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M. Ishiyama
Nippon Dental University

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ENAMEL STRUCTURE IN ODONTOCETE WHALES

M. Ishiyama

Department of Oral Anatomy, Nippon Dental University, Niigata
1-8 Hamaura-cho, Niigata 951, JAPAN

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Abstract

With regard to the enamel structure of mammals, a large number of studies have been reported in the past. Of them, however, the enamel structure of odontocetes has not yet been sufficiently elucidated. The author therefore observed the enamel structure of 11 species in 7 families of living odontocetes.

A clear prism structure in the enamel is noted in delphinids and Pontoporia blainvillei. Neophocaena phocaenoides has a very simple-structured prism, but even this structure is obvious only in the deep layer of the enamel, disappearing gradually from the mid layer to surface layer.

The prism pattern of delphinids differs significantly depending on the site of the enamel; that of Pontoporia shows as a whole pattern 1. On the other hand, the enamel of Physeter catodon, Berardius bairdi, Phocoena phocoena, Phocoenoides dalli and Delphinapterus leucus is prismless. The enamel of Physeter and Phocoena shows pseudoprisms; that of Phocoenoides contains enamel tubuli. The enamel of Berardius and Delphinapterus is 3 to 8 μm thick, which is extremely thin for mammalian enamel. No enamel was noted in Monodon monoceros teeth.

The enamel structure of living odontocetes is thus very variable. Several characteristic structures having been present during the evolutionary course of this tissue are still present in some of them. As the results of comparative histologic study, it is considered that the variable enamel structure of living odontocetes is a secondary phenomenon produced during the degenerative history of the enamel.

Key Words: Odontocete whales, dental enamel, enamel structure, prism patterns, prismless enamel.

*Address for correspondence:
Mikio Ishiyama, Department of Oral Anatomy,
Nippon Dental University,
1-8 Hamaura-cho,
Niigata 951, Japan
Phone No. 025(267)1500

Introduction

Cetaceans, belonging to mammalia, appeared in the early Tertiary times in the evolutionary history of vertebrates (Colbert, 1980) and are highly adapted to ocean life. Consequently marked changes took place in various regions in their bodies, resulting in the deformation or disappearance of even some fundamental characters of mammals. This tendency is also conspicuously exhibited in the teeth. For instance, the teeth have disappeared in adults of Mysticeti, and not only has the fundamental dental formula of mammals been lost but also the property of heterodonty in odontocetes.

Specialization of odontocetes teeth is noted also in the dental structure, and there has been a report of the absence of enamel in the teeth of Physeter catodon and Berardius bairdi(Kuroe, 1961; Osawa et al., 1981). However, there has also been a report of the presence of enamel at an extremely narrow site at the tip in Physeter teeth (Ohsumi et al., 1963). Therefore, whether the enamel is present or absent in the teeth of these species is probably a question that should first be elucidated when the dental structure of odontocetes is studied.

As a whole, definite reports concerning the enamel structure of odontocetes are few: only Shobusawa (1952) and Kawai (1955) have stated brief findings on 2 or 3 kinds of odontocetes in the comparative histological study of mammalian enamel. Boyde (1964, 1969) has mentioned structure of the prism pattern of odontocetes in his study of mammalian enamel structure, employing several species of odontocetes. Furthermore, Boyde (1980) has summarized the enamel structure of odontocetes.

Recently, Ishiyama (1984) has reported the enamel structure (mainly using scanning electron microscopy) in 7 species and has revealed the great variabilities of the enamel structure among the species. This paper is intended to review the enamel structure of odontocetes adding new findings.

Materials and Methods

The species used in this investigation are listed here: Physeter catodon Sperm whale (Physeteridae), Berardius bairdi Baird's Beaked whale (Ziphiidae), Monodon monoceros Narwhal (Monodontidae), Delphinapterus leucus White whale (Monodontidae), Stenella frontallis Bridled Dolphin (Delphinidae), Globicephala macrorhyncha Pilot whale (Delphinidae), Lagenorhynchus acutus Atlantic White Sided Dolphin

(Delphinidae), Pontoporia blainvillei La Plata River Dolphin (Platanistidae), Phocoena phocoena Common Porpoise (Phocaenidae), Neophocaena phocaenoides Finless Black Porpoise (Phocaenidae), Phocoenoides dalli Dall's Porpoise (Phocaenidae)

Materials were dry teeth kindly provided by the Far Seas Fisheries Research Laboratory, Japan (Physeter, Berardius, Stenella and Pontoporia); National Science Museum, Japan (Globicephala, Phocoena and Phocoenoides); Department of Anatomy, Nippon Dental University, Niigata, Japan (Neophocaena) and Arctic Biological Station, Canada (Monodon, Delphinapterus and Lagenorhynchus).

Most of the teeth were ground in a longitudinal, cross or tangential plane and then etched with 1/10 N HCl for 15 to 45 sec., dried, coated, and examined with a Hitachi, S-500 scanning electron microscope. In some species, 70 to 80 μm thick ground sections were prepared and examined by polarizing microscopy (Olympus, BHS-P). Contact microradiographs of these sections were made on Kodak Spectrographic Plates 649-0 (8 minutes, using CuK_α radiation generated at 24 kV and 40 mA).

Results

Monodon monoceros and Delphinapterus leucus

These 2 species belong to the Monodontidae, and distributed in the Arctic seas. Although many morphological similar points categorize the two into the same family, the forms of their teeth are quite different. Monodon usually has two teeth in the maxilla. Of them, the male's teeth on the right side and female's teeth do not develop in the form of the tusk, but remain unerupted. Delphinapterus teeth are conical, 8 to 10 being found in each side of both the maxilla and mandible.

For Monodon, the unerupted right teeth of males were used. The tooth is approximately 20 cm in length showing a slender bar-like form. Amputating 1 cm or so at the tip and observing the ground surface by SEM revealed that a major portion of the tooth consists of dentin, and cementum covers it completely up to the tip without enamel (Fig. 1). Many Howship's lacunae-like configurations are present on the surface of the dentin; there is an incomplete, very narrow gap between the dentin and cementum, leading to an incomplete contact between them (Fig. 2). The cementum covering the tip is divided into 2 layers, the inner layer of which is compact acellular cementum and the outer one of which is cellular cementum. The cellular cementum has many cavities that blood vessels presumably entered.

Delphinapterus exhibited markedly different structure between the erupted teeth and non-erupted ones. Dentin is exposed at the tip of erupted teeth. Enamel is present at the tip of the unerupted teeth (Fig. 3). The enamel is prismless, 7 to 10 μm thick (Fig. 4). In the enamel, incremental lines approximately parallel to the surface layer of the tooth are noted. The enamel is made of fine crystal groups arranged perpendicular to the tooth surface.

Physeter catodon

This species has more than 20 conical teeth 10 to 15 cm in length in each side of the mandible which work as functional teeth. More than 10 conical teeth, much smaller in size than mandibular at 4 to 8 cm in length are found in each side of the maxilla, and they are usually unerupted. Although the tip of the mandibular tooth exhibits conspicuous abrasion and exposure of the dentin, the maxillary teeth reveal scarcely any evidence of abrasion because they are embedded.

Observation of the surface of a longitudinal ground section of the maxillary tooth tip by means of SEM discloses the enamel between the dentin and coronal cementum (Fig. 5). The enamel is approximately 200 μm in thickness but varies considerably from one tooth to another. The enamel is localized at the tooth tip and never noted more than 3 mm from the tip. Observation of the enamel at a high magnification demonstrates the presence of incremental lines at intervals of 3 to 4 μm in the enamel and further the presence of several finer incremental lines among them (Fig. 6). The enamel is prismless, and the crystals radiate perpendicular to the dentinal surface. Careful observation shows that there is a definite pattern in the arrangement condition of these crystals observed between crossed polars. When the ground section is observed, the structure appears as pseudo-prismatic (Fig. 7).

Berardius bairdi

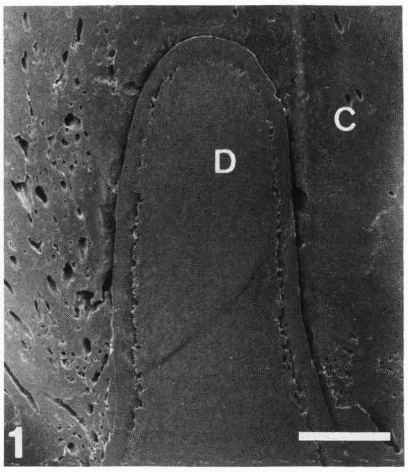
This species lacks teeth in the maxilla but has two-paired teeth on each side in the anterior portion of the mandible. The teeth show a triangular pyramidal shape compressed and flattened labio-lingually: the front teeth are 8 to 10 cm in length, while the rear ones are 4 to 5 cm.

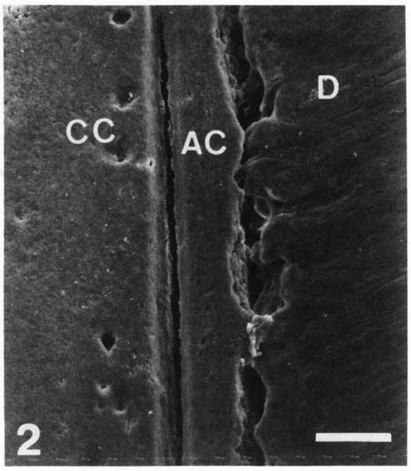
Polarizing microscopic observation of the ground sections shows that the tooth tip consists of dentin and cementum. Although the cementum covers up to near the dental tip, it does not completely cover it, and the dentin seems to be exposed for approximately 6 to 8 mm at the tip. However more careful observations reveal the presence of a thin layer that shows strong "negative birefringence" on the outside of apparently exposed dentine (Fig. 8). When the observation is gradually extended down the teeth, the thin layer is also found between the dentin and cementum (Fig. 9), up to 1 cm from the tip. Microradiography proves that this thin layer has a low degree of X-ray penetration and is obviously the enamel (Fig. 10). SEM shows that the enamel is very thin, at 3 to 5 μm, and consists of fine crystal groups arranged perpendicular to the dentinal surface (Fig. 11).

Stenella frontalis, Globicephala macrorhyncha and Lagenorhynchus acutus.

These species belong to Delphinidae and have in common the large number of teeth of the same shape and size in both jaws. The appearance of the tooth is sharply conical at the tip with a lingually curved crown. The teeth show a distinct crown-root junction; that is, they have a neck.

Stenella teeth are 1.2 to 1.5 cm in length with enamel 120 to 150 μm thick. The enamel is prismatic, and when observed in longitudinal sections, the prisms proceed from the enamel-dentin junction toward the tooth surface, showing a slight sigmoid curvature (Fig. 12). In the outer layer of the enamel, prismless regions are very frequently noted and occupy nearly 1/4 to 1/5 of the whole thickness of the enamel. In extreme cases there are teeth wherein even as much as 1/3 is prismless. Observation of the prism patterns discloses that in the case of this species they differ with the enamel layers. In the deep and mid layers of the enamel, patterns 2 and 3 and intermediate forms are mainly

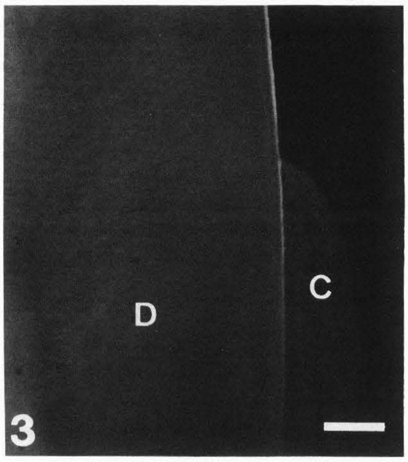


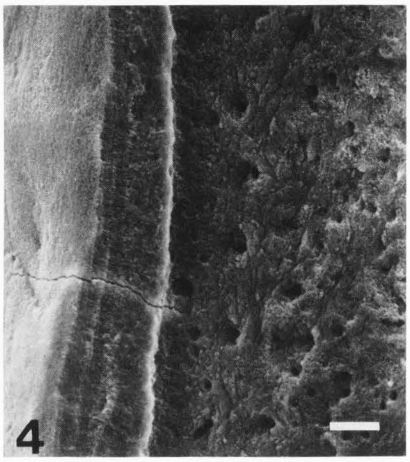


Figs. 1, 2. Scanning electron micrographs of ground section of tooth tip in Monodon.

Fig. 1. Low-power view of the tip of a tooth. The tip of a tooth consists of dentin (D) and cementum (C). Bar = 500 μm.

Fig. 2. Enlarged view of Fig. 1. Many lacunae are present on the surface of dentin (D). CC:cellular cementum, AC:acellular cementum. Bar = 50 μm.

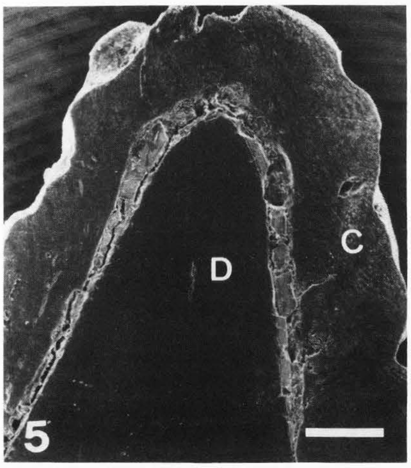


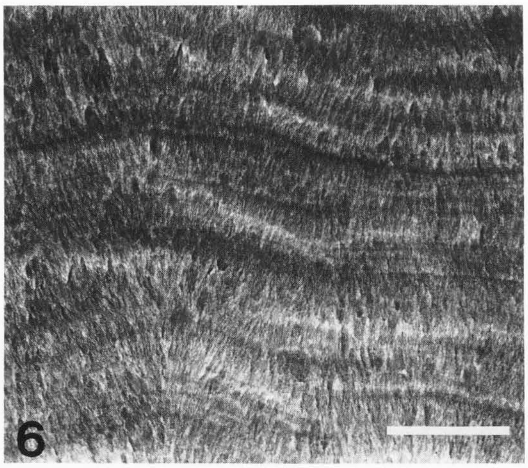


Figs. 3, 4. Delphinapterus tooth.

Fig. 3. Microradiograph of ground section. Note the very thin enamel on the dentinal surface. D:dentin, C:cementum. Bar = 200 μm.

Fig. 4. Scanning electron micrograph, showing incremental lines in the enamel. Bar = 5 μm.





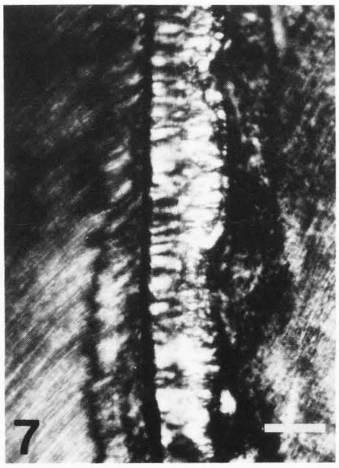
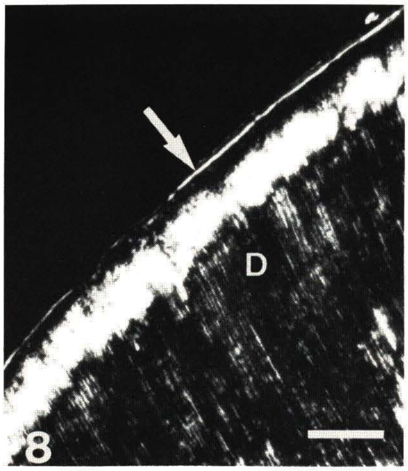
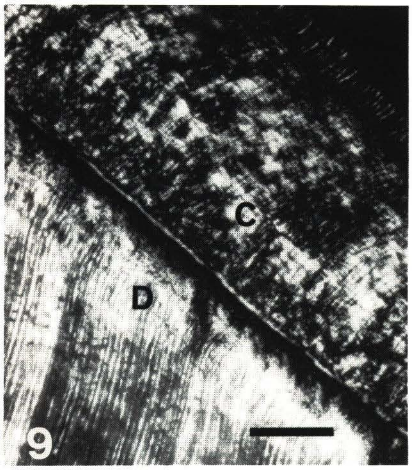


Fig. 5. Scanning electron micrograph of maxillary tooth tip of Physeter in low power view. A thin layer of enamel exists between dentin (D) and cementum (C). Bar = 500 μm.

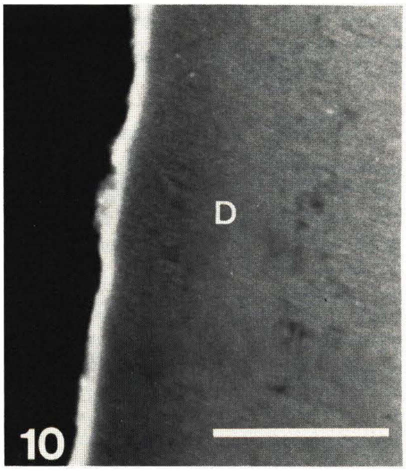
Fig. 6. Enlarged view of enamel of maxillary tooth in Physeter. The enamel is aprismatic and reveals a number of incremental lines. The crystallites are arranged in sinusoidal pseudo-prisms. Bar = 5 μm.

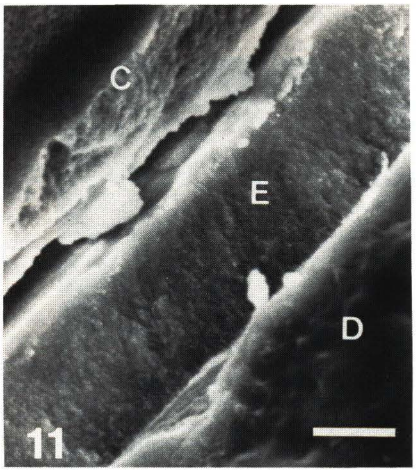
Fig. 7. Polarized light micrograph of ground section of Physeter maxillary tooth. The enamel exhibits a pseudo-prismatic structure at the extinction position. Bar = 100 μm.

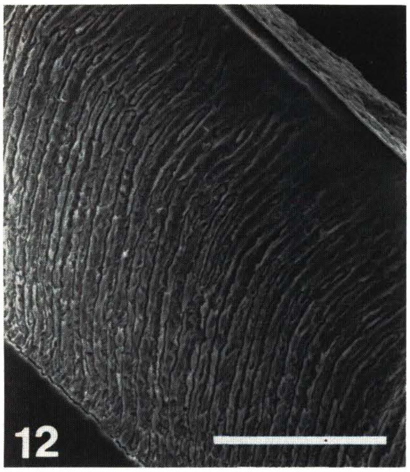


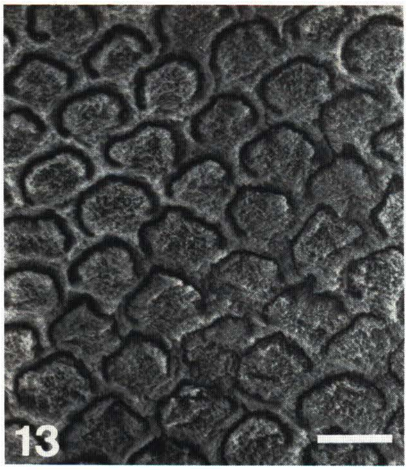


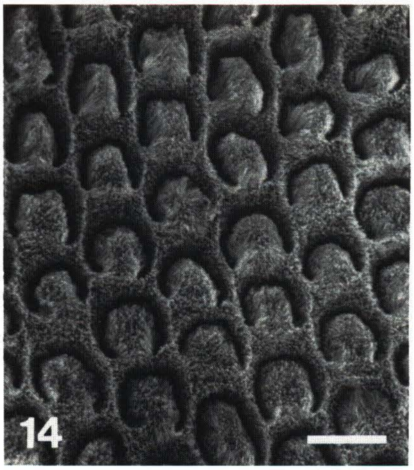
Figs. 8, 9. Polarized light micrographs of ground sections of mandibular teeth of Berardius. **Fig. 8.** A superficial thin layer (arrow) shows strongly negative birefringence. D:dentin. Bar = 100 μm. **Fig. 9.** The thin layer showing negative birefringence exists also between dentin (D) and cementum (C). Bar = 100 μm.











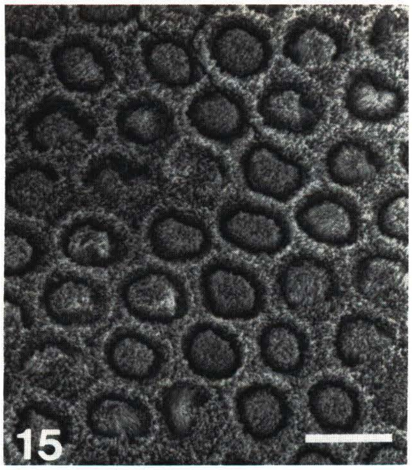
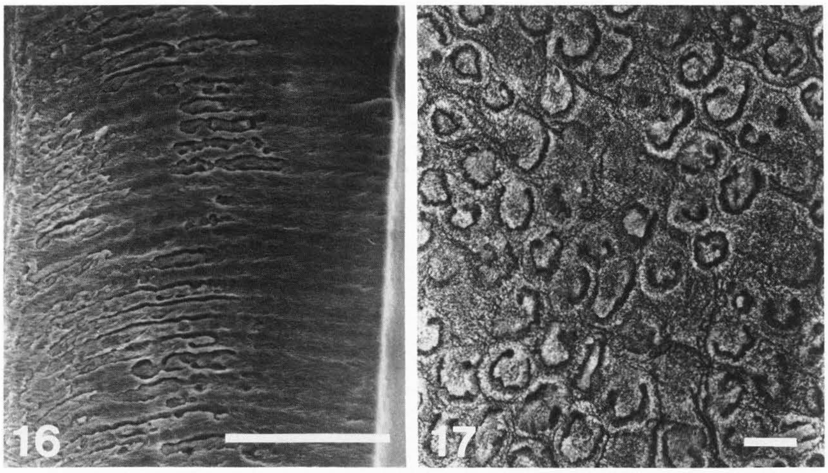


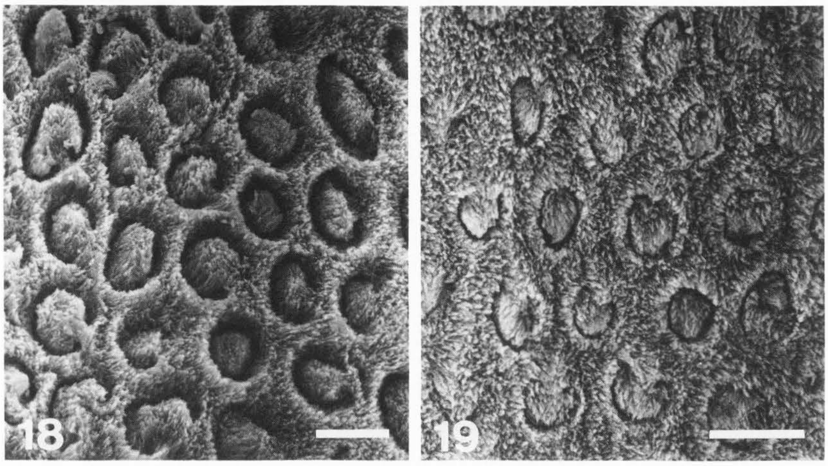
Fig. 10. Microradiograph corresponding to the region of Fig. 8. The thin hypermineralized layer is the enamel. D : dentin. Bar = 50 μm.

Fig. 11. Scanning electron micrograph showing enamel layer. The enamel (E) consists exclusively of crystallite materials arranged perpendicular to the surface of the dentin (D). C:cementum. Bar = 1 μm.

Figs. 12-15. Scanning electron micrographs of ground section of enamel in Stenella. **Fig. 12.** Longitudinal ground surface of enamel. The enamel is prismatic, and each prism slightly curves. Note the prismless region at the superficial layer. **Figs. 13-15.** Tangential ground surface of enamel. **Fig. 13.** "Keyhole" shaped prisms (pattern 3) in the middle layer. **Fig. 14.** "Horseshoe" shaped prisms (pattern 2) in the middle layer. **Fig. 15.** "Circular" shaped prisms (pattern 1) in the superficial layer. Bar = 50 μm (Fig. 12) and = 5 μm (Figs. 13-15).



Figs. 16, 17. Scanning electron micrographs of ground sections of enamel in Lagenorhynchus. **Fig. 16.** Longitudinal ground section of enamel. The enamel is prismatic. Note the very marked presence of the prismless region. Bar = 50 μm. **Fig. 17.** Tangential ground surface of enamel. Prisms are sparsely present and both large and small in size. Bar = 5 μm.



Figs. 18, 19. Scanning electron micrographs of tangential ground surface of enamel in Pontoporia. **Fig. 18.** "Circular" shaped prisms in the middle layer of enamel. Bar = 5 μm. **Fig. 19.** "Circular" shaped prisms in the superficial layer of enamel. Note the notable interprismatic substance. Bar = 5 μm.

noted, whereas in the surface layer only pattern 1 is found (Figs. 13,14,15).

The form and tissue structure of Globicephala teeth are similar to those of Stenella. However, this species is large among the Delphinidae, and the teeth are also large and 3 to 5 cm in length. The enamel is prismatic with a thickness of 250 to 300 μm. Changes in the prism patterns in the enamel are the same as those in Stenella, but the presence of the prismless region in the surface layer of the enamel is not so conspicuous as in the former species.

The form and size of Lagenorhynchus teeth also resemble those of Stenella. The enamel is 100 to 120 μm thick and prismatic. Although the enamel prisms show a slight curvature in the deeper layer, they then run linearly from there to the surface layer. The enamel structure of this species has characteristically the very marked presence of the prismless region. Note infrequent cases are encountered in which even as much as a half of the whole enamel layers becomes prismless (Fig. 16). The prism pattern centers mainly on pattern 1, but as a whole the prisms are sparse and tend not to show a regular arrangement (Fig. 17).

Pontoporia blainvillei

The form of the teeth of this species resembles that of delphinids. The tooth is 0.8 to 1.0 cm in length with enamel 90 to 100 μm thick. The enamel is prismatic, and the prisms show a slight sigmoid curvature. Unlike delphinids, the presence of the prismless region on the surface layer of the enamel is insignificant. The prism pattern centers on pattern 1 over the whole layers with extremely few patterns 2 and 3 (Fig. 18). The diameter of the prism in the surface layer is less than in the mid layer, resulting in a wider interprismatic component (Fig. 19).

Phocoena phocoena, Neophocaena phocaenoides and Phocoenoides dalli

These species belong to the Phocaenidae, having a mutually similar tooth form. Whereas most odontocetes have sharply-tipped conical teeth, this group shows a spatulate-shape with rounded apical margins.

Phocoena teeth are 1 to 1.2 cm in length with 60 to 100 μm thick prismless enamel with many incremental lines (Fig. 20). The crystals are not arranged in one direction homogeneously from the enamel-dentin junction, but show sinusoidal change in orientation observed in Physeter. Polarizing microscopic observation of ground sections also shows the structure as pseudo-prismatic (Fig. 21).

Neophocaena teeth are 0.7 to 1.0 cm in length with the enamel 250 to 300 μm thick. Considering the tooth size, it can be said that the enamel develops very well. Prisms are clearly outlined near the enamel-dentin junction. In the center, the prisms become unclearly marked showing a gradual change to prismless enamel (Fig. 22). The prism structure in the deep layer as seen in etched preparations in the

SEM is also very simple when compared with that of other mammals. A groove corresponding to the prism boundary is noted, but the interprismatic regions cannot be distinguished (Fig. 23). Etched cross sectioned prisms in the central layer of the enamel already show no prism, but only indistinct round prominences corresponding to the prism in size (Fig. 24).

Phocoenoides teeth are 0.5 to 0.8 cm long with enamel 200 to 250 μm thick. Considering the tooth size, it has, like *Neophocaena*, a well developed enamel. The enamel is prismless, but contains a number of tubuli (Fig. 25). Although these tubuli are mainly abundant in the inner half of the enamel, they partly reach close to the surface. Clear incremental lines are noted at intervals of 15 to 20 μm. As shown in Figure 26, whereas *Stenella* enamel shows the degree of mineralization generally found in mammals, the enamel of this specie shows too low a degree of mineralization to rate it as proper enamel.

Discussion

Species with the poorly-developed enamel

On observation of *Physeter* and *Berardius* enamel, the author paid particular attention to the two following points: firstly, since the presence of enamel was practically negligible in both species, the enamel is possibly localized if present, at an extremely limited site at the tip; secondly, since odontocete teeth are monophyodont, the same tooth functions throughout life, so that marked abrasion is noted in the adult teeth and many teeth have lost the tip, the important site. In the study of these odontocete teeth, if the teeth subjected for observation are selected without considering these two points, correct results might probably not be obtained. This problem also applies to *Delphinapterus*.

Physeter enamel is approximately 200 μm thick despite considerable variation between teeth. It is not so thin as that of delphinids, and seems insignificant in comparison with the tooth size. Delphinid enamel is 90 to 300 μm thick, with a prismatic structure, whereas those of *Physeter* and *Phocoenoides* enamel have no prismatic structure although they are 200 to 250 μm thick. Consequently no relationship is likely to be found between "the thickness of the enamel" and "the presence of a prismatic structure" in odontocetes.

Polarizing microscopic observation revealed the pseudo-prismatic arrangement both in *Physeter* and *Phocoena* enamel. Poole (1956) has found this structure in the enamel of mammal-like reptiles, and Moss (1969) and Schmidt and Keil (1971) have also described it. With regard to this polarizing-microscopic appearance, they have explained that the enamel shows this striped pattern because of the sinusoidal arrangement. Direct observation by SEM confirms this regular sinusoidal arrangement of the enamel crystals in the species. According to present views of evolution of enamel, this structure should be primitive. However, looking at vertebrate evolution, cetaceans are advanced Mammalia belonging to the theria, and it may be that no phylogenetic meaning could be attached to the fact that pseudoprisms are noted in the enamel of these two species.

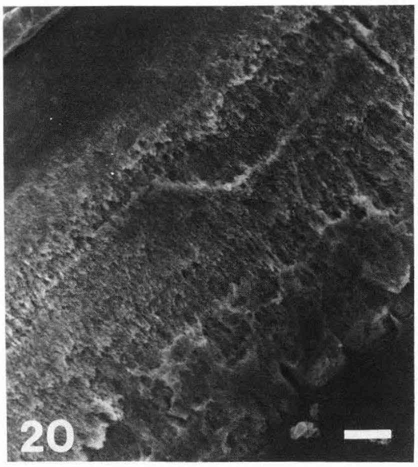
Berardius and *Delphinapterus* enamel was found to be extremely thin at only 3 to 10 μm. Such enamel is exceptional and unique amongst mammals. Enamel only a few microns thick is found in *Latimeria* (Smith, 1978; Shellis and Poole, 1978) and dipnoans (Smith, 1979; Ishiyama and Ogawa, 1983) in Pisces, amphibians (Sato, 1983), and Ophidia (Ishiyama et al., 1983) in reptiles and is often thought to be the most primitive kind of enamel. Even if monophyodont odontocetes have enamel of this thickness, it would disappear soon after eruption because of abrasion and thus probably frequently become unobservable. No enamel was noted in *Monodon* teeth. In this regard further study is indicated, because the number of teeth observed is still small at this time. Lacunae at the dentinal surface at the tip is noticeable in the teeth of this species. These are similar in form to the lacunae at the cement-dentin junction in rat molars described by Lester (1969) and may have a similar origin from the inclusion of the epithelial root sheath debris of Mallassez.

Changes in prism pattern and the phenomenon of becoming prismless

Hitherto it has been a common opinion that the odontocetes prism type is pattern 1 (Shobusawa, 1952; Boyde, 1964). However, the present observation found that stable pattern 1 is noted throughout the whole layer of enamel only in *Pontoporia*, while it is noted only in the surface layers of the enamel in *Stenella* and *Globicephala*. The prisms in the mid layer of the enamel in these species are mainly patterns 2 and 3 and transitional forms, without the typical pattern 1. It is probably attributable to the fact that observations have centered mainly on the surface layer of the enamel that in the past odontocetes have been reported to have the pattern 1. It should be noted, however, that this has been found to be a common feature in most mammals, just as has the tendency for the prisms to become pattern 1 in the subsurface zone (Boyde, 1964; Boyde and Martin, 1982).

A feature in common in delphinid enamel is the presence of a significant prismless region in the surface layer. The prism free layer occupies 1/4 to 1/5 of the surface layer side in *Stenella* and *Globicephala*, but more marked in *Lagenorhynchus*, occupying as much as nearly 1/2 in some teeth. In the latter species the prism pattern was indefinite, with prisms of variable shape and size. This phenomenon is obviously attributable to the fact that the ameloblast cannot form a definite Tomes' process, suggesting a sort of degenerative phenomenon or a less active enamel formation. The author suggests that delphinid enamel is as a whole proceeding to become prismless, and prism structure is degenerating.

The degeneration of the prismatic structure in delphinids seems to become most marked in porpoises. Despite belonging to the same family, these three kinds form a specific group with enamel structure differing from one another. Of these, *Neophocaena* is likely to be important for a consideration of the degenerative course of the prism structure. Prisms in this species are very simple, and even this degree of structure disappears gradually from the mid layer to the surface layer. This species is in a transitional position between the kind with prismatic enamel and that with prismless enamel and probably provides suitable evidence suggesting that the prismless enamel of porpoises is a degenerative phenomenon derived from prismatic enamel. *Phocoena* shows enamel that degenerated structurally one stage



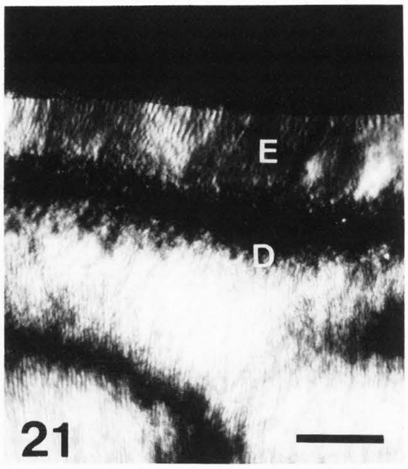
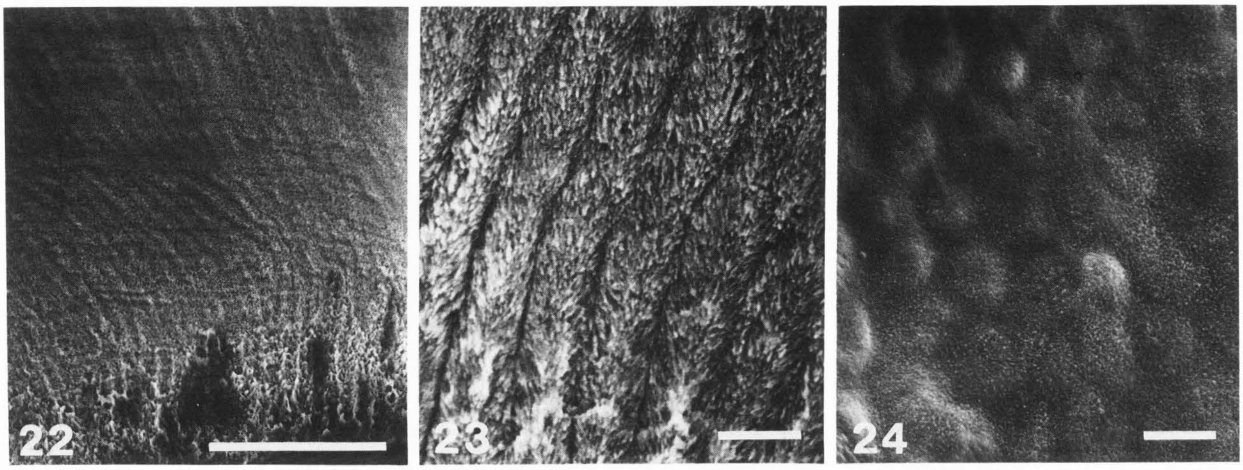
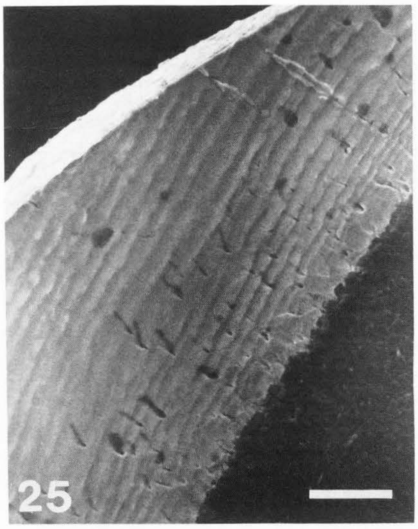


Fig. 20. Scanning electron micrograph of longitudinally ground surface of enamel in *Phocoena*. The enamel is *aprismatic*. Bar = 5 μm.

Fig. 21. Enamel exhibits typical pseudo-prism in polarized light at the extinction position. Bar = 50 μm.



Figs. 22-24. Scanning electron micrographs of the ground surface of enamel in *Neophocaena*. **Fig. 22.** Longitudinal surface of enamel in low-power view. On approaching the tooth *surface the prism* structure becomes indistinct. Bar = 50 μm. **Fig. 23.** Longitudinal surface of enamel in the deep layer. Prisms are seen, but the arrangement of crystallities is simpler than that of other mammals. Bar = 5 μm. **Fig. 24.** Tangential surface of the middle layer of enamel. Note the indistinct circular structure. Bar = 5 μm.



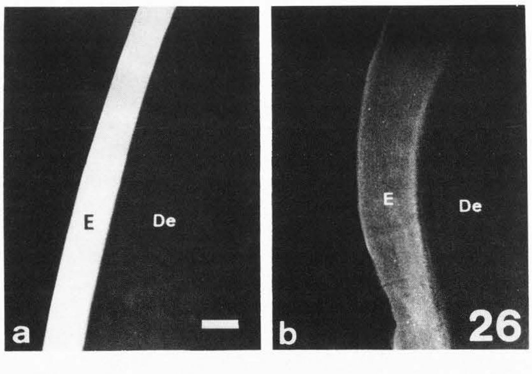


Fig. 25. Scanning electron micrograph of longitudinally ground surface of enamel in *Phocoenoides*. The enamel includes many tubuli, and a number of *incremental* lines. Bar = 50 μm.

Fig. 26. Microradiographs of ground sections in *Stenella* (a) and *Phocoenoides* (b). *Phocoenoides* enamel show a *notably low* degree *of mineralization*. *De:dentin, E*:enamel. Bar = 100 μm.

further than that in *Neophocaena*. The enamel of this species has no prism structure, but shows clearly the presence of pseudo-prisms. Going one step further, even the pseudo-prism structure is not noted in *Phocoenoides* enamel. In this species it would seem that even the mineralization mechanism has undergone degeneration; the degree of mineralization of the enamel is extremely low. The enamel contains a number of enamel tubuli, which may also be a secondary phenomenon associated with the low degree of mineralization of the enamel. Such a study of the enamel structure of porpoises impresses strongly that odontocete enamel is a degenerative tissue.

The overall results indicate that the structure of the odontocete enamel is extremely variable. It exhibits each evolutionary stage in vertebrate enamel (for instance, thin enamel several μm thick, prismless enamel, pseudo-prismatic enamel, tubular enamel, and prismatic enamel). All the stages in enamel evolution are seen in this group, but the main question is, in which direction the changes (which are occurring) have occurred. Sahni (1981) has reported on the enamel structure of an archaeocete *Protocetus* and indicated that the enamel showed Hunter-Schreger bands and pattern 1 prisms. This animal is thought to be the ancestor of the living odontocetes. It is suggested, however, that the significant changes in the tissue structure noted in the living odontocetes is a secondary degenerative phenomenon rather than an evolutionary trend in the opposite direction.

A gross scheme of the teeth and enamel structure of odontocetes is given in Fig. 27.

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Discussion with Reviewers

A. Boyde: The incomplete narrow gap that you show in your etched sections of *Monodon* tooth tip is very interesting. It should be confirmed as present in unetched preparations.

Author: I have confirmed the incomplete narrow gaps in unetched sections.

R.P. Shellis: The marked deviation of the prisms observed in *Stenella* (Fig. 12) interest me, as the same phenomenon occurs in the mole *Talpa* and the treeshrew *Tupaia*. As in both toothed whales and in these small insectivorous mammals, there is a large vertical component of tooth movement, it seems possible that this structure could have some mechanical significance. Does the author agree?

Author: Yes, I agree with your opinion.

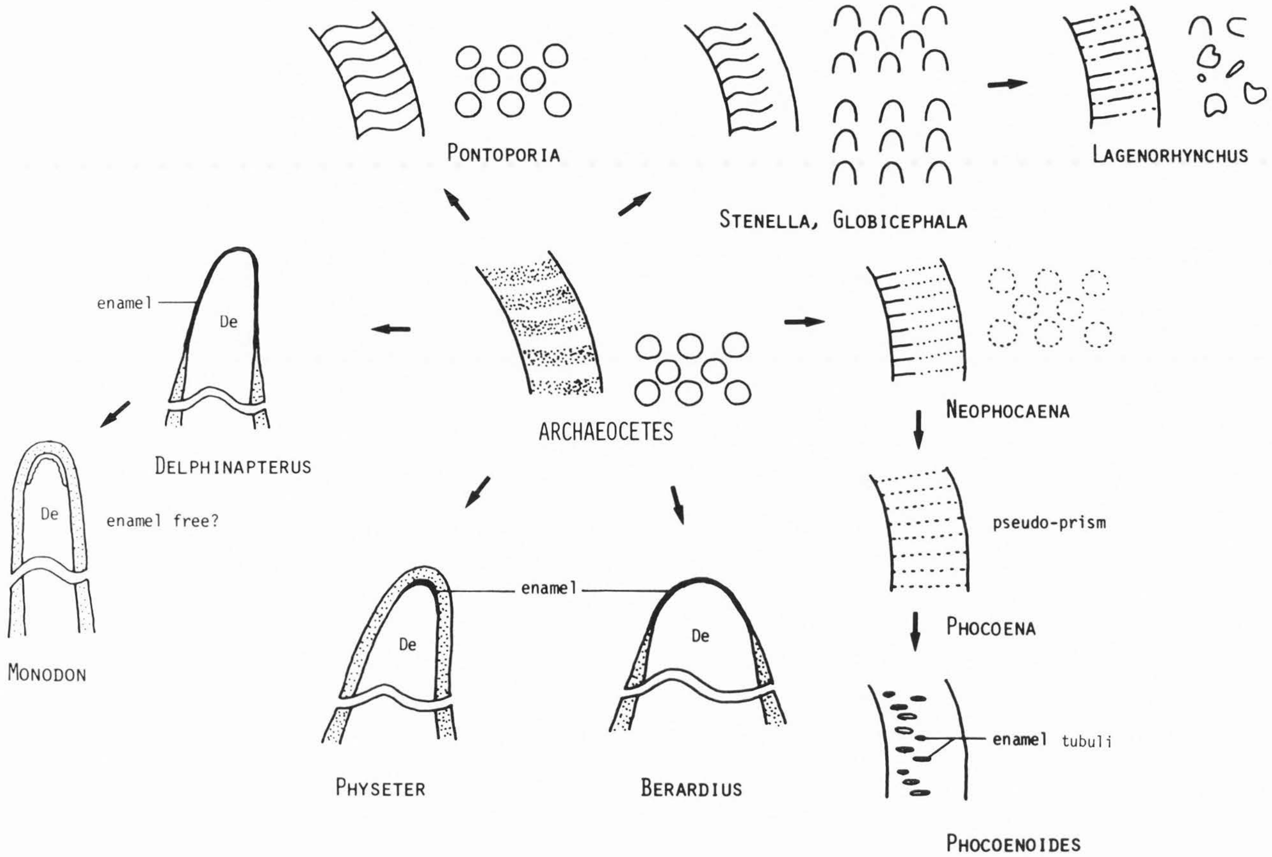

Fig. 27. The variation of teeth and enamel structure in odontocete whales used in this study.