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[Original Article]

Histological study of the enamel band from a Miocene proboscidean incisor

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Abstract

An extinct proboscidean incisor (INM-4-013796: Kitashiogo C specimen, Ibaraki Nature Museum) was discovered in Miocene sediment near Hitachiomiya City, Ibaraki Prefecture, Japan in 1978. A narrow enamel band extended along the lateral surface of the incisor. The incisor enamel of living elephants is difficult to study because it is lost early after the eruption, and histological reports of fossil proboscidean incisors are rare. As for cementum, there have been reported many studies of coronal cementum on molars, but few studies of cementum covering incisors. In this study, we report on the fungiform cross-sectional morphology of the enamel band of the incisor, including the irregular Hunter-Schreger band and the arcaded to keyhole type enamel prism. We then reveal the presence of the cementum covering the enamel band and describe the histology of the cellular cementum. And the cementoenamel junction is analyzed to indicate different patterns of smoothness and limited resorption. Although this incisor may belonged to a *Stegolophodon* sp. because of the estimated location and the similar proboscidean fossils excavated in the vicinity, it should be prudent to identify its classification from a histological point of view until it is compared with a confirmed specimen.

Key words: Enamel band, Proboscidean incisor, Miocene proboscidea

Introduction

In 1978, a proboscidean incisor lacking both ends was discovered in Miocene sediment near Hitachiomiya City, Ibaraki Prefecture, Japan and the geological background of this specimen has been investigated. A grayish-white narrow band stretched along almost the entire length of the lateral surface of the incisor. This band was proved to be made of enamel and was identified as an "enamel band". We had the opportunity to examine this enamel band for a histological study. Since enamel is lost early in the eruption of incisors in living Asian and African elephants (Miller 1890), it is difficult to research it, so a few studies of incisor enamel in fossil proboscideans were available for comparison. While Ferretti (2008) has described the presence of thin cementum in some parts of the enamel band found in a *Cuvieronius hyodon* specimen, little information is available regarding the coronal cementum of proboscidean incisors compared to molars. In this study, we evaluated the cross-sectional morphology of this enamel band, the Hunter–Schreger band (HSB), and the morphology of the enamel prisms. Moreover, this study sought to

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find the presence of coronal cementum covering the enamel band and investigated the histology of the cementum and the cementoenamel junction (CEJ).

Materials and Methods

The Kitashiogo specimen C (Ibaraki Nature Museum: INM-4-013796) was part of a cylindrical maxillary proboscidean left incisor lacking both proximal and distal parts. This specimen was excavated from the vicinity of Kitashiogo, Hitachiomiya City, Ibaraki Prefecture, Japan. Miocene sediments such as the Kuninaga Formation, Ogaino Formation, Sakuramoto Formation, and Tamagawa Formation were distributed in this area (Fig. 1). The horizon of the specimen could not be determined precisely because the landscape at the time of its discovery was currently changing.

The experimental sample was collected at a thickness of approximately 5 mm from a cut mark placed around the specimen during excavation. The examined parts, including the grayish band structure, were cut out and treated as tissue samples. These samples were cut into tangential, horizontal, and vertical sections for scanning electron microscope (SEM). Each block was then embedded in polyester resin, polished by diamond paste (particles: 3 to 1/4 μm in diameter), and etched with 1/20 N HCl for 20 s. The samples were then sputter-coated with gold-palladium (Eiko: IB-3) and observed using an optical stereomicroscope (Olympus: SZ) and SEM (Hitachi: S2700, S3400N). By using a reflected light microscope (Zeiss: Stemi 305) for the SEM sample, bands with different inclination of the HSB were exposed effectively.

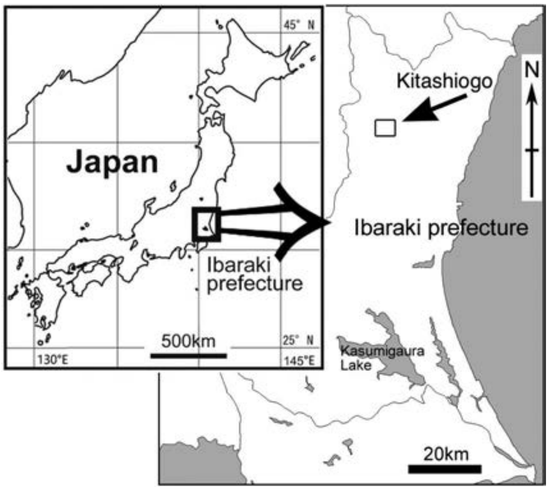

Fig. 1. Map showing the locality of the specimen (Kitashiogo C specimen). Topographical map "Hitachiomiya", 1:50,000 in scale by the Geographical Survey Institute of Japan.

Results

1. General findings

The cylindrical specimen colored with dark brown was approximately 109 mm length and a cross section with a major axis of 64 mm and a minor axis of 52 mm. The specimen exhibited a slightly inflated round shape on one side and a blunt edge on the other (Fig. 2, right, left). Grayish-white to grayish-brown enamel ran almost along the long axis on the side and

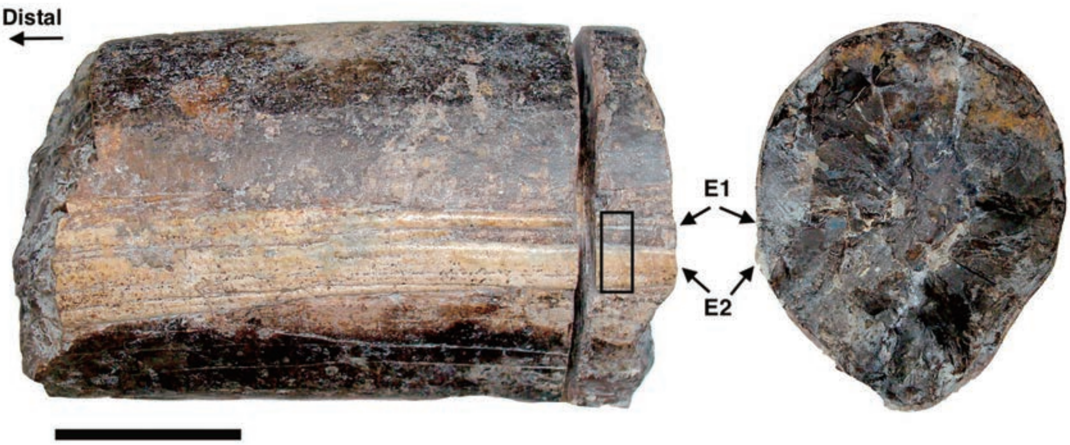

Fig. 2. Kitashiogo C specimen: (Ibaraki Nature Museum: INM-4-013796).
Lateral (left) and mesial (right) view. E1: enamel band (narrow), E2: enamel band (wide).
Box: area of Fig.3 (cementum sandwiched between two bands of the enamel). Scale bar: 30 mm

fine ridges were observed on the surface. The enamel width was not uniform, narrowing slightly toward the proximal region, and the ridges were interrupted in some places (Fig. 2, left). Almost the entire circumference of the specimen was covered with bright cementum of 1–2 mm thickness, and the central part of the specimen was filled with dark-brown to grayish-brown dentin and the pulp cavity did not exist (Fig. 2, right). In the cross section of the observation sample, the enamel was divided into two parts: wide part of the enamel was 6.8 mm in width and narrow part of the enamel was 1.5 mm in width. The surface of the wide part was smooth, but the surface of the narrow part was dotted with colored fillers in shallow pits of variable size and shape (Fig. 3, E1, E2). The cementum interposed between them was about 2.8 mm in width and covered with grayish-white or dark-brown deposits, and was in contact with enamel on both sides (Fig. 3, C). The transvers sections of the two parts of the enamel were both fungiform in shape, and both ends of the pileus (like an open umbrella) extended outward and embedded in the cementum (Fig. 4). In the center of the wide part of the enamel which was about 2 mm in thickness, about 0.3 mm of the surface layer was milky white and the underlayer was grayish-white (Fig. 4, E2), while the narrow part which was about 1.2 mm in thickness was grayish-white as a whole (Fig. 4, E1).

The dentinoenamel junction (DEJ) exhibited a small degree of ruggedness in both parts, and bundles of enamel prism penetrated almost linearly throughout the grayish-white enamel layer from DEJ (Fig. 4). The dentin that occupied most of the incisors was dark-brown to brown beneath the DEJ (Figs. 2, 4).

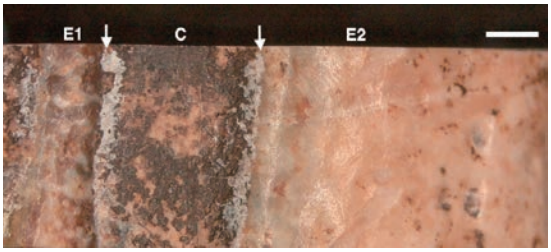

Fig. 3. Surface of the enamel band.
C: cementum, E1: enamel (narrow), E2: enamel (wide).
Arrows: CEJ. Scale bar: 1 mm

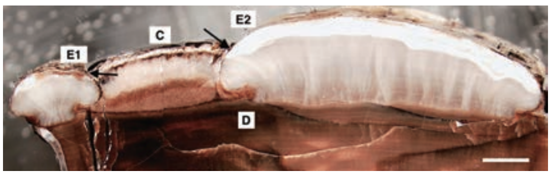

Fig. 4. Transverse section of the enamel bands.
C: cementum, D: dentin, E1: enamel (narrow),
E2: enamel (wide). Arrows: CEJ. Scale bar: 1 mm

The cementum sandwiched between the two parts of the enamel was similar to the cementum covering the entire surface of the specimen. The upper 2/3 of the cementum was brownish milky-white, and irregular dark-brown streaks were observed in the outermost layer. The lower 1/3 of the cementum exhibited a rough brown area (Figs. 4, 8①).

2. Results of reflected light microscopy

The transverse section of dentin possessed a lattice structure (Schreger pattern), which exhibited a clear checkered pattern, with a Schreger angle (pulp side) of 99° to 122° (average 113°) and a wavelength width of 1 mm or less (Fig. 5①).

The reflection micrographs of the SEM samples revealed intertwined and branched enamel prism bundles in 3/4 of the inner layers. However, there was a nearly homogeneous structure in about 1/4 of the surface layer in both the transverse (Fig. 5②) and longitudinal (Fig. 5③) sections. In the tangential section, circular and grooved structures filled with cementum were observed on the enamel surface (Fig. 5④). Enlargement of the enamel surface with an angled light revealed irregular and complex striae of enamel prisms (Fig. 5⑤).

3. Results of SEM

The dentinal tubules were clearly visible, and the vestiges of dentinal fiber were observed in some of the tubules. The peritubular dentin was poorly developed. In addition, small round granules were observed to be scattered within the sections (Fig. 5⑥). In the cementum, thick fibrous structures and cementum corpuscles were observed in the matrix (Fig. 6①).

In the transverse section of the surface enamel in the wideband, a layer composed of aprismatic enamel or nearly aprismatic enamel was distributed about 100 μm with an irregular border, followed by rough enamel with prominent prism sheaths and striations about 150–200 μm in thickness. The normal enamel which occupied the lower layer exhibited enamel prisms that advanced radially (Fig. 6②). A similar layered structure was observed in the tangential section at the contact surface with the cementum penetrating the enamel. Cross-sections of the enamel prisms adjacent to the

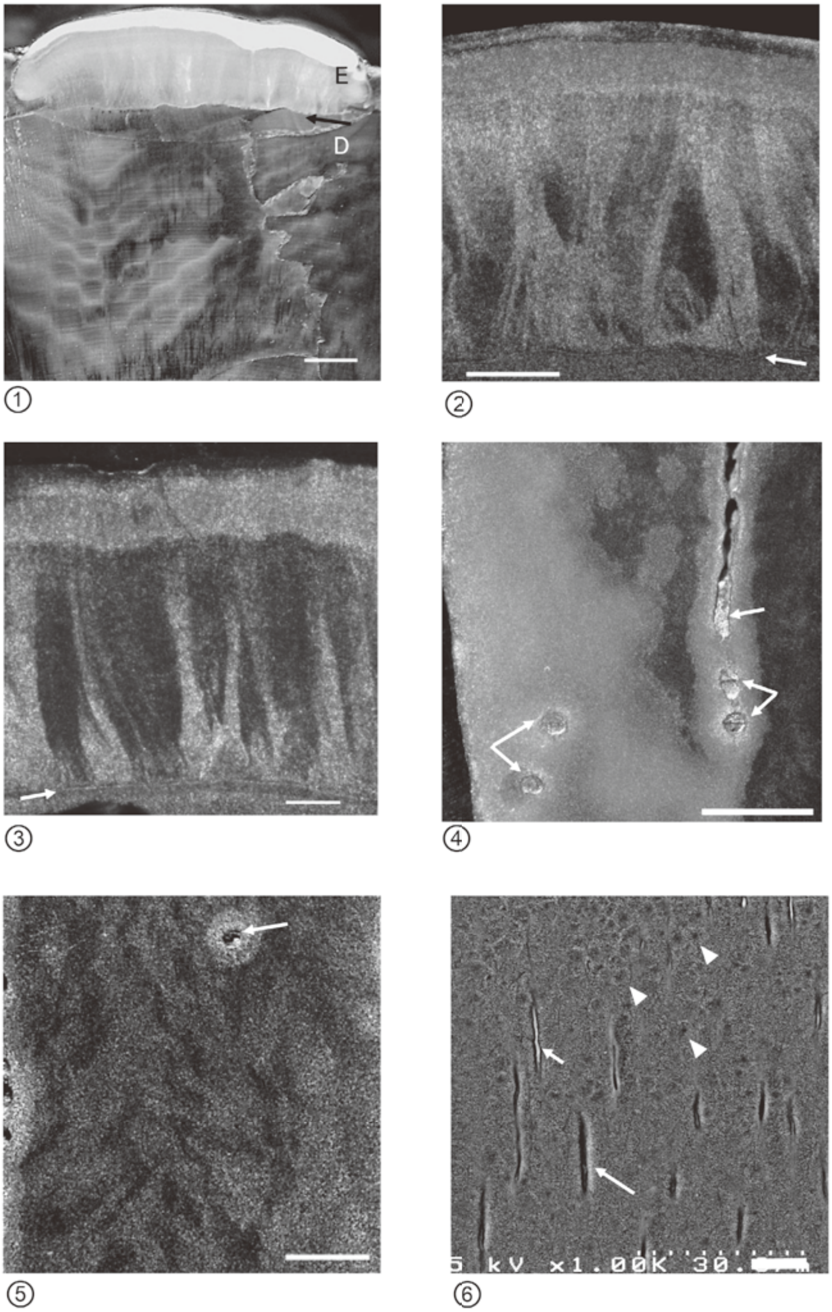

Fig. 5. (①-⑤: Reflected light microscopy, ⑥: SEM image)

①. Transverse section of the incisor at the wide enamel band (E2). Polished dentin shows the Schreger pattern (lattice pattern). D: dentin, E: enamel, Arrow: DEJ. Scale bar: 1 mm

②. Transverse section of enamel. Irregular Hunter-Schreger band (HSB) occupied 3/4 of the enamel and the superficial 1/4 was homogeneous area. Arrow: DEJ. Scale bar: 0.5 mm

③. Longitudinal section of enamel. Irregular Hunter-Schreger band (HSB) occupied 3/4 of the enamel and the superficial 1/4 was homogeneous area. Arrow: DEJ. Scale bar: 0.5 mm

④. Tangential section of enamel. Circular or grooved indentations filled with cementum. Scale bar: 0.5 mm

⑤. Tangential section. Irregular HSB and a circular indentation filled with cementum (Arrow). Scale bar: 0.5 mm

⑥. Dentinal tubule (Long arrow) and dentinal fiber (Short arrow). Arrowhead: patchy area. Scale bar: 10 μm

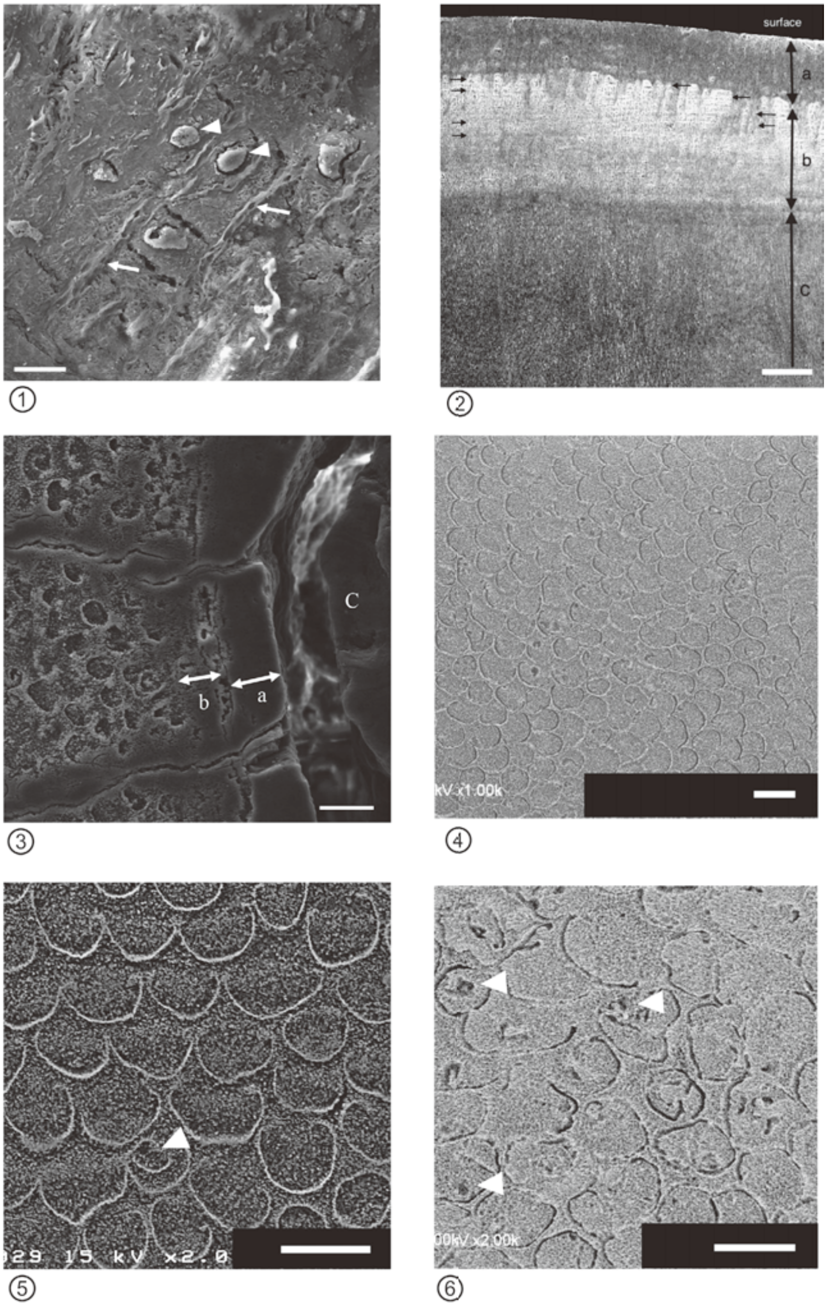

Fig. 6. (SEM image)

①. Cementum corpuscules (Arrowheads) with coarse fibers (Arrows) in the matrix. Scale bar: 10 μm

②. The transverse section. Aprismatic enamel (a), followed by rough enamel layer (b), and normal enamel (c) in the surface layer. Small arrow: incremental line. Scale bar: 100 μm

③. Tangential section at the hole area where cementum penetrating into enamel. Aprismatic enamel (a), followed by rough enamel layer (b) . Note irregular or nearly circular enamel prisms followed. C: cementum. Scale bar: 10 μm

④. Tangential section. Round and arcaded formed enamel prisms. Scale bar: 10 μm

⑤. Enlarged image of Arcade shaped enamel prisms in tangential section. An enamel prism inserted into another prism (Arrowhead). Scale bar: 10 μm

⑥. Tangential section. Enamel prisms intermingled with irregular shapes and various sizes of cross-sectional shapes. Note pits and holes (Arrowheads) in the enamel prisms. Scale bar: 10 μm rough enamel showed irregular or nearly circular shapes surrounded by wide interprismatic substances (Fig. 6③). At the tangential surfaces in the middle layer of the enamel, round to arcaded formed enamel prisms with a diameter of 5–10 μm were observed. However, the enamel prisms were not arranged regularly (Fig. 6④). Even in the regions where the arcaded forms were aligned, the boundary between the enamel prisms was unclear. In some cases, an enamel prism inserted into another prism was observed (Fig. 6⑤). In the regions where the arrangement of the enamel prisms had changed, there were pits and holes in the enamel prisms, and irregular shapes and sizes of the enamel prisms were observed (Fig. 6⑥). In the transverse section, from the DEJ to approximately 30 μm, the enamel was aprismatic with indistinct or invisible borders (Fig. 7①). The arcaded formed enamel prisms were observed in the middle layer, and irregular shapes were seen in the areas where the direction of the HSB had changed (Fig. 7②). By expanding the boundary between the diazone (which is composed of cross-sectioned enamel prisms) and the parazone (which is composed of longitudinally sectioned enamel prisms) of HSB, a coalescence of the enamel prisms and remarkable deformations were observed (Fig. 7③). Similar morphological changes were observed in the longitudinal sections at the boundary of the zones with different directions of HSB. Coalescence of the enamel prisms and small holes were observed (Fig. 7④). When the enamel prisms with small holes were enlarged, that the pores were not only circular but also intricate shapes (Fig. 7④ box). Even in regions where the cross-sectional shaped enamel prism dominated, the enamel prisms coalesced, and the double arcaded form was often visible (Fig. 7⑤). In some regions, keyhole and keyhole-like shaped enamel prisms were observed (Fig. 7⑥).

4. Findings of CEJ

The cross section of the enamel band showed a fungiform shape, and cementum covered the side of the pileus and further penetrated the lower part of the pileus and contacted the sides of the stipe (Fig. 8①). The cementum contained numerous cementum lacunae (Fig. 8②). The CEJ was smooth from the side of the enamel to under the surface of the pileus, while the portion contacting the stipe formed an uneven boundary (Fig. 8②). The underpart of the pileus had a smooth edge with converging enamel prisms, but the stipe had a rugged surface (Fig. 8③). The CEJ exhibited an uneven border in the middle part of the stipe. Dissolution of the enamel prisms was also observed (Fig. 8④ box). The enamel and cementum had a smooth contact surface with the dentin, but the boundary between the enamel and cementum had an irregular shape. In some regions, thin aprismatic enamel formed a layer adjacent to the DEJ, and almost circular prism surrounded by thick interprismatic substance were observed above it (Fig. 8⑤). Enamel was caved in and replaced by cementum in a portion of the DEJ (Fig. 8⑥).

Discussion

The Kitashiogo C specimen is part of a left maxillary proboscidean incisor , which has lost both ends, with belted tissue on the outside. The grayish-white band running along most of the long axis was recognized as an “enamel band”, which was present on the lateral surface of the permanent incisors (Shoshani and Tassy 1997). External shape, form of a cross-section and the differences in the diameter of enamel band were compared with the incisors of the following *Stegolophodon* (*Eostegodon*) *pseudolatidens* (Yabe 1950) and *Stegolophodon tsudai* (Shikama and Kirii 1956), the incisors of *Stegolophodon cautleyi progressus* (Osborn 1929, 1942), and the Miocene incisors of Thailand (*Gomphoterium* sp.: Ducrocq 1994, *Gomphoterium* cf. *browni*: Chavasseau et al. 2008). This specimen has a feature that the eminence of the edge of the lower surface is weak and the cross-sectional form is close to circular. The enamel band of this incisor is characterized by narrower, and bifurcation proximally (Fig. 2).

Most of this incisor was comprised of dentin, which contacted the enamel band at an almost smooth dentinoenamel junction (DEJ). The Schreger (lattice) pattern observed in the transverse section of the incisor dentin is used to discern a living elephant and a mammoth (Ishibashi et al. 1998). This specimen was a type C with a clear checkered pattern and a Schreger angle (pulp side) of 99° to 122° (average 113°) and a wavelength width of 1 mm or less. Therefore, this specimen appears to be similar to a *Mastodon* (Teapani and Fisher 2003). However, the position of the remaining parts is insufficient for definite identification. Histological findings showed a little branching in the dentinal tubule, and small patchy circles with indistinct boundaries that may indicate inequable calcification but are too small for a

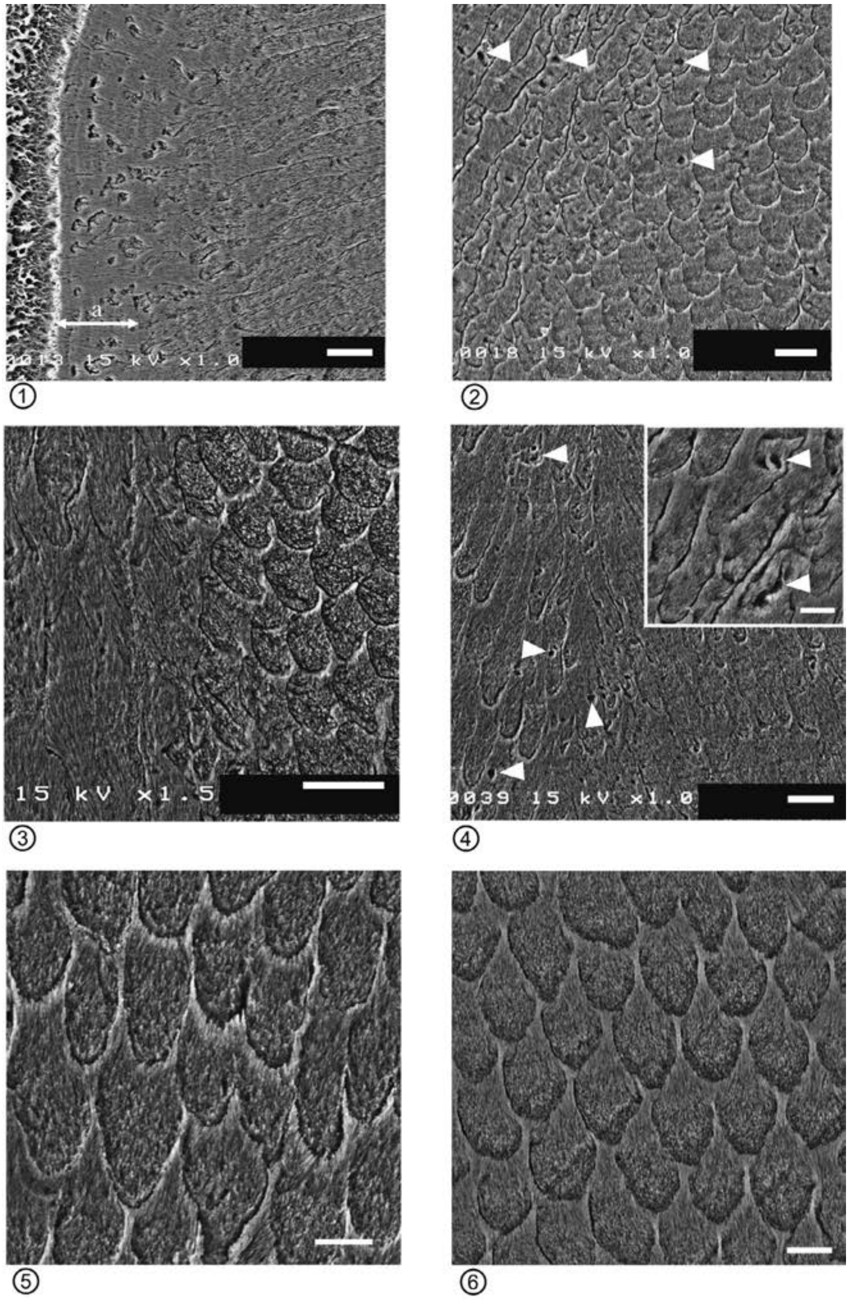

Fig. 7. (SEM image)

①. DEJ at the transverse section. a: aprismatic enamel area and invisible borders of the enamel prisms. Scale bar: 10 μm

②. Crossing area between vertical and horizontal bands of HSB in the middle layer of transverse section. Holes showed by arrowheads imply tubular enamel. Arcaded type enamel prism dominants in the horizontal band. Scale bar: 10 μm

③. Extension of crossing area between diazone and parazone of HSB in the transverse section. Remarkable deformations of the prisms. Scale bar: 10 μm

④. Boundary area of the zones with different directions of HSB in the longitudinal section. Note the small holes in the enamel prisms (Arrowheads). Scale bar: 10 μm. Box: Enlarged view of the enamel prisms. Note that the pores were not only circular but also in various shapes (Arrowheads). Scale bar: 5 μm.

⑤. Enamel prisms in the longitudinal section. Coalesced and/or double arcaded form of the enamel prisms. Scale bar: 5 μm

⑥. Keyhole and keyhole-like shaped enamel prisms in the transverse section. Scale bar: 5 μm

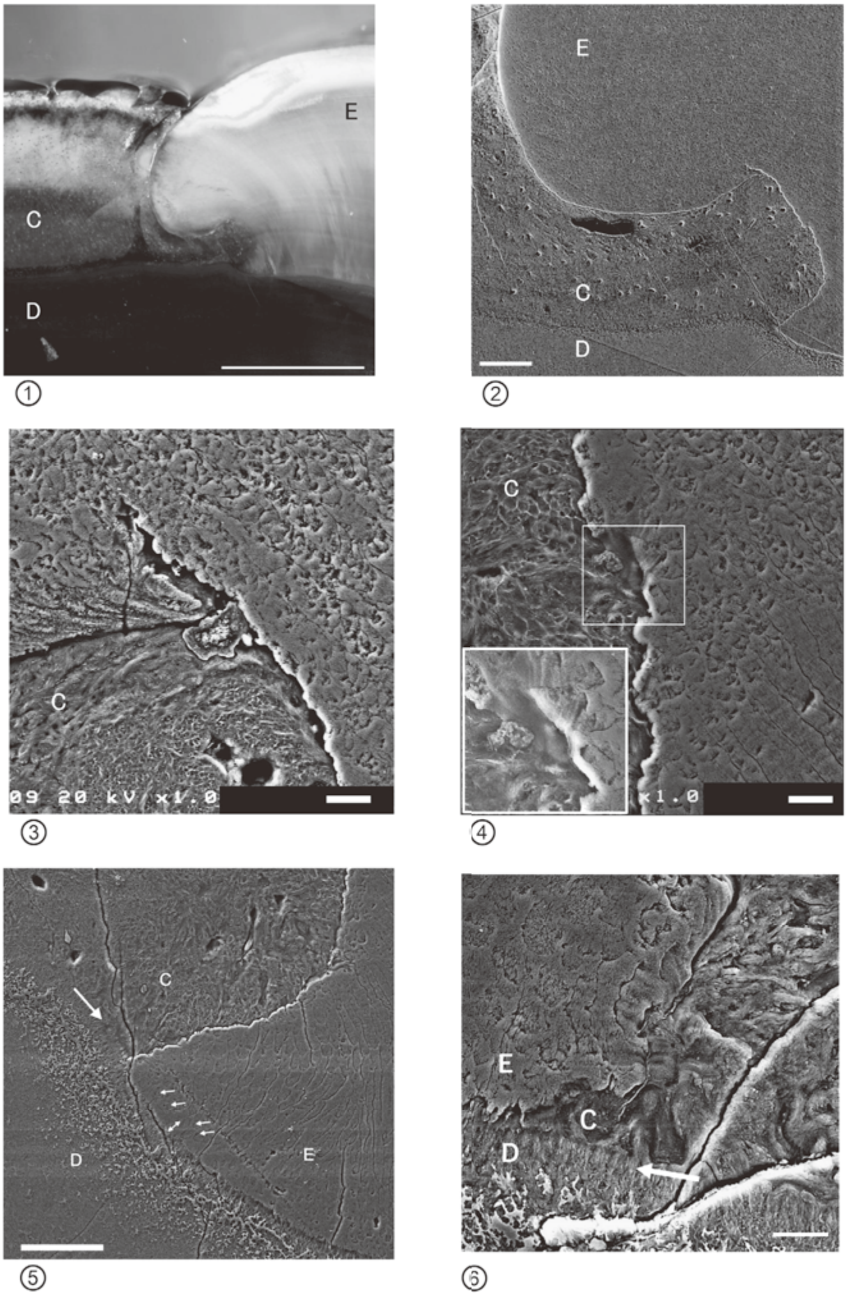

Fig. 8. (①: Reflected light microscopy, ②-⑥: SEM image)

①. Transverse section of the enamel band. C: cementum. D: dentin. E: enaml (E2). Scale bar: 1 mm

②. Enlargement of the base of the enamel band. Note the smooth borders of the pileus of fungiform and numerous lacunae in the cementum. C: cementum. D: dentin. E: enamel. Scale bar: 100 μm

③. The undersurface of the pileus and the upper part of the stipe of the fungiform enamel band. C: cementum. Scale bar: 10 μm

④. Middle part of the stipe of the fungiform. Uneven border of CEJ. Box: dissolution of enamel prisms. C: cementum. Scale bar: 10 μm

⑤. CEJ and DCJ. Arrow: DCJ. Small arrow: circular prism surrounded by the thick interprismatic substances. Double-headed arrow: aprismatic enamel. C: cementum. D: dentin. E: enamel. Scale bar: 50 μm

⑥. Collapse of enamel at the DEJ and replacement of cementum. Dissolution of enamel prisms and fibrous processes can be seen. Arrow: DCJ. C: cementum. D: dentin. E: enamel. Scale bar: 10 μm calcospherite. (Fig. 5⑥).

The fungiform cross-sectional shape of the enamel band has not yet been reported and suggests a complex histogenesis between enamel and cementum. The HSB exhibits characteristic decussation because of irregular width and direction in the 3/4 of the enamel layer, and radial direction in the surface 1/4 of the enamel (Fig. 5②, ③). A similar irregular HSB pattern was observed previously in the enamel of fossil proboscidean incisors (*Gomphotherium angustidens*, *Mastodon* sp.: Kozawa and Kamiya 1991; *Cuvieronius hyodon*: Ferretti 2008). Although the milky-white zone on the surface layer approximately 0.3 mm thick in the middle area of the wide band is divided into aprismatic enamel and rough enamel (likely etched recesses), the continuous incremental lines indicate that the enamel layers have undergone normal development (Fig. 6②). The fact that a similar layered structure was observed in the tangential section of the cementum-filled hole indicates that the sidewall of this hole is continuous with the superficial enamel layer and not formed by absorption (Figs. 5④, 6③). The structural organization of enamel (schmelzmuster) (Koenigswald et al. 1993; Koenigswald and Sander 1997) of this incisor is categorized as a type of 3DE-RE when applies to Ferrette's (2008) classification of proboscidean enamel, but a thin layer of aprismatic enamel is present close to DEJ and enamel surface (Abbreviations. 3DE: enamel type with irregular decussation. RE: enamel type of radial prisms).

The cross-section morphology of the enamel prisms was variable in size and shape, particularly at the conversional region of the diazone and parazone of HSB. There might be an alteration of morphology due to the fusion of the enamel prisms and pressure at the boundaries during amelogenesis. In the middle layer of enamel, the arcaded type to keyhole type dominated (Fig. 7⑤, ⑥), whereas the upper region of the middle layer tended to have a circular or vortex shape with a large opening and weak continuity of the prism sheath. There were small holes in some of the prisms in many areas of enamel (Fig. 6⑥, 7②, ④). Although dentin fibers could not be identified in the pores, a possibility of tubular enamel is considered.

As for the enamel prism of proboscidean incisor, Kamiya (1985) and Kozawa and Kamiya (1991) reported arcaded to keyhole type enamel prisms for *Gomphotherium angustidens* and *Mastodon andium*. Moreover, Ferretti (2008) reported keyhole and arcaded types dominant in *Cuvieronius hyodon* of the Gomphotheriidae. The keyhole type prism has also been observed in a deciduous incisor (15mm in diameter and 0.7mm thickness, presumed cap enamel) from *Elephas maximus* (Kozawa 1982; Kozawa and Kamiya 1991).

A keyhole-shaped enamel prism was considered "primate-type" by Shobusawa (1952) and classified as a "pattern 3B" by Boyde (1965). This type has been reported in the Miocene hominid primates (Gantt et al. 1977; Vrba and Grain 1978), as well as Taeniodonta (Koenigswald et al. 2010) in North America, *Pyrotherium* molars (Fortelius 1985; Koenigswald et al. 2015; Hirayama and Suzuki 2020) in South America, and Eocene proboscideans from Morocco (Tabuce et al. 2007). The keyhole type prism is, therefore, distributed in different groups of mammals, with a disjunctive phylogenetic relationship. In comparison with molar enamel, the cross-section of the keyhole to ginkgo-leaf type enamel prism was reported in the molar of a *Stegolophodon pseudolatidens* discovered from Miocene sediment (Asakawa Formation) in the same region (Kitashiogo, Hitachiomiya City, Ibaraki Prefecture) as this specimen (Kamei and Kamiya 1981: Locality was described as Kitashioko, but the correct place name is Kitashiogo.) (Fig. 9).

The surface of this specimen is surrounded by a 1-2 mm thick layer of cementum, and the cavities and pores in the exposed enamel surface are also filled with cementum (Fig. 3). The cementum presumably covered the entire enamel band. This layer corresponds to "coronal cementum", which covers the periphery of the molar crown. The coronal cementum of the molars from living elephants has been studied for long time (Kawai 1955; Muraki 1958), and has been reported in the fossil proboscideans (Kobayashi, 1985; Kozawa and Kamiya 1985; Kobayashi et al. 1991; Ferretti 2003; Kamiya 2005; Hirayama and Suzuki 2020). However, enamel was rarely observed in (permanent) incisors in living elephants (Miller 1890). Thus, reports of coronal cementum covering enamel were limited to the deciduous incisors of the *Elephas maximus* (Kozawa 1982; Kozawa and Kamiya 1991). It was uncertain whether cementum covered the enamel in the *Gomphotherium* enamel band described by Fox (2000). Ferretti (2008) mentioned the presence of a thin cementum in some places of the enamel band of *Cuvieronius hyodon*, but did not give a specific description. The cementum of this specimen also exhibited cellular mixed fiber cementum, and thick

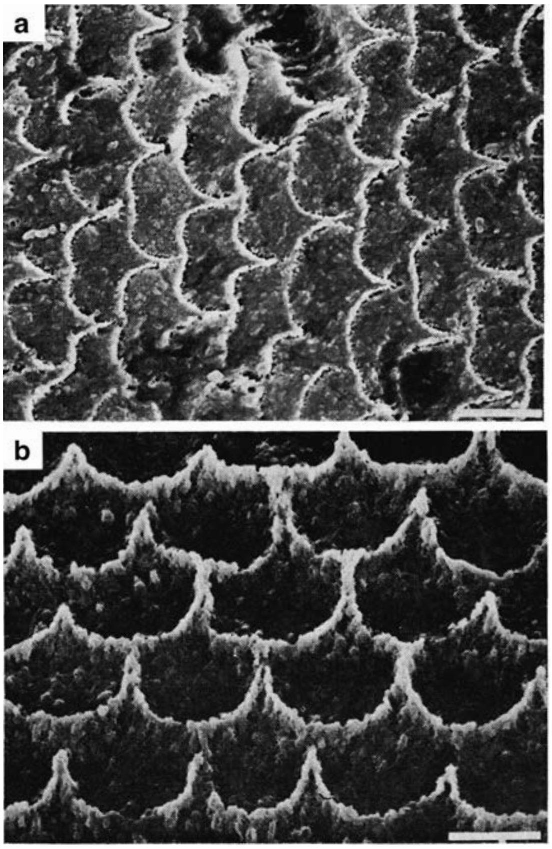

Fig. 9. SEM images of enamel prisms of molar of *Stegolophodon pseudolatidens* (Miocene, Kitashiogo, Ibaraki Prefecture, Japan).
a: The ginkgo-leaf shaped transverse section of the enamel prism. From Kamei and Kamiya (1981, Pl.2, Fig.4).
b: The keyhole shaped transverse section of the enamel prism. From Kamei and Kamiya (1981, Pl.2, Fig.5).
Scale bar in the figs.: 5 μm.

extrinsic fibers lacking the central portion (Fig. 6①) correspond to Sharpey's fiber derived from the periodontal ligament (Nanci 2013). This might be related to the formation rate and functional maintenance in continuously growing incisors.

From the lateral surface of the pileus (umbrella-like feature) of the fungiform enamel band (Fig. 8①) to the undersurface of the pileus, the enamel was complete in structure, and the enamel prisms converged at the base of the pileus. (Fig. 8②, ③). The enamel shows normal development and no resorption to create this form. In the lateral part of the stipe, an uneven boundary and dissolution of the enamel prisms were seen. However, resorption was not clearly identified in the CEJ (Fig. 8③, ④, ⑤). In the meantime, a part of the enamel collapsed and was replaced with cementum in the DEJ at the base of the stipe (Fig. 8⑥). Unlike the coronal cementum of elephant molars, the enamel resorption was very restricted at the CEJ of this incisor specimen.

In the proboscidean tooth, the dentin of rootless incisor became huge while the enamel significantly degenerated and reduced. In this specimen, the enamel band extended in the proximal direction and gradually narrowed, and its proximal end was reduced to almost half the width of the distal end. Presumably, the enamel separated along the long axis running through the grooves and striae, and the cementum filled the gaps. The enamel bands gradually decreased and disappeared into thin ridges toward the proximal end (Figs. 2, 3, 4). In the cross section of the enamel band, the enamel prisms extended outward from the DEJ during amelogenesis and cementum entered to complete the fungiform morphology (Figs. 4, 8①, ②). However, the developmental relationship between enamel and cementum has not yet been elucidated.

Miocene sediment was widely distributed in the vicinity of the Kitashiogo C site, where the studied proboscidean fossils were found. Kitashiogo A specimens as left upper Dp4 and Kitashiogo B specimens as left upper M1 of *Stegolophodon pseudolatidens* were also reported from Hitachiomiya City (Kamei and Kamiya 1981). The Katsura specimen of the left mandible of a *Stegolophodon* sp., in which 3 molars were implanted, was reported from Shiosato Town, in Higashiibaraki County (Koda et al. 2003). These specimens were presumed to be derived from the Asakawa Formation (middle Miocene). Moreover, new cranial specimens of *Stegolophodon pseudolatidens* (INM-4-013853, Ibaraki Nature Museum) with almost perfect incisors with enamel bands were discovered in 2011 at the lower part of the Tamagawa Formation (Miocene, about 16.6 Ma) in Hitachiomiya City (Koda et al. 2018).

Although the Kitashiogo C specimen may belong to a *Stegolophodon* sp. because of the estimated location and the similar proboscidean fossils excavated in the vicinity, it should be prudent to identify its classification from a histological point of view until it is compared with a confirmed specimen. Since histological studies of proboscidean incisors are rare, we hope that this examination of the enamel band will complement previous studies of other proboscidean incisors from the Miocene epoch in Japan, including those of *Stegolophodon*

(*Eostegodon*) *pseudolatidens* (Yabe 1950), *Stegolophodon tsudai* (Shikama and Kirii 1956) and *Gomphotherium anectens* (mandibular incisor: Makiyama 1838), and our understanding of proboscidean evolution.

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