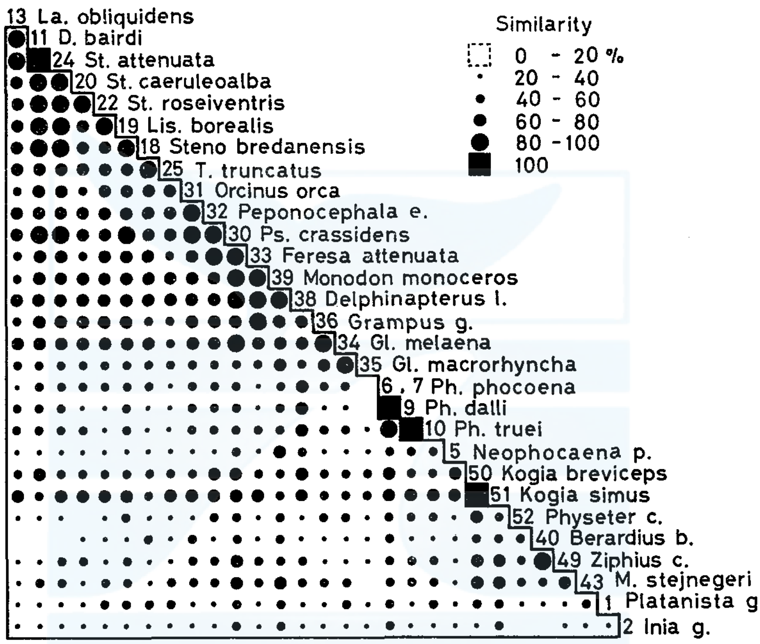


Fig. 71. Matrix of similarity coefficient calculated from morphological measurement of tympano-periotic bones of recent toothed whales. On the scale, the upper limits are not included in the range. The numbers coincides with those shown in Table 2. For other explanation see text.

In the calculation of the similarity indices, the standard lengths (measurement nos. 1 and 13) were compared in the value shown in mm but other measurements were calculated into the percentage of the standard length and then compared, because it is not desirable to compare repeatedly the size of the tympano-periotic bone by using the actual measurements. The 95% confidence limit of the mean value were calculated in each measurement and species. Then the ranges were compared between the selected two species. The number of overlapped measurements shown by the percentage of compared characteristics was used as the similarity index between the two species. Same comparizon was made between each combination of the species. For the non-numerical characteristics, nos. 11, 12, 20, and 21, the calcula-

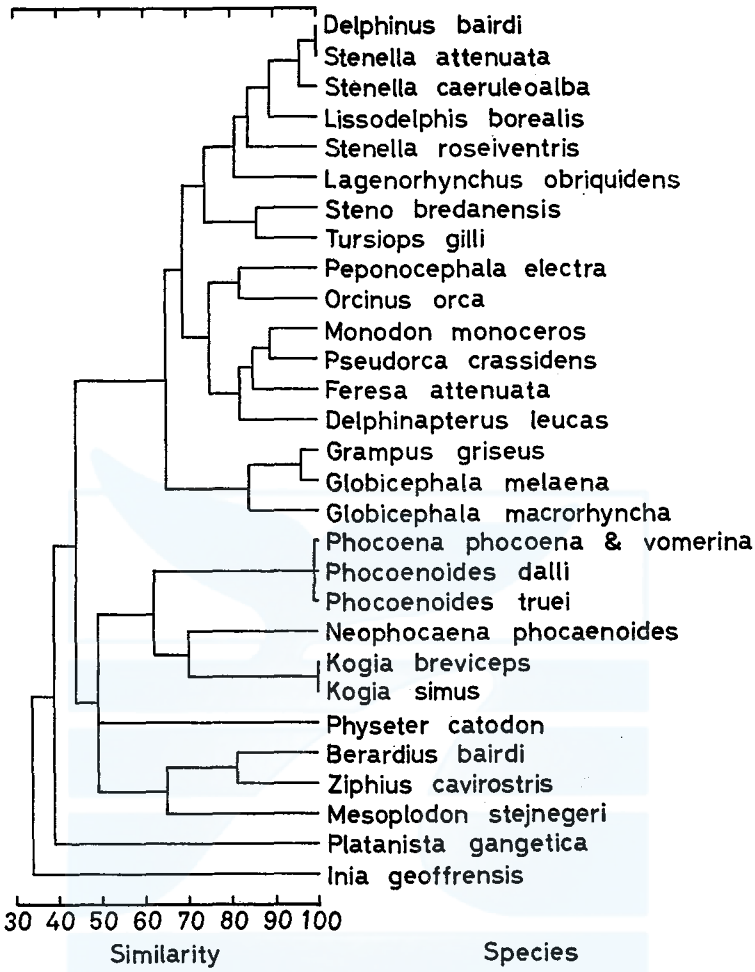


Fig. 72. Phenogram calculated from the matrix in Fig. 71. For explanation see text.

tion of the confidence limits was not made but compared in the similar manner mentioned above. This resut is shown by the matrix in Fig. 71. The phenogram shown in Fig. 72 was obtained from this matrix combining repeatedly the species of higher similarity with the average linkage method (Sokal and Sneath 1963).

The result obtained here is influenced by the number of samples in each unit, especially when the number of sample is small. And even when this result correctly indicates the morphological resemblance of tympano-periotic bone, it is incorrect to consider that it shows perfectly the phylogenetic relationships of the species, because the compared organ is very limitted.

In Fig. 71, the species from *Lagenorhynchus* to *Globicephala* show a higher similarity, which are species included into Delphinoidea in this study. In the Delphinoidea, *Delphinus*, *Lagenorhynchus*, *Stenella*, *Lissodelphis*, *Steno*, and *Tursiops* show the higher similarity than the other genera of Delphinoidea. The former group coincides with Delphininae, but the latter includes not only Globicephalinae and Orcininae but also *Monodon* and *Delphinapterus*. This will mean that Globicephalinae, Orcininae, Monodontidae, and Delphinapteridae can not be separated by the similarity index.

As shown in the matrix the tympano-periotic bone of Phocoenidae shows large morphological distance from that of other members of Delphinoidea. And the phenogram in Fig. 72 shows the higher similarity between the genera of Phocoenidae and *Kogia*. But as indicated in the latter chapter their tympano-periotic bones have a fundamental structural difference in the connection to the skull, and those of Phocoenidae seems to be the very specialized of Delphinoidea type tympano-periotic.

The low similarity between *Platanista* and *Inia* suggests their low phylogenetic affinity. The species of Physeteridae and Ziphiidae show a low similarity to other taxa.

## EVOLUTION OF THE TYMPANO-PERIOTIC BONE

When the morphology of tympano-periotic bone is compared between the taxa of toothed whales, there are found various kind of morphological pecuriorities which are common to several taxa, show successive change from one taxon to another, or can be lead from that of another taxon. These characteristics are considered to have been attained as the result of evolution of toothed whales. And their analysis will reveal the process of specialization of tympano-periotic bone which have occurred in the history of Odontoceti. This chapter is to consider the process of the evolution of some important morphological features of tympano-periotic bone of toothed whales.

### *Interrelationships between tympanic bulla, periotic, and skull*

In the land mammals the pars tympanic and pars petrosa, which correspond to the tympanic bulla and periotic of Cetacea, are connected to squamosal and exoccipital by processus mastoideus, and form a part of cranial wall. But in the toothed whales the tympano-periotic bone does not form a part of cranial wall. I consider that the pars mastoidea or mastoid process is fused to tympanic bulla and corresponds to the posterior process of tympanic bulla.

Fraser and Purves (1960, p. 77) classified the interrelationships between mastoid process and skull into the following 3 types, or the type where all the element of mastoid process is fused to tympanic bulla (*Kogia*), the type where all the element of mastoid process is fused to squamosal (*Platanista*, Delphinoidea) and the intermediate type where part of mastoid process is fused to tympanic bulla and the remaining to squamosal (*Physeter*, Ziphiidae).

But on my observation on *Physeter catodon* and other Physeteroid species, another interpretation is possible. On the skull of smaller fetus of *Physeter catodon* (Pl. I Fig. 1), mastoid process (posterior process of tympanic bulla) is imperfect, and the " mastoid element " of Fraser and Purves (1960) on the posterior region of squamosal

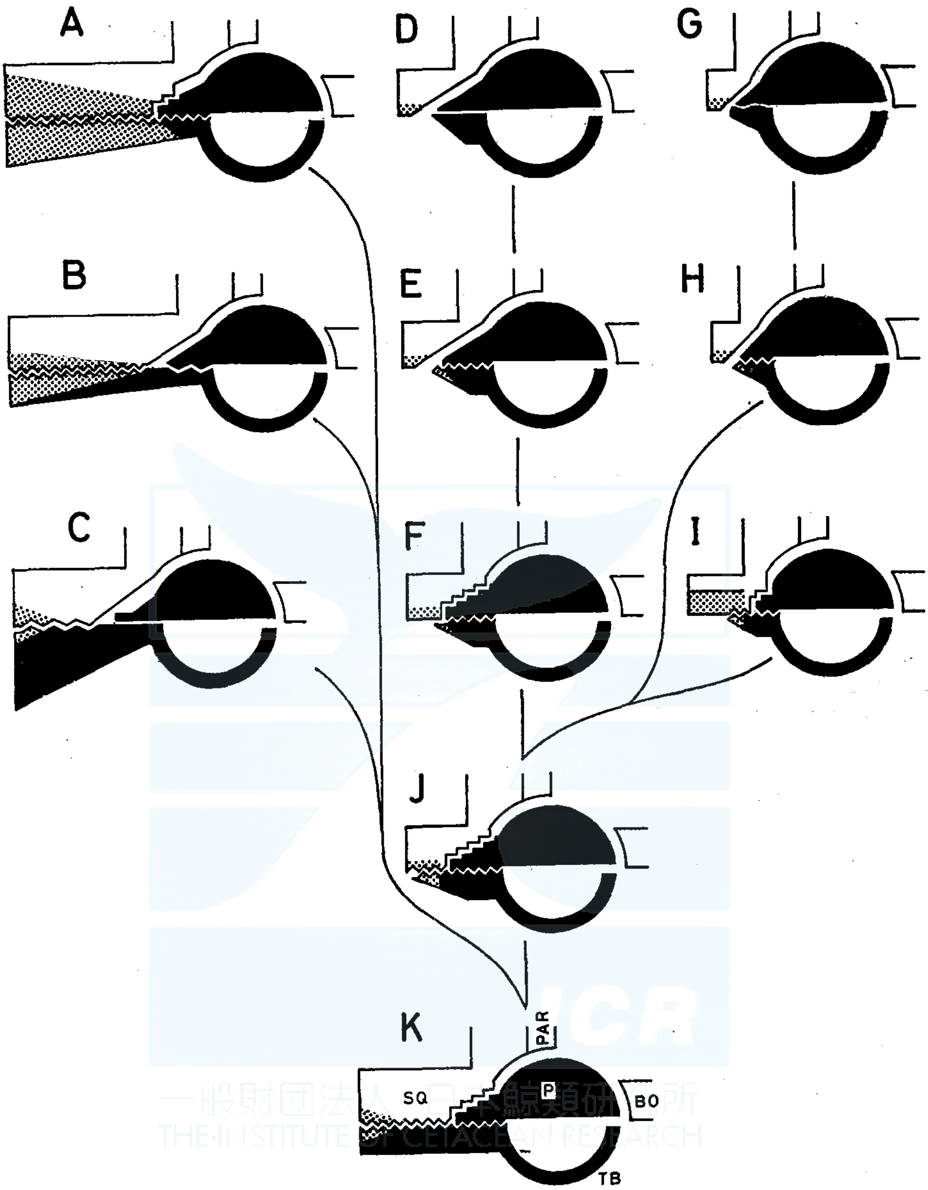


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Fig. 73. Tympano-periotic bones of toothed whales, arranged according to the degree of specialization of the connection between tympanic bulla, periotic, and skull. Waved edge indicates suture or tight connection of bones, and dotted area the laminated structure. A, *Physeter*. B, Ziphiidae. C, *Kogia*. D, Phocoenidae. E, Delphinoidea except D and F. F, *Delphinapterus*. G, *Pontoporia*. H, Iniidae. I, *Platanista*. J and K, Hypothetical primitive toothed whale. BO, Basioccipital. P, Periotic. PAR, Parietal. SQ, Squamosal. TB, Tympanic bulla.

is less developed and its structures is continuous to squamosal. The size and laminated structure of this part becomes larger on 5.0 m newborn calf (Pl. I Fig. 2), and finally in the adult attains the similar laminated structure as that of posterior process of tympanic bulla (Pl. I Fig. 3). The vague laminated structure is observed on the posterior region of squamosal even on *Kogia* and Ziphioid species which posterior process scarcely shows the laminated structure (Pl. I Figs. 4 and 5). Accordingly I consider that the posterior region of squamosal suturing to posterior process of tympanic bulla have developed the similar laminated structure, in the toothed whales, accompanied with the development of laminated structure on the posterior process of tympanic bulla. This hypothesis can explain more simply the evolution of the interconnection of tympanic bulla and skull.

Though there are observed, in the recent toothed whales, various patterns of interrelationship between tympano-periotic bone and the skull. They are continuous in some point of view, and can be classified into the following 7 patterns.

*Platanista-type*

This type is observed only in *Platanista gangetica*. It resembles *Physeter*-type but differs in the posterior process of tympanic bulla.

The small posterior process of tympanic bulla is loosely sutured to squamosal and exoccipital with about 2/3 area of the distal lateral portion of the process. The remaining inner proximal 1/3 area forms the loose suter with posterior process of periotic (Pl. I Fig. 7). There is developed a fine laminated structure, as in the case of *Physeter*, on the postero-ventral portion of squamosal to which the posterior process of tympanic bulla attaches. This laminated portion of squamosal is separated by a slit extending from the postero-dorsal margin, and has a connection with the main part only at the antero-ventral part (Pl. I Fig. 6). The posterior process of tympanic bulla is slightly seen on the surface of skull in the jevenile, but is hidden in the adult. The dorsal and posterior surface of the posterior process of periotic have a contact with the squamosal. One of the peculiar feature of this species is the small conical process projecting from the postero-dorsal wall of upper tympanic aperture. This process, posterior process of tympanic bulla, and squamosal interlock each other. As the result it is impossible to separate the three, without destroying one of them. This structure may have developed as the result of the specialization of *Platanista*.

The fossil Platanistid, *Zarhachis flagellator* (Kellogg 1924) belongs to this type. It is supposed from its shape that the posterior process of periotic of some of Eurhinodelphinid species (*Shizodelphis sulcatus*, Van Beneden and Gervaise 1868–1879) had the connection with squamosal but not in another species (*Eurhinodelphis longirostris*, Abell 1902). Anyway they differs from *Platanista* in the larger size of posterior process of periotic.

*Physeter-type*

This type is found only in *Physeter*, and differs from the former type in the large and highly laminated posterior process of tympanic bulla and weaker connection of periotic and squamosal.

The long and strongly laminated posterior process of tympanic bulla is wedged between squamosal and exoccipital. The postero-ventral portion of squamosal is also strongly laminated, and to this part the posterior process of tympanic bulla sutures. Though the suture is loose, it is impossible to separate the two part without destroying some of the suture.

The posterior surface of posterior process of periotic is rugose suggesting a contact with squamosal. On the miocene Physeteroid species, the periotic bone of *Orycterocetus crocodilinus* (Kellogg 1965) is supposed from the long posterior process and the rugosity to have had a stronger connection with squamosal, but *Aurophyseter morricei* in the same age (Kellogg 1931) had the smaller posterior process of periotic, which suggest the probable variety of posterior process of periotic among Physeteroid species.

There are observed longitudinal shallow grooves and ridges of the similar intensity as that of *Platanista* on the facets of posterior processes of tympanic bulla and of periotic, which does not form such a strong suture found on Delphinidae.

*Ziphius-type*

This type is observed on all the Ziphioid species. The interrelationships between squamosal, exoccipital, and posterior process of tympanic bulla is same with the *Physeter*-type. But this differs from it in the less developed laminated structure of squamosal and of the posterior process of tympanic bulla, in the separation of periotic and squamosal, and in the almost smooth facets on both posterior processes.

There is not observed such a highly laminated structure of squamosal and of posterior process of tympanic bulla as found in *Physeter*, but the laminated structure is restricted on their suturing surfaces. The posterior process of tympanic bulla is slender. This type is considered to be the intermediate of *Physeter*-type and *Kogia*-type.

*Kogia-type*

This is found on *Kogia*. The posterior process of tympanic bulla is short and the distal end is widely expanded in a funnel shape. The laminated structure of posterior process of tympanic bulla and of squamosal is restricted to the narrow area on the surface of the skull (Pl. I Fig. 5). The facets on the both posterior processes are perfectly smooth and forms no suture. Posterior process of periotic has no contact with squamosal.

*Delphinapterus-type*

This type is represented by only one species *Delphinapterus leucas*. The posterior process of periotic is firmly sutured with squamosal (Pl. I Fig. 8, Kleinenberg *et al.* 1964). On the removed periotic bones (AMNH 180017 and USNM 275075), the dorsal surface of the posterior process of periotic has the irregular deep grooves which are considered to help the connection between periotic and squamosal. But this structure is not observed on the juvenile specimen (USNM 7356). The connection between the posterior process of tympanic bulla and squamosal was not confirmed. Other characteristics are same with the *Delphinus*-type.

Probably this type will retain the more primitiveness than the next *Delphinus*-type.

*Delphinus-type*

This type is represented by all the species of Iniidae and Delphinoidea except those of Phocoenidae. The tympano-periotic bone looses the direct sutural connection with the surrounding elements of the skull, but is fixed with ligament in the cavity formed by basioccipital, exoccipital, and squamosal.

The posterior process of tympanic bulla is usually longer than that of periotic. At the tip of the former there is a small spongy structure, which will probably be the remaining of the laminated or spongy structure found in the proceeding types. The postero-ventral part of squamosal also retaines the small laminated structure. The both posterior processes are, as mentioned by Yamada (1953), firmly sutured by the help of ridges and grooves on the facets.

*Phocoena-type*

This type is seen in *Pontoporia* and all the species of *Phocoenidae*. This is characterized by the absence of the spongy osseous tissue at the tip of posterior process of tympanic bulla, and by the smooth or almost smoth facets of the posterior processes of tympano-periotic bone. Other features are same with the former *Delphinus*-type.

*Relationships between the types*

Fig. 73 shows the various types of the relation between tympanoperiotic bone and skull arranged in accordance with the degree of the specialization. This indicates that there are three main series of evolution in the tympano-periotic bone of recent toothed whales. The tendency of the degeneration of sutural connection between tympanic bulla, periotic, and squamosal is observed in every three series. It is also passible to say that the connection between skull and periotic through the tympanic bulla is getting weaker. This specialization may have some relation with the adaptation of acoustic systems into the water.

In the first series, or that of Physeteroidea, the posterior process of tympanic bulla is not atrophied but attained the increase of the size, and in some species high specialization of the structure of posterior process of tympanic bulla and of squamosal is observed. This does not necessarily mean the rigid connection between skull and tympano-periotic bone, but it is becoming weaker in the Physeteroidea series as in the case of other series. Though the connection between the periotic and squamosal seems to be rather strong in *Physeter catodon*, the connection between squamosal and posterior process of tympanic bulla is not strong as the result of the development of the laminated structures on the corresponding portion. And the connection between the both posterior process is also not strong. These are considered to have produced in some degree the weaker connection between skull and periotic through the posterior process of tympanic bulla. In *Kogia*, on the other hand, the structure of posterior process of tympanic bulla and squamosal is not so specialized, but the connection between the two parts, and that between both posterior processes have become very weak. These features suggest that the two genera of Physeteroidea, or *Kogia* and *Physeter* have attained slightly different modes of specialization. Ziphiidae shows the intermediate character of *Physeter* and *Kogia* in this point of view.

The second series, or the types found in Delphinoidea are considered to have derived from an ancestral type common with that of Physeteroidea, where the connection between skull and tympano-periotic bone was present. The both posterior processes of tympanic bulla and of periotic are atrophied in size. And there are observed various stages of specialization from the most primitive *Delphinapterus* to the most specialized Phocoenidae. Probably the tympano-periotic bone of the most of the species in the recent Delphinoidea may have attained the present condition, in which it is usually separated from the skull, through the stage found in *Delphinapterus leucas*.

The 3rd series is formed by the species of Platanistoidea. Though the ralation between skull, tympanic bulla, and periotic of *Inia*, *Lipotes*, and *Pontoporia* belongs to the *Delphinus*-type or to *Phocoena*-type, they should be separated from the 2nd series because of the stronger atrophy of the size of the posterior processes which is found also in *Platanista*, and of other morphological features common to Platanistoidea. Among the 4 species of Platanistoidea, the relationships between tympanic bulla, periotic, and skull is most specialized in *Pontoporia* and least in *Platanista*. As *Platanista* has too highly specialized structure of squamosal, the ear bone of two other families can not be directly led from *Platanista*. The structure of ear bones of the two families may have derived from a original type which is probably close to the ear bone of primitive *Platanista*. There is expected hypothetical type which connects the 2nd and 3rd series, where the decrease of the length of posterior process is started but the connection between the two processes and squamosal is retained together with the small part of laminated structure.

*Platanista* and *Physeter*, and in lesser degree all Physeteroidea species, retain the primitiveness in having the connection between skull and tympano-periotic bone. But their skulls show high specialization in the developed maxillary or premaxillary crests. If these crests have the relation with the acoustics (Norris 1968), it may be presumed that these species have developed a mechanism of hearing slightly different from other species.

As mentioned in the former chapter, the specialized posterior processes of periotic and tympanic bulla observed in Phocoenidae and Pontoporiidae resemble that of juvenile individuals of less specialized Delphinidae. This suggests that the specialization occured on the posterior processes of tympanic bulla and of periotic of Platanistoidea and Delphinoidea is one of the neoteny.

*Sigmoid process and lateral furrow*

The sigmoid process is a prominent plate projecting dorsally on the lateral wall of tympanic bulla and forming the anterior wall of lower tympanic aperture. This process is observed in all the species of Cetacea, and shows the pecuriorities in each taxa. Lateral furrow is a groove found on the lateral wall of tympanic bulla in front of sigmoid process. Here is discussed the morphological variations and the interrelationships.

In Physeteroidea the sigmoid process is square and the length of the dorsal margin is not less than that of lateral margin. The lateral furrow varies among the three families. In Ziphiidae, as the lateral margin of sigmoid process is twisted posteriorly, its front surface is directed antero-laterally. The lateral margin is not longer than the dorsal and the thickness is thin. The lateral furrow is deep and conspicuous. On the other hand, in *Physeter*, the lateral furrow is entirely disappeared. And the dorsal margin of sigmoid process is so long as 1.7 times of the lateral, and the front surface is exactly directed to the anterior axis of tympanic bulla. The thickness of sigmoid process of *Physeter* is thin as in the case of Ziphiidae. The sigmoid process of *Kogia* is globular, but it is not twisted. As seen in Pl. VII Fig. 5 and Pl. VIII Figs. 2 and 17, the contour and direction of sigmoid process of *Kogia* resembles those of *Physeter*.Lateral furrow is absent in *Kogia*.

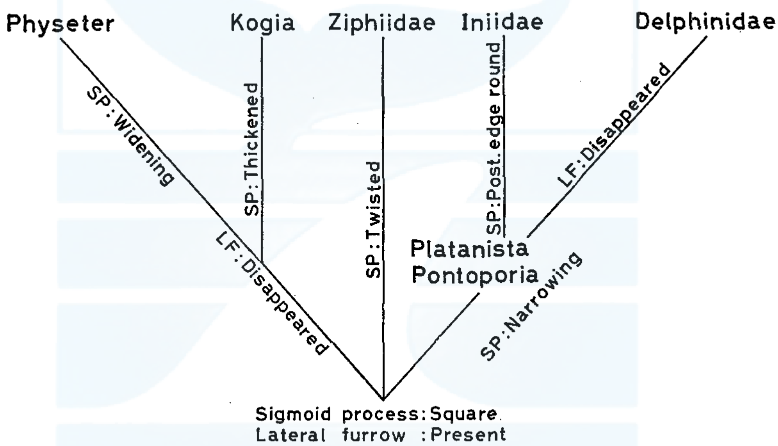


Fig. 74. Diagram showing the specialization of the sigmoid process (SP) and lateral furrow (LF) in recent toothed whales.

Though Platanistoidea resembles Physeteroidea in the wide sigmoid process, its lateral margin is parallel to the lateral wall of tympanic bulla similar with that in Delphinoidea. Lateral furrow is present in all species of Platanistoidea. In *Platanista* the front surface of sigmoid process is placed to coincide with the antero-posterior direction of tympanic bulla, and the lateral margin and the dorsal margin cross at a right angle. The sigmoid process of *Pontoporia* is similar with that of *Platanista*, but the thickness is slightly larger. In both genera the lateral furrow is shallow. In two genera of Iniidae, *Lipotes* and *Inia*, the lateral margin of sigmoid process is round and twisted to the posterior. This feature can be lead from that of *Platanista*. The lateral furrow is deep.

The sigmoid process of the species in Delphinoidea coincides with that of *Platanista* in important features, but differs from it in the smaller thickness and width.

The lateral view is L-shaped. The lateral furrow is usually absent, but in some cases it remains vestigeally. These features are able to be lead from those of *Platanista* by small modification.

In the fossile species, the sigmoid processes of *Zygorhyza kochii* and *Dorudon osiris* of Archaeoceti which may not be the direct ancestor of Odontoceti, are thin and square with long dorsal margin (Kellogg 1936) as that of *Physeter catodon*. The lateral furrow was vaguely present on the both Archaeoceti species. But, of course, it is not impossible to lead the sigmoid process of Mysticeti from that of Archaeoceti. The tympanic bulla of upper miocene Odontoceti, *Phocageneus venustus* (Kellogg 1957) and *Zarhachis flagellator* (Kellogg 1924) resemble that of *Platanista* in the wide and thick sigmoid process and in the presence of shallow lateral furrow. An Eurphinodelphinid species *Schizodelphis sulcatus* has the sigmoid process similar to that of *Platanista*, but it seems not to have retained the lateral furrow. The moderm delphinid species *Kentriodon pernix* (Kellogg 1927) has the lateral furrow.

From the comparison of the sigmoid process of Odontoceti species described in the above, the following consideration is possible. The sigmoid process of the three species of platanistoidea can easily be led from that of *Platanista gangetica*, and even that of Delphinoidea from that of *P. gangetica* in another process.

The various shape of sigmoid process observed in Physeteroidea seems to have originated from a common type which is square, flat, not twisted, and prepared a lateral furrow in front of it. The sigmoid process of *Platanista gangetica* also able to be led from this imaginative original type through the decrease of the width. This original type may probably derived in Oligocene or earlier ages from some species of Agorophiidae or Squalodontidae, on which sigmoid process I have no information.

Fig. 74 shows one of the most probable procedure which may have happened in the process of evolution of sigmoid process and lateral furrow of tympanic bulla.

*Elliptical foramen*

The elliptical foramen (Yamada 1953) and vertical cleft of Archaeoceti and Mysticeti (Kellogg 1936) are homologous. In the Mysticeti, by the absence of inner pedicle of tympanic bulla the vertical cleft forms a concavity connected to lower tympanic aperture. But in Archaeoceti and Odontoceti, as posterior process of tympanic bulla is connected by outer and inner pedicles to conical process and in-involucrum respectively, vertical cleft is separated from lower tympanic aperture, and the elliptical foramen is formed.

In some taxa of recent Odontoceti, the elliptical foramen is closed or going to be closed. This tendency seems to have happened independently in various small taxa. Its featurs are as follows.

*Physeteroidea*

Elliptical foramen is perfectly disappeared in Physeteridae and Kogiidae. The elliptical foramen exists in all species of Ziphiidae, but the opening is irregularly shaped and sometimes narrowed by a thin plate of bone. This indicates that the elliptical foramen of Ziphiidae is on an earlier stage of the closure.

*Platanistoidea*

In the two species of Iniidae the elliptical foramen opens round except one individual of *Inia*. On this individual of *Inia geoffrensis* (LACM 19588) elliptical foramen opened only on the right side. In *Platanista gangetica* elliptical foramen was present on all individuals observed. But its opening is constricted by thin bone tissue and it opens only through several small holes penetrating it. Probably the elliptical foramen of this species is also on the process of the closure. Elliptical foramen is perfectly disappeared on *Pontoporia blainvillei*.

*Delphinoidea*

In all the species constituting Delphinapteridae and Phocoenidae elliptical foramen is closed. In Delphinoidea its condition varies among the subfamilies. The elliptical foramen is oval and its margin is thickened in all the species of Delphininae. But the percentage of the opened elliptical foramen varies in the species of Globicephalinae. In *Peponocephala electra* it was present on all the 6 animals studied, in *Feresa attenuata* on 2 individuals among 7 studied, in *Globicephala macrorhyncha* on 1 among 26, in *Grampus griseus* on 3 among 12. This observation suggests that Globicephalinae is a group of species where the closure of elliptical foramen is progressing in various degree.

In Orcininae *Pseudorca crassidens* has the elliptical foramen opened, but it is closed in *Orcinus orca*. This indicates that tympanic bulla of *Orcinus* is more specialized than that of *Pseudorca*. *Sousa teuszii*, *Sotalia* spp., and *Cephalorhynchus* spp., which are included tentatively into Sotaliinae, usually have the elliptical foramen entirely closed.

The elliptical foramen of *Monodon monoceros*, included into Monodontidae, was open on 1 individual among 4 animals studied.

*Flatness, Ventral keel, and median furrow of tympanic bulla*

The flatness of tympanic bulla mentioned below is the characteristics concerning the angle at which the lateral wall and ventral wall cross. This feature is prodused, in Delphinoidea, by the bilateral compression of tympanic bulla. On primitive tympanic bulla the two walls crosses at nearly a right angle, but on some specialized or flat one they cross at larger angle. The developement of ventral keel and the disappearence of median furrow are observed often in accompanied with the progress of flattening.

The tympanic bullae of the two species of Archaeoceti mensioned in the chapter of " sigmoid process and lateral furrow ", and of three fossile Odontoceti *Phocageneus venustus*, *Zarhachis flagellator*, and *Schizodelphis sulcatus* have the ventral wall crossing with the lateral wall at about 90° or slightly smaller angle, and the median furrow extending anteriorly from the interprominential notch. And ventral keel is not developed on these species. But in *Kentriodon pernix*, though the bilateral compression is not developed, the median furrow is almost disappeared and ventral keel is developed.

These observations suggest that the primitive tympanic bulla shows no flattening and no development of ventral keel but possesses the median furrow, and that the tympanic bulla of recent Odontoceti attained, starting from the primitive type, various combination of the specialization in median furrow, ventral keel, and the bilateral compression. Discussions on the process of these specialization are made below.

*Physeteroidea*

Median furrow is entirely lost in Physeteridae and Ziphiidae, but in two species of Kogiidae is retained the slight vestige of the furrow. On the tympanic bulla of *Kogia* the ventral keel is not developed and the lateral and ventral walls cross at a right angle, which is one of the characteristics showing the primitiveness of the tympanic bulla.

The dorsal part of the lateral wall of tympanic bulla is, in Ziphiidae, strongly rolled into the inner direction, and the inner posterior prominence moved to the reverse. This modification is quite different from the usual bilateral compression observed in other famillies of Odontoceti, but produces one of the flat feature of the bulla. This flatness is strongest in *Ziphius* in which the lateral wall and ventral wall form nearly continuous arc, and gradually decreases in the order of *Mesoplodon*, *Berardius*, and *Hyperoodon*. The ventral keel is inconspicuous in all Ziphioid species, and especially in *Ziphius*.

The tympanic bulla of *Physeter catodon* is cylindrical and shows a pecurior transformation of the both posterior prominences (see page 23). This shape can be led from the tympanic bulla of primitive *Kogia* as a result of the reduction of outer posterior prominence and the movement of inner posterior prominence toward the direction reverse of that occurred in Ziphiidae.

*Platanistoidea*

The tympanic bullae of the species of this superfamilly show no flattening. Median furrow is observed in all species. The tympanic bullae of *Platanista gangetica*, *Inia geoffrensis* and *Lipotes vexillifer* have common features in the weak ventral keel, swollen base of outer posterior prominence, and the conical anterior tip.

The general shape of the tympanic bulla of *P. gangetica* shows close resemblance to that of the fossile species *Phocageneus venustus*, *Shizodelphis sulcatus*, and *Zarhachis flagellator*, except for the many needle-shaped processes in the ventral furrow of *P. gangetica*.

The tympanic bulla of *Pontoporia blainvillei* slightly differs from that of other Platanistoidea species in the slight development of ventral keel and the shape of anterior tip.

*Delphinoidea*

In this superfamily, the flattening or bilateral compression of tympanic bulla is well observed in the species included into Monodontidae and Globicephalinae. The median furrow is found clearly only on some species included into Sotaliinae, but ventral keel on various species of Delphinoidea. Further explanation is made below on each families or subfamilies.

In *Delphinapterus leucas* and *Orcaella brevirostris*, which constitute Delphinapteridae, the tympanic bulla is not flattened and ventral keel is low.

In Phocoenidae, rudimental median furrow is present in all species, and flattening is not observed. The ventral keel is not conspicuous in *Phocoena*, but develops well in *Neophocaena* and highest in *Phocoenoides*.

The tympanic bulla of *Monodon monoceros* shows the strong flatness and has developed ventral keel. In these respect it looks like to situate at the extremity of Globicephalinae series (Fig. 75).

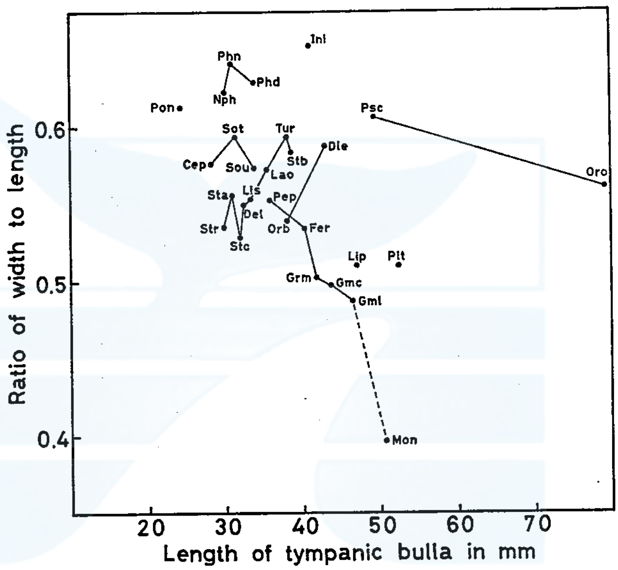


Fig. 75. Relation between mean length of tympanic bulla and mean ratio of the width to the length. Cep, *Cephalorhynchus* spp. Del, *Delphinus bairdi*. Dle, *Delphinapterus leucas*. Fer, *Feresa attenuata*. Gmc, *Globicephala macrorhyncha*. Gml, *Globicephala melaena*. Grm, *Grampus griseus*. Ini, *Inia geoffrensis*. Lao, *Lagenorhynchus obliquidens*. Lip, *Lipotes vexillifer*. Lis, *Lissodelphis borealis*. Nph, *Neophocaena phocaenoides*. Mon, *Monodon monoceros*. Oro, *Orcinus orca*. Orb, *Orcaella brevirostris*. Pep, *Peponocephala electra*. Phd, *Phocoenoides* spp. Phn, *Phocoena phocoena*. Plt, *Platanista gangetica*. Pon, *Pontoporia blainvillei*. Psc, *Pseudorca crassidens*. Sot, *Sotalia* spp. Sou, *Sousa teuszii*. Sta, *Stenella attenuata*. Stb, *Steno bredanensis*. Stc, *Stenella caeruleoalba*. Str, *Stenella roseiventris*. Tur, *Tursiops truncatus* (W. Pacific). Solid lines connect the members in a family or subfamily.

In Delphinidae, the morphology of tympanic bulla shows several characteristic features in each subfamily or lesser taxa. In the three genera tentatively included into Sotaliinae, the tympanic bulla is not flattened and ventral keel is slightly developed. Shallow median furrow is observed in *Sotalia* and *Sousa*, but inconspicous in *Cephalorhynchus*. This is one of the primitive features of the tympanic bulla of these species.

In Delphininae there is not observed the flattening of tympanic bulla nor median furrow. The genera of this subfamily is divided into two groups by the character of ventral keel. The first group includes *Tursiops*, *Stenella*, and *Lissodelphis*. Their ventral keel is long and reaches the anterior part of ventral wall of tympanic bulla. Its height is largest in *Tursiops* and lowest in *Lissodelphis*. The second group includes *Delphinus*, *Lagenorhynchus*, and *Steno*. In these genera the ventral keel does not reach the anterior part, but disappears near the middle of tympanic bulla. As the result the anterior part of tympanic bulla is cylindrical. Among the latter group the height of ventral keel is smallest in *Delphinus* and largest in *Steno*, but its length is in the reverse. This characteristics is considered to be continuous between the two genera situating at the extremities or *Lissodelphis* and *Delphinus*.

In Orcininae, the tympanic bulla shows no trace of flattening as in the case of Sotaliinae and Delphininae. The median furrow is absent. Though the low atrophied ventral keel is observed in *Pseudorca* in the posterior region of the tympanic bulla, it is almost entirely disappeared in *Orcinus*. These features resembles the tympanic bulla of *Delphinus* and *Lagenorhynchus*, and can be led from them.

In Globicephalinae the ventral keel develops well and ventral furrow is absent. The flattness is strong in all genera of this subfamily, but its degree varies between the genera (Fig. 75).

*The posterior process of periotic*

As mentioned in the former chapter, the posterior process of periotic is considered to have had the connection with squamosal in the primitive form. In these primitive Odontoceti the posterior process of periotic is bent to ventral direction at

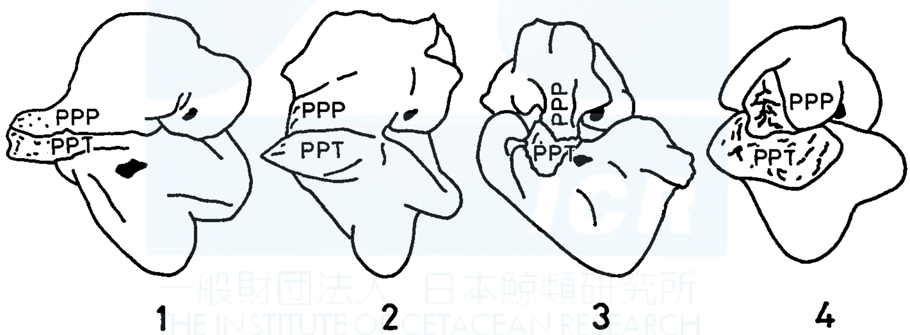


Fig. 76. Posterior view of tympano-periotic bone, showing the direction of the posterior processes. Lateral side is at the left. 1, *Peponocephala electra*. 2, *Monodon monoceros*. 3, *Platanista gangetica*. 4, *Orcaella brevirostris*.

a right angle with the antero-posterior axis of superior process. The facet for posterior process of tympanic bulla is situated on its tip. In the recent Odontoceti, this structure is observed on *Physeter catodon* and *Platanista gangetica*. I consider that various types of posterior process of periotic of other Odontoceti may have derived from the primitive type now found only in *Physeter* and *Platanista*.

In other two families of Physeteroidea the direction of posterior process of periotic is same with that of *Physeter* in principle. But the length is shorter, and the distal tip is widened in Ziphiidae, or changed into thin plate in Kogiidae.

Though the posterior process in Iniidae and Pontoporiidae is continuous to superior process and shorter than that of *Platanista*, the direction is similar to *Platanista*. The atrophy of the posterior process is stronger in Pontoporiidae. *Platanista* and *Lipotes* show the same feature where posterior process and superior process of periotic are clearly distinguished externally.

The posterior process of periotic of Delphinoidea is thicker and longer than that of Platanistoidea. Its direction is classified into two types (Fig. 76). In one type the posterior process is extended to the posterior in parallel with the axis of superior process. All species of Delphinapteridae and Phocoenidae are included in this type. This type may have derived from the primitive type mentioned in the above. In another type the posterior process is bent laterally or postero-laterally. Delphinidae and Monodontidae are included in this type. Though it is not impossible to lead this type from the former, it may be more reasonable to lead directly from the primitive type seen in *Platanista* or *Physeter*.

In the miocene Delphinids, *Kentriodon pernix* belongs to the latter type, but its posterior process of tympanic bulla is directed posteriorly retaining the primitive character. *Delphinodon dividum* (True 1912) belongs to the former type. The posterior process of periotic of *Lophocetus* spp. (Kellogg 1955, Pl. 5–6) is extending to the ventral and connection with squamosal is expected.

In Platanistoidea and Delphinoidea the direction of the posterior process of tympanic bulla coincides with that of the periotic. But in Physeteroidea they do not necessarily coincide because the posterior process of tympanic bulla is usually bent at the distal part.

*Anterior process of periotic*

In all the species which have the primitive posterior process of periotic mentioned in the preceding chapter, or several species of Squalodontidae, Physeteridae, and Platanistidae, the anterior process of periotic is shaped of a rod tapering at the tip. And this type of anterior process is found only on the species which have primitive posterior process of periotic or on its allied species. From these facts, it is suggested that the rod-shaped anterior process of periotic retains the primitive form, and that the various forms found in the recent Odontoceti may have derived from it. In this chapter the probable process of specialization of the anterior process of periotic is discussed.

The anterior process of *Berardius bairdi* is most slender among the species of Ziphiidae and retains the most primitive feature, the trigonal pyramidal or hemispheric anterior process of other species of this family is considered to have originated from this slender type seen in *Berardius*. The anterior process of periotic of *Kogia* may have been formed through another process by loosing the length and thickness.

In *Platanista gangetica*, though the slenderness of the anterior process of periotic shows the primitiveness, there are observed some specialization in usually observed small protuberence on the dorsal surface of the base of the anterior process (Pl. IX Fig. 9). The anterior process of periotic of *Lipotes vexillifer* resembles that of *Platanista* in the curved and pointed shape, but its proportional length is shorter. In *Inia geoffrensis* the length is shorter and the anterior margin is square, showing a slight resemblance to that of Delphinoidea. In *Pontoporia blainvillei* the process is strongly shortened.

The anterior process of Delphinoidea is shaped of thick plate and anterior margin is square. Its length is short. In the fossile species, the anterior process of periotic of the miocene *Kentriodon pernix* (Kellogg 1927) and *Delphinodon dividum* (True 1912) had attained the feature similar to that of recent Delphinoidea.
Though that of *Lophocetus* spp. (Kellogg 1955) is also same, its posterior process of periotic slightly differes from that of recent Delphinoidea.

## CONCLUSION

The classification of recent toothed whales used in this report is shown in Table 15. This classification is based mainly on the morphology of the tympano-periotic bone, paying the attention not to largely modify the classification generally have been accepted. But the classification of Delphinoidea is slightly modified, affected by the wide variation of the morphology of the tympano-periotic bones.

This chapter considers the phylogenetic interrelationships of the taxa of recent toothed whales based on the morphology of tympano-periotic bones.

*Interrelationships among Archaeoceti, Mysticeti, and Odontoceti*

According to the description of Kellogg (1936) and his photographs, the tympano-periotic bones of *Zygorhiza kochii* and *Dorudon osiris* show the following character.

The ventral wall of tympanic bulla is flat and wide, with which the lateral wall crosses at a right angle. The inner border of ventral wall is straight. The anterior border of tympanic bulla or opening of Eustachian tube is partly closing and resembles that of Mysticeti than that of Odontoceti. Sigmoid process is square as in the case of *Physeter*. Posterior process of tympanic bulla is fixed to tympanic bulla with the inner and outer pedicles, and here opens an elliptical foramen (vertical cleft) on the posterior wall of tympanic bulla. These features are similar with that of Odontoceti. But the outer pedicle is reported to be smaller than the inner (Kellogg 1936). Though the both posterior prominences are prominent, the outer posterior prominence is larger than the inner. Interprominential notch is shallow, and median furrow is inconspicuous.

The periotic is sutured to squamosal and exoccipital at the anterior, superior and posterior processes forming a part of cranial cavity as in the case of Mysticeti. The long posterior process of periotic is wedged between squamosal and exoccipital, and its tip reaches to the external surface of the skull. The ventral surface of the posterior process of periotic prepares longitudinal shallow grooves and keels to which the posterior process of tympanic bulla sutures. Though the posterior process of tympanic bulla is thinner than that of periotic, the lengths are nearly same. Judging from the large width of the posterior process of tympanic bulla and the structure of the corresponding part of squamosal (Kellogg 1936, Pls. 15, 20, 24, 25, and 28), I consider that its anterior part may have sutured with squamosal as in the case of recent Physeteroidea and *Platanista* (Fig. 77).

In all the recent Mysticeti the involucrum of tympanic bulla is highly developed. There are found two types in the shape of posterior prominences. In all the species other than Balaenidae, as the outer posterior prominence is strongly atrophied or disappeared, the tympanic bulla is nearly hemispheric. But in Balaenidae outer and inner posterior prominences clearly exist, and the ventral side of tympanic bulla is shaped of a flat square (*Balaena*) or of a triangle (*Eubalaena*). Though in recent Mysticeti the interprominential notch is absent, the *Isocetus* sp. from tertiary (Kellogg 1944) retains both the posterior prominences and interprominential notch. I consider that this condition is more primitive than that observed in recent Mysticeti. The sigmoid process is flat and shaped of a semicircular (Balaenidae) or of a triangle (other than Balaenidae). The tympanic bulla is connected to posterior process of tympanic bulla only by the inner pedicle, which is a feature entirely different from the condition in Archaeoceti and Odontoceti (Kellogg 1936).

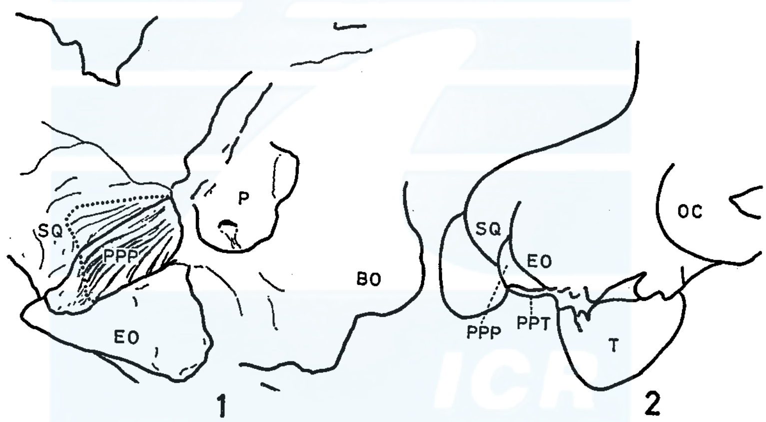


Fig. 77. Skull of Archaeoceti showing the connection between ear bone and skull, drawn based on Kellogg 1936, Pl. 15, Fig. 1, and Pl. 25, Fig. 2. Dotted line indicates the presumed area to which the posterior process of tympanic bulla was sutured. 1, *Zygorhyza kochii*, ventral aspect. 2, *Dorudon stromeri*, posterior aspect. BO, Basioccipital. EO, Exoccipital. OC, Occipital condyle. P, Periotic. PPP, Posterior process of periotic. PPT, Posterior process of tympanic. SQ, Squamosal. T, Tympanic bulla.

As in the case of Archaeoceti, the periotic bone of Mysticeti forms a part of the brain cavity, and the anterior and posterior processes are elongated in rod shape and the latter is wedged between squamosal and exoccipital. Its distal tip nearly reaches to the outer surface of the skull. Though Yamada (1953) showed another opinion, it is clear on a fetus *B. borealis* (Pl. I Fig. 9) that the posterior process of Mysticeti is

TABLE 15. CLASSIFICATION OF RECENT TOOTHED WHALES BASED ON THE MORPHOLOGY OF TYMPANO-PERIOTIC BONES.

| | |
|---|---|
| Suborder | Odontoceti |
| Superfamily | Physeteroidea |
| Family | Physeteridae |
| Subfamily | Physeterinae |
| Genus | *Physeter* |
| Family | Ziphiidae |
| Subfamily | Ziphiinae |
| Genus | *Mesoplodon, Berardius, Tasmacetus, Ziphius, Hyperoodon* |
| Family | Kogiidae |
| Subfamily | Kogiinae |
| Genus | *Kogia* |
| Superfamily | Platanistoidea |
| Family | Platanistidae |
| Subfamily | Platanistinae |
| Genus | *Platanista* |
| Family | Iniidae |
| Subfamily | Iniinae |
| Genus | *Inia, Lipotes* |
| Family | Pontoporiidae |
| Subfamily | Pontoporiinae |
| Genus | *Pontoporia* |
| Superfamily | Delphinoidea |
| Family | Delphinapteridae |
| Subfamily | Delphinapterinae |
| Genus | *Delphinapterus* |
| Subfamily | Orcaellinae |
| Genus | *Orcaella* |
| Family | Phocoenidae |
| Subfamily | Phocoeninae |
| Genus | *Phocoena, Neophacoena, Phocoenoides* |
| Family | Delphinidae |
| Subfamily | Sotaliinae |
| Genus | *Sotalia, Sousa, Cephalorhynchus* |
| Subfamily | Orcininae |
| Genus | *Orcinus, Pseudorca* |
| Subfamily | Delphininae |
| Genus | *Steno, Lagenorhynchus, Delphinus, Lissodelphis, Stenella, Tursiops* |
| Subfamily | Globicephalinae |
| Genus | *Peponocephala, Feresa, Globicephala, Grampus* |
| Family | Monodontidae |
| Subfamily | Monodontinae |
| Genus | *Monodon* |

composed of the elements of posterior process of tympanic bulla and of posterior process of periotic. But the relative ratio of the two elements in adult individual is not clear.

When the above features are compared with that of *Platanista gangetica* and *Physeter catodon* which are considered to retain the primitive condition in the interrelationships between skull and tympano-periotic bone, Archaeoceti has some common features both with Mysticeti and Odontoceti, but shows no perfect coincidence. In order to lead the structure seen in Mysticeti from that of Archaeoceti, only the disappearence of the outer pedicle of tympanic bulla which is smaller than the inner, and the fusion of the posterior process of tympanic bulla and that of periotic are the fundamental modification needed to Archaeoceti (Fig. 78). But to lead the ear bone of some primitive Odontoceti, at first the periotic bone must be freed from the wall of cranial cavity and at secand the posterior process of periotic must greatly degenerate to loose the strong connection with squamosal and exoccipital and to leave the sutural connection between the posterior process of tympanic bulla, squamosal, and exoccipital.

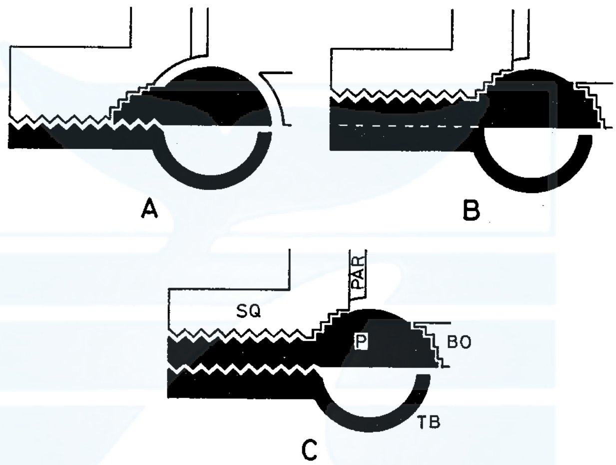


Fig. 78. Schematic diagrams showing the connection between tympano-periotic bone and skull. Waved edge indicates the tight connection or suture of bones, and dotted line the fused bone. A, Hypothetical primitive Odontoceti. B, Mysticeti. C, Archaeoceti, in which the connection between squamosal and posterior process of tympanic bulla is not shown. For other marks see Fig. 73.

As the reduction of the outer pedicle of tympanic bulla had already started in Archaeoceti, I consider that it is easier to lead the ear bone of Mysticeti from that of Archaeoceti than to do that of Odontoceti, which will suggest that Archaeoceti has closer relationship with Mysticeti than with Odontoceti. This coincides with the conclusions obtained by Miller (1923) and Slijper (1946). But this does not necessarily mean that Mysticeti had originated from Archaeoceti.

*Squalodontidae*

According to Kellogg (1928) Squalodontidae is known in oligocene and miocene, and its primitive relative is in lower eocene. The description of the two periotic bones of Squalodontidae is based on the drawings and photographs reported by Kellogg (1923, 1931). No information on the tympanic bulla was obtained.

On the periotic bone of *Squalodon calvertensis*, the anterior process and posterior process are long and separated from the superior process by the grooves at the bases. And when seen from the lateral side the dorsal borders of the anterior and posterior processes cross at a right angle. The former feature resembles that of *Platanista* and *Lipotes*, and the latter that of *Physeter* and many Ziphiids. As the posterior process of periotic is slender at the tip and has the rugose area on the posterior surface, it is supposed that it had the similar connection with squamosal seen in *Physeter catodon*. The slenderness of the anterior process resembles both *P. catodon* and *P. gangetica*. But the flat and low cochlear portion and slit-like opening of fundus of internal auditory meatus is peculiar.

On the other hand, the periotic bone of *Squalodon errabundus* has the swallen anterior process resembling that of recent Ziphiidae. The large round cochlear portion and the round opening of the fundus of internal auditory meatus are different from those of *S. calvertensis* but resemble that of Platanistidae and Physeteridae. Anterior process is continuous to superior process. On the reffered specimen the posterior process was lost.

Above discussion shows that the periotic bone of Squalodontidae have many characteristics common with that of Physeteroidea or Platanistoidea, though it is suggested that there exist some differentiation among the periotics of Squalodontidae. As the conclusion it is suggested from the morphology of periotic that the recent Odontoceti at least Physeteridae and Platanistidae had derived, as *Squalodon*, from a primitive *Squalodon*-like species.

*Physeteroidea*

One of the most conspicuous features of the tympano-periotic bone of Physeteroidea is the developed structure connecting it to skull. The similar but less developed structure is found even in some species of Platanistidae, Delphinapteridae and Eurhinodelphinidae. This suggest that, though there is found wide variation in the morphology of the tympano-periotic bone of recent Odontoceti, all of them have derived from one primitive type.

Though there are observed wide difference in the morphology of tympano-periotic bones of the three families constituting the Physeteroidea, there is observed some continuity in several features which permits the following discussion on the interrelationships of these families.

When the tympano-periotic bones of the three families are compared, the morphology of the anterior and posterior processes of periotic, and the connection between both posterior processes are most specialized in *Kogia* and least in *Physeter*. But the laminated structure of posterior process of tympanic bulla is most developed in Physeter and less in *Kogia* and Ziphiidae. The arrangement of posterior prominences and the shape of sigmoid process show the most primitive condition in *Kogia*, and the greatly modified in *Physeter*. But in Ziphiidae they have changed the relative position in a way different from that occurred in *Physeter*. On this point of view, the tympanic bullae of Physeteridae and of Ziphiidae seems to have been specialized in different direction probably starting from the common original type.

Accordingly it is considered that the three families had differentiated in the early stage of history of Physeteroidea and the specializations of the anterior and posterior processes of periotic and posterior process of tympanic bulla mentioned above might have been attained as the result of evolution happened independently. The features of sigmoid process, lateral furrow, and elliptical foramen of Kogiidae resembles more to those of Physeteridae than those of Ziphiidae. Though it is one of the pecuriority of the periotic of recent *Physeter* that the aquaeductus Fallopii and ductus endolymphaticus open inside of the opening of fundus of internal auditory meatus, in the miocene Physeterid species *Aurophyseter morricei* (Kellogg 1931) and *Orycterocetus crocodilinus* (Kellogg 1965) they open independently as in the case of recent *Kogia*. These resemblances of tympano-periotic bone between Kogiidae and Physeteridae will indicate the slightly closer phylogenetic relationships between Kogiidae and Physeteridae. But it is of course sure that the phylogenetic distance between Physeteridae and Kogiidae is not small as indicated by the difference of general featurs of tympano-periotic bone, the process of telescoping of the skull (Miller 1923), and by the condition of the fusion of the cervical vertebrae (Nishiwaki 1963, 1964).

Among several genera of Ziiphiidae, *Berardius* and *Mesoplodon* have well developed posterior prominences of tympanic bulla and interprominential notch. But on the tympanic bulla of *Ziphius*, the outer posterior prominence has a wedge-shaped keel on its postero-lateral part, and both posterior prominences are thin. Its interprominential notch is almost disappeared. In *Tasmacetus*, though the outer posterior prominence retains the thick cylindrical form, there is observed the similar keel found in *Ziphius* (Oliver 1937, Pl. III). *Hyperoodon* also resembles to *Ziphius* in the atrophied inner posterior prominence and interprominential notch.

Based on these characteristics, the genera of Ziphiidae are divided into two groups. One has less specialized tympanic bulla and includes *Berardius* and *Mesoplodon*, the other has the more specialized and includes *Ziphius*, *Tasmacetus* and *Hyperoodon*. The former is composed of the species which retain developed tooth even on the part of mandible other than anterior tip (with an exception of *M. mirus*), and the latter only at the tip of mandible. Though the phylogenetic rela-relationships among the species of *Mesoplodon* can not be presumed from the morphology of tympano-periotic bone, it should be noted that *M. ginkgodens* and *M. europaeus* show a common feature in the pecuriority of the superior process of periotic.

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*Platanistoidea*

The tympano-periotic bones of this taxon show the common primitive features of unflattened tympanic bulla, existance of median and lateral furrows, large posterior prominences, and the shape of anterior, superior and posterior processes of periotic, together with the specialized feature of the degenerated size of posterior process.

As mentioned before the tympano-periotic bone of *Platanista gangetica*, which retains the most primitive features among the recent species of this family, shows some resemblance to that of *Physeter*. Furthermore the arrangement of anterior and posterior processes of periotic and the constrictions at their bases suggest the probable relationships to Squalodontidae.

The miocene Eurhynodelphinid species *Schizodelphis sulcatus* (Van Beneden and Gervais 1868–1879) has the tympanic bulla highly resembling that of *P. gangetica* except the existance of needle-shaped processes in the median furrow. Its periotic bone also resembles that of *P. gangetica* in the shape of cochlear portion especially the opening of fundus of internal auditory meatus, and in the relationships with the skull. But it greatly differs from *P. gangetica* in the larger size of the posterior process of periotic. When the skull of *S. sulcatus* is compared with that of *Platanista*, the former has larger brain case and weaker intertemporal constiction, and the proximal part of maxillae is expanded horizontally and covers the temporal fossa. As these features are similar to the modern Delphinoidea and different from Platanistoidea, it is unreasonable to lead Platanistoidea directly from the Eurhyodelphinids. Probably the two taxa had originated from a same origin, and Platanistoidea attained the tendency to form the maxillary crest through the vertical extension of the lateral margin of the proximal part of maxillae.

The tympano-periotic bone of a miocene Platanistoid species, *Zarhachis flagelator* (Kellogg 1924), is almost perfectly coincides with that of *Platanista gangetica* except the needle-shaped processes in the median furrow of *Platanista*, but the maxillary crest of *Z. flagelator* is far smaller than that of *P. gangetica*. This suggests that *Platanista* did not gain large specialization of the tympano-periotic bone in the process of evolution, but did the strong modification on the maxillae and on the pterygoid (Miller 1923; Fraser and Purves 1960).

The tympano-periotic bone of Iniidae is more specialized than that of Platanistidae in the degeneration of the connection with skull and in the shape of the sigmoid process, median furrow, and of the three processes of periotic. Between the two genera of Iniidae, *Lipotes* is considered to be more primitive in the form of the tympano-periotic bone.

The strength of the development of the maxillary crest decreases in the order of *Platanista*, *Zarhachis*, *Inia*, and *Lipotes*. This order is rather reverse of the degree of the specialization of the tympano-periotic bones. This will indicate that the three genera had been separeted at the very early stage of the evolution.

There have been reported two different consideration on the taxonomical position of *Pontoporia blainvillei*. The one considers *Pontoporia* close to Delphinoidea (Gray 1866; Kellogg 1928; Miller 1923), and the other to Platanistoidea (Flower 1867; Winge 1918; Fraser and Purves 1960; Nishiwaki 1963). Though the interrelationships between skull and tympano-periotic bone and the square-shaped anterior border of the tympanic bulla are the very specialized features not observed in Platanistidae or in Iniidae, all the primitive features concerning the sigmoid process, shape of outer posterior prominence, median furrow, unflattened tympanic bulla, and round opening of fundus of internal auditory meatus are common to Platanistidae and Iniidae. and the specialized characteristics such as wide lower tympanic aperture can be led from the primitive condition found in Platanistidae and Iniidae. As the conclusion, when based on the morphology of tympano-periotic bone, *Pontoporia blainvillei* is considered to situate at the extremity of the specialization occurred in Platanistoidea. Furthermore the shape of anterior and posterior processse of periotic resembles that of *Inia*, and the development of the vertical maxillary crest and the horizontal spreading of the proximal part of maxilla are intermediate of *Inia* and *Lipotes*. A tympanic bulla reportedly belonging to iniid species *Kampholophos serrulus* (Rensberger 1969) is much similar, except the size, to that of *Pontoporia* than *Inia*. They might suggest that *Pontoporia* is a relative of the Iniidae. But *Pontoporia* should be separated from Iniidae considering the high specialization of the tympano-periotic bone.

*Delphinoidea*

The features of the tympano-periotic bones of this superfamily are described in the preceeding chapters. As the relatives of this modern dolphins, *Delphinodon dividum* (True 1912) and *Kentriodon pernix* (Kellogg 1927) are known from middle miocene. Their tympano-periotic bones are, same as the features of the skull, resembles to the recent Delphinoidea and differs from those of Eurhynodelphinidae. But their tympanic bulla still retains the primitive features in the presence of median furrow, lateral furrow (no data on *Delphinodon*) and swallen inner posterior prominence.

Though, other miocene species *Lophocetus* spp. (Kellogg 1955) have the tympanic bulla and the anterior process of periotic resembling those of the former *Delphinodon* and *Kentriodon*, its posterior process of periotic shows the primitiveness suggesting the connection between posterior process of periotic and squamosal as observed in recent *Delphinapterus*.

Though the tendency of the separation of the tympano-periotic bone and skull is also observed in Platanistoidea it cannot be considered to be the direct ancestor of the Delphinoidea, because the strong reduction of the posterior process of periotic is not observed in Delphinoidea. On the other hand the posterior process of periotic bone of *Shizodelphis sulcatus* (Eurhynodelphinidae) is large enough to lead that of recent Delphinoidea. And its shape of the maxillae shows the similar specialization to that of recent Delphinoidea. Accordingly it is reasonable to think that the recent Delphinoidea had originated from a close ancestor of Eurhynodelphinidae. As there had been established in the middle miocene both Eurhynodelphinid and Delphinid species (Kellogg 1928), it seems to be in lower miocene or earlier date when the primitive Delphinoids started.

In this study, the recent Delphinoidea is divided into Delphinapteridae, Phocoenidae, Monodontidae, and Delphinidae. These four families are classified into two groups by the shape and the direction of the posterior process of periotic. One includes Delphinapteridae and Phocoenidae, and the other Delphinidae and Monodontidae.

The first two families seem to have derived from a common origin, in which posterior extension of posterior process of periotic and possibly the tendency of widening of rostrum will be attained. I consider that this group constitutes one of the three groups in Delphinoidea which have attained the wide rostrum. Other two groups with wide rostrum are Orcininae and Globicephalinae. Though there is observed a strong resemblance between the two species constituting Delphinapteridae in the morphology of tympano-periotic bones, the sutural connection between squamosal and periotic observed in *Delphinapterus leucas* will be a good reason to separate them into two subfamilies or Delphinapterinae and Orcaellinae. Probably, after the differentiation from the stock common with that of Phocoenidae, *Delphinapterus* and *Orcaella* might have differentiated in the arctic and tropical waters respectively.

In spite of the resemblance of the external appearance of Delphinapteridae and Globicephalinae, it is reasonable to consider that they are not in close relatives when considered from the morphology of tympano-periotic bones. Because, other than the difference of the direction of the posterior processes, all the characteristic features of the tympanic bulla of Globicephalinae, or bilateral compression of tympanic bulla, conspicuous ventral keel, anterior spine, short inner posterior prominence, and narrow posterior branch of lower tympanic aperture lack in both *Orcaella* and *Delphinapterus*. Though Fraser and Purves (1960) found a resemblance of the air sinus system between *Orcaella* and *Orcinus-Globicephala* group, the morphology of tympano-periotic bones of the three genera is quite different. Miller (1923) indicated the resemblance of the pterygoid among *Orcaella*, *Monodon*, and all species of Delphinidae. But this will indicate only that the pterygoid of *Delphinapterus* is specialized, and not the close phylogenetic relationships of *Orcaella* and *Monodon* to Delphinapteridae.

TABLE 16. COMPARISON OF THE MORPHOLOGY OF TYMPANO-PERIOTIC BONES IN PHOCOENIDAE

| Genus | *Phocoena* | *Neophocaena* | *Phocoenoides* |
|---|---|---|---|
| High ventral keel | + | ++ | +++ |
| Wide LTA | + | ++ | ++ |
| Outer post. prominence | Flat, Thick | Cylindrical | Flat, Thin |
| Post. proc. of tympanic bulla | Square, Thick | Conical | Square, Thin |
| Post. proc. of periotic | Thick | Slender | Thick |

LTA: Lower tympanic aperture

The tympano-periotic bone of Phocoenidae is characteristic in the direction and structure of posterior processes of tympanic bulla and of periotic. The structure of posterior processes is more specialized than that of Delphinapteridae. Similar tendency of higher specialization of Phocoenidae is observed also in the degeneration of tooth and fusion of cervical vertebrae. Many other features of tympanic bulla are common to those of Delphinapteridae. Among the three genera of Phocoenidae the tympano-periotic bone of *Phocoena* retains the most primitive features in all the characteristics compared, especially in the condition of the ventral keel, but the mode of specialization of outer posterior prominence, posterior process of tympanic bulla, and of posterior process of periotic differ between *Neophocaena* and *Phocoenoides*. And the tympanic bulla of the one genus cannot be led from that of the other. This will suggest that these two genera have independently derived from a stock which is close to *Phocoena*.

The family Delphinidae contains most numerous and wide variety of species. This group will have originated from a same stock with that of Delphinapteridae and Phocoenidae, and attained the character in which the posterior process of periotic extends to the lateral direction. There is a decreasing tendency in the width of the posterior branch of lower tympanic aperture. This family is divided into 4 subfamilies of Sotaliinae, Delphininae, Orcininae, and Globicephalinae based on the morphology of tympanic bulla.

Sotaliinae includes *Sotalia*, *Sousa*, and *Cephalorhynchus*. The closure of their elliptical foramen indicates one of the specialization, but the existance of median furrow or similar structure, weak ventral keel, and no bilateral compression of tympanic bulla indicate the primitiveness. Their posterior branch of lower tympanic aperture is wider than those of other 3 subfamilies. This feature is also considered to be a primitive character, showing no extraordinary widened status found in Pontoporiidae, Phocoenidae, and Delphinapteridae, nor the narrowed condition of other subfamilies of Delphinidae. As this subfamily is established based on many primitive features and modification of elliptical foramen which is very variable, there remains a question on the phylogenetic uniformity of this group. Among the three genera of this subfamily, *Sotalia* and *Sousa* show the higher resemblance in the morphology of tympano-periotic bone. Anyway the tympano-periotic bone of these genera shows higher resemblance to that of Delphininae.

The tympanic bulla of Delphininae is weakly specialized, and retains the most primitive condition in Delphinidae. This subfamily includes *Steno*, *Lagenorhynchus*, *Delphinus*, *Lissodelphis*, *Stenella*, and *Tursiops*. They are classified into two groups by the feature of the ventral keel of tympanic bulla, the one includes the first three genera and the other the last three. On the two genera at the boundary, *Delphinus* and *Lissodelphis*, the height of ventral keel is the smallest, which will probably retain the unspecialized original feature of the tympanic bulla of Delphininae. In Fig. 78, these two groups are shown in *Delphinus* group and *Tursiops* group. The genus *Stenella* includes many species which varidity is not established yet. When considered from the morphology of tympanic bulla, the North Pacific species *S. longirostris* and *S. roseiventris*, and *S. attenuata* and *S. graffmani* seems to be in close relations respectively. And *S. caeruleoalba* is in closer affinity with the latter pair of species than the former.

Oricininae is constituted by *Orcinus orca* and *Pseudorca crassidens*. As their tympanic bullae show the resemblance to those of *Delphinus* and *Lagenorhynchus*, this subfamily seems to have derived from the stock which has such an unspecialized tympanic bulla. The tympano-periotic bone of *Orcinus orca* shows the higher specialization in the perfect disappearance of ventral keel, closure of elliptical foramen, and the massiveness of anterior and superior process of periotic.

The two species included here in Orcininae have been often included in the Globicephalinae here adopted. Though they resembles in the width of rostrum, Orcininae greatly differs from Globicephalinae in the features of tympanic bulla and periotic. In other characteristics of skull, Orcininae seems to have developed the augmentation of tooth together with the decrease of tooth number. On the other hand, in Globicephalinae, the number of tooth seems to be decreasing without accompanied by the much increase of size, and the function of the tooth in taking the food is decreasing. Accordingly, I consider that the resemblance of the width of the rostrum between Orcininae and Globicephalinae is not significant.

Globicephalinae includes *Peponocephala*, *Feresa*, *Globicephala*, and *Grampus*. They are distinguished from other genera of Delphinidae by the morphology of tympanic bulla, especially by the bilateral compression, presence of anterior spine and ventral keel, and the closing tendency of elliptical foramen. In the least specialized species *Peponocephala electra*, the flatness of tympanic bulla is not strong and all individuals retain the elliptical foramen open. This suggests that Globicephalinae derived from a primitive Delphinidae which possessed such a tympanic bulla now found in Delphininae, and diverged to wide variety of species.

TABLE 17. COMPARISON OF THE MORPHOLOGY OF TYMPANO-PERIOTIC BONES AND OTHER TAXONOMICAL CHARACTERS.

| Species | Mean tympanic width (%) | Opened elliptical foramen (%) | *Rostrum length /width | *No. of upper tooth | *No. of united cervicals |
|---|---|---|---|---|---|
| *Peponocephala electra* | 55.3 | 100 | 1.83 | 21–25 | 3 |
| *Feresa attenuata* | 53.5 | 28.6 | 1.58 | 8–11 | 3–4 |
| *Globicephala macrorhyncha* | 49.8 | 3.8 | 1.16 | 6– 9 | 5–6 |
| *Grampus griseus* | 50.1 | 8.3 | 1.04 | 0 | 6 |
| *Monodon monoceros* | 39.6 | 25.0 | 1.31 | 0– 1 | 0 |
| *Pseudorca crassidens* | 60.6 | 100 | 1.49 | 8–11 | 6 |
| *Orcinus orca* | 56.1 | 0 | 1.36 | 10–13 | 4 |
| *Delphinapterus leucas* | 58.9 | 0 | 1.50 | 8–10 | 0 |
| *Orcaella brevirostris* | 54.9 | 0 | 1.10 | 15–17 | 2 |
| *Neophocaena phocaenoides* | 64.4 | 0 | 1.03 | 15–19 | 5 |
| *Phocoena phocoena* | 62.3 | 0 | 1.39 | 23–27 | 6 |
| *Phocoenoides* spp. | 62.3 | 0 | 1.47 | 23–27 | 7 |

* Refered from Nishiwaki (1963, '64), Nakajima and Nishiwaki (1965), Nishiwaki *et al* (1965), and Kasuya (unpublished).

As shown in Table 17, there is observed a correlation between the strength of specialization of tympanic bulla and that of other taxonomical characteristics of Globicephalinae. But this correlation can not be extended to other taxa of Delphinoidea. This will indicate that Globicephalinae should be separated from other taxa which have wide rostrum. Among the species constituting Globicephalinae, *Peponocephala electra* was indicated to have a strong resemblance to Delphinidae in the morphology of skull (True 1889; Nakajima and Nishiwaki 1965). And True (1889) included this species into *Lagenorhynchus*. Though its tympanic bulla retains the most primitive condition in the Globicephalinae species, it surely shows the taxonomical characteristics of Globicephalinae and quite different from the tympanic bulla of *Lagenorhynchus*. Accordingly *Peponocephala* should be included into Globicephalinae.

The specialized features of tympanic bulla of *Monodon monoceros* are seen in the strong bilateral compression, short inner posterior prominence, high ventral keel,

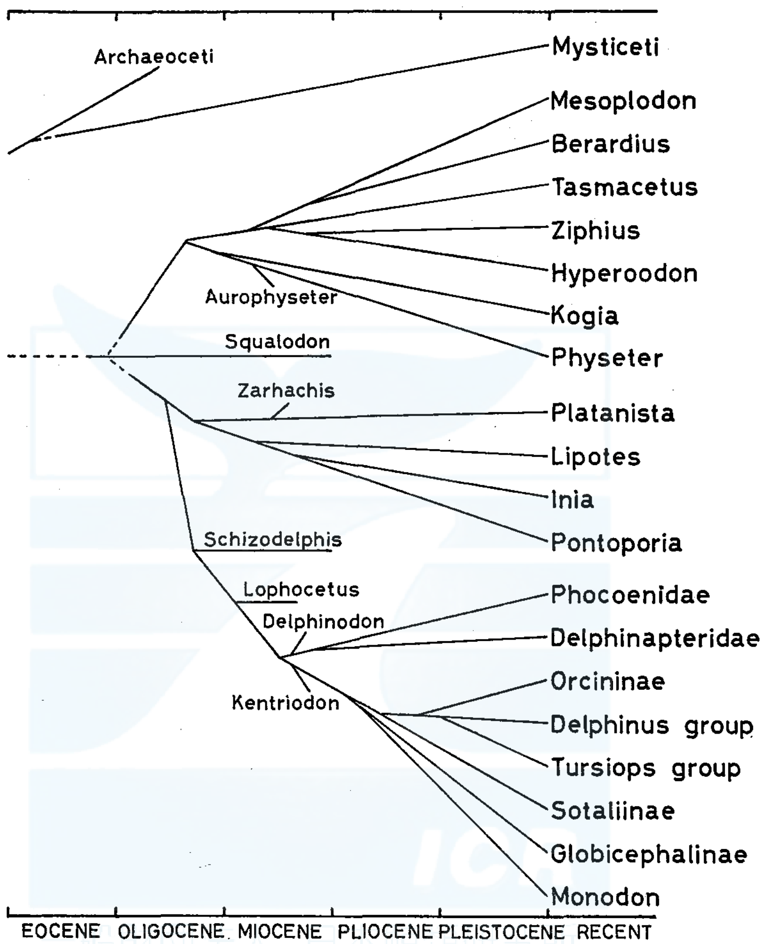


Fig. 79. Dendrogram of the recent Odontoceti considered from the morphology of tympano-periotic bone. For other explanation see text.

and in sigmoidally curved inner margin of the involucrum. These characteristics are not found in *Delphinapterus leucas*, but show higher resemblance to Globicephalinae, especially with *Grampus*. However, different from the general feature of Globicephalinae, tympanic bulla of *Monodon* has no anterior spine and the compression of the bulla is stronger than any Globicephalinae species. The periotic of *Monodon* shows specialization in the presence of thick and wide anterior process and postero-laterally directed long posterior process of periotic. The former resembles more to *Globicephala* and *Grampus* than *Delphinapterus*, and the latter especially its direction is quite different from *Delphinapterus* but is common to all Delphinidae. On the other hand tympano-periotic bone of *Monodon* retains some primitive features of slightly wide posterior branch of lower tympanic aperture, round opening of fundus of internal auditory meatus, and of elliptical foramen opened in higher frequency than in some Globicephalinae. But they are not of great importance in taxonomical point of view.

As the conclusion, though tympano-periotic bone of *Monodon monoceros* has some primitive features not observed in Globicephalinae, most of features are considered to be common to Globicephalinae or are the specialized form of it. This will suggest that *M. monoceros* and Globicephalinae derived from a common stock which had started the specialization for *Globicephala* group, or the various modification of tympano-periotic bone, and the decrease in number of tooth, and increase in the width of rostrum. The presence of a conspicuous tusk on the male *Monodon* is one of the extremity of the decrease of the tooth. But in this study *Monodon* is classified into Monodontidae considering the slightly primitive features in the tympano-periotic bone and in the cervical vertebrae, and the specialized tooth.

In the past, *Monodon* was included in one group together with *Delphinapterus* (Winge 1918; Nishiwaki 1963), based mainly on the condition of the cervicals. But the condition where all the 7 cervicals are separated is commonly observed in the miocene dolphins, and it will not be necessarily correct to conclude the phylogenetic relationships based on this kind of primitive characteristics.

Fig. 79 shows the phylogenetic relationships of the recent toothed whales presumed in the above discussions. Some fossile species refered in this study are also shown in it. The geological age is based on Kellogg (1923) and adaptable mainly to the fossile species.

## SUMMARY

The tympano-periotic bone of toothed whales has attained the peculiar morphological features and between species differences suggesting the probable efficiency as the taxonomical characteristics. This study intends, at first, to clarify the morphology of tympano-periotic bones of recent toothed whales, and then to discuss the phylogenetic relationships of the genera of recent Odontoceti based on the tympano-periotic bones representing 313 individuals in 30 genera.

In the preliminary morphological study of the tympano-periotic bones, the following results were obtained.

1. The bilateral difference of tympano-periotic bones between the both sides of one individual was studied on 6 species of Delphinoidea. Though most of measurements showed no bilateral asymmetry, the asymmetry was expected in few points. But it is small enough compared with the range of individual variation to be neglected in the present study.

2. The growth of tympano-periotic bone accompanied with the growth of the animal was studied on 3 species of Delphinoidea. The length of tympanic bulla

shows slight increase after the birth, but the length of periotic does almost no increase. The proportional dimensions of tympanic bulla or of periotic vary in relation to their lengths and in species.

3. It is usually possible to identify the genus with hte morphology of tympanic bulla or of periotic, but sometimes difficult to identify the species. The morphological characteristics of tympano-periotic bone for the identification of the species or genus are described.

4. A similarity coefficient of the tympano-periotic bone was calculated based on the 22 morphological characteristics. By this coefficient, Delphinidae, Phocoenidae, Kogiidae, Physeteridae, Ziphiidae, Platanistidae, and Iniidae are separated, but Monodontidae and Delphinapteridae are not separated from Delphinidae.

The following results were obtained on the probable processes of the specialization of several morphological characteristics, through the comparizon of the tympano-periotic bones of various taxa of recent toothed whales and fossil species.

1. In the primitive condition, the posterior process of tympanic bulla, posterior process of periotic, and squamosal are considered to have been sutured each other. But in the specialized species, these connections are disappearing in various degree.

2. The most primitive condition concerning the above characteristics is found, in the recent Odontoceti, on *Physeter catodon* and *Platanista gangetica.* But these species show the higher specialization on the structure of the postero-ventral region of squamosal where the posterior process of tympanic bulla sutures.

3. The degeneration of sutural connection between skull and tympano-periotic bone is considered to have advanced independently in Physeteroidea, Platanistoidea, and Delphinoidea. The suture between squamosal and posterior process of tympanic bulla is retained in all species of Physeteroidea. In Platanistoidea and Delphinoidea the connection between squamosal and posterior process of tympanic bulla is disappearing in various degree. Pontoporiidae and Phocoenidae situate at the extremity where the suture is fully lost.

4. The primitive form of sigmoid process is considered to be of a thin square, which is retained better in *Physeter catodon.* The form of sigmoid process found widely in Delphinoidea seems to have derived from this primitive type through the condition of *Platanista.* The lateral furrow seems to have disappeared in several taxa.

5. The closure of elliptical foramen is considered to have occurred parallelly in various taxa, and to be still progressing in some taxa. The elliptical foramen is perfectly retained in Delphininae.

6. In primitive tympanic bulla, the ventral wall and the lateral wall cross at a right angle. In Physeteridae, Ziphiidae, Monodontidae, and in Globicephalinae their relation is modified. The median furrow is retained well in Platanistoidea, but only slightly in Kogiidae, Delphinapteridae, Phocoenidae, and Sotaliinae.

7. There are observed two cases in the mode of specialization of ventral keel which afford a base for the ligament connecting the tympanic bulla and basioccipital crest, in one case it increases in height and in the other decreases.

8. In the primitive condition, the posterior process of periotic is directed to postero-ventral direction. This condition is observed in some species of Physetero-

idea and Platanistoidea. In one of the specialized type it is directed to the posterior direction, which is observed in Delphinapteridae and Phocoenidae. And in the other it is directed to postero-lateral or to lateral direction, which is observed in Monodontidae and Delphinidae.

9. The anterior process of periotic seems to have changed from the primitive rod-shape which is observed in *Physeter*, *Platanista*, and *Lipotes*, to the triangular pyramid shape of Ziphiidae, to spool shape of *Kogia*, or to square shape of Delphinoidea, and *Inia*.

The following conclusions on the phylogenetic relationships of the taxa of recent Odontoceti were obtained from the consideration of the process of the evolution of tympano-periotic bone.

1. The fundamental structure of tympano-periotic bones of Archaeoceti coincides neither with that of Mysticeti nor that of Odontoceti, but it shows higher resemblance with the former.

2. The recent Odontoceti is considered to have derived from a primitive *Squalodon* group, and classified into two groups. One is Physeteroidae, and the other includes Platanistoidea and Delphinoidea.

3. The group of Physeteroidea retains the suture between squamosal and posterior process of tympanic bulla, and shows a conspicuous specialization of these parts. In its early stage of evolution, Kogiidae, Ziphiidae, and Physeteridae seems to have been separated.

4. The recent Ziphiidae is classified by tympanic bulla into two groups, one indludes *Berardius* and *Mesoplodon*, and the other *Ziphius*, *Hyperoodon*, and *Tasmacetus*.

5. The 2nd group of recent Odontoceti shows the tendency of the separation of tympano-periotic bone from the skull, accompanied with the degeneration of posterior processes of tympanic bulla and of periotic. This group is devided into Platanistoidea and Delphinoidea, which are presumed to have derived from a common origin.

6. In Platanistoidea, the regression of the size of posterior processes is stronger but retains many primitive features of tympano-periotic bones than those of Delphinoidea. The differentiation of Platanistidae, Iniidae, and Pontoporiidae seems to have occurred in the early period of evolution of Platanistoidea.

7. Delphinoidea is composed of the two groups. One includes Delphinapteridea and Phocoenidae, and the other Delphinidae and Monodontidae. These two groups in Delphinoidea had originated from a common stock.

8. Delphinidae is composed of Sotaliinae, Delphininae, Oricininae, and Globicephalinae.

9. It is presumed from the morphology of tympanic bulla that Orcininae may have derived from a stock which is close to that of *Delphinus* or *Lagenorhynchus*.

10. Globicephalinae and Monodontidae show some resemblance in the mo·phology of tympano-periotic bone.

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## APPENDIX I

Key to genus or species by means of the morphology of tympanic bulla or periotic.

*Tympanic bulla*

a¹ Sigmoid process is globular. Tympanic bulla is not compressed laterally. Anterior spine and elliptical foramen are absent. Posterior process is large and funnel shaped. Interprominential notch is wide and opens posteriorly. Involucrum is thick. Length of tympanic bulla 24 to 39 mm.
.................................................. *Kogia*

b¹ Anterior margin of the lateral wall is convexed.
.................................................. *K. breviceps*

b² Anterior margin of the lateral wall is concaved.
.................................................. *K. simus*

a² Sigmoid process is of a large square and thin. Its dorsal margin is longer than the lateral.

c¹ Lateral furrow is absent. Outer and inner posterior prominences are small, and they situate on a plane including the lateral margin of sigmoid proces. Involucrum is thick. Elliptica lforamen is absent. Posterior process is long and finely laminated. Length of tympanic bulla 55 to 63 mm.
.................................................. *Physeter catodon*

c² Lateral furrow is conspicuous. Lateral margin of sigmoid process is twisted posteriorly.
.................................................. Ziphiidae

d¹ Posterior prominences are large. Interprominential notch is wide.

e¹ In the ventral view the anterior part of tympanic bulla is triangular and narrow. Length of tympanic bulla 63 to 71 mm.
.................................................. *Berardius*

e² In the ventral view the anterior part of the outer and inner border is nearly parallel.

f¹ A small crest is present on the postero-lateral tip of outer posterior prominence.
.................................................. *Tasmacetus*

f² Outer posterior prominence is globular or cylindrical. Length of tympanic bulla 39 to 54 mm.
.................................................. *Mesoplodon*

g² Ventral keel situates on the line extended from inner posterior prominence.
.................................................. *M. carlhubbsi*, *M. stejnegeri*, *M. europaeus*, *M. mirus*

g² Ventral keel situates outer side of the line extended from inner posterior prominence.
.................................................. *M. densirostris*, *M. ginkgodens*

d² Interprominential notch is shallow and narrow.

h¹ Outer posterior prominence is thin and has a small keel on the posterolateral tip. Tympanic bulla is flat. Length of tympanic bulla 51 to 60 mm.
.................................................. *Ziphius cavirostris*

h² Outer posterior prominence is thick and has no keel on the postero-lateral tip. Tympanic bulla is cylindrical. Length of tympanic bulla 54 mm (1 example).
.................................................. *Hyperoodon*

a³ Dorsal margin of sigmoid process is equal or shorter than the lateral margin.
i¹ Lateral and median furrows are present. Sigmoid process is thick.
j¹ Anterior part of the ventral wall is conical. Elliptical foramen usually opens.
k¹ Median furrow is wide and deep, and has fine needle-like processes in it. Anterior spine is long. Lateral margin of sigmoid process is straight. Length of tympanic bulla 47 to 64 mm.
.................................................. *Platanista gangetica*

k² No needle-like process in the median furrow. Lateral margin of sigmoid process convexes posteriorly.
l¹ Tympanic bulla is wide (63 to 71% of the length) with the inner projection of involucrum. Median furrow is narrow. Length of tympanic bulla 38 to 46 mm.
.................................................. *Inia geoffrensis*

l² Involucrum does not project interiorly. Width of tympanic bulla is 51% of the length (1 example). Length of tympanic bulla 47 mm (1 example).
.................................................. *Lipotes vexillifer*

j² Inner border of ventral wall is concaved, and the anterior part is square. Posterior branch of lower tympanic aperture is wide (17.7% of the length, 1 example). Elliptical foramen closed. Length of tympanic bulla 24 mm (1 example).
.................................................. *Pontoporia blainvillei*

i² Lateral furrow is absent. Median furrow is absent or vaguely present. Sigmoid process is thin and long.
m¹ Posterior process of tympanic bulla extends posteriorly. Posterior branch of lower tympanic aperture is wide. Tympanic bulla is not compressed bitaterally. Anterior spine is absent.
n¹ Facet for posterior process of periotic has ridges and keels. Involucrum convexes.
o¹ Anterior tip of tympanic bulla and outer posterior prominence project ventrally, and when seen from the lateral side the ventral contour is saddleshaped. Length of tympanic bulla 40 to 45 mm.
.................................................. *Delphinapterus leucas*

o² When seen from the lateral side, the ventral contour is nearly straight. Shallow median furrow is present. Length of tympanic bulla 36 to 40 mm.
.................................................. *Orcaella brevirostris*

n² Facet for posterior process of periotic is smooth. Weak median furrow is present.
p¹ Outer posterior prominence is cylindrical. Posterior process is thick and spindle-shaped. Length of tympanic bulla 27 to 32 mm.
.................................................. *Neophocaena phocaenoides*

p² Outer posterior prominence is flat. Posterior process is flat and square.
q¹ Ventral keel is high. Length of tympanic bulla 30 to 37 mm.
.................................................. *Phocoenoides*

q² Ventral keel is low. Length of tympanic bulla 28 to 34 mm.
.................................................. *Phocoena*



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$m^2$ Posterior process of tympanic bulla extends to postero-lateral or lateral direction. Anterior spine is usually present. Posterior branch of lower tympanic aperture is not wide.

$r^1$ Tympanic bulla is strongly compressed laterally. Inner posterior prominence is short, and not extended posteriorly beyond the base. Ventral keel is prominent. Median furrow is absent.

$s^1$ Width of tympanic bulla is 37 to 42% of the length. Ventral keel is high and sigmoidal. Anterior spine is absent and elliptical foramen is usually absent. Length of tympanic bulla 50 to 51 mm.

.................................................. *Monodon monoceros*

$s^2$ Width of tympanic bulla is more than 42% of length. Anterior spine is present.

$t^1$ In the ventral view anterior margin is triangular, and the anterior spine situates at the center. Anterior part of lateral wall is narrow. Inner margin of ventral wall is straight. Surface of ventral keel is smooth. Length of tympanic bulla 34 to 38 mm.

.................................................. *Peponocephala electra*

$t^2$ Inconspicuous anterior spine situates nearly at the center. Anterior part of lateral wall is wide. Involucrum is short. Inner margin of the bulla concaves. Length of tympanic bulla 39 to 42 mm.

.................................................. *Feresa attenuata*

$t^3$ A plate-like or semitubal anterior spine situates in front of ventral keel. Anterior parts of ventral wall and of lateral wall are narrow and pointed. Inner margin of ventral wall is slightly convexed. Ventral keel is lower at the center. Length of tympanic bulla 36 to 52 mm.

.................................................. *Globicephala*

$t^4$ Anterior spine situates in front of involucrum. Anterior part of the lateral wall is wide. Ventral keel is conspicuous. Inner margin of the ventral wall slightly concaves. Length of tympanic bulla 38 to 47 mm.

.................................................. *Grampus griseus*

$r^2$ Tympanic bulla is not compressed laterally.

$u^1$ Ventral keel continues from inner posterior prominence to anterior end of involucrum. Inner posterior prominence projects posteriorly beyond the base. Median furrow is absent. Length of tympanic bulla is less than 45 mm.

$v^1$ Contour of anterior margin of ventral wall is oval. Ventral keel is high. The thickness of inner posterior prominence is nearly same with that of outer posterior prominence. Length of tympanic bulla 34 to 42 mm.

.................................................. *Tursiops*

$v^2$ Contour of anterior margin of ventral wall is rectangular, and has small tubal anterior spine at the center. Ventral keel is high. Inner posterior prominence is thinner than outer posterior prominence. Length of tympanic bulla 28 to 35 mm.

.................................................. *Stenella*

$v^3$ Contour of anterior margin of ventral wall is narrow rectangular. Ventral keel is wide and flat. Length of tympanic bulla 32 to 35 mm.

.................................................. *Lissodelphis borealis* u² Ventral keel does not reach the anterior end of tympanic bulla. Inner posterior prominence projects posteriorly beyond the base. Median furrow absent.

w¹ Ventral keel is inconspicous and fades at slightly anterior of the middle of the bulla. Ventral wall is nearly smooth except a hemispheric prominence at the antero-mesial corner. Interprominential notch is wide and U shaped. Length of tympanic bulla 30 to 35 mm.
.................................................. *Delphinus*

w² Ventral keel is high only at the posterior part, and ends nearly at the middle of the bulla. Two vague longitudinal keels are present on the median line and in front of outer posterior prominence. Length of tympanic bulla 32 to 39 mm.
.................................................. *Lagenorhynchus*

w³ Ventral keel is high and reaches at the point about 1/3 from the anterior. There is a deep groove on the ventral surface along the anterior end of ventral keel. Anterior part of the bulla is cylindrical. Vague longitudinal keels are observed same with *Lagenorhynchus*. Length of tympanic bulla 36 to 42 mm.
.................................................. *Steno bredanensis*

u³ Ventral keel is almost absent. Median furrow absent. Tympanic bulla is cylindrical. Length of tympanic bulla is more than 45 mm.

x¹ Both posterior prominences are arranged in parallel. Inner margin of the bulla is straight. Length of tympanic bulla 49 to 51 mm.
.................................................. *Pseudorca crassidens*

x² Posterior prominences opens posteriorly at the angle of about 45°. Elliptical foramen is absent. Length of tympanic bulla 70 to 85 mm.
.................................................. *Orcinus orca*

u⁴ Median furrow or similar structure is present. Ventral keel low. Elliptical foramen is usually absent. Small in size.

y¹ Inner posterior prominence projects posterioly beyornd the base. Vague keels is present at the outer border of median furrow. The inner angle on the anterior border of ventral wall is steep. Length of tympanic bulla 34 mm (1 example).
.................................................. *Sousa teuszii*

y² Inner posterior prominence projects posteriorly beyond the base. Anterior base of outer posteriorly prominence swells. Anterior margin of ventral wall is oval. Length of tympanic bulla 27 to 29 mm.
.................................................. *Cepholorhynchus*

y³ Inner posterior prominence does not project posteriorly beyond the base. Anterior margin of ventral wall is oval. Length of tympanic bulla 31 to 32 mm.
.................................................. *Sotalia*

*Periotic*

a¹ Anterior process is shaped of a curved rod. Posterior process is bent postero-bentrally at a right angles with superior process. Facet for posterior process of tympanic bulla is small, and has weak keels and grooves.

b¹ Large accessory ossicle touches the cochlear portion and covers the dorsal part of tympanic cavity. Superior process is massive and continuous in structure to the base of posterior process. Aquaeductus Fallopii, foramen singulare, and ductus endolymphaticus open in the fundus of internal auditory meatus. Length of periotic 57 to 69 mm.

.................................................. *Physeter catodon*

b² Accessory ossicle is small. Superior process is slender. Slender posterior process is separated from superior process by a groove. Ductus endolymphaticus opens outside of the opening of fundus of internal auditory meatus.

c¹ Cochlear portion is flat. Anterior process is separated from superior process by a groove. A protuberance projects postero-ventrally from the antero-ventral base of posterior process. Length of periotic 33 to 43 mm.

.................................................. *Platanista gangetica*

c² Cochlear portion is globular. Anterior process is continuous to superior process. No protuberence at the antero-ventral base of posterior process. Length of periotic 52 mm (1 example).

.................................................. *Lipotes vexillifer*

a² Anterior process is hemispheric or triangular pyramidal. Anterior and Posterior processes are distinct from superior process. Posterior process is short. Facet for posterior process of tympanic bulla is almost smooth.

d¹ Tip of posterior process is fan shaped.

e¹ Anterior process is elongted triangular pyramidal. Length of periotic 66 to 76 mm.

.................................................. *Berardius*

e² Anterior process is short, and the triangular pyramidal part is roundish. Length of periotic 54 to 63 mm.

.................................................. *Ziphius cavirostris*

d² Posterior process is slender, and not wide.

f¹ Anterior process forms a long triangular pyramid with the clear ridges. Length of periotic 61 mm (1 example).

.................................................. *Hyperoodon*

f² Anterior process is hemispheric, and has a small protuberance at the anterior tip. The surface of periotic is smooth and roundish. Small in size, 41 to 52 mm.

.................................................. *Mesoplodon*

g¹ Dome shaped protuberance is formed on the dorsal surface of superior process. Length of periotic 41 to 45 mm.

.................................................. *M. europaeus*
*M. ginkgodens*

g² No dome shaped protuberance on the superior process. Length of periotic 44 to 52 mm.

.................................................. *M. densitostris*
*M. carlhabbsi*
*M. stejnegeri*

a³ Anterior process is flat and spool shaped. A plate-like protuberance is on the tip of posterior process. Aquadeuctus Fallopii opens out side of the opening of fundus of internal auditory meatus.

.................................................. *Kogia*

h¹ Dorsal contour of upper tympanic aperture forms small semicircle. Length of periotic 24 to 31 mm.

.................................................. *K. breviceps*

h[2] Dorsal contour of upper tympanic aperture is nearly straight. Length of periotic 22 to 30 mm.

.................................................. *K. simus*

a[4] Anterior process is flat, and its anterior margin is rectangular.

i[1] Posterior process is short. Cochlear portion is spheric, and its diameter is more than 54% of the tympanic length.

j[1] Periotic is short. Anterior process very short. Length of periotic 20 mm (1 example).

.................................................. *Pontoporia blainvillei*

j[2] Periotic is large. Length of periotic 25 to 31 mm.

.................................................. *Inia geoffrensis*

i[1] Posterior process extends posteriorly and not short. Cochlear portion is less than 53% of periotic length.

k[1] Facet for posterior process of tympanic bulla is smooth. Posterior process is rod shaped. Length of periotic 26 to 32 mm.

l[1] Posterior process is slender and conical, and the tip is pointed.

.................................................. *Neophacaena phocaenoides*

l[2] Tip of posterior process is blunt. Faint constriction is on the base of posterior process.

.................................................. *Phocoenoides*

l[3] Tip of posterior process is blunt. No constriction on the base of posterior process.

.................................................. *Phocoena*

k[2] Facet for posterior process of tympanic bulla has ridges and grooves. Posterior process is stout.

m[1] Posterior process is wedge-shaped. Irregular grooves are present on the dorsal surface of posterior process. Length of periotic 37 to 41 mm.

.................................................. *Delphinapterus leucas*

m[2] Posterior process is of triangular rod with spongy structure on the tip. Length of periotic 34 to 41 mm.

.................................................. *Orcaella brevirostris*

i[3] Posterior process extends laterally or postero-laterally and is not short.

n[1] Periotic is large. Anterior, posterior, and superior processes are very massive, but cochlear portion is relatively small (diameter is 31 to 39% of periotic length). Periotic length 73 to 88 mm.

.................................................. *Orcinus orca*

n[2] Periotic is small, less than 50 mm in length. *Monodon* and most of the genera of Delphinidae are included, and their identification is usually difficult.

o[1] Needle-shaped processes are formed on the dorsal surface of superior process. They are conspicuous in older individuals, and weaker in the following order.

p[1] Opening of fundus of internal auditory meatus is round. Crista transversa is high (characteristics found only in this genus among the following 4 genera). No flat area is on the dorsal surface of superior process. Length of periotic 37 to 50 mm.

.................................................. *Monodon monoceros*

p[2] Wide and elevated flat area is conspicuous on the dorsal surface of superior process. Posterior process is thick and short, and has the spongy structure on the tip (found only in this genus among the 4 genera). Length of periotic 34 to 46 mm.

................................................ *Grampus griseus*

$p^3$ Flat area on the superior process is low, and distinguished unclearly from the rest of the part. Tip of posterior process is thin. The contour of anterior, superior, and posterior processes is smoothly round. Length of periotic 33 to 44 mm.

................................................ *Globicephala*

$p^4$ Flat area on the dorsal surface of superior process is oblique and not elevated from the rest of the area. Longitudinal keel is present on the inner side of dorsal surface of superior process. Opening of fundus of internal auditory meatus is long. Length of periotic 31 to 38 mm.

................................................ *Tursiops*

$o^2$ No needle-shaped process is formed on the dorsal surface of superior process. Crista transversa is low.

$q^1$ Longitudinal keel is conspicuous on the dorsal surface of superior process, and its outer area forms a flat slope. Anterior process is nearly straight. Length of periotic 42 to 49 mm.

................................................ *Pseudorca crassidens*

$q^2$ Anterior process is thick. In the lateral view, the dorsal contour of anterior and superior processes is straight. Dorsal surface of superior process is not wide. Length of periotic 35 to 38 mm.

................................................ *Feresa attenuata*

$q^3$ Dorsal surface of superior process is wide and flat. Length of periotic 30 to 35 mm.

................................................ *Peponocephala electra*

$q^4$ The area posterior of the opening of fundus of internal auditory meatus is wide and flat. Length of periotic 33 to 36 mm.

................................................ *Steno bredanensis*

$q^5$ Aquaeductus cochleae and ductus endolymphaticus are surrounded by a flat area, and open in a same plane. Length of periotic 30 to 33 mm.

................................................ *Lissodelphis borealis*

$q^6$ In the lateral view, the dorsal contour of anterior, superior, and posterior processes is round. Length of periotic 28 to 33 mm.

................................................ *Lagenorhynchus*

$q^7$ Superior process is slender, and surrounded by two planes of dorsal and and lateral sides. Length of periotic 33 mm (1 example).

................................................ *Sousa teuszii*

$q^8$ Superior process is slender, and surrounded by three planes. Length of periotic 27 mm (1 example).

................................................ *Sotalia*

$q^9$ Opening of aquaeductus cochleae projects posteriorly. One longitudinal keel is present on the dorsal surface of superior process. Length of periotic 26 mm (1 example).

................................................ *Cephalorhynchus*

$q^{10}$ Small periotics (24 to 32 mm in length) other than the above genera probably belong to *Delphinus* or *Stenella*. As the individual variation is large, the identification is most difficult in these genera.

APPENDIX II. TABLE OF MEASUREMENTS AND SOME CHARACTERISTICS OF TYMPANO-PERIOTIC BONE.

| A | 1 *Platanista gangetica* | | | | 2 *Inia geoffrensis* | | | | 3 *Lipotes vexillifer* | | | 4 *Pontoporia blainvillei* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | E | B | C | D | E | B | C | D | B | C | D |
| 1 | 7 | 47.1, 63.5 | 100 | 52.4 | 5 | 38.2, 45.6 | 100 | 41.1 | 1 | 47.1 | 100 | 1 | 24.3 | 100 |
| 2 | 7 | 43.7, 58.3 | 90.0, 91.8 | 91.3 | 5 | 32.0, 41.1 | 83.8, 91.5 | 88.0 | 1 | 44.4 | 94.3 | 1 | 21.9 | 90.0 |
| 3 | 7 | 34.3, 37.2 | 58.6, 73.2 | 68.2 | 5 | 25.3, 28.1 | 59.4, 68.5 | 64.5 | 1 | 29.3 | 62.3 | 1 | 17.1 | 70.3 |
| 4 | 7 | 27.3, 30.1 | 47.4, 59.6 | 54.6 | 5 | 16.6, 18.9 | 39.1, 44.8 | 42.7 | 1 | 22.4 | 47.6 | 1 | 13.2 | 54.3 |
| 5 | 7 | 24.7, 29.2 | 44.3, 54.4 | 50.9 | 5 | 25.5, 28.0 | 60.3, 70.3 | 65.3 | 1 | 24.0 | 51.0 | 1 | 14.9 | 61.3 |
| 6 | 7 | 33.3, 38.9 | 61.3, 74.8 | 69.2 | 5 | 29.8, 34.8 | 74.0, 81.4 | 77.4 | 1 | 27.3 | 58.0 | 1 | 20.1 | 83.0 |
| 7 | 7 | * | | | 5 | * | | | 1 | 24.1 | 51.2 | 1 | 13.5 | 55.5 |
| 8 | 7 | 2.4, 3.6 | 4.5, 5.7 | 5.3 | 5 | 2.8, 3.4 | 6.3, 8.5 | 7.8 | 1 | 4.8 | 10.2 | 1 | 3.0 | 12.4 |
| 9 | 7 | 11.0, 13.1 | 20.3, 25.9 | 23.4 | 5 | 9.7, 10.2 | 22.6, 27.5 | 25.1 | 1 | 5.0 | 10.6 | 1 | 6.0 | 24.6 |
| 10 | 7 | 2.7, 4.3 | 4.7, 9.1 | 6.4 | 5 | 3.5, 4.2 | 7.9, 11.5 | 9.5 | 1 | 1.3 | 2.8 | 1 | 4.3 | 17.7 |
| 11 | 6 | 0.9, 4.5 | 1.9, 8.2 | 4.9 | 5 | 1.9, 5.0 | 4.3, 11.0 | 8.5 | 1 | 2.2 | 6.0 | 1 | 0 | 0 |
| 12 | 7 | Inner | | | 5 | Outer≑Inner | | | 1 | Outer | | 1 | Inner | |
| 13 | 7 | 33.4, 42.3 | 100 | 37.6 | 5 | 25.7, 30.4 | 100 | 26.9 | 1 | 52.0 | 100 | 1 | 20.0 | 100 |
| 14 | 7 | 9.4, 15.2 | 23.9, 35.9 | 30.3 | 5 | 10.7, 15.6 | 41.6, 58.3 | 48.7 | 1 | 14.0 | 26.9 | 1 | 9.5 | 47.5 |
| 15 | 7 | 21.9, 24.8 | 55.3, 66.5 | 61.7 | 5 | 21.4, 25.2 | 79.6, 90.0 | 87.0 | 1 | 24.0 | 46.2 | 1 | 16.2 | 81.0 |
| 16 | 7 | 3.6, 5.3 | 9.9, 13.7 | 11.8 | 5 | 3.8, 4.8 | 14.7, 18.3 | 15.2 | 1 | 3.0 | 5.8 | 1 | 4.0 | 20.0 |
| 17 | 7 | 2.2, 3.8 | 5.6, 9.8 | 8.1 | 5 | 2.6, 3.6 | 9.7, 13.6 | 11.7 | 1 | 3.0 | 5.8 | 1 | 2.8 | 14.0 |
| 18 | 6 | 10.0, 13.0 | 26.3, 35.0 | 30.8 | 5 | 8.2, 11.1 | 31.9, 36.6 | 34.3 | 1 | 10.0 | 19.2 | 1 | 8.4 | 42.0 |
| 19 | 7 | 14.5, 16.2 | 38.3, 44.8 | 41.7 | 5 | 14.2, 18.2 | 54.3, 68.5 | 63.7 | 1 | 19.5 | 37.5 | 1 | 13.6 | 68.0 |
| 20 | 7 | + | | | 5 | + | | | 1 | + | | 1 | — | |
| 21 | 7 | + | | | 5 | — | | | 1 | — | | 1 | — | |
| 22 | 7 | | 64.7, 77.0 | 71.4 | 5 | | 60.8, 67.6 | 65.7 | 1 | | 110.4 | 1 | | 82.3 |

* Unmeasurable

A : Position of measurement or observed characters (see Table 3 in the text).

B : Number of individuals observed.

C : Observed minimum and maximum in mm.

D : Observed minimum and maximum in percentage of the standard length.

E : Mean value in mm (positions 1 and 13) or in percentage of the standard length.

APPENDIX II. Continued.

| A | 5 *Neophocaena phocaenoides* | | | | 6 *Phocoena ph. vomerina* | | | | 7 *Phocoena ph. phocoena* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | E | B | C | D | E | B | C | D | E |
| 1 | 19 | 27.7, 31.5 | 100 | 30.1 | 3 | 30.5, 33.7 | 100 | 31.9 | 3 | 28.4, 31.4 | 100 | 29.5 |
| 2 | 19 | 28.4, 32.1 | 98.7, 108.0 | 101.7 | 3 | 28.3, 30.3 | 89.3, 92.8 | 91.6 | 3 | 27.8, 30.1 | 95.9, 97.9 | 97.0 |
| 3 | 17 | 21.7, 25.4 | 74.8, 83.2 | 80.4 | 3 | 23.2, 24.4 | 70.3, 77.4 | 74.6 | 3 | 21.9, 22.5 | 71.7, 77.5 | 75.3 |
| 4 | 17 | 16.1, 19.4 | 56.1, 63.2 | 61.1 | 3 | 17.7, 18.0 | 53.1, 58.0 | 56.0 | 3 | 15.7, 16.3 | 52.0, 56.3 | 54.4 |
| 5 | 18 | 16.0, 20.0 | 57.8, 65.8 | 62.3 | 3 | 19.4, 21.0 | 62.8, 63.7 | 63.4 | 3 | 18.5, 19.9 | 59.0, 70.1 | 65.3 |
| 6 | 17 | 24.1, 28.1 | 81.5, 94.3 | 88.3 | 3 | 24.2, 25.0 | 75.2, 80.3 | 77.1 | 3 | 22.7, 24.9 | 79.3, 87.3 | 82.0 |
| 7 | 19 | 16.7, 19.3 | 56.2, 63.5 | 59.4 | 3 | 15.2, 17.0 | 49.1, 50.4 | 49.5 | 3 | 14.8, 16.9 | 51.7, 55.3 | 53.6 |
| 8 | 19 | 2.9, 5.4 | 10.4, 17.8 | 14.1 | 3 | 4.6, 5.4 | 13.6, 17.7 | 16.2 | 3 | 3.6, 4.9 | 12.6, 15.6 | 14.6 |
| 9 | 17 | 6.1, 7.4 | 20.1, 24.6 | 22.0 | 3 | 5.1, 5.8 | 16.7, 18.0 | 17.4 | 3 | 5.3, 5.9 | 18.2, 20.8 | 19.2 |
| 10 | 18 | 2.4, 3.9 | 7.6, 12.8 | 10.3 | 3 | 3.1, 3.9 | 9.2, 12.8 | 10.6 | 3 | 2.7, 3.3 | 9.5, 10.8 | 10.3 |
| 11 | 19 | 0 | 0 | Closed | 3 | 0 | 0 | Closed | 3 | 0 | 0 | Closed |
| 12 | 19 | Outer | | | 3 | Inner | | | 3 | Inner | | |
| 13 | 19 | 27.1, 31.4 | 100 | 29.9 | 3 | 26.9, 30.0 | 100 | 28.3 | 3 | 28.2, 30.4 | 100 | 29.0 |
| 14 | 19 | 8.1, 9.9 | 26.6, 33.6 | 29.7 | 3 | 10.1, 10.6 | 34.2, 39.0 | 36.8 | 3 | 9.4, 9.8 | 32.6, 34.8 | 33.7 |
| 15 | 19 | 16.2, 18.4 | 55.5, 64.3 | 58.5 | 3 | 15.2, 16.4 | 52.7, 57.6 | 54.9 | 3 | 15.3, 16.1 | 53.0, 56.9 | 54.8 |
| 16 | 19 | 3.1, 5.0 | 10.2, 16.4 | 12.7 | 3 | 3.3, 4.8 | 11.8, 16.2 | 13.7 | 3 | 3.6, 4.3 | 12.8, 15.2 | 13.7 |
| 17 | 19 | 1.4, 2.8 | 4.5, 9.2 | 7.0 | 3 | 2.5, 3.7 | 10.0, 12.3 | 11.4 | 3 | 2.8, 3.4 | 9.9, 12.0 | 11.0 |
| 18 | 15 | 8.9, 15.8 | 30.4, 51.6 | 47.3 | 1 | 8.6 | 32.0 | | 3 | 10.8, 11.8 | 37.6, 41.8 | 39.7 |
| 19 | 19 | 13.2, 15.2 | 45.1, 51.4 | 47.3 | 3 | 12.0, 12.6 | 40.0, 44.6 | 43.0 | 3 | 11.2, 11.9 | 38.9, 42.0 | 40.8 |
| 20 | 19 | — | | | 3 | — | | | 3 | — | | |
| 21 | 19 | — | | | 3 | — | | | 3 | — | | |
| 22 | 19 | | 93.7, 105.8 | 99.7 | 3 | | 87.0, 91.0 | 88.7 | 3 | | 96.8, 99.6 | 98.3 |



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APPENDIX II. Continued.

| A | 8 *Phocoena sinus* | | | 9 *Phocoenoides dalli* | | | | 10 *Phocoenoides truei* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | B | C | D | E | B | C | D | E |
| 1 | 1 | 29.5 | 100 | 6 | 32.1, 36.9 | 100 | 33.9 | 6 | 30.9, 34.1 | 100 | 32.3 |
| 2 | 1 | 27.8 | 94.3 | 6 | 29.4, 34.2 | 90.9, 97.2 | 92.9 | 6 | 27.5, 31.5 | 89.0, 93.9 | 91.1 |
| 3 | 1 | 23.0 | 78.0 | 6 | 24.1, 26.9 | 72.9, 77.5 | 75.4 | 6 | 23.4, 25.7 | 68.5, 81.9 | 75.4 |
| 4 | 1 | 16.1 | 54.5 | 6 | 19.4, 21.0 | 54.2, 60.8 | 58.7 | 6 | 17.8, 19.4 | 54.0, 61.8 | 58.0 |
| 5 | 1 | 17.0 | 57.6 | 6 | 19.1, 22.5 | 59.0, 69.8 | 63.0 | 6 | 18.5, 20.5 | 55.4, 60.8 | 61.6 |
| 6 | 1 | 22.8 | 77.3 | 6 | 25.3, 29.2 | 76.4, 82.4 | 79.2 | 6 | 22.8, 25.9 | 67.9, 82.5 | 74.5 |
| 7 | 1 | 15.6 | 63.0 | 6 | 15.1, 18.3 | 44.9, 52.4 | 48.2 | 6 | 12.9, 16.8 | 37.8, 53.5 | 45.4 |
| 8 | 1 | 4.3 | 14.6 | 6 | 4.9, 6.7 | 14.7, 20.8 | 17.6 | 6 | 4.4, 6.4 | 12.9, 20.4 | 17.0 |
| 9 | 1 | 6.1 | 20.6 | 6 | 5.4, 8.0 | 16.8, 21.7 | 19.8 | 6 | 6.4, 7.3 | 19.6, 23.6 | 20.8 |
| 10 | 1 | 2.2 | 7.5 | 5 | 2.5, 3.7 | 7.7, 11.5 | 8.9 | 6 | 2.8, 4.3 | 9.1, 12.6 | 10.5 |
| 11 | 1 | 0 | 0 | 5 | 0 | 0 | Closed | 6 | 0 | 0 | Closed |
| 12 | 1 | Outer≑Inner | | 6 | Inner | | | 6 | Inner | | |
| 13 | 1 | 26.8 | 100 | 6 | 28.7, 33.2 | 100 | 31.2 | 6 | 29.0, 31.6 | 100 | 30.1 |
| 14 | 1 | 10.3 | 38.4 | 6 | 10.9, 12.5 | 35.8, 39.4 | 37.5 | 6 | 10.8, 11.7 | 36.4, 38.6 | 37.3 |
| 15 | 1 | 15.2 | 56.7 | 6 | 15.7, 17.5 | 50.9, 56.5 | 53.8 | 6 | 15.7, 17.1 | 52.8, 54.1 | 53.6 |
| 16 | 1 | 3.4 | 12.7 | 6 | 2.9, 4.6 | 8.7, 16.0 | 12.6 | 6 | 3.1, 5.5 | 10.2, 18.7 | 13.2 |
| 17 | 1 | 2.7 | 10.4 | 6 | 1.9, 3.2 | 7.3, 11.2 | 8.6 | 6 | 2.4, 3.6 | 8.3, 12.4 | 10.1 |
| 18 | | | | 5 | 11.4, 14.4 | 38.8, 44.4 | 41.7 | 5 | 11.7, 12.1 | 37.9, 41.4 | 39.6 |
| 19 | 1 | 12.6 | 47.0 | 6 | 11.9, 13.8 | 37.5, 43.5 | 40.7 | 6 | 12.2, 13.2 | 41.5, 43.2 | 42.3 |
| 20 | 1 | — | | 6 | — | | | 6 | — | | |
| 21 | 1 | — | | 6 | — | | | 6 | — | | |
| 22 | 1 | | 91.0 | 6 | | 86.2, 97.8 | 92.0 | 6 | | 89.0, 100.6 | 93.5 |

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APPENDIX II. Continued.

| A | 11 *Delphinus bairdi* B | C | D | E | 12 *Delphinus delphis* B | C | D | 13 *Lagenorhynchus obliquidens* B | C | D | E |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 6 | 30.5, 35.0 | 100 | 32.6 | 2 | 31.8, 34.4 | 100 | 14 | 33.0, 38.4 | 100 | 35.4 |
| 2 | 6 | 28.3, 33.5 | 92.9, 97.5 | 95.8 | 2 | 29.5, 31.8 | 91.2, 93.7 | 14 | 30.9, 36.8 | 92.0, 98.8 | 96.0 |
| 3 | 6 | 20.4, 22.9 | 64.0, 70.0 | 67.6 | 2 | 22.1, 22.9 | 66.3, 69.5 | 14 | 22.4, 25.2 | 64.0, 70.3 | 67.4 |
| 4 | 6 | 16.1, 17.5 | 48.4, 53.8 | 51.7 | 2 | 16.2, 17.6 | 48.4, 53.8 | 14 | 17.2, 19.8 | 49.3, 54.8 | 52.3 |
| 5 | 6 | 16.8, 18.6 | 50.9, 58.0 | 55.0 | 2 | 18.6, 19.7 | 55.6, 58.4 | 14 | 18.8, 22.2 | 53.2, 64.1 | 57.3 |
| 6 | 6 | 21.4, 22.4 | 64.0, 70.2 | 67.9 | 2 | 22.1, 23.2 | 66.1, 72.0 | 14 | 22.1, 25.2 | 64.4, 71.2 | 67.8 |
| 7 | 6 | 15.0, 15.9 | 44.6, 49.5 | 47.8 | 2 | 15.2, 16.4 | 44.2, 49.8 | 14 | 14.2, 17.7 | 42.0, 49.4 | 45.5 |
| 8 | 6 | 4.0, 5.2 | 12.5, 16.0 | 14.4 | 2 | 4.6, 4.8 | 13.7, 15.1 | 14 | 4.3, 5.7 | 12.5, 16.8 | 14.4 |
| 9 | 6 | 4.1, 5.0 | 13.2, 15.2 | 14.4 | 2 | 4.8, 5.7 | 14.0, 17.0 | 14 | 4.2, 6.1 | 12.5, 17.1 | 14.8 |
| 10 | 6 | 0.9, 1.4 | 3.0, 4.5 | 3.6 | 2 | 0.8, 1.0 | 2.3, 3.1 | 14 | 0.6, 2.1 | 1.7, 5.9 | 3.9 |
| 11 | 6 | 3.4, 6.3 | 10.7, 18.5 | 15.6 | 2 | 4.9, 6.2 | 14.6, 18.1 | 14 | 4.0, 6.3 | 10.4, 18.4 | 14.0 |
| 12 | 6 | Outer | | | 2 | Outer | | 14 | Outer | | |
| 13 | 6 | 27.4, 31.1 | 100 | 28.6 | 2 | 27.9, 30.1 | 100 | 14 | 29.0, 32.7 | 100 | 30.6 |
| 14 | 6 | 10.0, 11.6 | 35.8, 38.6 | 37.4 | 2 | 10.0, 11.0 | 33.7, 39.4 | 14 | 10.9, 14.0 | 37.1, 43.1 | 40.0 |
| 15 | 6 | 18.9, 20.4 | 65.6, 72.6 | 68.7 | 2 | 19.0, 19.8 | 63.1, 68.1 | 14 | 18.6, 21.7 | 61.5, 70.5 | 66.4 |
| 16 | 6 | 1.2, 2.6 | 4.1, 9.5 | 7.0 | 2 | 1.2, 2.2 | 4.0, 7.9 | 14 | 1.3, 3.8 | 4.4, 12.2 | 9.4 |
| 17 | 6 | 1.3, 3.0 | 4.2, 10.9 | 7.7 | 2 | 1.6, 3.4 | 5.4, 12.2 | 14 | 2.0, 3.8 | 6.7, 12.3 | 9.1 |
| 18 | 6 | 10.3, 14.0 | 37.3, 46.8 | 44.1 | 2 | 12.2, 12.2 | 43.7, 43.7 | 14 | 10.9, 16.4 | 37.2, 54.5 | 42.4 |
| 19 | 6 | 12.1, 13.8 | 42.8, 48.6 | 45.5 | 2 | 13.4, 14.1 | 45.2, 49.1 | 14 | 13.3, 14.5 | 44.6, 49.5 | 46.1 |
| 20 | 6 | + | | | 2 | + | | 14 | + | | |
| 21 | 6 | — | | | 2 | — | | 14 | — | | |
| 22 | 6 | | 85.4, 92.0 | 88.1 | 2 | | 83.3, 92.8 | 14 | | 78.4, 91.8 | 86.4 |

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APPENDIX II. Continued.

| A | 14 *Lagenorhynchus acutus* | | | | 15 *L. albirostris* | | | | 16 *L. obscurus* | | | 17 *L. australis* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | E | B | C | D | E | B | C | D | B | C | D |
| 1 | 3 | 32.3, 33.4 | 100 | 33.0 | 3 | 36.6, 37.6 | 100 | 37.1 | 1 | 33.5 | 100 | 1 | 32.7 | 100 |
| 2 | 3 | 30.6, 31.6 | 91.7, 98.0 | 94.7 | 3 | 35.0, 35.8 | 94.3, 98.0 | 96.2 | 1 | 32.8 | 98.0 | 1 | 30.9 | 94.5 |
| 3 | 2 | 22.4, 23.3 | 69.5, 69.6 | 69.6 | 1 | 24.5 | 65.0 | | 1 | 23.3 | 69.5 | 1 | 22.5 | 69.0 |
| 4 | 3 | 16.6, 17.3 | 51.5, 51.7 | 51.6 | 2 | 19.1, 19.3 | 51.4, 51.5 | | 1 | 23.2 | 69.3 | 1 | 16.8 | 51.4 |
| 5 | 2 | 17.4, 18.0 | 54.0, 54.0 | 54.0 | 2 | 22.3, 22.4 | 59.4, 60.4 | | 1 | 19.1 | 57.0 | 1 | 19.0 | 58.0 |
| 6 | 2 | 22.3, 23.3 | 69.0, 69.7 | 69.4 | 1 | 27.8 | 74.0 | | 1 | 23.7 | 70.7 | 1 | 13.1 | 40.1 |
| 7 | 3 | 16.0, 16.5 | 48.0, 49.6 | 49.0 | 3 | 20.1, 20.5 | 54.2, 56.0 | 54.9 | 1 | 16.5 | 49.2 | 1 | 15.5 | 47.4 |
| 8 | 3 | 4.0, 4.4 | 12.0, 13.6 | 12.5 | 3 | 5.0, 5.7 | 13.7, 15.2 | 14.6 | 1 | 4.2 | 12.5 | 1 | 4.7 | 14.4 |
| 9 | 2 | 5.5, 6.2 | 16.5, 19.2 | 17.9 | 1 | 5.7 | 15.2 | | 1 | 5.5 | 16.4 | 1 | 4.8 | 14.7 |
| 10 | 2 | 0.9, 0.9 | 2.7, 2.8 | 2.7 | 1 | 1.1 | 2.9 | | 1 | 1.1 | 3.3 | 1 | | |
| 11 | 3 | 3.1, 4.4 | 9.6, 13.2 | 11.7 | 2 | 1.7, 2.7 | 4.6, 7.2 | | 1 | 4.0 | 11.9 | 1 | 0 | 0 |
| 12 | 3 | Outer | | | 2 | Outer | | | 1 | Outer | | 1 | Outer | |
| 13 | 3 | 28.4, 30.0 | 100 | 29.1 | 2 | 31.8, 32.4 | 100 | | 1 | 31.6 | 100 | 1 | 30.1 | 100 |
| 14 | 3 | 10.8, 11.8 | 37.2, 29.4 | 38.6 | 2 | 13.5, 14.1 | 42.5, 43.5 | | 1 | 12.7 | 40.2 | 1 | 13.9 | 46.2 |
| 15 | 3 | 17.9, 19.5 | 63.0, 67.3 | 64.6 | 2 | 20.9, 21.4 | 65.8, 66.0 | | 1 | 22.0 | 69.8 | 1 | 19.7 | 65.5 |
| 16 | 3 | 1.1, 1.3 | 3.9, 4.3 | 4.1 | 2 | 1.8, 1.8 | 5.6, 5.7 | | 1 | 1.7 | 5.4 | 1 | 1.5 | 5.5 |
| 17 | 3 | 1.8, 2.2 | 6.3, 7.6 | 6.8 | 2 | 2.9, 3.3 | 7.7, 10.4 | | 1 | 2.8 | 8.9 | 1 | 1.8 | 6.0 |
| 18 | 3 | 13.4, 14.3 | 46.2, 47.6 | 47.1 | 2 | 15.5, 15.6 | 48.1, 48.8 | | 1 | | | 1 | | |
| 19 | 3 | 13.1, 14.0 | 46.2, 48.3 | 46.9 | 2 | 14.2, 14.3 | 43.8, 45.0 | | 1 | 15.0 | 47.6 | 1 | 12.8 | 42.6 |
| 20 | 3 | + | | | 3 | + | | | 1 | + | | 1 | + | |
| 21 | 3 | — | | | 3 | — | | | 1 | — | | 1 | — | |
| 22 | 3 | | 87.0, 90.0 | 88.3 | 2 | | 85.8, 88.5 | | 1 | | 94.5 | 1 | | 92.0 |

APPENDIX II. Continued.

| A | 18 *Steno bredanensis* B | C | D | E | 19 *Lissodelphis borealis* B | C | D | E | 20 *Stenella caeruleoalba* B | C | D | E |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 7 | 36.8, 41.8 | 100 | 38.5 | 6 | 32.6, 34.1 | 100 | 33.4 | 14 | 28.9, 34.3 | 100 | 32.0 |
| 2 | 7 | 35.7, 40.8 | 96.5, 99.7 | 98.0 | 6 | 32.1, 34.3 | 96.5, 100.3 | 99.0 | 14 | 28.0, 34.3 | 90.0, 95.5 | 93.1 |
| 3 | 7 | 25.5, 27.7 | 66.3, 72.0 | 69.4 | 6 | 22.0, 23.5 | 65.6, 71.2 | 68.8 | 14 | 19.9, 22.9 | 62.4, 72.4 | 68.6 |
| 4 | 7 | 18.8, 21.5 | 51.3, 55.0 | 52.9 | 6 | 16.5, 18.1 | 49.2, 55.4 | 52.5 | 14 | 15.8, 17.8 | 49.3, 55.8 | 52.7 |
| 5 | 7 | 20.3, 25.0 | 55.3, 60.3 | 58.5 | 6 | 17.8, 19.6 | 53.0, 58.9 | 55.3 | 14 | 15.4, 18.8 | 49.0, 55.8 | 52.8 |
| 6 | 7 | 25.5, 28.7 | 67.7, 74.9 | 71.5 | 6 | 23.1, 25.1 | 68.3, 75.0 | 70.9 | 13 | 20.9, 24.4 | 63.3, 74.7 | 70.2 |
| 7 | 7 | 19.1, 21.7 | 50.7, 57.2 | 53.2 | 6 | 14.0, 15.9 | 42.0, 48.5 | 45.5 | 14 | 12.9, 16.0 | 41.5, 47.6 | 44.1 |
| 8 | 7 | 4.3, 5.6 | 11.3, 14.7 | 12.9 | 6 | 5.1, 6.3 | 15.4, 18.9 | 16.6 | 14 | 3.1, 5.1 | 11.9, 15.2 | 13.1 |
| 9 | 7 | 4.5, 6.3 | 12.2, 17.2 | 14.4 | 6 | 4.7, 5.3 | 13.8, 16.0 | 14.7 | 13 | 4.6, 5.6 | 13.6, 17.9 | 15.9 |
| 10 | 7 | 1.1, 2.5 | 2.6, 6.4 | 4.4 | 6 | 0.9, 1.3 | 2.6, 3.9 | 3.2 | 14 | 0.7, 1.8 | 2.2, 5.8 | 3.7 |
| 11 | 7 | 3.4, 6.1 | 9.0, 16.6 | 12.0 | 6 | 2.6, 4.3 | 7.8, 12.9 | 10.4 | 14 | 3.0, 5.6 | 8.8, 17.7 | 14.5 |
| 12 | 7 | Outer | | | 6 | Outer | | | 14 | Outer | | |
| 13 | 7 | 33.1, 36.0 | 100 | 34.3 | 6 | 30.2, 32.5 | 100 | 30.9 | 15 | 28.0, 31.9 | 100 | 29.7 |
| 14 | 7 | 11.3, 13.6 | 32.1, 40.7 | 36.3 | 6 | 10.4, 11.8 | 34.2, 39.1 | 36.7 | 15 | 10.8, 14.1 | 36.2, 45.6 | 40.0 |
| 15 | 7 | 21.2, 24.3 | 62.0, 73.5 | 67.2 | 6 | 19.3, 20.4 | 62.5, 64.3 | 63.3 | 15 | 18.3, 20.6 | 60.3, 69.1 | 65.6 |
| 16 | 7 | 1.0, 2.3 | 3.0, 6.8 | 5.4 | 6 | 1.4, 2.4 | 4.6, 7.8 | 6.3 | 15 | 0.7, 2.1 | 2.4, 8.1 | 4.5 |
| 17 | 7 | 2.4, 3.8 | 7.2, 11.3 | 9.1 | 6 | 2.0, 2.9 | 6.1, 9.3 | 7.9 | 15 | 1.1, 4.0 | 3.9, 12.7 | 8.0 |
| 18 | 6 | 13.7, 17.8 | 41.1, 52.3 | 48.0 | 6 | 10.2, 13.5 | 33.4, 44.8 | 39.3 | 15 | 9.0, 14.0 | 30.4, 47.6 | 37.5 |
| 19 | 7 | 15.5, 18.3 | 46.4, 54.5 | 49.6 | 6 | 13.0, 14.9 | 41.8, 48.8 | 44.9 | 15 | 13.5, 14.3 | 43.2, 47.6 | 46.7 |
| 20 | 7 | + | | | 6 | + | | | 15 | + | | |
| 21 | 7 | — | | | 6 | — | | | 15 | — | | |
| 22 | 7 | | 84.7, 98.0 | 89.2 | 6 | | 90.0, 97.5 | 92.7 | 14 | | 88.1, 102.1 | 92.8 |

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APPENDIX II. Continued.

| A | 21 Stenella styx | | | 22 (?) Stenella roseiventris | | | | 23 (?) Stenella longirostris | | | 24 Stenella attenuata | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | B | C | D | E | B | C | D | B | C | D | E |
| 1 | 1 | 32.1 | 100 | 6 | 28.0, 30.8 | 100 | 29.9 | 2 | 28.4, 30.4 | 100 | 7 | 30.1, 33.8 | 100 | 31.3 |
| 2 | 1 | 30.5 | 95.0 | 6 | 27.5, 29.2 | 93.5, 96.9 | 94.8 | 2 | 27.2, 28.4 | 93.4, 95.8 | 7 | 28.2, 32.8 | 89.7, 105.0 | 95.4 |
| 3 | 1 | 27.0 | 84.1 | 6 | 19.4, 22.1 | 65.8, 71.8 | 68.8 | 2 | 20.3, 24.6 | 69.1, 72.1 | 7 | 21.0, 22.5 | 62.4, 73.5 | 68.6 |
| 4 | 1 | 17.6 | 54.8 | 6 | 14.9, 16.7 | 50.7, 54.2 | 52.4 | 2 | 15.8, 16.0 | 51.9, 56.0 | 7 | 15.3, 17.3 | 45.2, 54.5 | 51.7 |
| 5 | 1 | 18.6 | 57.9 | 6 | 15.0, 16.9 | 50.8, 55.0 | 53.6 | 2 | 15.9, 17.0 | 55.4, 57.4 | 7 | 17.1, 18.1 | 51.0, 59.0 | 55.6 |
| 6 | 1 | 23.1 | 72.0 | 6 | 20.1, 22.2 | 68.5, 72.1 | 70.7 | 2 | 20.0, 21.5 | 70.4, 70.7 | 7 | 22.0, 23.9 | 68.3, 77.0 | 71.4 |
| 7 | 1 | 14.8 | 46.1 | 6 | 12.6, 15.5 | 43.3, 50.4 | 46.4 | 2 | 14.1, 15.2 | 46.4, 53.5 | 7 | 14.3, 15.6 | 42.9, 49.4 | 46.8 |
| 8 | 1 | 4.3 | 13.4 | 6 | 3.3, 4.7 | 11.2, 15.8 | 13.5 | 2 | 4.2, 4.5 | 13.8, 15.7 | 7 | 4.2, 5.6 | 12.8, 17.6 | 14.9 |
| 9 | 1 | 5.3 | 16.5 | 6 | 3.6, 4.5 | 12.2, 14.7 | 13.9 | 2 | 4.3, 4.7 | 14.5, 16.5 | 7 | 4.0, 5.7 | 14.0, 18.7 | 15.7 |
| 10 | 1 | 1.2 | 3.7 | 6 | 0.8, 1.4 | 2.7, 4.8 | 3.5 | 2 | 0.8, 1.0 | 2.8, 3.3 | 7 | 0.5, 1.2 | 1.5, 4.0 | 2.5 |
| 11 | 1 | 5.5 | 17.1 | 6 | 2.8, 5.3 | 9.5, 18.1 | 11.7 | 2 | 2.1, 4.0 | 6.9, 14.1 | 7 | 0.7, 4.7 | 2.3, 14.1 | 7.2 |
| 12 | 1 | Outer | | 6 | Outer | | | 2 | Outer | | 7 | Outer | | |
| 13 | 1 | 28.8 | 100 | 6 | 25.4, 28.5 | 100 | 27.0 | 2 | 24.3, 24.4 | 100 | 7 | 26.2, 29.6 | 100 | 28.2 |
| 14 | 1 | 11.5 | 39.9 | 6 | 9.5, 10.9 | 34.9, 41.3 | 37.9 | 2 | 9.4, 9.5 | 38.5, 39.1 | 7 | 9.8, 12.4 | 36.3, 42.5 | 38.3 |
| 15 | 1 | 19.1 | 66.3 | 6 | 17.0, 18.8 | 58.1, 67.9 | 64.8 | 2 | 16.7, 17.0 | 68.4, 70.0 | 7 | 18.0, 20.0 | 61.9, 69.5 | 66.6 |
| 16 | 1 | 1.3 | 4.5 | 6 | 1.7, 3.1 | 6.7, 11.6 | 8.2 | 2 | 1.9, 2.0 | 7.8, 8.2 | 7 | 0.9, 1.8 | 3.1, 4.9 | 4.7 |
| 17 | 1 | 1.7 | 5.9 | 6 | 1.2, 2.8 | 4.8, 10.3 | 7.6 | 2 | 1.7, 2.0 | 7.0, 8.2 | 7 | 2.2, 3.4 | 7.5, 12.5 | 9.7 |
| 18 | 1 | 10.9 | 37.8 | 6 | 9.0, 11.8 | 33.1, 44.9 | 38.9 | 2 | 8.3, 8.3 | 34.0, 34.2 | 7 | 11.0, 14.5 | 35.3, 49.6 | 46.1 |
| 19 | 1 | 13.2 | 45.8 | 6 | 12.4, 13.5 | 43.9, 53.2 | 47.6 | 2 | 12.3, 12.3 | 50.4, 50.6 | 7 | 13.0, 14.0 | 46.9, 50.5 | 48.5 |
| 20 | 1 | + | | 6 | + | | | 2 | + | | 7 | + | | |
| 21 | 1 | — | | 6 | — | | | 2 | — | | 7 | — | | |
| 22 | 1 | | 89.7 | 6 | | 85.1, 97.9 | 90.1 | 2 | | 84.7, 85.9 | 7 | | 80.5, 95.7 | 88.0 |

APPENDIX II. Continued.

| A | 24a *Stenella graffmani* B | C | D | 24b *Stenella plagiodon* B | C | D | E | 25 *Tursiops truncatus* (w. Pacific) B | C | D | E |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 29.8, 32.0 | 100 | 3 | 33.8, 34.4 | 100 | 34.1 | 43 | 34.7, 41.5 | 100 | 38.1 |
| 2 | 2 | 27.4, 29.8 | 91.5, 93.1 | 3 | 31.2, 32.2 | 90.6, 95.2 | 92.6 | 43 | 33.1, 40.0 | 80.6, 99.2 | 95.2 |
| 3 | 2 | 21.0, 21.3 | 65.9, 71.1 | 2 | 22.5, 22.6 | 65.6, 66.5 | 66.1 | 42 | 23.9, 28.1 | 65.6, 74.0 | 69.8 |
| 4 | 2 | 15.9, 16.4 | 51.1, 53.6 | 3 | 16.8, 17.3 | 49.1, 50.3 | 49.8 | 43 | 17.7, 21.7 | 48.6, 55.9 | 52.6 |
| 5 | 2 | 17.8, 18.3 | 55.6, 60.7 | 3 | 17.6, 19.8 | 51.4, 54.9 | 53.6 | 43 | 18.9, 25.5 | 52.5, 63.4 | 59.3 |
| 6 | 2 | 21.1, 21.7 | 65.9, 72.6 | 2 | 23.4, 23.6 | 68.0, 69.8 | 68.9 | 42 | 25.3, 30.2 | 65.4, 79.2 | 72.8 |
| 7 | 2 | 14.5, 15.7 | 48.6, 50.8 | 3 | 15.0, 15.7 | 43.6, 46.4 | 45.1 | 43 | 17.4, 21.3 | 45.2, 55.6 | 51.1 |
| 8 | 2 | 4.1, 4.8 | 13.7, 15.0 | 3 | 4.3, 5.0 | 12.5, 14.8 | 13.6 | 43 | 4.0, 5.9 | 10.7, 15.5 | 13.1 |
| 9 | 2 | 4.5, 4.7 | 14.1, 15.7 | 2 | 4.7, 4.9 | 13.9, 14.2 | 14.1 | 42 | 4.6, 6.9 | 11.3, 18.6 | 15.0 |
| 10 | 2 | 0.8, 1.0 | 2.5, 3.2 | 3 | 0.8, 1.2 | 2.3, 4.1 | 3.3 | 43 | 0.8, 3.5 | 2.2, 9.2 | 4.5 |
| 11 | 2 | 3.5, 4.3 | 11.1, 14.4 | 3 | 3.4, 4.0 | 9.9, 11.6 | 11.0 | 43 | 0 , 7.3 | 3.8, 20.3 | 12.1* |
| 12 | 2 | Outer | | 3 | Outer | | | 43 | Outer | | |
| 13 | 3 | 25.9, 27.2 | 100 | 3 | 28.9, 29.6 | 100 | 29.1 | 43 | 31.7, 37.8 | 100 | 35.0 |
| 14 | 3 | 8.3, 9.6 | 30.6, 36.2 | 3 | 10.4, 12.1 | 36.0, 41.9 | 38.4 | 43 | 12.0, 18.0 | 36.2, 52.6 | 42.0 |
| 15 | 3 | 16.6, 18.4 | 64.0, 69.4 | 3 | 18.9, 19.9 | 63.8, 68.9 | 66.5 | 43 | 20.5, 24.3 | 56.7, 70.1 | 64.3 |
| 16 | 2 | 0.6, 1.0 | 2.3, 3.7 | 3 | 1.3, 1.4 | 4.4, 4.8 | 4.7 | 43 | 0.4, 3.4 | 2.8, 10.1 | 4.9 |
| 17 | 2 | 2.1, 2.7 | 7.9, 10.1 | 3 | 2.0, 2.3 | 6.8, 8.0 | 7.4 | 43 | 1.2, 4.7 | 3.4, 14.1 | 9.1 |
| 18 | 2 | 10.4, 12.1 | 39.2, 44.6 | 3 | 10.8, 13.6 | 36.5, 47.0 | 40.3 | 42 | 12.0, 19.0 | 35.1, 52.8 | 43.0 |
| 19 | 2 | 13.4, 13.6 | 49.4, 51.3 | 3 | 12.8, 13.9 | 43.6, 47.7 | 45.2 | 43 | 14.9, 17.5 | 41.9, 52.8 | 46.3 |
| 20 | 2 | + | | 3 | + | | | 43 | + | | |
| 21 | 2 | — | | 3 | — | | | 43 | — | | |
| 22 | 2 | | 84.6, 89.2 | 3 | | 81.5, 85.5 | 83.7 | 43 | | 80.4, 99.5 | 91.9 |

* Closed on 1



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APPENDIX II. Continued.

| A | 25a *Tursiops truncatus* (Atlantic) | | | | 26 *T. gilli* (e. Pacific) | | | 27 *Cephalorhynchus spp.* | | | 28 *Sotalia spp.* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | E | B | C | D | B | C | D | B | C | D |
| 1 | 3 | 38.3, 39.2 | 100 | 38.6 | 2 | 37.5, 38.9 | 100 | 2 | 27.8, 28.7 | 100 | 2 | 31.4, 31.7 | 100 |
| 2 | 3 | 36.6, 38.8 | 95.9, 99.0 | 97.5 | 2 | 36.6, 37.4 | 96.5, 97.5 | 2 | 24.8, 26.1 | 89.3, 90.9 | 2 | 28.7, 28.9 | 91.3, 91.4 |
| 3 | 3 | 25.4, 26.2 | 64.8, 68.3 | 67.3 | 2 | 25.3, 26.4 | 67.5, 68.0 | 2 | 18.4, 19.4 | 66.2, 67.6 | 1 | 21.0 | 67.0 |
| 4 | 3 | 18.3, 19.0 | 45.2, 48.6 | 47.3 | 2 | 18.8, 20.6 | 50.1, 53.0 | 2 | 14.5, 14.8 | 51.6, 52.2 | 2 | 15.7, 16.0 | 49.6, 51.0 |
| 5 | 3 | 20.5, 21.0 | 53.2, 54.0 | 53.5 | 2 | 20.8, 23.5 | 55.4, 60.5 | 2 | 15.9, 16.7 | 57.2, 58.2 | 2 | 17.8, 18.0 | 56.2, 57.3 |
| 6 | 3 | 26.2, 27.2 | 68.3, 69.5 | 68.9 | 2 | 27.7, 28.1 | 72.3, 74.0 | 2 | 18.3, 19.8 | 65.8, 69.0 | 1 | 22.1 | 70.4 |
| 7 | 3 | 18.2, 19.5 | 46.4, 51.0 | 49.1 | 2 | 16.7, 20.5 | 44.6, 52.8 | 2 | 12.8, 12.9 | 44.6, 46.4 | 2 | 15.3, 15.7 | 48.6, 49.4 |
| 8 | 3 | 4.4, 5.0 | 11.2, 13.0 | 12.6 | 2 | 3.9, 4.8 | 10.4, 12.3 | 2 | 2.8, 3.2 | 10.1, 11.1 | 2 | 3.3, 4.3 | 10.3, 13.5 |
| 9 | 3 | 4.9, 6.5 | 12.8, 16.6 | 14.6 | 2 | 4.8, 6.1 | 12.3, 16.3 | 2 | 4.4, 4.8 | 15.3, 17.3 | 1 | 4.1 | 13.0 |
| 10 | 3 | 1.6, 2.3 | 4.2, 6.0 | 5.2 | 2 | 2.6, 2.8 | 6.9, 7.2 | 1 | 1.1 | 4.0 | 1 | 1.7 | 5.4 |
| 11 | 3 | 2.3, 5.2 | 6.0, 13.6 | 10.5 | 2 | 2.8, 5.4 | 7.2, 5.4 | 2 | 0 | 0 | 2 | 0 , + | 0 , + |
| 12 | 3 | Outer | | | 2 | Outer | | 2 | Outer | | 2 | Outer | |
| 13 | 3 | 31.9, 33.6 | 100 | 33.1 | 2 | 33.4, 34.4 | 100 | 1 | 25.7 | 100 | 2 | 26.5, 26.7 | 100 |
| 14 | 3 | 11.7, 13.7 | 36.6, 41.3 | 37.4 | 2 | 14.0, 14.0 | 40.7, 42.0 | 1 | 10.1 | 40.9 | 2 | 8.4, 9.4 | 31.5, 35.5 |
| 15 | 3 | 21.1, 22.2 | 62.8, 66.5 | 66.9 | 2 | 20.8, 23.9 | 62.3, 69.5 | 1 | 16.6 | 64.6 | 2 | 18.1, 19.5 | 67.9, 73.5 |
| 16 | 3 | 0.5, 1.9 | 1.5, 5.7 | 3.5 | 2 | 1.2, 2.2 | 3.6, 6.4 | 2 | 2.6, 3.0 | | 2 | 1.4, 1.5 | 5.3, 5.7 |
| 17 | 3 | 3.0, 3.8 | 8.9, 11.2 | 10.2 | 2 | 2.1, 2.6 | 6.1, 7.8 | 2 | 3.6, 4.6 | | 2 | 1.5, 1.8 | 5.7, 6.8 |
| 18 | 3 | 14.7, 19.9 | 44.2, 59.2 | 42.2 | 1 | 15.2 | 45.4 | 1 | 9.5 | 37.0 | 1 | 12.9 | 48.4 |
| 19 | 3 | 15.8, 17.0 | 49.4, 50.3 | 49.9 | 2 | 15.3, 15.9 | 44.5, 47.6 | 2 | 12.1, 13.9 | | 2 | 12.2, 12.8 | 45.8, 48.3 |
| 20 | 3 | + | | | 2 | + | | 2 | + | | 2 | + | |
| 21 | 3 | — | | | 2 | — | | 2 | — | | 2 | — | |
| 22 | 3 | | 83.3, 87.5 | 85.7 | 2 | | 88.5, 89.0 | 1 | | 92.5 | 2 | | 83.5, 85.0 |

APPENDIX II. Continued.

| A | 29 *Sousa teuszii* | | | 30 *Pseudorca crassidens* | | | | 31 *Orcinus orca* | | | | 32 *Peponocephala electra* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | B | C | D | E | B | C | D | E | B | C | D | E |
| 1 | 1 | 34.2 | 100 | 4 | 47.7, 50.5 | 100 | 49.5 | 7 | 70.2, 85.0 | 100 | 79.2 | 6 | 34.0, 37.9 | 100 | 35.9 |
| 2 | 1 | 33.3 | 97.4 | 4 | 42.3, 46.0 | 88.7, 90.9 | 90.3 | 7 | 62.1, 76.0 | 83.8, 90.8 | 87.2 | 6 | 30.3, 33.8 | 88.1, 93.4 | 89.8 |
| 3 | 1 | 23.4 | 68.4 | 2 | 32.5, 36.6 | 68.1, 72.5 | | 5 | 50.3, 62.7 | 68.2, 74.5 | 71.6 | 6 | 25.4, 26.7 | 67.0, 73.7 | 71.8 |
| 4 | 1 | 17.9 | 52.3 | 3 | 25.6, 28.8 | 53.7, 58.0 | 55.6 | 6 | 38.5, 46.9 | 49.6, 55.8 | 53.6 | 6 | 19.2, 20.9 | 53.6, 58.3 | 56.1 |
| 5 | 1 | 19.6 | 57.3 | 2 | 28.5, 31.1 | 59.7, 61.8 | | 6 | 39.8, 49.4 | 52.5, 58.8 | 56.1 | 6 | 19.1, 20.6 | 50.4, 58.9 | 55.3 |
| 6 | 1 | 24.1 | 70.5 | 2 | 34.9, 38.3 | 73.2, 75.8 | | 6 | 50.9, 63.7 | 67.3, 75.8 | 71.8 | 6 | 26.8, 28.1 | 69.7, 80.3 | 75.7 |
| 7 | 1 | 18.5 | 54.1 | 4 | 21.6, 24.5 | 43.5, 49.3 | 46.3 | 7 | 34.7, 46.9 | 47.3, 55.8 | 51.5 | 6 | 16.0, 18.1 | 42.2, 53.2 | 47.5 |
| 8 | 1 | 4.0 | 11.7 | 4 | 6.5, 7.7 | 13.3, 15.2 | 14.1 | 7 | 7.6, 16.1 | 10.8, 19.8 | 15.6 | 6 | 4.7, 5.3 | 12.6, 15.6 | 13.9 |
| 9 | 1 | 4.6 | 13.5 | 2 | 6.2, 10.2 | 12.9, 20.2 | | 5 | 7.3, 10.9 | 9.5, 13.8 | 12.3 | 6 | 4.7, 6.0 | 12.9, 17.6 | 14.6 |
| 10 | 1 | 2.5 | 7.3 | 3 | 2.0, 2.3 | 4.0, 4.8 | 4.3 | 6 | 2.2, 3.8 | 3.2, 4.9 | 4.2 | 6 | 1.0, 1.7 | 2.7, 4.0 | 3.6 |
| 11 | 1 | 0 | 0 | 4 | 2.1, 8.0 | 4.2, 16.1 | 12.8 | 7 | 0 | 0 | Closed | 6 | 4.0, 5.2 | 9.7, 14.7 | 12.5 |
| 12 | 1 | Outer | | 4 | Outer | | | 7 | Outer | | | 6 | Outer | | |
| 13 | 1 | 33.3 | 100 | 4 | 42.8, 49.0 | 100 | 45.4 | 7 | 73.6, 87.5 | 100 | 79.8 | 6 | 30.8, 34.2 | 100 | 32.1 |
| 14 | 1 | 10.8 | 32.4 | 4 | 17.2, 18.9 | 38.6, 42.1 | 40.1 | 6 | 30.0, 36.0 | 38.0, 48.6 | 42.1 | 6 | 13.5, 15.7 | 40.6, 48.9 | 45.0 |
| 15 | 1 | 20.0 | 60.1 | 4 | 27.8, 33.4 | 64.7, 70.9 | 67.6 | 7 | 46.8, 57.3 | 53.5, 70.8 | 65.3 | 6 | 21.3, 22.8 | 65.5, 69.8 | 67.8 |
| 16 | 1 | 3.2 | 9.6 | 4 | 2.1, 2.5 | 4.6, 5.4 | 5.0 | 7 | 1.2, 3.2 | 1.4, 7.9 | 3.1 | 6 | 0.4, 1.2 | 1.6, 3.9 | 2.4 |
| 17 | 1 | 1.8 | 5.4 | 4 | 0.8, 2.4 | 1.6, 5.6 | 4.1 | 7 | 1.9, 5.2 | 2.2, 6.1 | 4.6 | 6 | 0.4, 1.9 | 1.2, 5.6 | 3.0 |
| 18 | 1 | 14.8 | 44.4 | 4 | 20.5, 25.2 | 42.5, 58.7 | 49.1 | 6 | 33.1, 46.3 | 43.5, 62.6 | 48.0 | 3 | 14.5, 16.0 | 45.4, 51.9 | 49.3 |
| 19 | 1 | 15.6 | 46.8 | 4 | 18.4, 20.5 | 41.1, 43.0 | 42.1 | 6 | 25.8, 32.6 | 31.8, 38.6 | 34.6 | 6 | 14.2, 15.9 | 43.8, 49.0 | 46.3 |
| 20 | 1 | + | | 4 | + | | | 7 | + | | | 6 | + | | |
| 21 | 1 | — | | 4 | — | | | 7 | — | | | 6 | — | | |
| 22 | 1 | | 97.4 | 4 | | 86.7, 98.5 | 91.9 | 7 | | 94.0, 105.0 | 100.9 | 6 | | 81.3, 93.8 | 89.5 |

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APPENDIX II. Continued.

| A | 33 *Feresa attenuata* | | | | 34 *Globicephala melaena* | | | | 35 *Globicephala macrorhyncha* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | E | B | C | D | E | B | C | D | E |
| 1 | 7 | 39.3, 41.2 | 100 | 40.3 | 4 | 46.2, 49.7 | 100 | 46.7 | 26 | 36.4, 52.1 | 100 | 43.7 |
| 2 | 7 | 33.5, 36.4 | 84.5, 90.5 | 87.6 | 4 | 37.6, 42.5 | 83.0, 85.5 | 84.4 | 26 | 34.2, 44.1 | 79.6, 98.0 | 88.4 |
| 3 | 7 | 28.2, 29.8 | 71.0, 73.5 | 72.5 | 4 | 30.1, 31.9 | 64.2, 69.0 | 66.6 | 26 | 26.8, 30.3 | 52.1, 73.6 | 65.9 |
| 4 | 7 | 20.3, 22.2 | 51.7, 55.4 | 53.7 | 4 | 23.3, 23.9 | 47.6, 52.9 | 50.7 | 26 | 19.6, 22.9 | 38.8, 53.3 | 48.7 |
| 5 | 7 | 20.8, 22.6 | 50.6, 57.5 | 53.5 | 4 | 21.7, 23.2 | 46.8, 51.3 | 48.9 | 26 | 19.2, 23.5 | 42.4, 55.5 | 49.8 |
| 6 | 7 | 29.4, 31.8 | 73.5, 77.6 | 75.9 | 4 | 31.1, 33.9 | 67.3, 71.6 | 69.2 | 26 | 28.2, 32.1 | 58.5, 82.7 | 70.0 |
| 7 | 7 | 17.5, 19.6 | 42.6, 49.6 | 46.1 | 4 | 18.8, 20.4 | 40.7, 43.8 | 42.1 | 26 | 15.8, 21.0 | 37.6, 50.3 | 43.1 |
| 8 | 7 | 4.5, 6.4 | 11.3, 16.1 | 13.5 | 4 | 4.2, 5.1 | 9.3, 11.0 | 10.0 | 26 | 2.9, 5.4 | 7.1, 12.3 | 10.0 |
| 9 | 7 | 5.4, 7.1 | 13.1, 17.6 | 15.1 | 4 | 5.9, 8.2 | 11.9, 18.1 | 15.0 | 26 | 4.9, 8.1 | 11.0, 18.0 | 14.8 |
| 10 | 7 | 0.4, 2.7 | 1.8, 6.7 | 3.0 | 4 | 1.4, 1.8 | 3.1, 3.7 | 3.4 | 26 | 0.8, 2.4 | 2.5, 5.7 | 3.8 |
| 11 | 7 | 0 , 2.8 | 0 , 6.9 | 1.5* | 4 | 0 | 0 | Closed | 26 | 0 , 1.3 | 0 , 3.1 | 0.1** |
| 12 | 7 | Outer | | | 4 | Outer | | | 26 | Outer | | |
| 13 | 7 | 35.3, 37.8 | 100 | 36.3 | 4 | 36.8, 43.4 | 100 | 39.1 | 26 | 33.2, 39.5 | 100 | 35.7 |
| 14 | 7 | 15.1, 16.4 | 40.2, 46.2 | 43.1 | 4 | 16.7, 23.9 | 41.2, 64.9 | 52.0 | 26 | 14.7, 22.8 | 43.1, 60.8 | 49.2 |
| 15 | 7 | 23.3, 27.2 | 63.0, 73.5 | 70.3 | 4 | 23.0, 25.0 | 57.6, 64.5 | 61.6 | 26 | 22.2, 26.5 | 58.0, 74.6 | 68.8 |
| 16 | 7 | 0.9, 2.4 | 2.6, 6.5 | 4.8 | 4 | 1.2, 3.0 | 3.3, 8.1 | 4.6 | 26 | 0.4, 2.3 | 1.1, 6.5 | 4.0 |
| 17 | 7 | 1.2, 2.3 | 3.3, 6.3 | 5.3 | 4 | 0.2, 1.5 | 0.5, 3.8 | 2.5 | 26 | 0.3, 3.5 | 0.8, 10.2 | 4.4 |
| 18 | 7 | 12.9, 17.4 | 35.9, 49.3 | 40.4 | 4 | 14.9, 22.4 | 40.1, 52.4 | 47.2 | 26 | 12.6, 25.1 | 37.0, 74.8 | 48.5 |
| 19 | 7 | 13.8, 16.6 | 37.6, 45.6 | 41.9 | 4 | 16.5, 17.6 | 40.0, 45.8 | 44.0 | 26 | 14.5, 17.8 | 41.9, 50.9 | 45.6 |
| 20 | 7 | + | | | 4 | + | | | 26 | + | | |
| 21 | 7 | — | | | 4 | — | | | 26 | — | | |
| 22 | 7 | | 86.5, 94.0 | 90.2 | 4 | | 79.7, 87.5 | 83.8 | 26 | | 69.2, 94.8 | 82.0 |

* Closed on 5   ** Closed on 25

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APPENDIX II. Continued.

| A | 36 *Grampus griseus* | | | | 37 *Orcaella brevirostris* | | | 38 *Delphinapterus leucas* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | E | B | C | D | B | C | D | E |
| 1 | 12 | 38.7, 46.8 | 100 | 41.9 | 2 | 36.9, 39.2 | 100 | 4 | 40.7, 45.0 | 100 | 42.9 |
| 2 | 12 | 31.8, 39.9 | 76.5, 88.9 | 34.2 | 2 | 34.5, 37.5 | 93.5, 96.3 | 4 | 39.7, 42.7 | 93.0, 98.4 | 96.6 |
| 3 | 11 | 27.6, 30.8 | 62.4, 75.4 | 70.1 | 1 | 24.1, 24.7 | 63.0 | 2 | 32.2, 33.1 | 78.4, 79.3 | 78.9 |
| 4 | 12 | 20.8, 24.0 | 46.8, 58.6 | 53.1 | 2 | 16.0, 17.4 | 42.9, 45.6 | 4 | 24.1, 24.9 | 54.2, 61.2 | 57.0 |
| 5 | 11 | 19.0, 23.9 | 43.8, 58.7 | 50.1 | 2 | 20.0, 21.2 | 52.0, 57.5 | 3 | 24.0, 26.0 | 58.0, 59.0 | 58.9 |
| 6 | 11 | 28.5, 31.0 | 64.8, 78.1 | 72.8 | 1 | 26.5, 26.8 | 67.6, 70.0 | 2 | 32.7, 33.9 | 80.3, 80.4 | 80.4 |
| 7 | 12 | 16.5, 22.0 | 36.1, 52.1 | 43.8 | 2 | 18.7, 21.5 | 50.7, 55.0 | 4 | 20.0, 21.5 | 47.8, 49.8 | 48.8 |
| 8 | 12 | 2.7, 6.7 | 6.1, 14.3 | 10.3 | 2 | 3.2, 4.3 | 8.2, 11.7 | 4 | 6.1, 6.8 | 14.2, 16.1 | 15.1 |
| 9 | 12 | 4.9, 9.2 | 12.1, 20.2 | 15.8 | 1 | 3.9 | 10.0, 10.2 | 2 | 6.0, 6.9 | 14.8, 16.3 | 15.6 |
| 10 | 12 | 0.7, 2.0 | 1.8, 5.1 | 3.0 | 2 | 1.9, 3.8 | 5.1, 9.7 | 3 | 4.1, 5.3 | 10.1, 11.8 | 10.8 |
| 11 | 12 | 0 , 4.0 | 0 , 9.9 | 0.7* | 2 | 0 | 0 | 4 | 0 | 0 | Closed |
| 12 | 12 | Outer | | | 2 | Outer | | 4 | Outer | | |
| 13 | 12 | 34.8, 45.2 | 100 | 38.5 | 2 | 34.3, 40.7 | 93.0, 103.8 | 4 | 37.7, 40.4 | 100 | 39.0 |
| 14 | 12 | 11.7, 25.0 | 31.1, 55.3 | 43.4 | 2 | 12.7 | 31.2, 37.0 | 4 | 13.9, 16.2 | 36.9, 42.2 | 39.4 |
| 15 | 12 | 23.6, 28.0 | 56.0, 75.9 | 67.3 | 2 | 20.5, 21.2 | 52.1, 59.8 | 3 | 26.4, 27.4 | 65.3, 72.8 | 69.5 |
| 16 | 12 | 0.5, 2.7 | 1.3, 7.1 | 4.3 | 2 | 0.9, 1.4 | 2.2, 4.1 | 3 | 1.2, 2.8 | 3.0, 7.3 | 5.0 |
| 17 | 12 | 0.8, 3.5 | 1.8, 7.2 | 4.1 | 2 | 1.7, 2.0 | 4.2, 5.8 | 3 | 2.5, 3.1 | 6.2, 8.1 | 7.4 |
| 18 | 11 | 13.4, 18.4 | 34.3, 47.5 | 40.9 | 1 | 17.0 | 49.6 | 3 | 16.8, 21.4 | 44.6, 53.0 | 48.9 |
| 19 | 12 | 15.4, 18.5 | 37.0, 48.9 | 43.3 | 2 | 15.1, 15.2 | 37.3, 44.0 | 4 | 19.2, 20.3 | 47.0, 52.9 | 49.9 |
| 20 | 12 | + | | | 2 | + | | 4 | + | | |
| 21 | 12 | — | | | 2 | — | | 4 | — | | |
| 22 | 12 | | 86.6, 100.0 | 92.4 | 2 | | 93.0, 103.8 | 4 | | 87.6, 94.5 | 90.4 |

* Closed on 11



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APPENDIX II. Continued.

| A | 39 *Monodon monoceros* | | | | 40 *Berardius bairdi* | | | | 41 *B. arnouxii* | | | 42 *Hyperoodon ampullatus* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | E | B | C | D | E | B | C | D | B | C | D |
| 1 | 4 | 50.1, 50.9 | 100 | 50.7 | 5 | 63.1, 70.4 | 100 | 66.7 | 1 | 63.2 | 100 | 1 | 54.5 | 100 |
| 2 | 4 | 42.8, 46.2 | 84.4, 90.8 | 87.2 | 5 | 50.3, 61.2 | 78.9, 84.6 | 81.0 | 1 | 47.5 | 75.0 | 1 | 47.3 | 86.8 |
| 3 | 4 | 36.8, 39.0 | 72.5, 76.6 | 74.8 | 5 | 47.0, 53.1 | 72.6, 76.7 | 74.7 | 1 | 47.4 | 75.3 | | | |
| 4 | 4 | 26.0, 27.8 | 51.3, 55.5 | 53.7 | 5 | 35.3, 40.8 | 54.3, 58.8 | 57.2 | 1 | 36.2 | 57.2 | | | |
| 5 | 4 | 19.0, 20.9 | 37.5, 41.4 | 39.6 | 5 | 38.7, 45.5 | 57.1, 67.7 | 64.3 | 1 | 44.1 | 69.8 | | | |
| 6 | 4 | 36.3, 38.6 | 71.6, 76.0 | 73.7 | 5 | 46.0, 51.2 | 70.0, 73.6 | 71.9 | 1 | 45.0 | 71.2 | | | |
| 7 | 4 | 20.8, 23.8 | 40.8, 46.8 | 44.0 | 5 | 33.6, 40.1 | 52.6, 57.0 | 54.5 | 1 | 36.5 | 58.0 | | | |
| 8 | 4 | 6.3, 7.8 | 12.4, 15.3 | 13.9 | 5 | 1.4, 3.8 | 21.4, 5.4 | 4.7 | 1 | 3.3 | 5.2 | | | |
| 9 | 4 | 7.1, 8.1 | 14.0, 15.9 | 15.0 | 5 | 18.8, 21.0 | 29.0, 31.4 | 29.7 | 1 | 21.6 | 30.2 | 1 | 16.5 | 30.3 |
| 10 | 4 | 2.0, 4.9 | 5.2, 9.7 | 7.5 | 4 | 5.9, 6.5 | 9.1, 9.6 | 9.3 | | | | | | |
| 11 | 4 | 0 , 3.1 | 0 , 6.1 | 1.5* | 5 | 0 , 14.5 | 0 , 20.9 | 5.9** | 1 | 0 | 0 | | | |
| 12 | 4 | Outer | | | 5 | Outer | | | 1 | 18.8 | 29.8 | 1 | Outer | |
| 13 | 4 | 37.0, 49.4 | 100 | 42.3 | 5 | 66.9, 75.8 | 100 | 71.0 | | | | 1 | 61.1 | 100 |
| 14 | 4 | 20.4, 23.5 | 41.3, 59.7 | 53.2 | 5 | 29.0, 38.1 | 43.4, 50.3 | 46.9 | | | | 1 | 20.3 | 33.2 |
| 15 | 4 | 25.4, 30.9 | 62.7, 68.8 | 66.5 | 5 | 34.7, 37.2 | 49.6, 54.1 | 51.7 | | | | 1 | 33.0 | 54.0 |
| 16 | 4 | 2.0, 3.1 | 4.1, 6.2 | 4.8 | 5 | 0.8, 4.8 | 1.2, 6.9 | 3.1 | | | | 1 | 0.5 | 0.8 |
| 17 | 4 | 2.5, 4.1 | 5.5, 9.5 | 7.4 | 5 | 1.9, 5.1 | 2.8 , 7.4 | 4.9 | | | | 1 | 1.5 | 2.5 |
| 18 | 4 | 25.5, 27.7 | 51.3, 68.4 | 63.3 | 5 | 23.4, 26.0 | 31.4, 37.1 | 33.3 | | | | 1 | 25.2 | 41.2 |
| 19 | 4 | 17.2, 20.9 | 40.1, 48.6 | 45.2 | 5 | 23.2, 25.1 | 33.1, 37.5 | 34.5 | | | | 1 | 23.0 | 37.6 |
| 20 | 4 | + | | | 5 | — | | | 1 | — | | 1 | — | |
| 21 | 4 | — | | | 5 | + | | | 1 | + | | 1 | + | |
| 22 | 4 | | 73.6, 98.6 | 83.5 | 5 | | 101.0, 113.4 | 106.6 | | | | 1 | | 112.0 |

* Closed on 3 ** Closed on 1

APPENDIX II. Continued.

| A | 43 *Mesoplodon stejnegeri* B | C | D | E | 44 *M. densirostris* B | C | D | E | 45 *M. ginkgodens* B | C | D |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 7 | 46.9, 49.0 | 100 | 47.7 | 4 | 49.7, 54.2 | 100 | 51.8 | 2 | 39.8, 44.1 | 100 |
| 2 | 7 | 42.2, 47.2 | 88.8, 97.5 | 94.8 | 4 | 47.0, 49.5 | 90.0, 95.6 | 93.4 | 2 | 37.4, 41.6 | 94.0, 94.5 |
| 3 | 6 | 33.0, 35.1 | 69.0, 74.9 | 72.0 | 3 | 36.1, 38.4 | 72.5, 73.5 | 72.9 | 2 | 30.3, 34.1 | 76.1, 77.3 |
| 4 | 6 | 25.3, 27.0 | 52.8, 56.6 | 54.1 | 1 | 29.4 | 54.2 | | 1 | 24.7 | 56.0 |
| 5 | 5 | 27.8, 33.9 | 67.0, 70.2 | 67.1 | 1 | 32.1 | 59.2 | | 2 | 28.0, 30.4 | 69.0, 70.4 |
| 6 | 5 | 37.8, 39.2 | 78.5, 82.0 | 80.5 | 3 | 39.8, 42.7 | 72.1, 80.5 | 75.3 | 2 | 31.6, 35.2 | 79.4, 79.9 |
| 7 | 7 | 23.1, 27.0 | 48.2, 55.8 | 50.8 | 4 | 22.9, 28.3 | 45.7, 52.2 | 49.2 | 2 | 20.3, 28.5 | 51.0, 64.6 |
| 8 | 7 | 2.5, 4.4 | 5.2, 9.1 | 7.2 | 4 | 1.7, 4.0 | 3.1, 8.1 | 6.3 | 2 | 1.7, 3.5 | 4.3, 7.9 |
| 9 | 6 | 14.8, 16.6 | 31.4, 34.8 | 32.2 | 3 | 15.3, 17.2 | 30.5, 34.6 | 32.0 | 2 | 14.0, 15.6 | 35.2, 35.4 |
| 10 | 3 | 3.7, 6.1 | 7.6, 13.0 | 8.2 | | | | | 1 | 2.9 | 6.6 |
| 11 | 7 | 6.1, 8.4 | 13.2, 17.6 | 10.5 | 4 | + | + | | 2 | + | + |
| 12 | 7 | Outer | | | 4 | Outer | | | 2 | Outer | |
| 13 | 4 | 44.3, 50.9 | 100 | 47.5 | 1 | 52.2 | 100 | | 2 | 41.0, 42.3 | 100 |
| 14 | 4 | 16.4, 18.3 | 33.4, 41.3 | 37.0 | 1 | 20.1 | 38.5 | | 2 | 20.4, 20.6 | 48.2, 50.2 |
| 15 | 4 | 26.9, 29.1 | 56.9, 61.3 | 59.2 | 1 | 28.0 | 53.6 | | 2 | 22.3, 23.1 | 54.4, 54.6 |
| 16 | 4 | 0.2, 1.7 | 0.4, 3.3 | 1.7 | 1 | 1.4 | 2.7 | | 2 | 0 , 0.4 | 0 , 0.9 |
| 17 | 4 | 2.6, 3.3 | 5.5, 6.5 | 6.1 | 1 | 4.3 | 8.2 | | 2 | 2.2, 3.0 | 5.4, 7.1 |
| 18 | 4 | 15.4, 17.7 | 34.8, 41.6 | 37.5 | 1 | 16.9 | 32.4 | | 2 | 13.8, 15.4 | 32.6, 37.6 |
| 19 | 4 | 19.0, 20.9 | 40.3, 43.0 | 41.5 | 1 | 22.0 | 42.1 | | 2 | 16.0, 17.8 | 39.0, 42.1 |
| 20 | 4 | — | | | 4 | — | | | 2 | — | |
| 21 | 4 | + | | | 4 | + | | | 2 | + | |
| 22 | 4 | | 92.8, 104.0 | 98.8 | 1 | | 96.3 | | 2 | | 96.0, 103.0 |

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APPENDIX II. Continued.

| A | 46 *Mesoplodon europaeus* B | C | D | E | 47 *M. carlhubbsi* B | C | D | 48 *M. mirus* B | C | D | 49 *Ziphius cavirostris* B | C | D | E |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 3 | 41.1, 45.7 | 100 | 44.1 | 2 | 48.4, 49.4 | 100 | 1 | 41.0 | 100 | 6 | 51.8, 59.7 | 100 | 55.9 |
| 2 | 3 | 38.4, 43.2 | 93.4, 95.0 | 94.1 | 2 | 46.2, 46.8 | 94.7, 95.5 | 1 | 37.1 | 90.5 | 5 | 43.8, 50.1 | 83.0, 93.3 | 87.8 |
| 3 | 3 | 34.2, 35.5 | 75.0, 86.4 | 79.5 | 1 | 34.6 | 71.5 | 1 | 32.7 | 79.5 | 6 | 41.9, 44.3 | 72.4, 81.0 | 77.3 |
| 4 | 3 | 25.8, 26.5 | 56.8, 64.5 | 59.6 | 1 | 21.8 | 44.1 | 1 | 23.8 | 58.0 | 5 | 32.6, 36.3 | 56.5, 66.4 | 61.7 |
| 5 | 1 | 30.3 | 66.3 | | 1 | 31.9 | 65.9 | 1 | 25.8 | 63.0 | 6 | 27.0, 37.6 | 52.1, 64.9 | 61.3 |
| 6 | 3 | 34.8, 38.7 | 79.3, 85.0 | 83.0 | 1 | 40.6 | 83.9 | 1 | 35.2 | 86.0 | 6 | 38.6, 44.8 | 72.8, 77.9 | 76.4 |
| 7 | 3 | 23.4, 23.9 | 52.5, 57.0 | 55.0 | 2 | 27.4, 28.7 | 56.6, 58.1 | 1 | 20.8 | 50.8 | 5 | 21.2, 26.0 | 38.6, 50.2 | 41.6 |
| 8 | 1 | 3.3 | 7.2 | | 1 | 3.8 | 7.7 | 1 | 13.9 | 9.5 | 5 | 1.0, 2.4 | 1.8, 4.6 | 3.0 |
| 9 | 3 | 13.8, 16.9 | 32.2, 37.1 | 34.1 | 1 | 14.8 | 30.6 | 1 | 15.6 | 38.0 | 6 | 15.1, 17.8 | 25.3, 31.7 | 29.6 |
| 10 | | | | | | | | | | | 2 | 2.1, 2.2 | 3.8, 4.0 | |
| 11 | 3 | + | + | | 1 | 7.5 | 15.2 | 1 | 8.7 | 21.2 | 7 | + | + | |
| 12 | 3 | Outer | | | 1 | Outer | | 1 | Outer | | 7 | Outer | | |
| 13 | 1 | 44.5 | 100 | | 1 | 49.4 | 100 | | | | 7 | 54.0, 62.4 | 100 | 57.6 |
| 14 | 1 | 18.5 | 41.6 | | 1 | 20.9 | 41.9 | | | | 7 | 22.3, 27.0 | 38.5, 45.0 | 41.7 |
| 15 | 1 | 25.0 | 56.2 | | 1 | 17.6 | 35.6 | | | | 7 | 29.5, 34.1 | 50.0, 58.0 | 55.1 |
| 16 | 1 | 0 | 0 | | 1 | 0.8 | 1.6 | | | | 7 | 0.4, 3.8 | 1.6, 6.9 | 3.7 |
| 17 | 1 | 2.8 | 6.3 | | 1 | 1.9 | 3.8 | | | | 7 | 1.2, 5.6 | 2.1, 10.4 | 6.8 |
| 18 | 1 | 16.7 | 37.6 | | 1 | 17.7 | 35.8 | | | | 7 | 20.5, 23.8 | 36.0, 39.6 | 38.2 |
| 19 | 1 | 16.0 | 36.0 | | 1 | 20.0 | 40.4 | | | | 7 | 18.8, 22.6 | 33.6, 40.1 | 36.6 |
| 20 | 3 | — | | | 1 | — | | 1 | — | | 7 | — | | |
| 21 | 3 | + | | | 1 | + | | 1 | + | | 7 | + | | |
| 22 | 1 | | 97.5 | | 1 | | 100.0 | | | | 6 | | 92.5, 116.0 | 103.6 |



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APPENDIX II. Continued.

| A | 50 *Kogia breviceps* | | | | 51 *K. simus* | | | | 52 *Physeter catodon* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | D | E | B | C | D | E | B | C | D | E |
| 1 | 5 | 26.2, 38.5 | 100 | 30.1 | 3 | 24.2, 27.5 | 100 | 26.2 | 8 | 55.4, 62.8 | 100 | 59.8 |
| 2 | 5 | 20.8, 24.1 | 61.0, 85.5 | 77.0 | 3 | 18.5, 25.0 | 89.8, 94.2 | 92.3 | 8 | 45.5, 57.1 | 75.8, 91.2 | 84.2 |
| 3 | 4 | 21.2, 22.5 | 76.3, 81.0 | 78.5 | 3 | 19.9, 21.9 | 74.0, 84.7 | 79.4 | 7 | 41.2, 44.4 | 68.3, 75.5 | 71.1 |
| 4 | 4 | 14.0, 16.5 | 50.3, 56.5 | 54.0 | 2 | 12.8, 14.5 | 47.6, 52.9 | | 6 | 30.1, 34.3 | 50.2, 56.9 | 53.6 |
| 5 | 4 | 12.0, 15.7 | 46.0, 56.3 | 50.4 | 3 | 14.3, 16.4 | 53.5, 66.1 | 59.7 | 8 | 33.4, 39.5 | 37.0, 66.5 | 59.6 |
| 6 | 4 | 23.6, 26.2 | 84.6, 93.2 | 88.4 | 3 | 22.9, 23.9 | 85.1, 97.5 | 89.8 | 8 | 47.7, 51.8 | 77.1, 87.2 | 79.1 |
| 7 | 5 | 17.4, 18.5 | 48.1, 66.5 | 61.3 | 3 | 14.4, 18.4 | 52.4, 64.9 | 60.1 | 7 | 24.1, 27.7 | 38.4, 46.2 | 42.8 |
| 8 | 2 | 1.2, 1.9 | 4.1, 6.8 | | 2 | 1.2, 2.1 | 6.5, 8.7 | | 7 | 1.5, 2.9 | 2.5, 4.9 | 3.4 |
| 9 | 4 | 7.8, 10.5 | 27.8, 37.6 | 31.6 | 3 | 7.4, 9.3 | 27.6, 33.8 | 31.6 | 8 | 25.5, 28.2 | 41.6, 48.9 | 45.4 |
| 10 | 4 | 0.5, 1.5 | 1.8, 5.7 | 4.1 | 2 | 0.7, 1.8 | 2.9, 6.5 | | 8 | — | — | — |
| 11 | 5 | 0 | 0 | Closed | 3 | 0 | 0 | Closed | 8 | 0 | 0 | Closed |
| 12 | 5 | Outer≑Inner | | | 3 | Outer≑Inner | | | 8 | Inuer | | |
| 13 | 4 | 24.0, 30.5 | 100 | 26.2 | 4 | 22.7, 29.2 | 100 | 26.6 | 8 | 57.7, 68.9 | 100 | 63.6 |
| 14 | 4 | 8.5, 11.5 | 29.2, 47.9 | 40.8 | 4 | 8.2, 11.4 | 31.1, 40.6 | 36.6 | 8 | 32.2, 36.8 | 50.2, 60.3 | 54.0 |
| 15 | 4 | 18.0, 20.9 | 59.7, 87.0 | 77.0 | 4 | 17.0, 19.2 | 63.0, 75.5 | 68.7 | 8 | 34.2, 42.1 | 53.0, 64.6 | 59.3 |
| 16 | 3 | 0.5, 1.0 | 1.6, 3.9 | 2.9 | 4 | 0 , 1.0 | 0 , 3.9 | 0 in 3 | 8 | 0 | 0 | 0 |
| 17 | 4 | 2.2, 3.8 | 7.2, 15.6 | 10.9 | 4 | 1.8, 2.7 | 6.4, 9.7 | 8.2 | 8 | 0.7, 3.0 | 1.2, 4.6 | 3.2 |
| 18 | 4 | 12.6, 16.0 | 45.2, 61.8 | 53.8 | 3 | 11.6, 13.9 | 41.4, 49.6 | 46.2 | 7 | 24.3, 30.1 | 37.6, 46.6 | 42.1 |
| 19 | 4 | 12.7, 14.4 | 41.6, 58.4 | 53.1 | 4 | 11.0, 12.8 | 41.7, 53.4 | 46.1 | 8 | 23.2, 28.8 | 36.0, 45.9 | 41.7 |
| 20 | 5 | — | | | 4 | — | | | 8 | — | | |
| 21 | 5 | + | | | 4 | + | | | 8 | + | | |
| 22 | 4 | | 83.4, 109.3 | 93.6 | 2 | | 106.2, 109.1 | | 8 | | 94.1, 116.5 | 106.7 |



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# EXPLANATION OF PLATES

## PLATE I

Posterior process of tympanic bulla and that of periotic, and their connection with the skull. BO, Basioccipital. EO, Exoccipital. P, Periotic. PPP, Posterior process of periotic. PPT, Posterior process of tympanic bulla. SQ, Laminated portion of squamosal. T, Tympanic bulla.

Fig. 1. *Physeter catodon*, TK85, fetus, skull length 75 cm, ventro-lateral view, right side.
Fig. 2. *Physeter catodon*, TK165, 5.0 m female, skull length 115 cm, same view.
Fig. 3. *Physeter catodon*, TK261, adult female, same view.
Fig. 4. *Mesoplodon densirostris*, TK256, 356 cm female, postero-lateral view, left side.
Fig. 5. *Kogia breviceps*, TK244, 197 cm female, postero-ventral view, right side.
Fig. 6. *Platanista gangetica*, TK363, 122 cm (juvenile) male, same view.
Fig. 7. *Platanisata gangetica*, TK 357, 200 cm male, ventral view of skull and periotic. Dotted area indicates the facet for posterior process of tympanic bulla.
Fig. 8. *Delphinapterus leucas*, SDNHM20046, ventral view, right side.
Fig. 9. *Balaenoptera borealis*, fetus, lateral view of right tympano-periotic bone.

## PLATE II

*Ziphius cavirostris*, TK296, tympano-periotic bone, left side.

## PLATE III

Tympano-periotic bones.
Figs. 1–10. *Berardius bairdi*, TK299, right side.
Figs. 11–13. *Mesoplodon mirus*, AMNH174293, right side.
Two black spots on Fig. 8 are artificial and insignificant.

## PLATE IV

Tympano-periotic bones.
Figs. 1– 9. *Mesoplodon stejnegeri*, TK97, right side.
Figs. 10–16. *Hyperoodon ampullatus*, USNM14449, left side.
Figs. 17–20. *Berardius arnouxi*, USNM21511, left side.

## PLATE V

Tympano-periotic bones.
Figs. 1–10. *Mesoplodon densirostris*, TK256, 356 cm female, right side.
Figs. 11–16. *Mesoplodon europaeus*, USNM306302, right side.

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## PLATE VI

Tympano-periotic bones.
Figs. 1–10. *Mesoplodon ginkgodens*, HCY specimen, left side.
Figs. 11–18. *Mesoplodon carlhubbsi*, USNM274591, right side.

## PLATE VII

Tympano-periotic bones.
Figs. 1–10. *Physeter catodon*, NUMS specimen, left side.
Fig. 11. *Physeter catodon*, TK304, left side.

## PLATE VIII

Tympano-periotic bones.

Figs. 1– 9. *Kogia simus*, TK47, 245 cm, right side.

Figs. 10–18. *Kogia breviceps*, TK244, 197 cm female, left side.

Figs. 10–18. *Kogia breviceps*, TK244, 197 cm female, left side. In Figs. 5 and 14, part of posterior process of tympanic bulla is removed.

## PLATE IX

Tympano-periotic bones.

Figs. 1–11. *Platanista gangetica*, TK357, 200 cm male, left side.

Figs. 12–13. *Platanista gangetica*, TK351, 171.5 cm male, right side, showing the ossicles attaching to anterior process of periotic.

Figs. 14–23. *Pontoporia blainvillei*, USNM49494 right side.

## PLATE X

Tympano-periotic bones.

Figs. 1– 8. *Inia geoffrensis*, LACM19589, left side.

Figs. 9–15. *Inia geoffrensis*, LACM19590, left side.

Figs. 16–20. *Lipotes vexillifer*, AMNH57333, left side.

## PLATE XI

Tympano-periotic bones.

Figs. 1–10. *Orcaella brevirostris*, USNM199743, left side.

Figs. 11–13. *Orcaella brevirostris*, ZSI 274, right side.

Figs. 14–20. *Delphinapterus leucas*, AMNH180017, right side.

## PLATE XII

Tympano-periotic bones, shadow lines on the tympanic bullae indicate contour lines.

Figs. 1– 9. *Neophocaena phocaenoides*, TK95, right side.

Figs. 10–18. *Phocoena phocoena phocoena*, TK84, left side.

## PLATE XIII

Tympano-periotic bones, shadow lines on the tympanic bullae indicate contour lines.

Figs. 1– 9. *Phocoenoides truei*, TK113, right side.

Figs. 10–18. *Phocoenoides dalli*, TK129, 186 cm female, left side.

## PLATE XIV

Tympano-periotic bones.

Figs. 1–13. *Sousa teuszii*, TK260, 191 cm female, left side.

Figs. 14–20. *Cephalorhynchus* sp. USNM252568, left side.

## PLATE XV

Tympano-periotic bones.

Figs. 1– 8. *Sotalia guianensis*, CNHM 34907, left side.

Figs. 9–12. *Sotalia fluviatilis*, AMNH94169, left side.

Figs. 13–15. *Tursiops gilli*, SDNHM20144, right side.

## PLATE XVI

Tympano-periotic bones.

Figs. 1–9. *Tursiops truncatus*, 292 cm male, right side, from the coast of Japan.

Figs. 10–14. *Tursiops truncatus*, 335 cm male, right side, same locality.

## PLATE XVII

Tympano-periotic bones.

Figs. 1–8. *Stenella caeruleoalba*, adult, right side.

Fig. 9. *Stenella caeruleoalba*, 92 cm male, fetus, left side.

Fig. 10. *Stenella caeruleoalba*, adult, right side.

Figs. 11–18. *Stenella attenuata*, TK103, right side, from the coast of Japan.

Fig. 19. *Stenella attenuata*, TK60, right side, same locality.

Fig. 20. *Stenella attenuata*, TK61, left side, same locality.

## PLATE XVIII

Tympano-periotic bones.

Figs. 1–9. *Stenella graffmani*, WAW44, 179 cm female, left side, 12°08′N, 105°46′W.

Figs. 10–12. *Stenella styx*, left side, from the north Atlantic.

## PLATE XIX

Tympano-periotic bones.

Figs. 1–8. (?) *Stenella roseiventris* (Hawaiian spinner dolphin), TK50, 180 cm male, left side.

Figs. 9–10. (?) *Stenella roseiventris* (Hawaiian spinner dolphin), TK295, 195 cm male, left side, from Hawaii.

Figs. 11–19. (?) *Stenella longirostris*, WAW52, 168 cm male, left side, 21°06′N, 106°16′W.

## PLATE XX

Tympano-periotic bones.

Figs. 1–9. *Lissodelphis borealis*, TK257, 245 cm male, left side.

Figs. 10–11. *Lissodelphis borealis*, TK258, 224 cm female, right side.

Figs. 12–19. *Delphinus bairdi*, TK255, 204 cm female, right side, from Formosa.

## PLATE XXI

Tympano-periotic bones.

Figs. 1–8. *Delphinus delphis*, TK specimen, left side, from the north Atlantic.

Figs. 9–16. *Lagenorhynchus obliquidens*, TK229, left side.

Figs. 17–19. *Lagenorhynchus obliquidens*, TK230, left side.

## PLATE XXII

Tympano-periotic bones.

Figs. 1–8. *Lagenorhynchus acutus*, USNM14265, right side.

Figs. 9–11. *Lagenorhynchs obsculus*, AMNH34935, left side.

Figs. 12–17. *Lagenorhynchus australis*, CNHM22248, left side.

## PLATE XXIII

Tympano-periotic bones.

Figs. 1–9. *Lagenorhynchus albirostris*, TK87, left side.

Figs. 10–18. *Steno bredanensis*, TK73, left side.

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## PLATE XXIV

Tympano-periotic bones.
Figs. 1–13. *Pseudorca crassidens*, TK specimen, left side.
Figs. 14–17. *Orcinus orca*, TK specimen, left side, (continue to Pl. XXV).

## PLATE XXV

Tympano-periotic bones.
Figs. 1– 2. *Orcinus orca*, TK specimen (continued from Pl. XXIV).
Figs. 3–15. *Peponocephala electra*, TK32, left side.

## PLATE XXVI

Tympano-periotic bones.
Figs. 1–10. *Feresa attenuata*, TK27, 214 cm male, left side.
Figs. 11–19. *Grampus griseus*, TK101, left side.
Figs. 20–22. *Grampus griseus*, TK specimen, left side.

## PLATE XXVII

Tympano-periotic bones.
Figs. 1–11. *Globicephala melaena*, TK specimen, left side, from the north Atlantic.
Figs. 12–20. *Globicephala macrorhyncha*, TK287, 358 cm female, left side.
Figs. 21–22. *Globicephala macrorhyncha*, TK292, 203 cm female, right side.
Figs. 23–24. *Globicephala macrorhyncha*, TK291, 141 cm male, left side.

## PLATE XXVIII

Tympano-periotic bones.
Figs. 1–10. *Monodon monoceros*, SDNHM7096, right side.
Figs. 11–13. *Monodon monoceros*, AMNH73318, left side.

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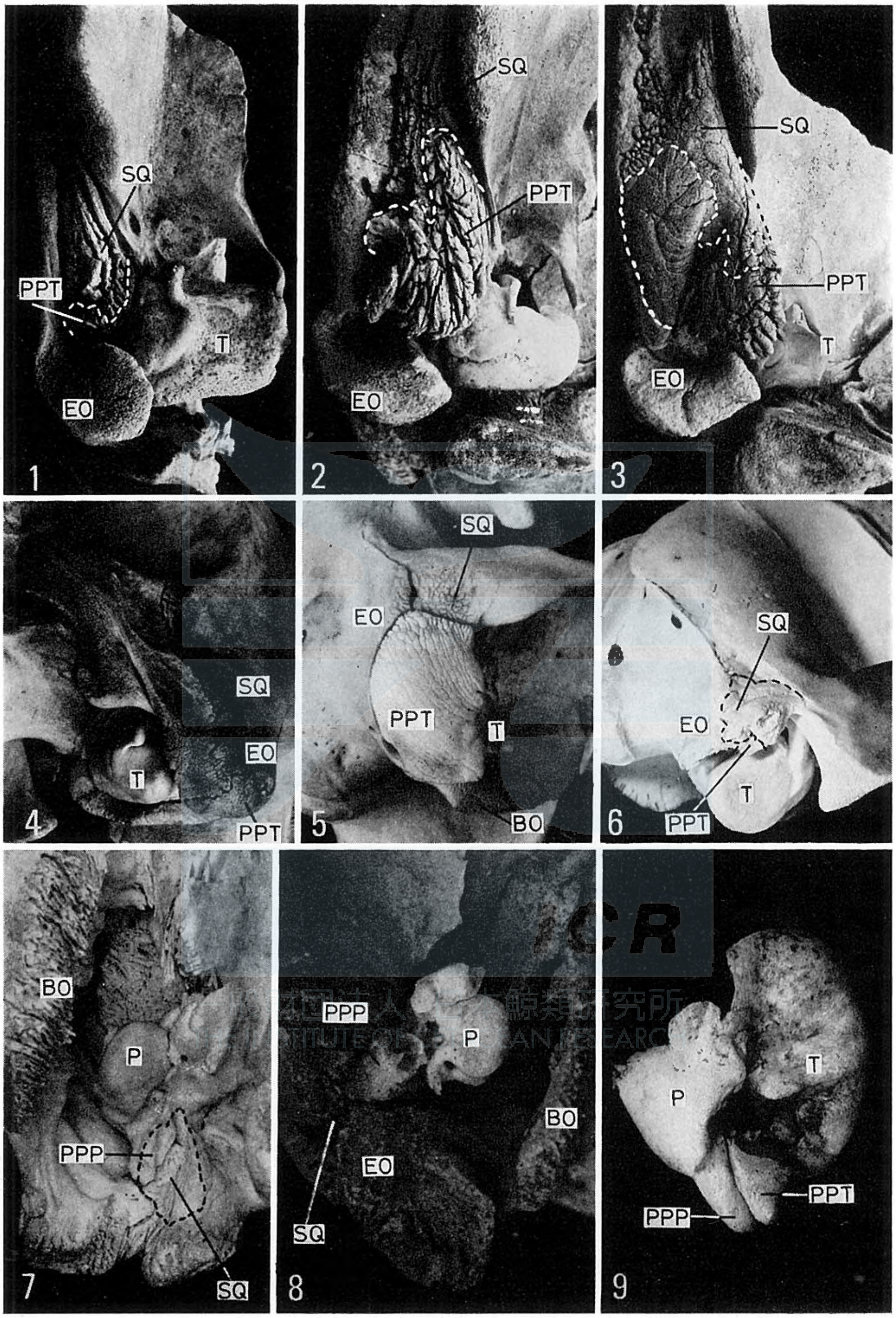
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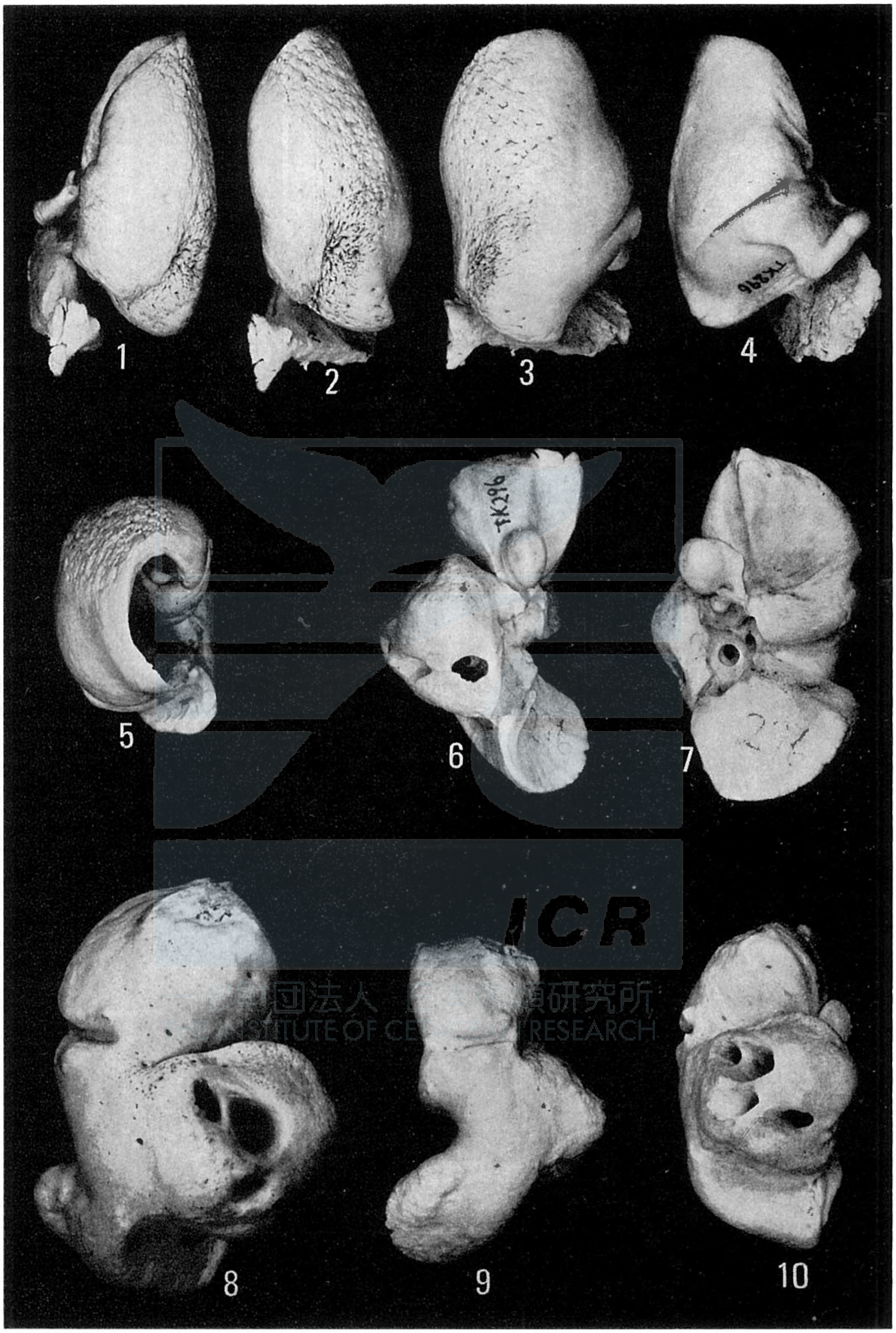
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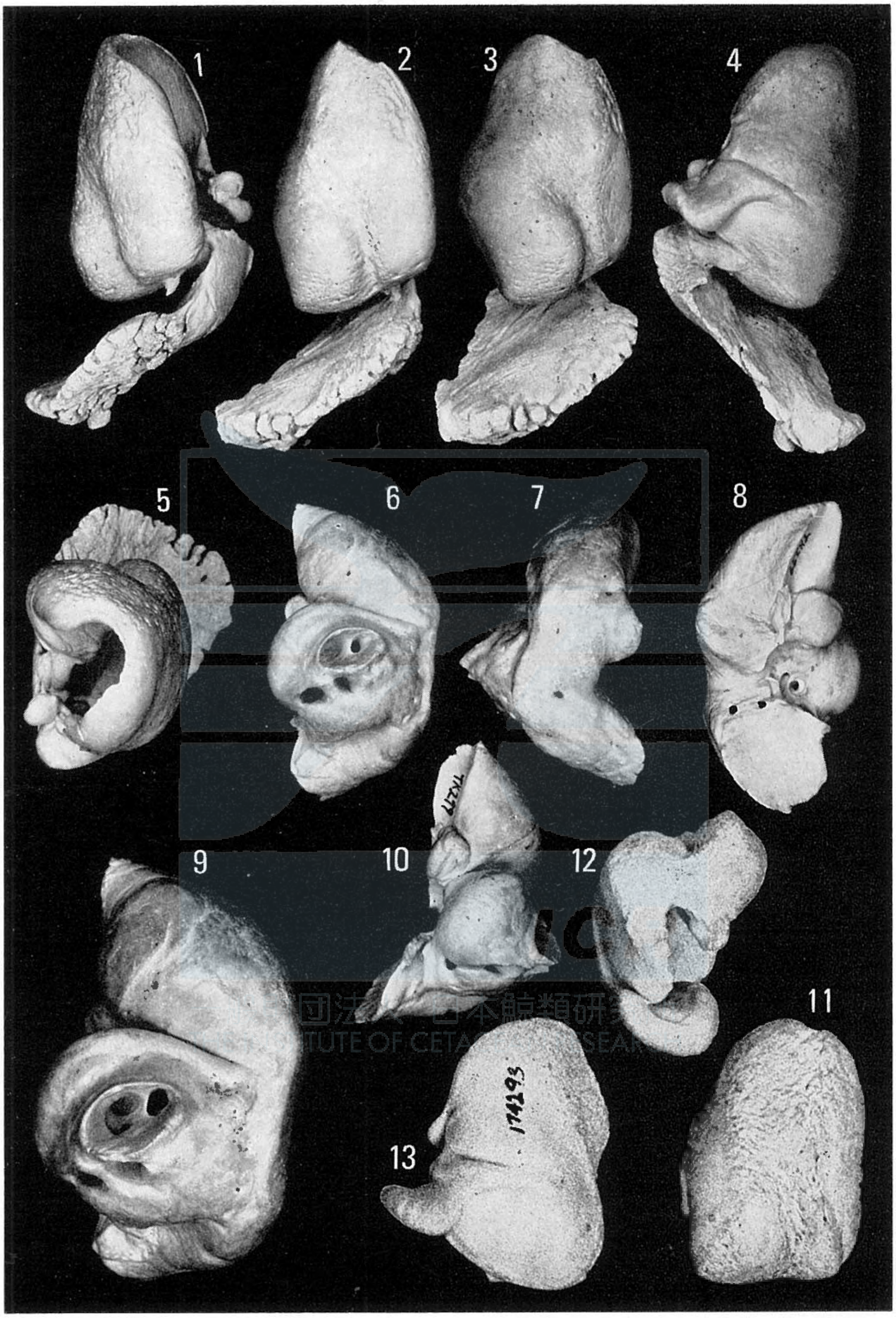
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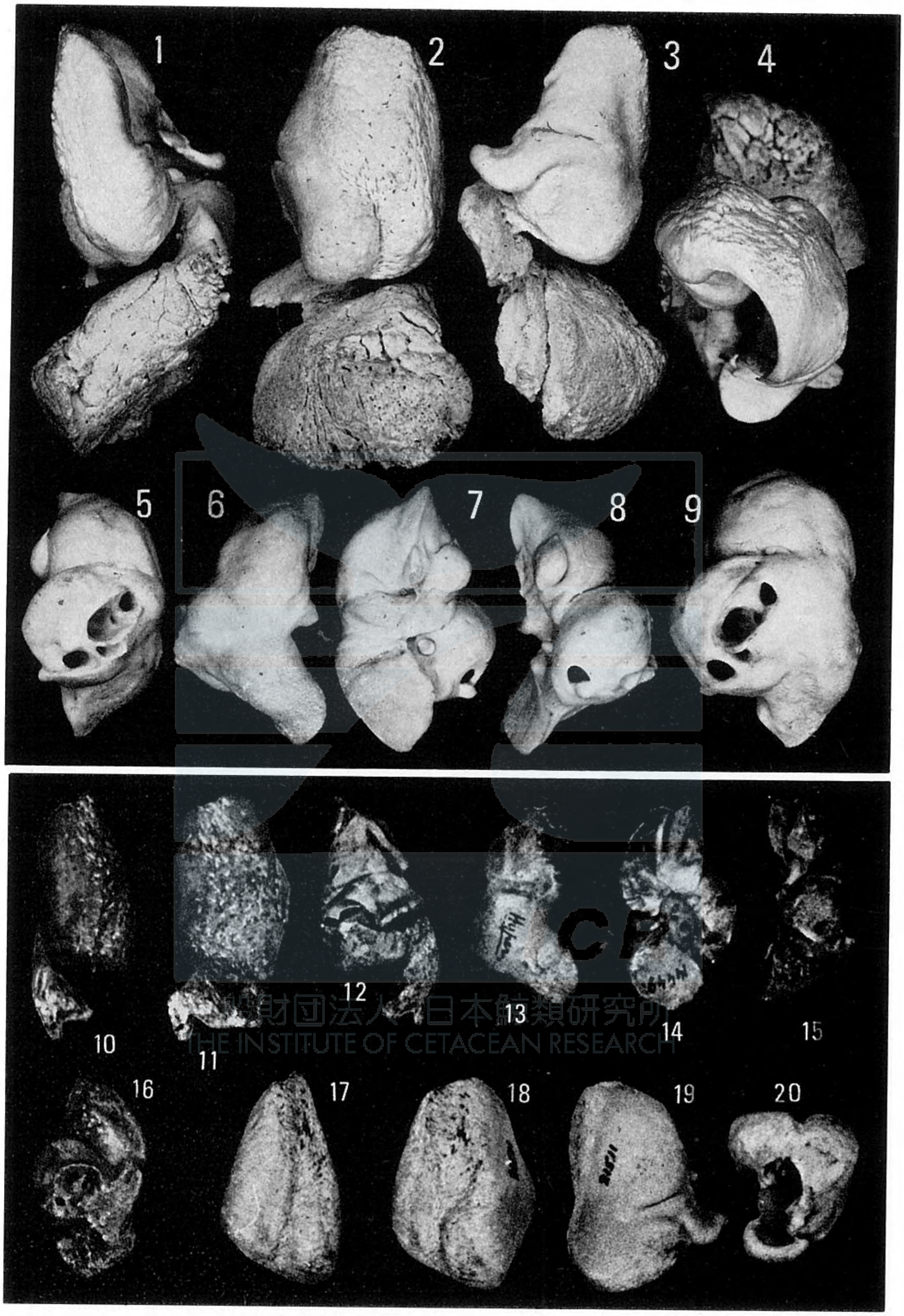


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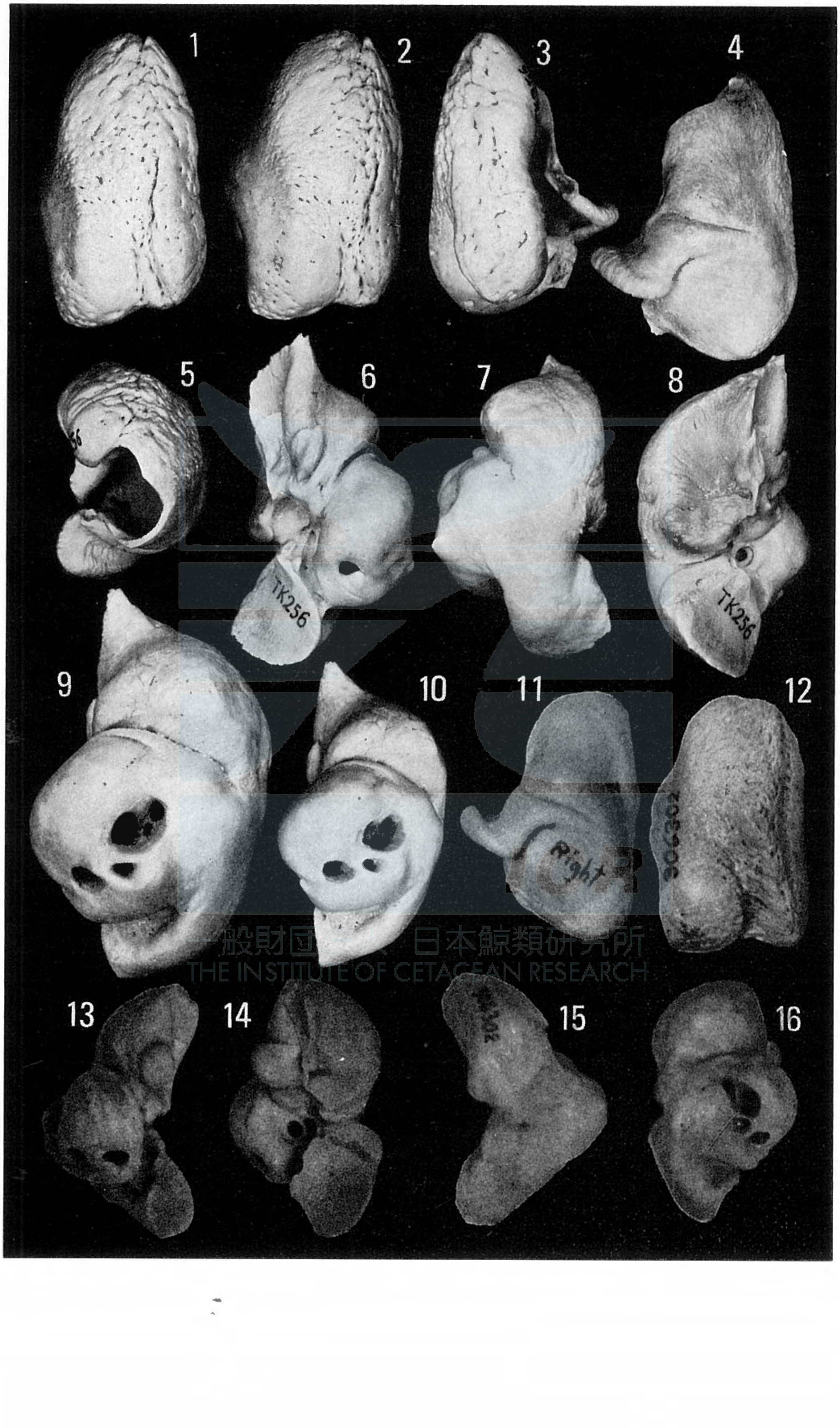


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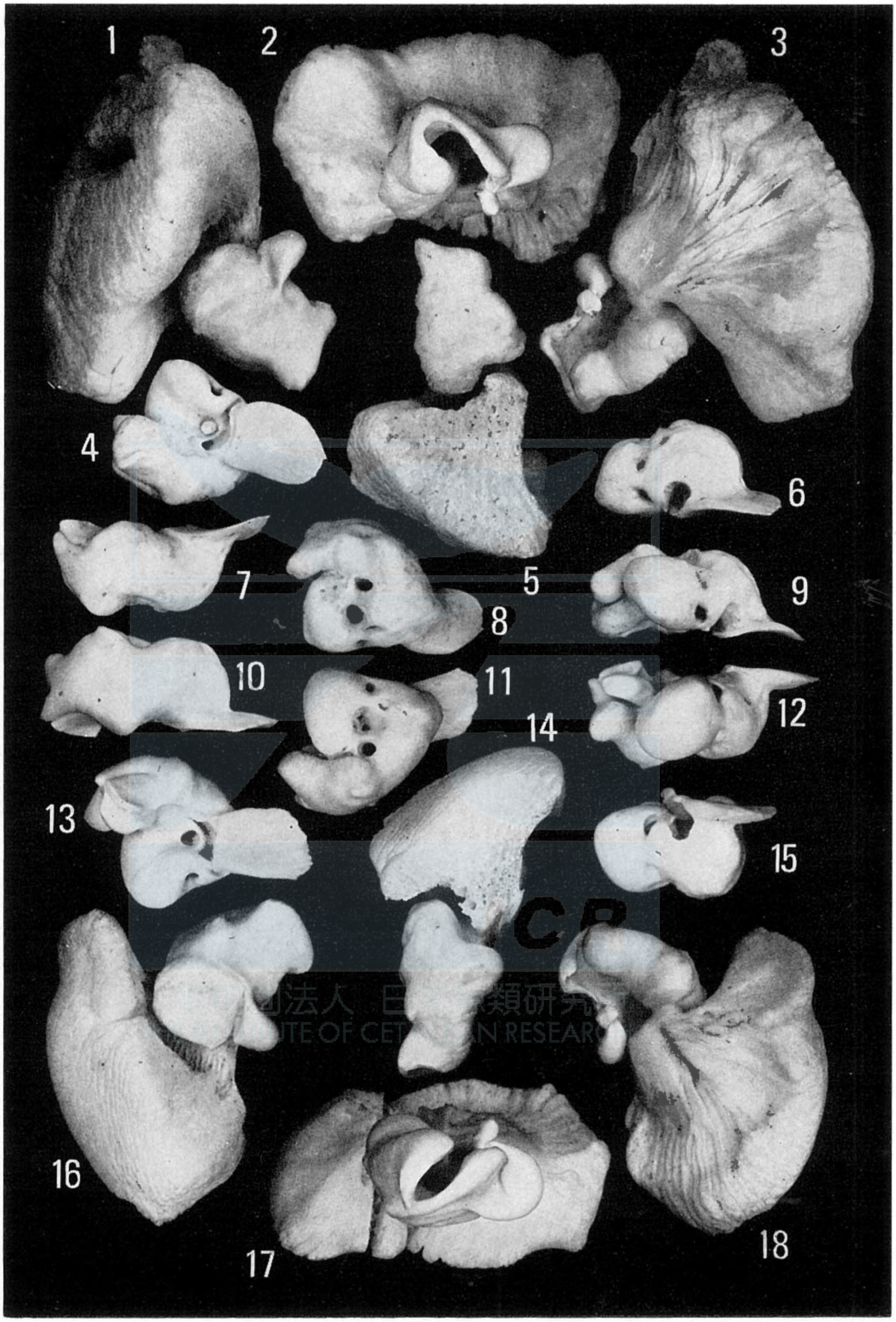
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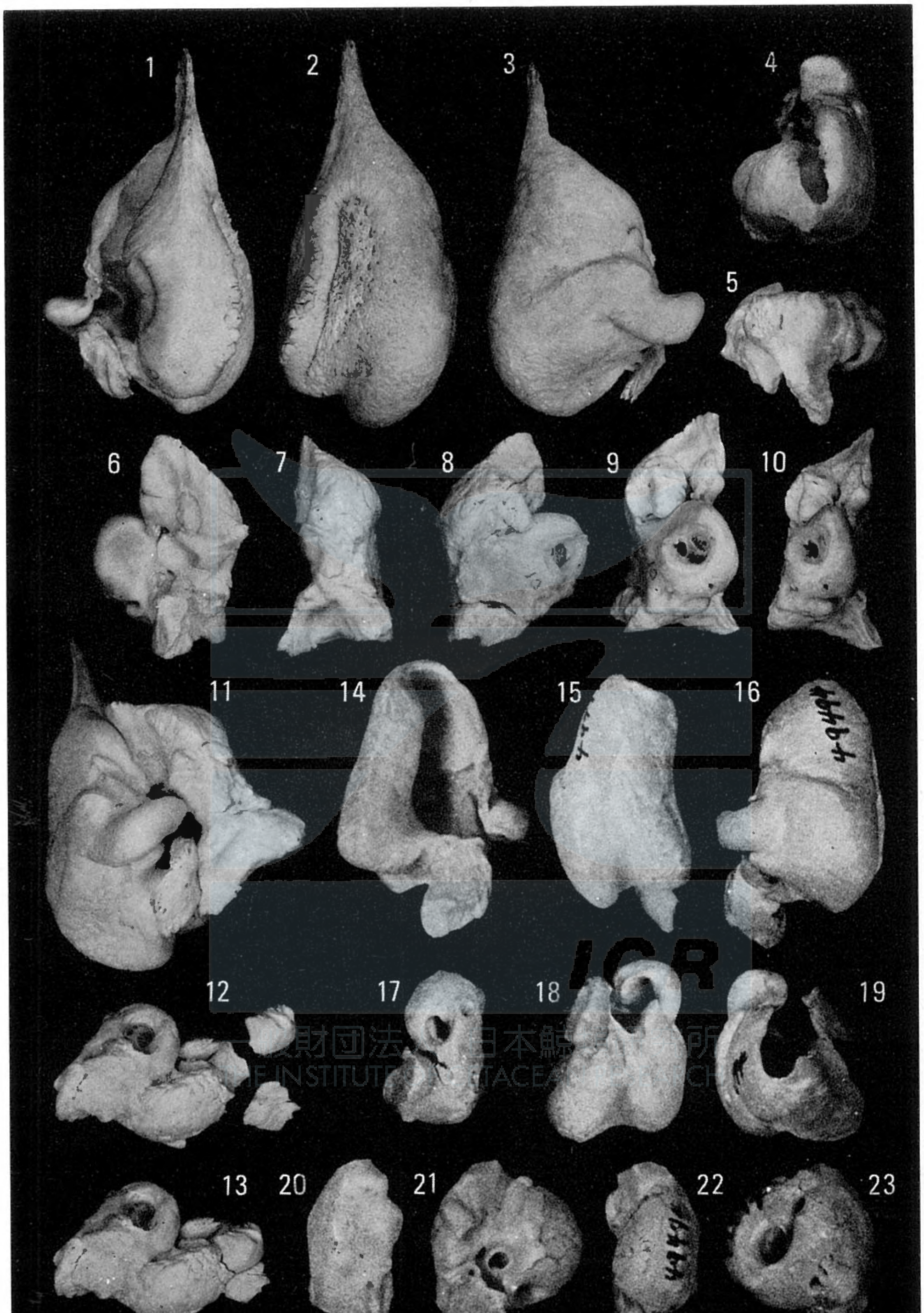
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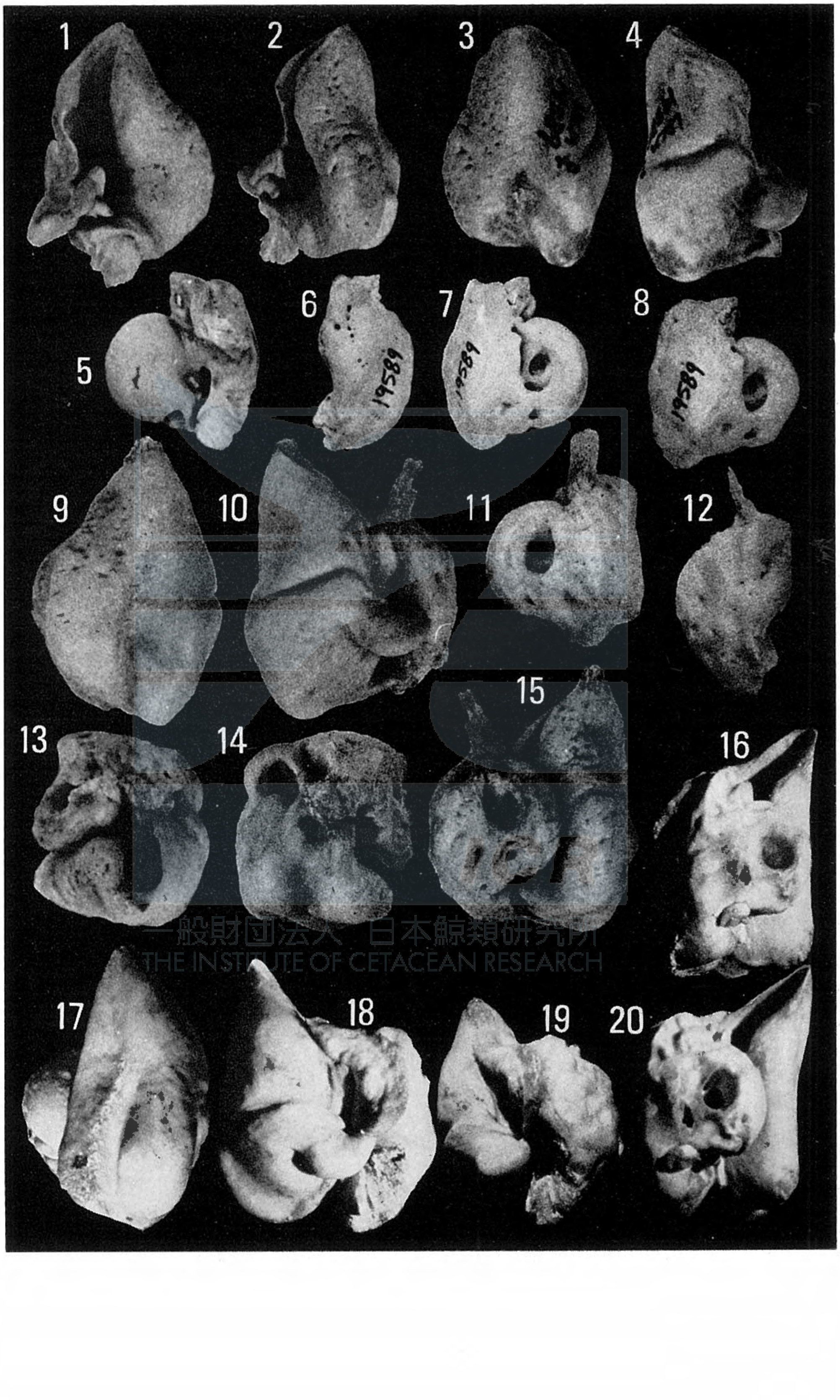


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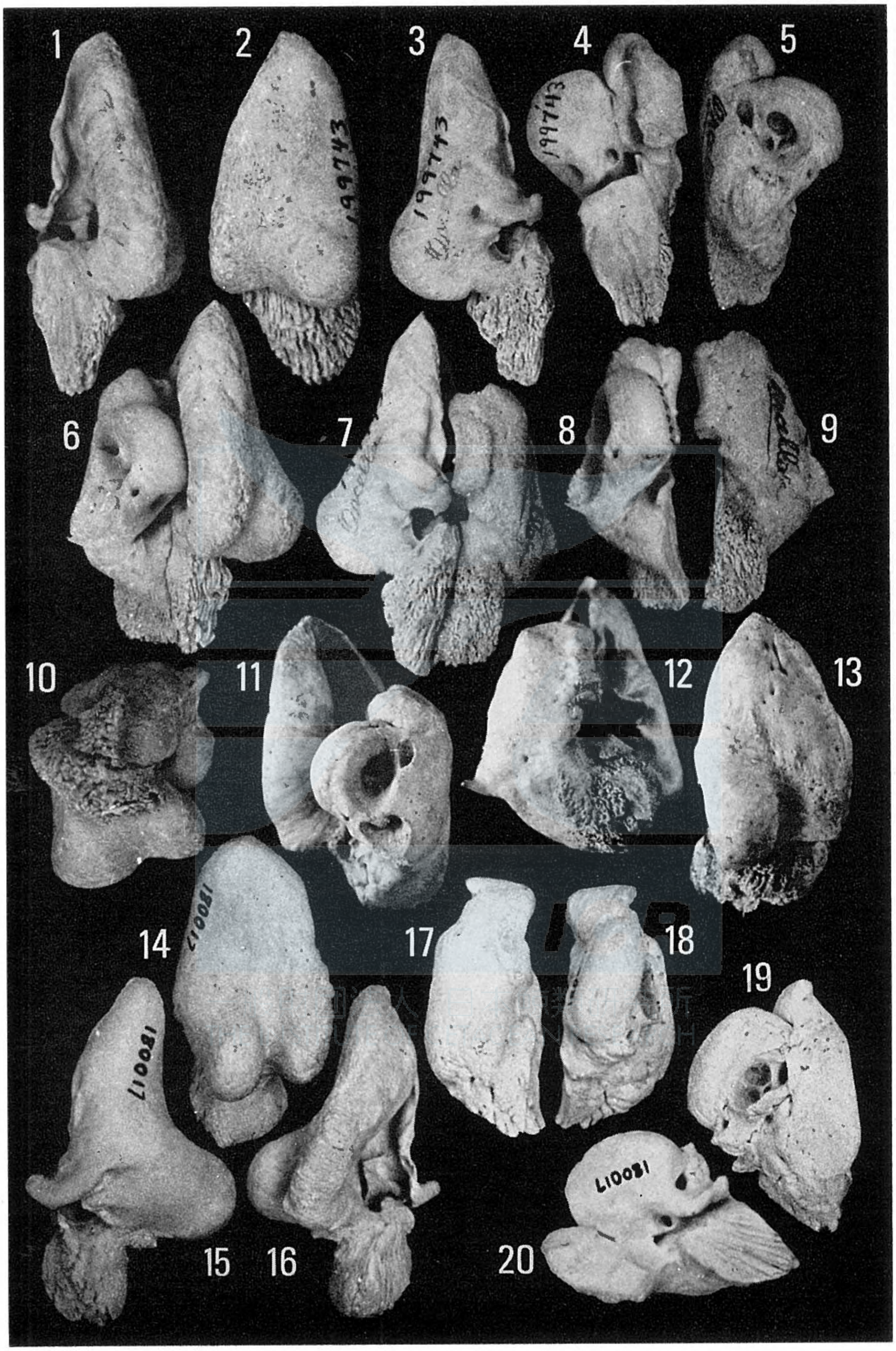
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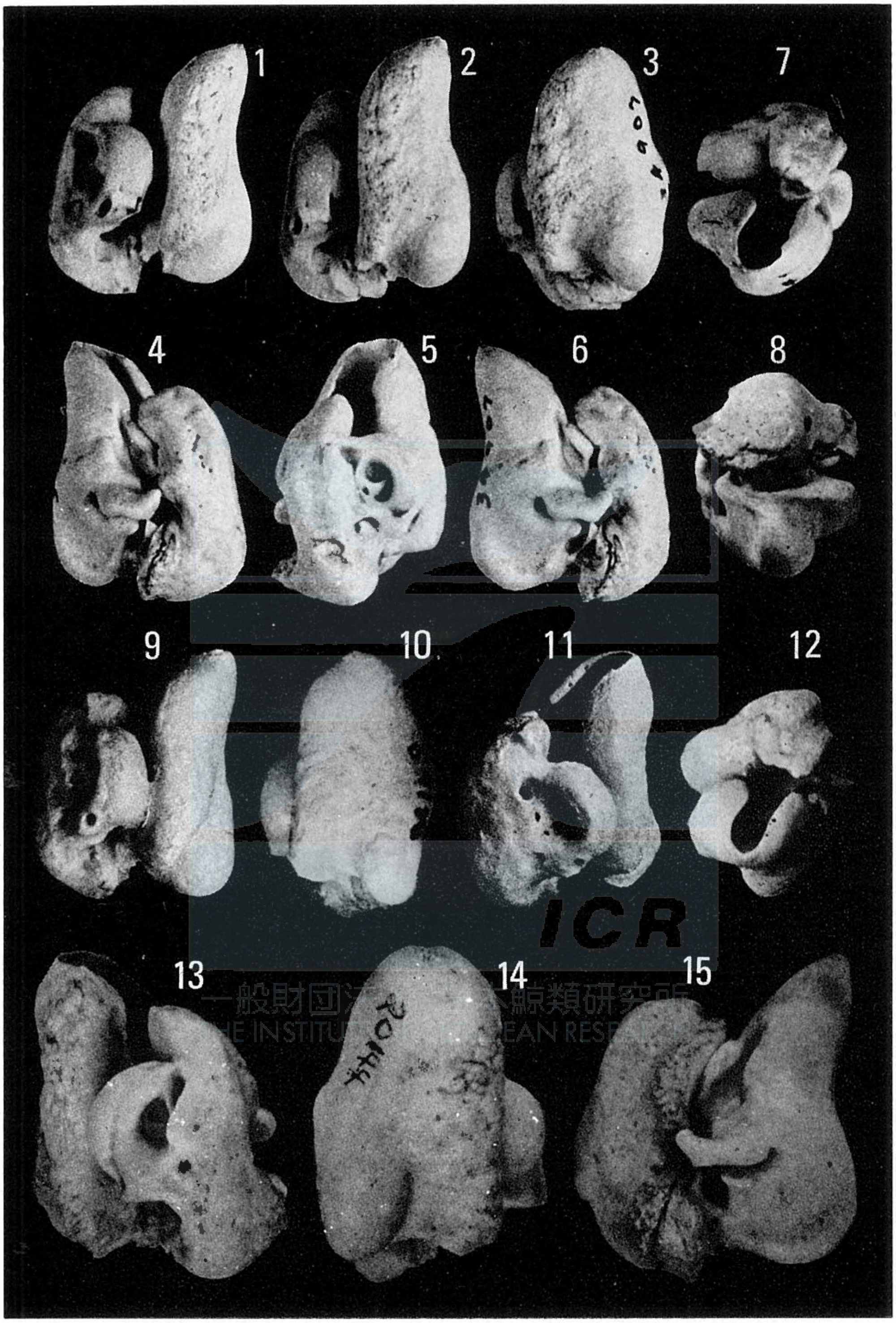
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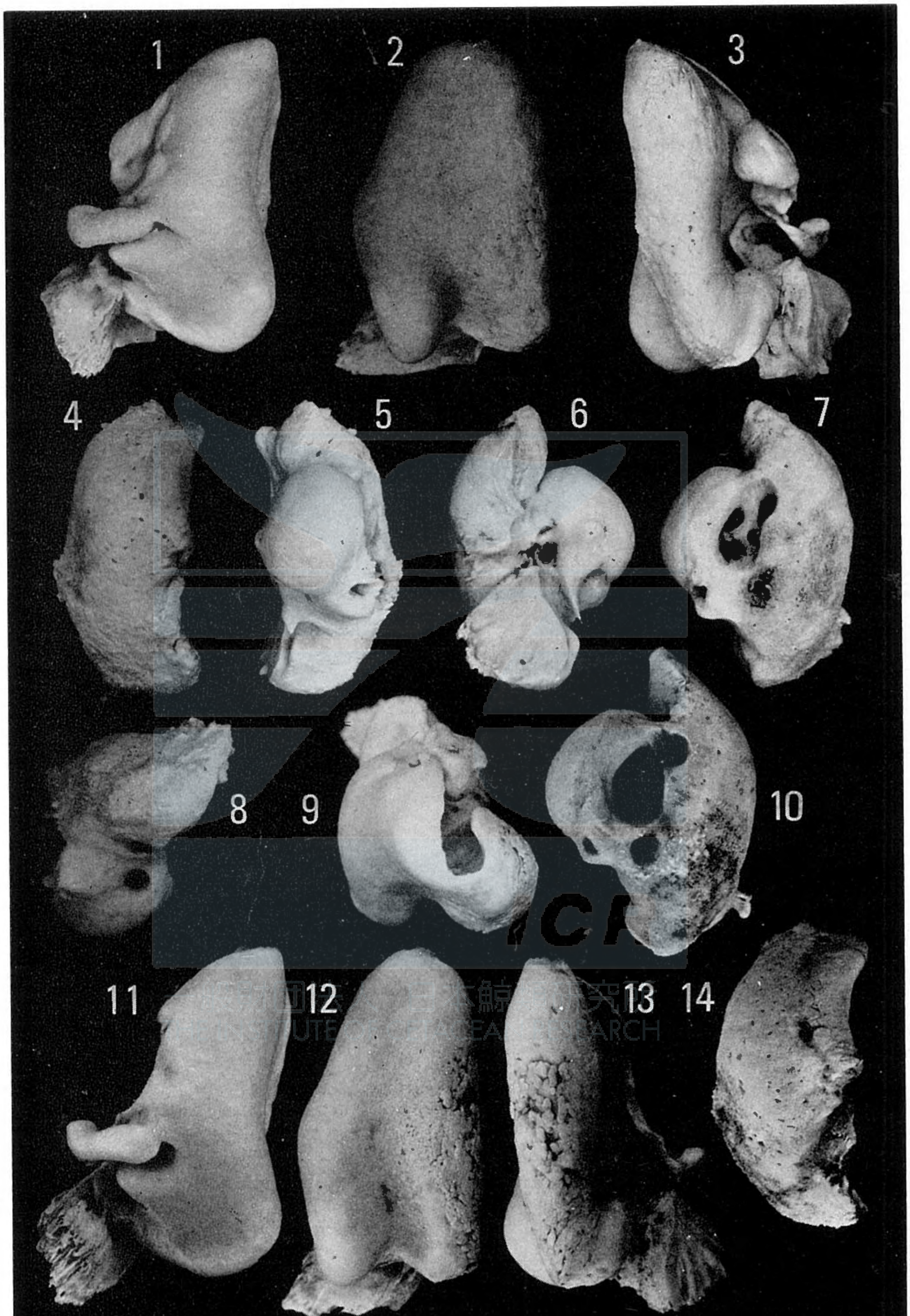
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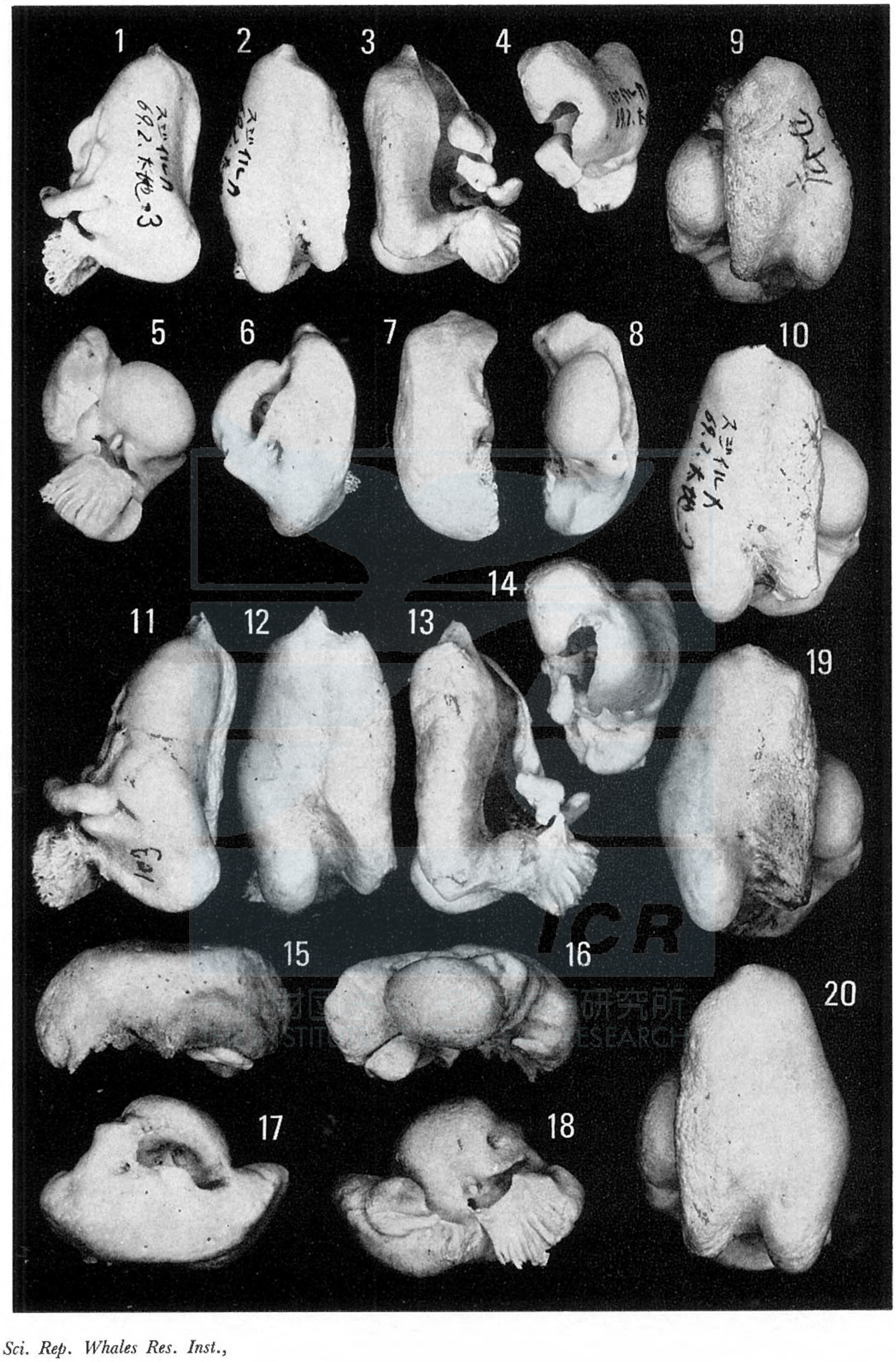

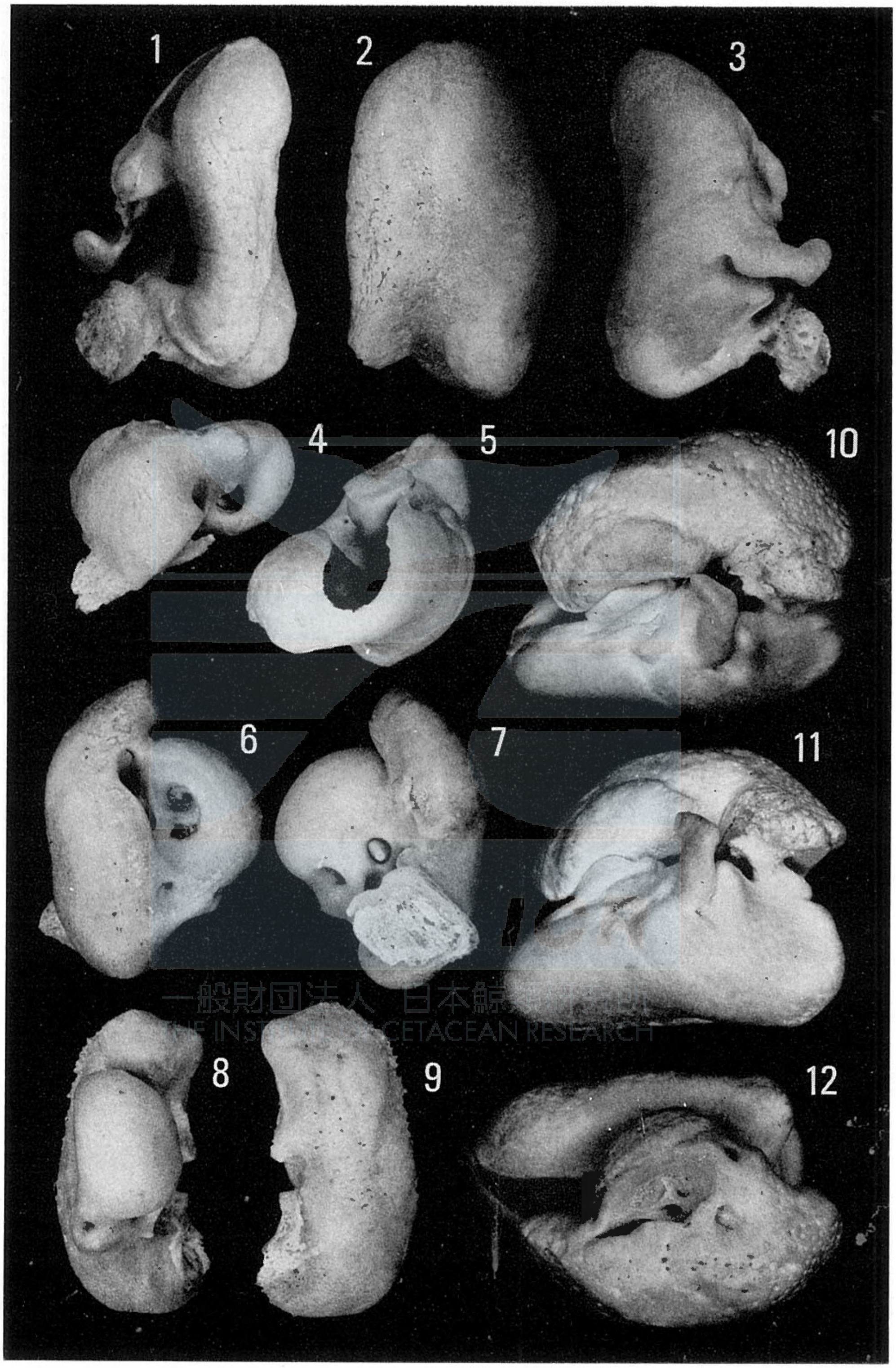


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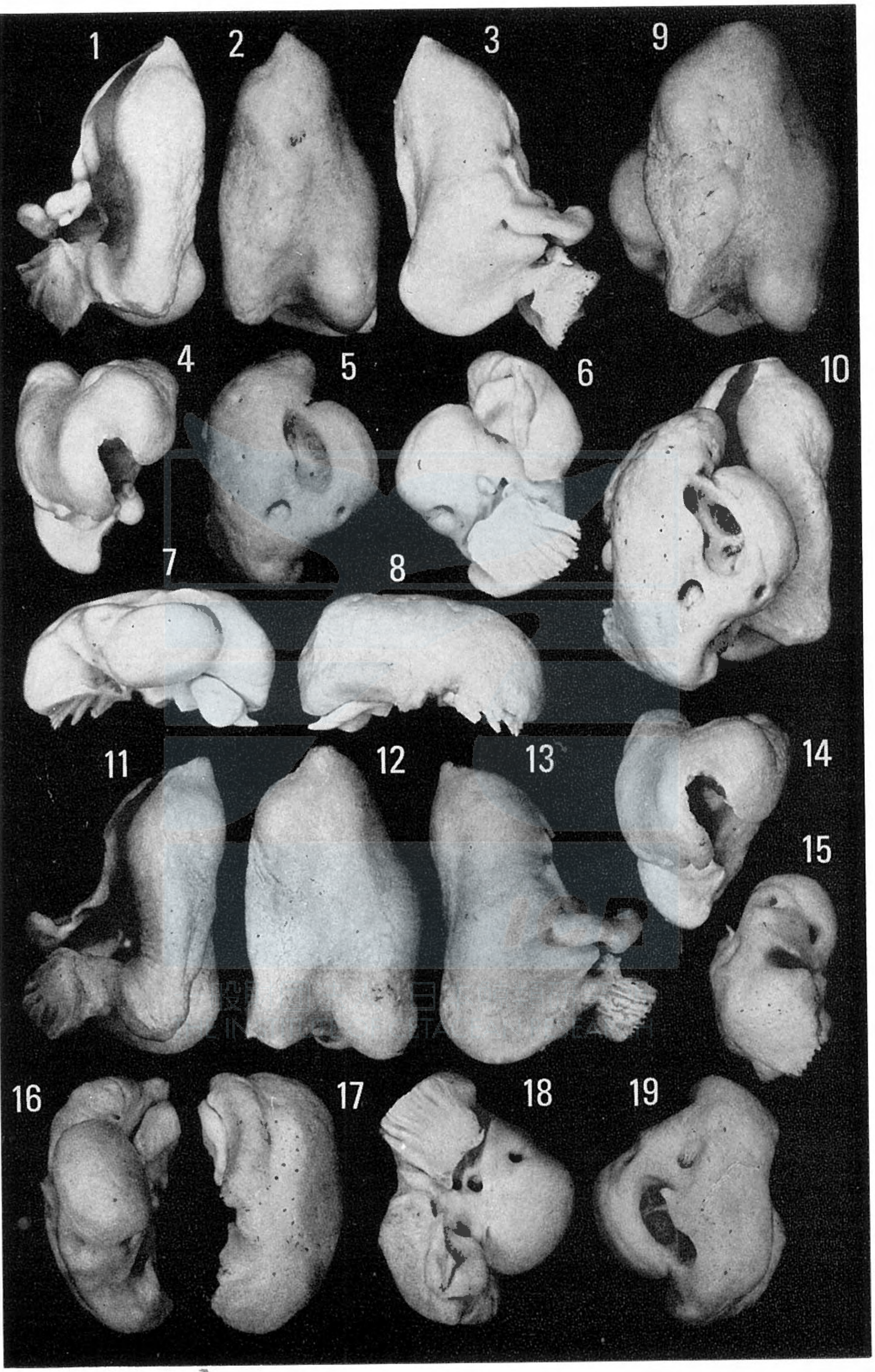
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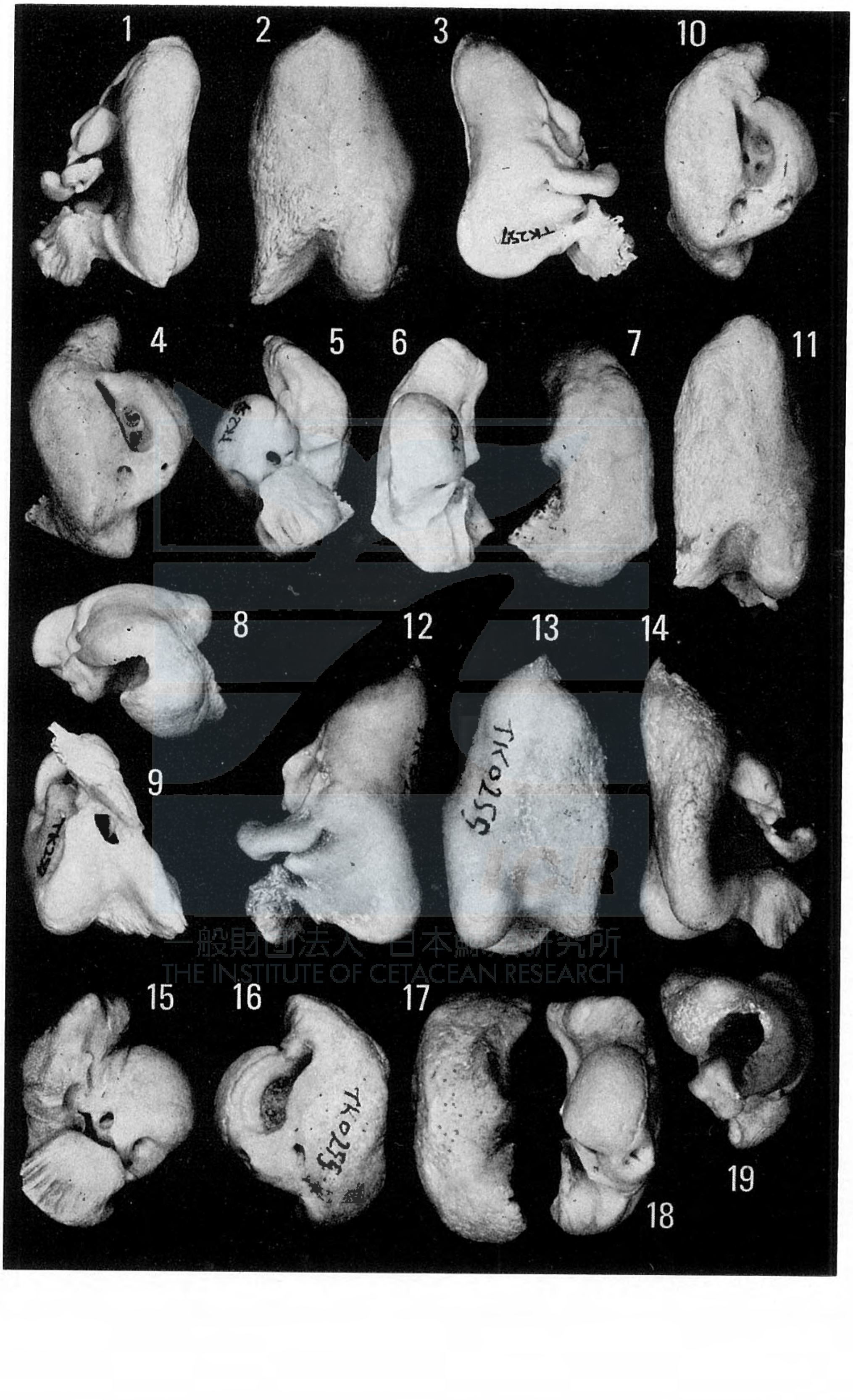


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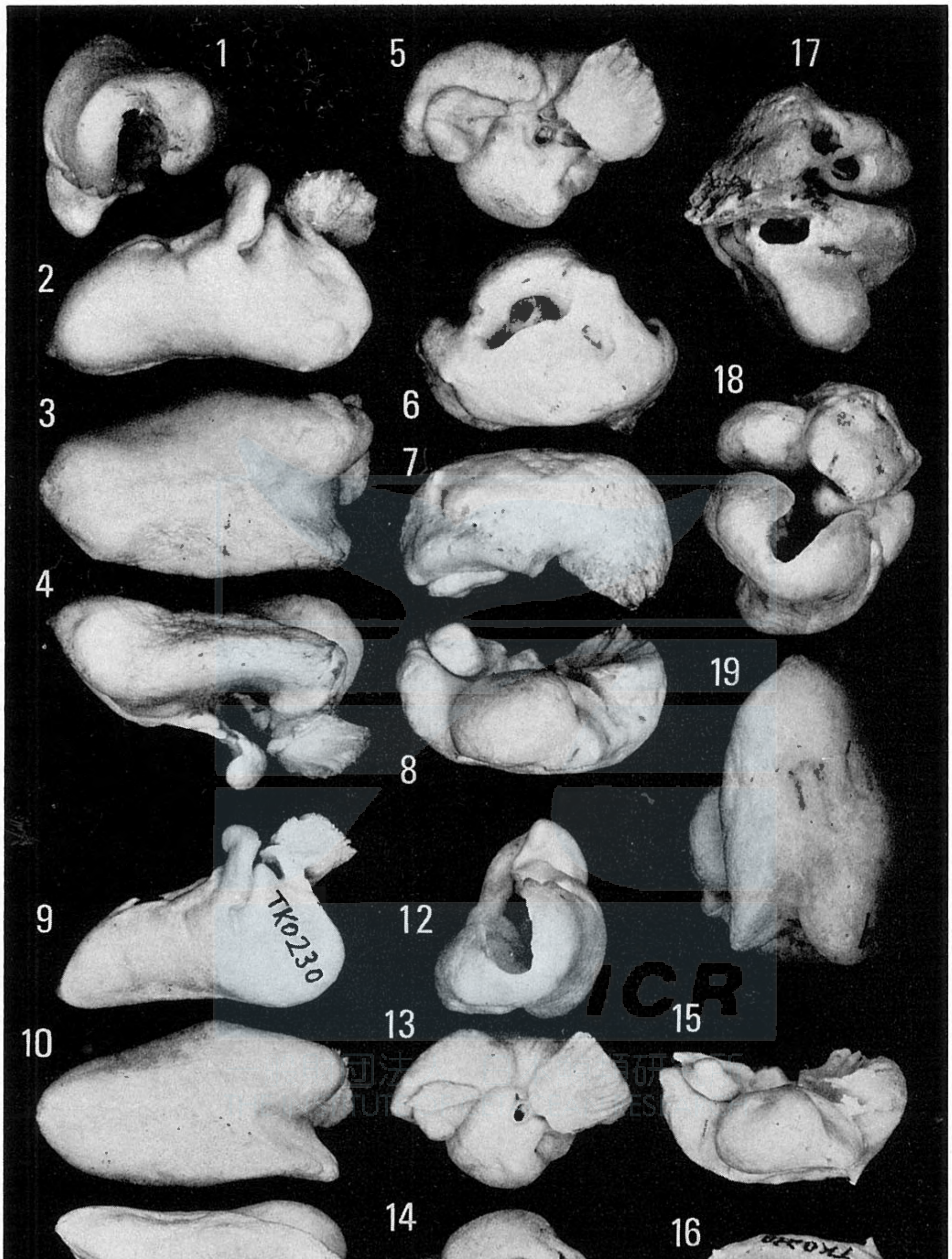
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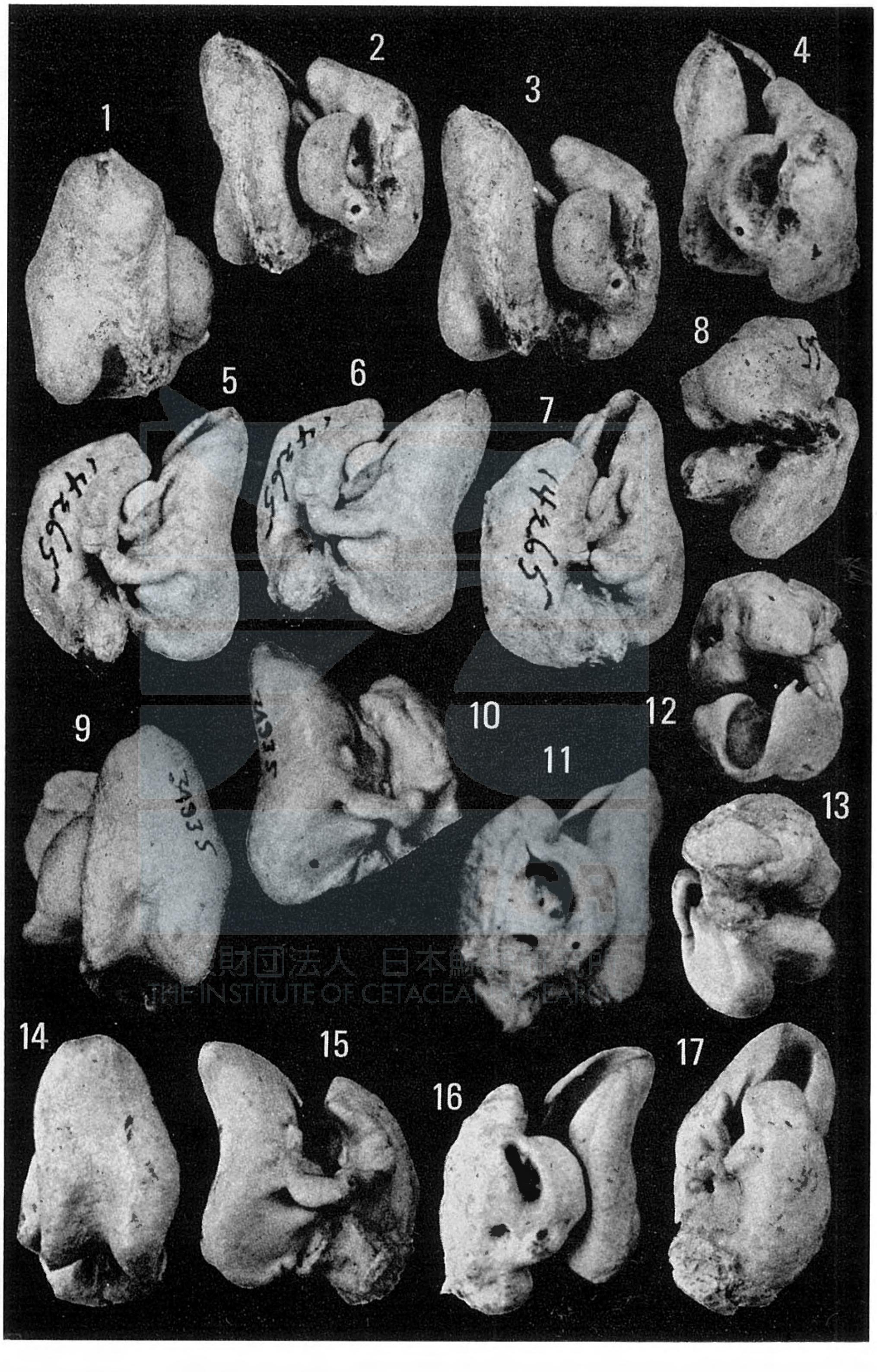
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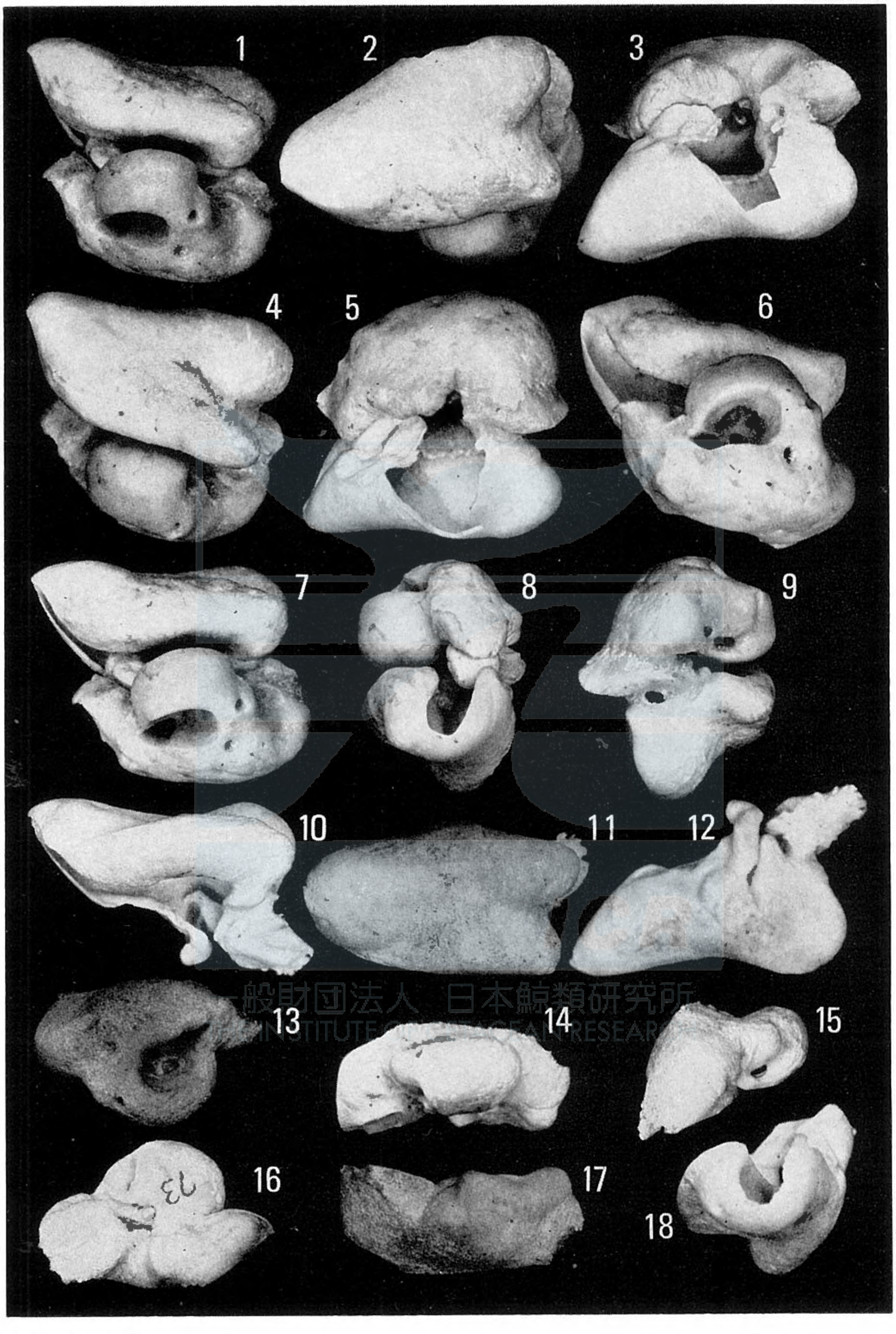
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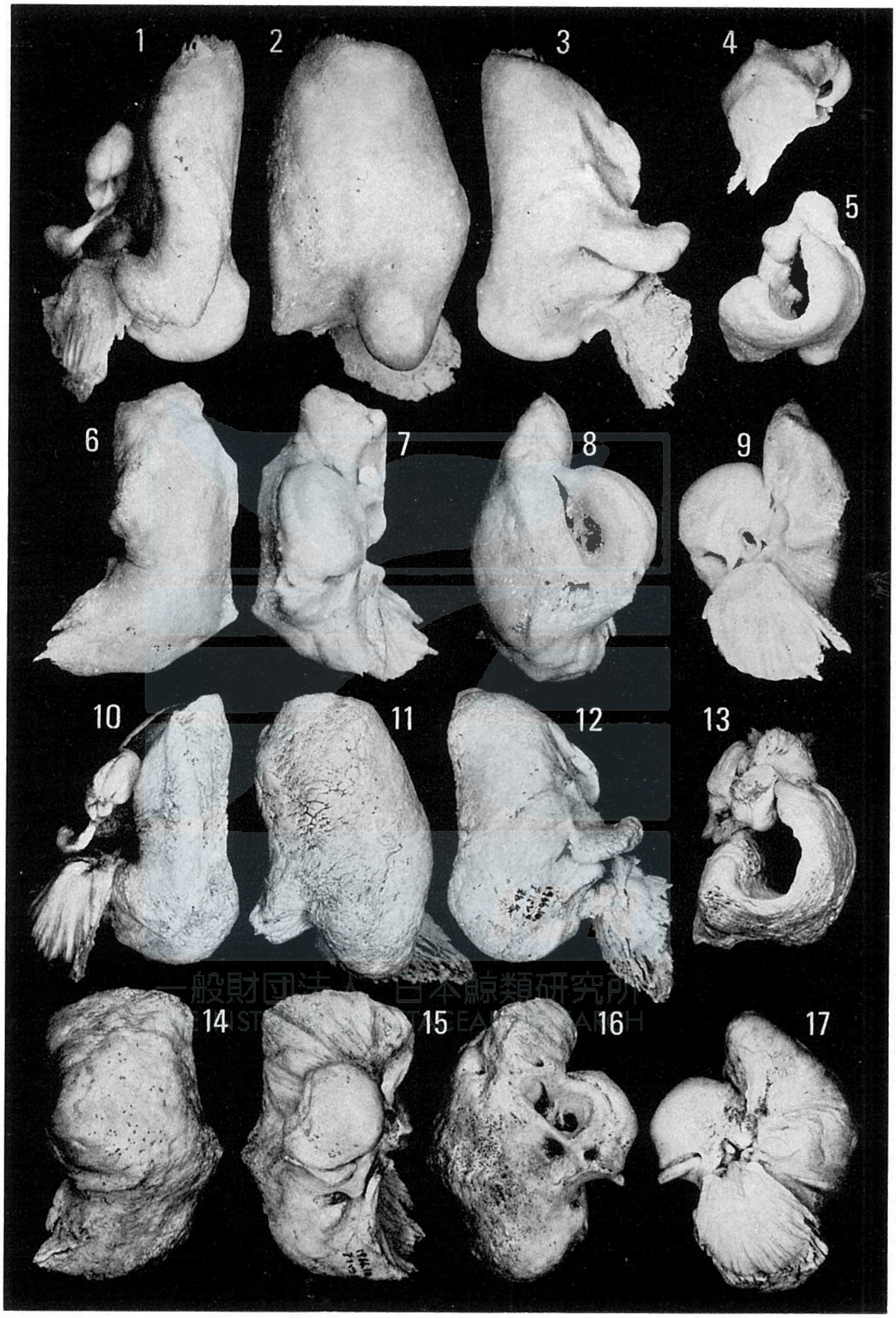
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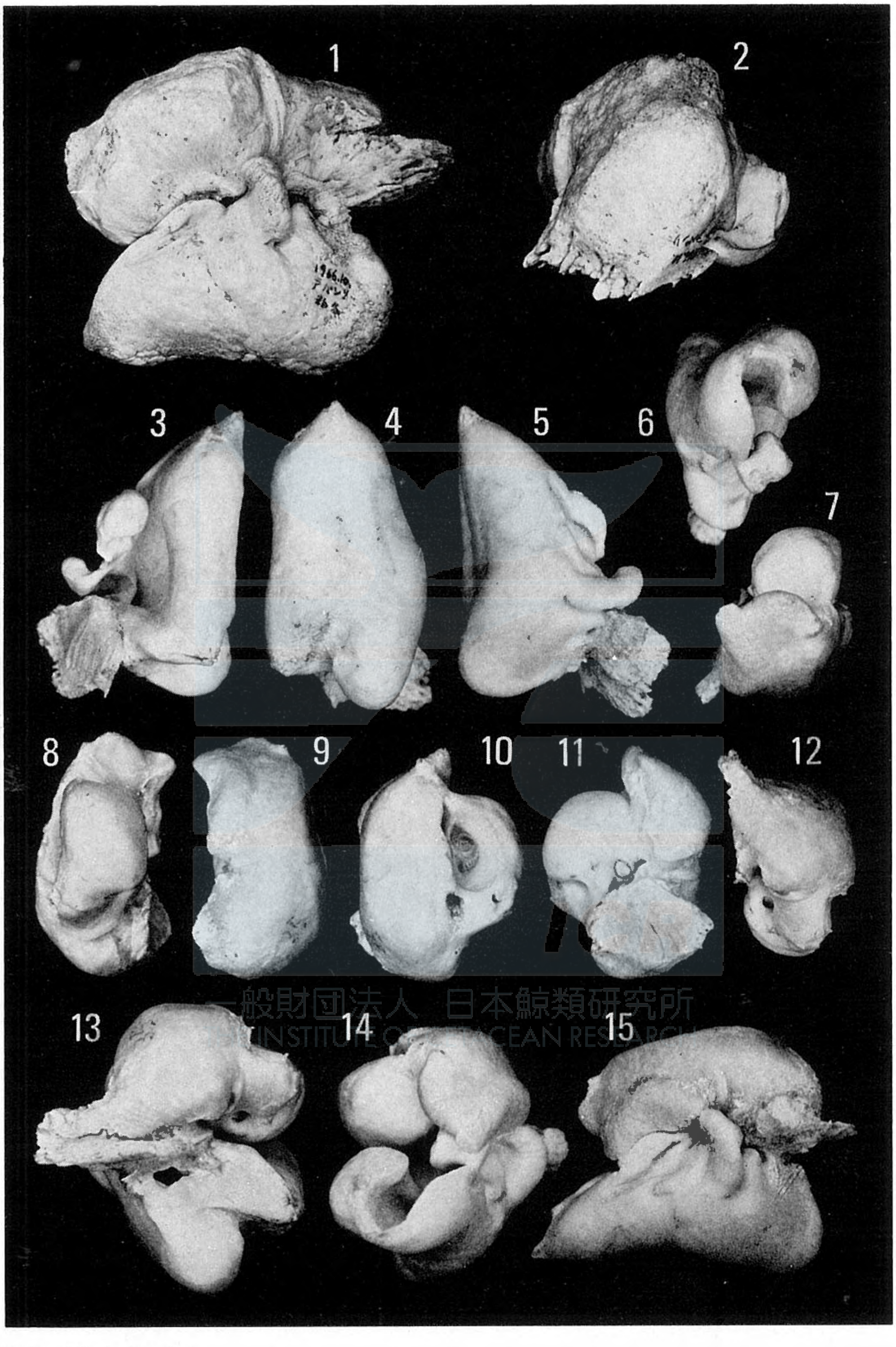
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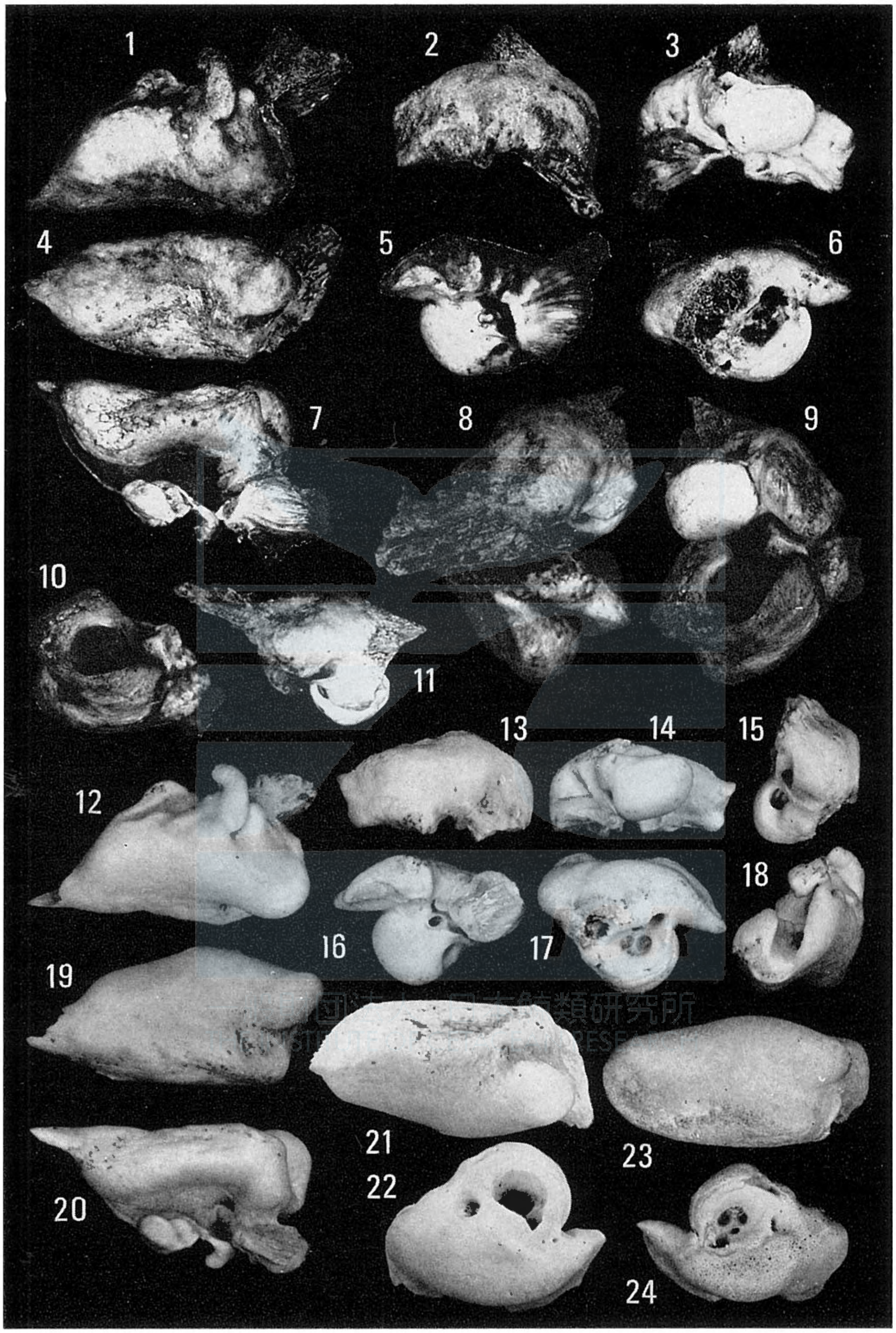
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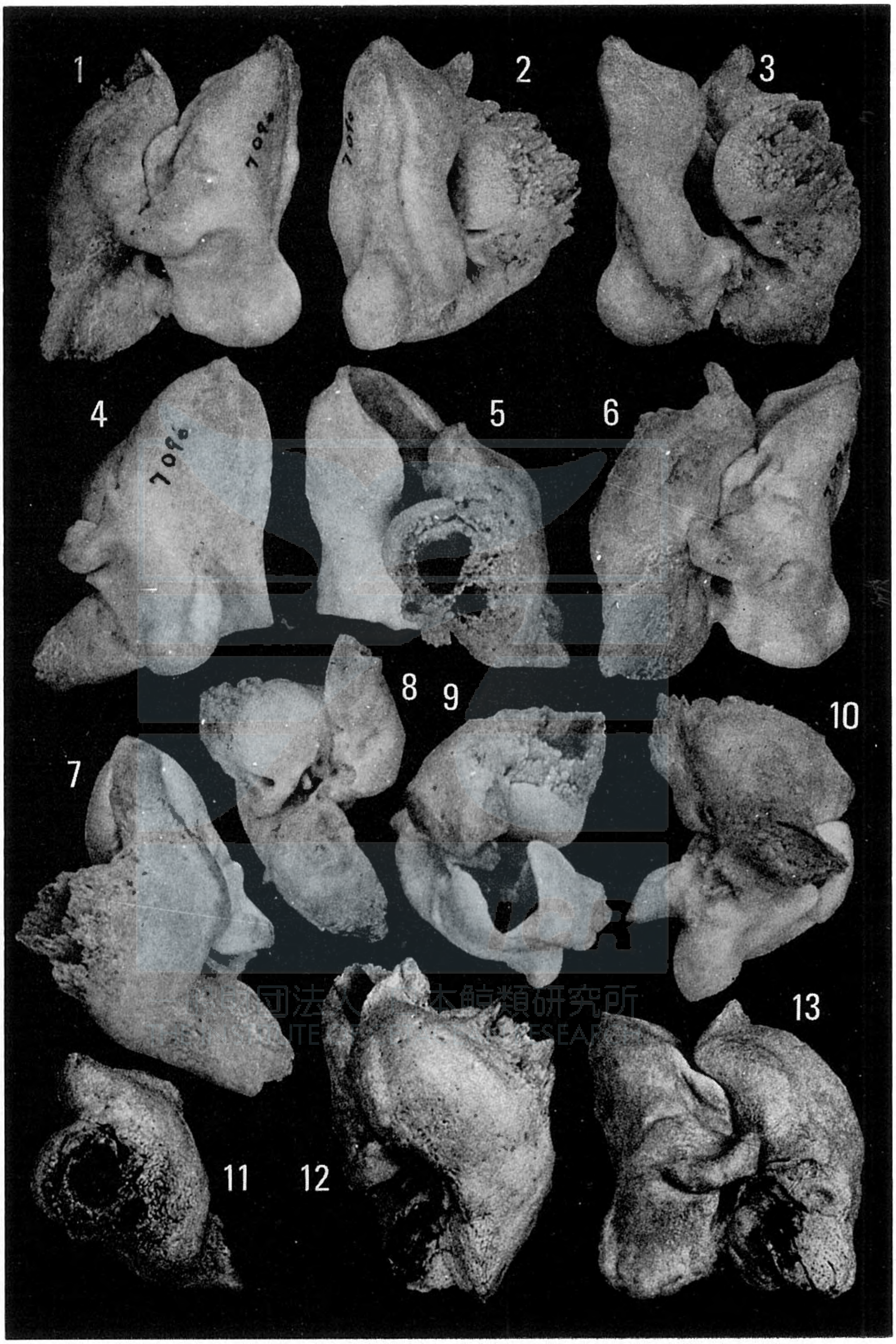


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