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AUTHOR(S): Kobayashi, Iwao; Kamei, Tadao


ISSUE DATE: 1973-09-10

URL: http://hdl.handle.net/2433/186591

RIGHT:
A Histological Study on a Tooth of Paleoparadoxia

By

Iwao Kobayashi* and Tadao Kamei

(Received May 10, 1973)

Abstract

A histological study has been made for a tooth of Paleoparadoxia tabatai (Tokunaga) found from the Tomikusa Group, Middle Miocene. The polished surface of the tooth has been prepared for the optical and electron microscopic observations. The observations on the micro-structures of enamel rods, bands of Schreger, dentinal tubules, cementum lacunae etc. are described in comparison with those of other mammals. As a conclusion, the presence of the common characteristics between Desmostylus and Paleoparadoxia is clarified from the histological viewpoint. The results suggest that the teeth of both Desmostylus and Paleoparadoxia have common histological characteristics with those of Ungulate group.

Introduction

As for the tooth of Desmostylid, the histological studies have been carried out by V. L. Vanderhoof (1937), S. Ijiri (1939) and S. Ijiri and T. Kamei (1961). Among them, in the last work taxonomy and paleoecology of Desmostylid have been discussed from the view point of the oral histology. Ijiri and Kamei have given a short description about the micro-structure of molars of Paleoparadoxia tabatai (Tokunaga) from Toki city and they have suggested that there is close relation between Paleoparadoxia and Desmostylus.

The authors have an opportunity to examine a fossil tooth which was described as a premolar of Paleoparadoxia sp. designated by Kamei (1967), found from Anan-chō, Nagano Prefecture. In this paper, the results of optical- and electron microscopic observations on that specimen are described and a view from the comparative histology of the tooth is discussed.

The authors take this opportunity to express their thanks to Dr. S. Ijiri from his continuing interest and encouragement and to Dr. M. Katagiri for suggestion on calcified spherulites. Thanks are also due to Professor K. Tanaka of Shinshu University and Mr. M. Kobayashi of Anan-chō for their facilities to study the material. The study was supported in part by a grant from the Foundation of the Ministry of Education.

* Department of Geology and Mineralogy, Faculty of Science, Niigata University, Niigata.
Material and Method

Material: The material is composed of a fossil tooth discovered by Mr. Masakazu Kobayashi in 1966. For this fossil tooth, Kamei (1967) gave identification as the right lower first premolar of *Paleoparadoxia* sp.

Locality: Upper stream of the Onzawa, about 100 m. from the Miyashita bridge, Anan-chō, Shimoina-gun, Nagano Prefecture.

Horizon: The lower part of Oshimojo formation of Tomikusa Group.—Middle Miocene—(Miyajima, 1958 in Tanaka, 1967)

Mode of Occurrence: According to K. Tanaka, the fossil tooth had been obtained from medium sandstone of dark brown in color which is abundant in molluscan fossils and shark teeth. Following fossils had been found associating with the fossil tooth:

- *Patinopecten egregius* Itoigawa
- *Lucinoma acutilineatum* Conrad
- *Carcharhinus* sp.
- *Negaprion* sp.
- *Galeocerdo* sp.
- *Squalus* sp.
- *Lamna* sp.
- *Isurus* sp. (abundant)
- *Venericardia cf. ferruginea* Cleassin
- *Culterius izumoensis* Yokoyama
- *?Dosinia* sp.
- *Acila* sp.
- Fish, crab, fossil cones, etc.

The occurrence of *Trionyx* sp. had been reported (Shikama, 1954), and the site of that fossil locality is probably assignable to the present locality.

Description of the material:

Family *Paleoparadoxidae* Reinhart, 1959

Genus *Paleoparadoxia* Reinhart, 1959

*Paleoparadoxia tabatai* (Tokunaga)

1961 *Paleoparadoxia tabatai* (Tokunaga); Ijiri and Kamei: pp. 6–17, Pl. V.
1963 *Paleoparadoxia tabatai* (Tokunaga); Mitchell: pp. 192–201, Fig. 1–6.
1967 *Paleoparadoxia* sp.; Kamei: pp. 129–130, Pl. 28, Fig. 1.

The material is composed of a isolated tooth of which the root is lacking due to the destruction. It is pale brown in colour and lustrous as a whole, but partly in white colour. The apex of the tooth crown is rounded, but it is canine-like in form, curving strongly toward liguo-distal side. In spite of the form of canine-like, a crestal pit filled with cementum is observed at apical portion of the crown. In addition to this, two accessory cusps with each crestal pit can be recognized at the basal part of the crown. Associating with a form of brachyodont tooth, therefore, it seems that the present material is a molar of Desmostylid, *Paleoparadoxia*. As the number of cusp is
one, this tooth is estimated to be the first premolar.

Extending from mesial side to distal side, there is a slightly marked keel-like ridge. By this ridge, the tooth crown is divided into four sides, viz., mesial, buccal, lingual and distal sides. Mesial and buccal sides are smooth and are made from somewhat convex surfaces, while lingual and distal sides are made from concave surfaces which are crossing perpendicular to each other. Accordingly, a cross section of the tooth appears to form a kind of fan shape. The enamel is thick and smooth. At the upper half of the crown, fine and waving striations of perichyma are clearly observed, but at the lower half some coarsely plicated folds which extend vertically are observed.

At the neck of the tooth, thin and non-lustrous cementum of pale brown in colour is attached. Though the root is missed, the dentine of dark brown in colour is exposed at a fracture of the crown base. A narrow opening of the pulp cavity is observed. Based upon the state of that opening, it is possible to suppose that the root of the tooth was long and inclined abruptly toward distal side. As the occlusion has proceeded slightly at distal and buccal sides, it is probable that this tooth belongs to one of the teeth of lower jaw.

The dimensions in mm. are:

<table>
<thead>
<tr>
<th>Specification</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesio-distal length of crown</td>
<td>15.6</td>
</tr>
<tr>
<td>Linguo-buccal length of crown</td>
<td>11.1</td>
</tr>
<tr>
<td>Height of crown (buccal)</td>
<td>24.0</td>
</tr>
<tr>
<td>Height of crown (lingual)</td>
<td>22.1</td>
</tr>
<tr>
<td>The maximal length of tooth</td>
<td>31.5</td>
</tr>
</tbody>
</table>

The morphology of the present tooth is quite similar to the lower first premolar of *Paleoparadoxia tabatai* (Tokunaga) from Toki city (Ijiri and Kamei, 1961). However, the latter has one accessory cusp. Two accessory cusps of the former may be explained to be in the range of variation. As the form of the second premolar has been unknown, it is impossible to compare the present material with it. The type specimens from Sado (Tokunaga, 1938) and *C. sp.* (Arai, 1954) are represented by incisor and molar teeth. The present tooth is similar in form and size to the San Clements specimen designated as the first premolar (Mitchell, 1963), but the latter is weaker in curvature and less in the development of the accessory cusp than the present.

In summary, from the process of the occlusion, the mode of the cervical line and the number of the cusp, it seems to be reasonable that the present tooth belongs to the lower first premolar of *Paleoparadoxia tabatai* (Tokunaga).

*Method:* As the material is composed of only one single tooth material, the observation was obliged to be carried through the work depending on the polished
surface of the median longitudinal and thin section made from a part of the tooth.

The specimen is prepared for observation by polishing on the glass plate with grinding material of carborundum no. 3000 and powder of aluminium oxide water ground in the mixture of water and glycerine (1:1). After the observation under reflection microscope, the following procedures are taken. The polished surface is replicated by a thin film of Bioden R.F.A. after three minutes etching with 0.1% HCl. For the electron microscopic observation, two-stage replication method is used. After etching for about twenty seconds in 0.1% HCl, the first replica is obtained by means of a thin film of Bioden R.F.A. In vacuum evaporator, the replica is shadowed with chromium and succeedingly, is uniformly covered with carbon (second replica). The first replica is now removed by methylacetate solution.

**Results**

1. Generals:

In the median longitudinal section of the tooth, it has been observed that the micro-structures of the enamel, the dentine and the cementum are well preserved (Fig. 1; Pl. 2, fig. 1). Consequently, fine structures such as enamel rods, dentinal tubules, cementum lacunae and so on were clearly figured.

The enamel is semi-transparent and white in color. It make thick covering as a protective layer on the entire surface of the tooth crown. Next, the dentine of pale
Fig. 2. Representation of lines for measurement of enamel thickness (below) and variation of enamel thickness in the longitudinal section of the tooth (above). A, Mesial side; B, distal side; C. Area of the accessory cusps.
brown to dark brown in colour occupies the whole part of the crown. The root-cementum is partly preserved only just below the distal cervical portion of the crown. As the main part of the root is lost in the present specimen, the observation is limited to the portion stated above. Although the observation of the coronal cementum is described in the morphological description, it is hard to observe it in this longitudinal section of the tooth. A part of the dental pulp is remained in the lower half of the crown, escaping from the destruction, but it is filled with secondary deposits completely.

2. Enamel:

The thick covering of the enamel is observed over the entire surface of the dentine in the region of the crown including cusp and accessory cusps.

a. Thickness of the enamel

In the section, the thickness of the enamel was measured at intervals of 1.5 mm. along the dentinoenamel border starting from the distal cervical point of the tooth. The measurement is taken in vertical direction to tangent line touching the outer dentinal surface (Fig. 2). The thickness ranges 1–4 mm., varying from place to place. As has been shown in Fig. 2, the distribution curve of the enamel thickness is represented to have high values at the mesial apical part of cusp and at each central part of mesial and distal sides in accessory and main cusps. It is measured as thick as 2.7 mm. at the crestal portion of cusp and 3.7 mm. at the accessory cusp region. Generally, the value of the thickness is larger in distal part than in mesial part, and it is minimum, about 1 mm., at cervical part.

b. Enamel rod and interprismatic substance

The forms of the enamel rod and the interprismatic substance can be well observed. The diameter of rod is 4–5μ, and the width of substance is 1–2μ in average respectively. In cross section, the rods appear variable in shape, namely arcade, semi-circular, long elliptical, polygonal and so on. As a whole, they resemble fish scales or tile-roof appearance. (Pl. 2, fig. 3)

c. Bands of Schreger

Well developed bands of Schreger are observed throughout whole layers of the enamel (Fig. 3). In the reflected light thrown obliquely, it is observed that those are composed of more or less regular alternations of white opaque and transparent zones. Both zones seem to be responsible for each parazone and diazone of rods bundle (Pl. 1, figs. 2, 4, 5, 6). The dimensions of those bands of Schreger are shown as follows.

<table>
<thead>
<tr>
<th></th>
<th>Width at mesial part</th>
<th>Width at distal part</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parazone</td>
<td>35–45μ (65μ, 25μ)</td>
<td>45–55μ (90μ, 25μ)</td>
</tr>
<tr>
<td>Diazone</td>
<td>45–50μ (65μ, 20μ)</td>
<td>35–45μ (55μ)</td>
</tr>
<tr>
<td>a set of Bands</td>
<td>90–100μ</td>
<td>90–100μ</td>
</tr>
</tbody>
</table>
The width of bands varies in the course of passing through the enamel, and that in the distal part of the tooth is more variable than in the mesial part.

The course of bands is observed rather clearly at the medial and distal sides of the cusp in the obliquely reflected light, but it becomes obscure in the crestal part of the crown and also in the area of the accessory cusp where the Retzius lines are indistinct. In observation of the polished surface by replica, it can be observed clearly that there are some disturbance in the course of bands and those of wavy appearance. In other part, the parallel arranged bands starting from the dentioenamel junction run ascendingly to form convex arch toward the crest of the crown. Those bands reach to the outer surface of the enamel. Especially, it is characteristic that some parallel arranged bands extend occasionally in straight direction.

At the outer layer of the enamel and in the neighbourhood of the dentioenamel junction, the bands of Schreger become rather obscure and resemble the appearance of diazone (Pl. 2, fig. 6).

Bifurcation and fusion of the bands are observed frequently in the neighbourhood of the dentioenamel junction, in the distal side of the tooth and at the apical part of the cusp.

The angle between dentioenamel border and the course of the bands is $70^\circ-55^\circ$ at the mesial central part of the crown and $80^\circ-90^\circ$ at the distal central part. It is represented as approximately as $90^\circ$ at the cervical part, at the accessory cusp area and at the crest of the crown.
On the basis of the observation of the bands in the electron microscope, the distinction between the rods and the interprismatic substances is rather easy in either case of the diazone and the parazone (Pl. 3, figs. 1 and 2). The observation exhibits that the border between the rods and the substances is somewhat uneven but clear. In the parazone, the enamel rods are arranged in parallel with the intervention of the interprismatic substances. An enamel rod is composed of the aggregates of long prismatic crystals (apatite) which are arranged in parallel with or slightly oblique to their long axes. The interprismatic substances are represented by the figure of polygonal granular structure.

d. RETZIUS lines

The RETZIUS lines can be recognized by the reflection microscopic observation. A place where distinct and continuous features of those lines are exhibited is shown in Fig. 4. Those lines make some combinations of alternating colourless transparent zones and white-colored opaque zones. Such structure as has been shown are observed in the entire area of the tooth crown, but it is rather indistinct at the apical parts of the main and accessory cusps. Otherwise, it is rather more evident in the mesial part than in the distal part.

Those RETZIUS lines make an angle with the surface of the tooth crown and with the dentioenamel junction, both in less than $10^\circ$. 

Fig. 4. A sketch of the longitudinal section of the tooth showing the course of RETZIUS lines.
e. Dentioenamel junction

The dentioenamel junction is sometimes represented by wavy border, but in general, it is observed by straight and weakly curved line.

3. Dentine:
   a. Dentinal tubules

   The dentinal tubules are well preserved and are 1–1.5μ in diameter. It seems that the interior of a tubule is left in empty or with secondary fillings. In observation, they are dark brown in colour. The course of the dentinal tubules are parallel with each other and slightly curved, resembling a S in shape, starting from the pulp surface toward the periphery of the tooth crown (Pl. 3, figs. 3, 4, 5). Concerning the observation on the termination figure of the tubules lying just beneath the enamel layer, it is difficult to describe in detail due to an unfavourable condition of the present specimen, but it is infallible that over their entire lengths the tubules are figured to make straight lines without any convexity and complicated bifurcation. The angle between the course of the tubules and the surface of the dentioenamel junction is usually measured about 50–60°, but it reaches to 90° only at the crestal edge of the cusp.

   b. Matrix

   The colour of the matrix observed in any case of the living dentine is usually white to milky, but in this case, it appears to be pale brown to dark brown in colour.

   c. Calcified spherulites

   It is generally accepted that mineralization appears to take place radially from common centers within the interglobular space (Fujita, 1958, pp. 53–61; Orbán in Schier, 1966, pp. 122–123). Throughout the entire part of the present tooth crown, the distribution of those calcified spherulites in large size is observed in a band which occupies inner 0.15–0.2 mm. layer from the dentioenamel junction (Fig. 3; Pl. 3, fig. 6). The width of a band is measured as 0.1–0.3 mm., but especially in the crestal part of the tooth crown, it reaches up to about 1 mm. Moreover, a band of about 1 mm. in thickness is observed to encircle the pulp cavity.

   d. Lines of Andreasen

   By the reflection microscopic observation, the figure of numerous fine striations which are composed of alternating transparent brown band and pale brown band is revealed. The course of those striation runs in parallel and makes slightly oblique angle with the course of the dentinal tubules.

   Those striations appear to be distributed rather widely throughout whole dentinal area. However, as the present specimen escapes from Hematoxylin-Eosin staining, it is hard to define whether the striations observed here correspond with the lines of Andreasen or not.
Table 1.

<table>
<thead>
<tr>
<th></th>
<th>Demoslylus japonicus</th>
<th>Demoslylus mirabilis</th>
<th>Paleoparadoxia tabulata (TOKUNAGA) Tomikusa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thickness of enamel layer</td>
<td>10 mm</td>
<td>1-4 mm</td>
<td></td>
</tr>
<tr>
<td>Diameter of enamel rod</td>
<td>4μ±(3-5μ)</td>
<td>4-5μ</td>
<td></td>
</tr>
<tr>
<td>Breadth of interprismatic substances</td>
<td>1μ±</td>
<td>1-2μ</td>
<td></td>
</tr>
<tr>
<td>Cross section of enamel rod</td>
<td>Polygonal (Penta-hexagonal) archade form</td>
<td>Polygonal scale form</td>
<td>Polygonal, long elliptical, arched or semi-circular in form</td>
</tr>
<tr>
<td>Bands of SCHREGER</td>
<td>Throughout whole layer (faint just below the dentioenamel junction)</td>
<td>Throughout whole layer</td>
<td>Nearly throughout whole layer</td>
</tr>
<tr>
<td>Course of bands of SCHREGER</td>
<td>Weakly curved resembling a S figure</td>
<td>Wavy</td>
<td>Tortuosity appearance</td>
</tr>
<tr>
<td>Mode of interprismatic substances</td>
<td>Tortuosity appearance with definite orientation</td>
<td>Tortuosity appearance</td>
<td></td>
</tr>
<tr>
<td>Width of diazone</td>
<td>50-80μ</td>
<td>35-55μ</td>
<td></td>
</tr>
<tr>
<td>Width of parazone</td>
<td>50-80μ</td>
<td>35-55μ</td>
<td></td>
</tr>
<tr>
<td>Angle between the course of band and dentioenamel junction</td>
<td>50-65°</td>
<td>50-65°</td>
<td>55-70° (mesial) 80-90° (distal)</td>
</tr>
<tr>
<td>Diameter of dentinal tubule</td>
<td>2μ</td>
<td>1-1.5μ</td>
<td></td>
</tr>
</tbody>
</table>

4. Cementum:

The root cementum is preserved partly only at the distal cervical portion of the tooth. The cementum covers the dentine directly. It covers also more or less on the free edge of the enamel, but it does not creep upwardly to form so-called “tongue of cementum” (Pl. 3, fig. 7). The thickness of the cementum is about 0.5 mm. A half of its outer surface is white in colour, while the inner half of it is brown in colour. Both parts seem to be made from cellular cementum in which lacunae of 1 mm. in diameter are distributed sparsely throughout the whole area (Pl. 3, fig. 6). The lamellar structure is not recognized.

5. Dental pulp:

The pulp cavity is completely filled with the secondary deposits.

**Conclusion**

In regard to the histology of the teeth of *Paleoparadoxia*, IJIRI and KAMEI (1961)
pointed out that the histological characteristics of the tooth of *Paleoparadoxia* resemble to those of *Desmostylus*. They stated it very briefly without any detail description. Therefore, in this case, the present specimen is compared with the material of *Desmostylus* described in *Ijiri* (1939) and *Ijiri* and *Kamei* (1961). On the other hand, specimen is examined to compare with the results of the comparative dental history of various mammals in the works of *Kawai* (1955), *Shobusawa* (1952) and *Maejima* (1961). The histological characteristics of the present specimen in comparison with *Desmostylus* are shown in Table 1.

The marked differences in histology between the present tooth and the teeth of *Desmostylus* will be noticed in the following points, such as the thickness of the enamel, the width of a band of Schügger and the figure of the dentioenamel border and so on. On the other hand, common characteristics are given in the following points, such as the form of the enamel rod, the pattern of arrangement made by rods and interprismatic substances, the size of the enamel rod, the course and features of bands of Schügger and so on.

On the basis of the form of the enamel rod, *Shobusawa* (1952) classified the mammalian teeth into five categories, viz., Primate-, Carnivora-, Ungulate-, Rodent- and Cetacea types. In connection with this, the present specimen has the nearest relation in the form of the enamel rod to Ungulate- and Primate types, but it differs considerably from those of other types.

*Kawai* (1955) made the comparative study on the bands of Schügger of the mammalian tooth enamel, and he classified them into four categories, viz., Carnivora-, Primate-, Ungulate- and Rodent types. According to the comparison with these types, it is clear that the present specimen has the bands of Schügger of Ungulate type in the appearances of the course of bands, the angle measured between the band and the dentioenamel junction.

For the histology of the mammalian tooth dentine, *Maejima* (1961) made a comparative study. In his work, the angles measured between the course of the dentinal tubules and the surface of the dentinal layer have been measured at ligual and labial sides of the tooth. Therefore, those measurements are inadequate to compare in the case of the present specimen. Notwithstanding of such objection, the value indicated as 50-60° of the present specimen suggests that value of *Paleoparadoxia* is rather nearer to those of Artiodactylian or Perisodactylian group of low angle more than to those of Rodent-Primate-Carnivora group of high angle.

Based upon a histological study of *Desmostylus japonicus* *Tokunaga* and *Iwasaki* from Togari, *Ijiri* (1939) pointed out the inadequacy against the opinion that for *Desmostylus* a new taxonomical position is to be given. According to him, *Desmostylus* may belong to a group of Ungulate apart from subungulata. *Ijiri* and *Kamei* (1961) have discussed about the taxonomical position of *Desmostylus mirabilis* *Nagao* of
Sakhalin. In the paper, they suggested from the oral histology together with comparative anatomy of the skull that both of *Desmostylus* and *Paleoparadoxia* have close relation to Perisodactylia.

As a conclusion of the present study, it is possible to say that the histological characteristics of the Tomikusa specimen suggests the similarity between *Paleoparadoxia* and Ungulates. And also, those characteristics are common in *Desmostylus*. However, in order to clarify the clean-cut distinction in the oral histology between *Paleoparadoxia* and *Desmostylus*, it is necessary to study in many respects more detail.

References


KAMEI, T. (1967): A Note on a fossil premolar of *Paleoparadoxia*, in “Fossils of Anan-chō”, Committee of Education, Anan-chō, Nagano Pref., pp. 129-130, pl. 27, Fig. 1. (in Japanese)


A Histological Study on a Tooth of *Paleoparadoxia*.

**Explanation of Plates**

**Plate 2.**

*Paleoparadoxia tabatai* (Tokunaga)

1. Median longitudinal section of a tooth, ×3.5.
2. Photomicrograph of enamel showing the bands of Schreger, ×125, crossed nicols.
3. Photomicrograph of the enamel rods in cross section, ×800.
4. Photomicrograph of the bands of Schreger in reflected light (mesial side), ×17.5.
5. Photomicrograph of the bands of Schreger in replica image (distal side), ×16.
6. Photomicrograph of the bands of Schreger in the neighbourhood of the dentioenamel junction in replica image, ×95.

**Plate 3.**

*Paleoparadoxia tabatai* (Tokunaga)

1. Electron microscopic photomicrograph of the diazone in the enamel layer, ×4000.
2. Electron microscopic photomicrograph of the parazone in the enamel layer, ×4000.
3. Photomicrograph of the dentine showing the course of the dentinal tubules in reflected light, ×21.
4. Electron microscopic photomicrograph of the dentine showing the dentinal tubules and the matrix, ×4000.
5. Photomicrograph of the dentine in replica image, ×240.
6. Photomicrograph of calcified large spherulites of the dentine in replica image, ×760.
7. Photomicrograph of the cementum (right in the figure) in reflected light, ×25.
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Kobayashi & Kamei: A Tooth of *Paleoparadoxia*