蜥臀目霸王龙及有鳞目沧龙牙齿
组织的微细结构

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本文是利用扫描电子显微镜对龙骨恐龙 tyrannosaurid 与海蜥蜴沧 mosasaourid 牙齿结构进行的比较解剖学研究。化石采自加拿大 Red Deer River Valley 上白垩统 Horse-shoe Canyon 组。研究过程中，通过研究地层中出现的生物化石，特别是动物牙齿的组织结构，可以了解动物适应生活环境而发生的进化过程。也可以推测它们的系统发育关系。

tyrannosaurid 与 mosasaourid 都拥有锥状的同形齿，牙齿侧扁平，且略有后曲。研究结果确认了 tyrannosaurid 的牙齿是具有黄柱状与柱状的齿质 (prismatic enamel) 与齿质的棱面而造成许多的凹凸构造。此螺纹状构造沿着牙齿的前缘，由牙齿的顶端分布至基部，因此 tyrannosaurid 的牙齿呈现着锐利的切缘；在这些凹凸状切缘的沟与小窝的深部可观察到有机物的沉积。但是类似的螺纹状构造能在在齿冠呈锥状的 mosasaourid 牙齿的基部附近观察到。我们以扫描电子显微镜(SEM) 检索，确认两性行类的齿质皆属于中间型的真性齿质(intermediate type orthodentine)；所谓 orthodentine 即是细管齿质(tubular dentine)。tyrannosaurid 的真性齿质的齿质小管只在齿质－釉质相接 (dentine－enamel junction) 附近散布出现性的分布于齿质。但 mosasaourid 的真性齿质的齿质小管，在齿质的中间层与基质中，呈现着由复杂的侧槽与联络枝条形成的网状构造。微细构造的观察显示，这两种齿型行类的真性齿质皆只有少数的齿质小管侵入其基质；并且管周齿质(peritubular dentine) 皆不甚发达，在非薄的非柱状质之下，都可观察到形态相似的球间齿质(interglobular dentine interglobular area) 的分布。本研究以牙齿组织的比较解剖学(comparative odontology) 的观点，讨论了鳞龙下纲与龙骨龙下纲爬行类牙齿组织的异同点，并推测牙齿组织的进化与生物进化的相互关系。

关键词 加拿大 白垩纪 霸王龙科 沧龙科 牙齿显微结构

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FINE STRUCTURE OF DENTAL TISSUES IN TEETH OF SAURISCHIAN TYRANNOSAURID AND SQUAMATE MOSASAURID

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Abstract  Teeth of saurischian tyrannosaurid and squamate mosasaurid are studied mainly by scanning electron microscopy. The teeth of both diapsids are conical-shaped homodontic teeth mediolaterally compressed and curved posteriorly. The sharp cutting edges at both anterior and posterior aspects of tyrannosaurid tooth are serrated with invagination of a quite thin prismatic enamel layer. Fissures and pits of the invaginations are packed with what is possibly a layer of laminarized organic substance.

In contrast, similar serrated cutting edges are only observed at the basal portion of lepidosaurian mosasaurid teeth. The present scanning electron microscopy (SEM) observes a similar intermediate type odontoblast (tabular dentine) with ill-developed peri-tubular dentine of both extinct reptiles. SEM reveals that dentinal tubules are regularly branched only in the vicinity of the flat dentino–enamel junction in tyrannosaurid tabular dentine, but are complicatedly branched in the mid– and superficial–layer of mosasaurid dentine. The present study also shows a few dentinal tubules invaded the enamel layer, with a similar configuration and an evident distribution of interglobular dentine beneath the thin enamel layer of both reptiles.

Based on the present fine structure study, we elucidate some histological similarities and dissimilarities of the enamel and dentine in the reptilian tyrannosaurid and mosasaurid of different infraclasses.

Key words  Canada, Cretaceous, Tyrannosauridae and Mosasauridae, fine structure of dental tissues

Tyrannosaurus, a massive reptile ruling the top of the food–chain, had a stout head, small fore legs, and had been described as one of the largest terrestrial carnivores. But it became extinct along with many members of plants and herbivore communities in the Late Cretaceous (Osborn, 1917; Newman, 1970; Lawson, 1976).

Mosasauroidea, which evolved during the Cretaceous has been reported to be a shell–eating reptile with dentition similar to the extant Delphinoidae in having cone–shaped teeth with a bluntes cusp (Williston, 1896; Osborn, 1899; Ijiri, 1981; Tsuchiya, 1984; Hewitt and Western, 1990). The authors obtained some tyrannosaurid and mosasaurid teeth, excavated from the Upper Cretaceous, Horseshoe Canyon Formation, Red Deer River Valley, Canada (plate III, lower part). In the
present study, scanning electron microscopy (SEM) for comparative odontological study on the fossil teeth of the terrestrial archosaurian tyrannosaurid and marine lepidosaurian mosasaurid is carried out, in order to observe the fine structure in the dental tissue of these ancient carnivorous reptilians. The samples were kindly identified by Dr. J. Nasu.

Materials and Methods

Four teeth of tyrannosaurid and six of mosasaurid are used for the present study. The study aimed mainly at the well—preserved coronal portion of the teeth. All the samples were sectioned through the axial plane passing through the anterior and posterior cutting edges. We preserve the specimens as best we could, but unavoidably left some marks on the ground surfaces because the fossil teeth are quite rigid and fragile. Some of the longitudinal halves were polished, rinsed and dried at room temperature. The other halves were further ground—sectioned or fractured in horizontal planes. All the specimens were set on aluminum stumps, coated with platinum and palladium (at 0.1 Torr, 20 mA for 10 min) in an IB—3 type ion—coater (Eiko Engineering, Tokyo, Japan) filled with Argon gas, then observed and photographed (15—20 kV, 50—15,000 X) under a S—570 scanning electron microscope equipped with a LaB6 electron gun (Hitachi, Tokyo, Japan).

Results

1. Structures on the tooth surface

Crowns of the conical, pointed homodontic tyrannosaurid teeth are mediolaterally compressed. They measured about 54 mm high, 19 mm in maximal antero—posterior dimension and 12 mm in maximal thickness (plate 1—1). In contrast, mosasaurid teeth are blunt conical teeth of various sizes, they are averagely 30 mm high and 20 mm in maximal diameter (plate 1—2). The teeth of both tyrannosaurid and mosasaurid curve posteriorly.

Low magnification shows that from the tip to basal portion of the tyrannosaurid teeth, the anterior and posterior cutting edges are serrated. A quite thin enamel layer invaginates towards the dentine, that forms a continuous skirt of small tubercles on the sharp cutting edges. The small tubercles are similar and measured 1.35 mm high (from base of the pit to the tooth surface) and 0.48 mm thick: they shift gradually to the inner and outer (lingual and buccal) aspects of the tooth (plate 1—1, 3).

On the contrary, continuous tubercles showing similar configuration are only observed on the basal portion of mosasaurid teeth (plate 1—2, 4). On the basal portion of the teeth, many characteristic longitudinal grooves of 400 to 500 μm intervals are present and running along the long axis of the teeth (plate 1—2). Between the major
grooves (about 30 μm wide and 3 mm long) exist some dispersed grooves, which are narrow (about 1 μm wide) and parallel to one another. Both the major broad and narrow grooves deeply invade into the enamel and reach to the surface of the dentine in mosasaurid teeth; versus, only narrow longitudinal grooves are observed on the tooth surface of tyrannosaurid teeth (plate 1–5, b).

2. Enamel

The enamel is a regular of 100 μm maximal thick in the tubercular regions and about 60 μm to 80 μm thick in the other regions. On the other hand, the enamel of mosasaurid teeth shows its maximal thickness at the apex but gradually thins towards the base of the teeth. Observations of the serrated cutting edges of both tyrannosaurid and mosasaurid teeth reveals that the enamel invades even 155 μm into the underlying dentine, resulting in continuous tubercles, fissures and pits. The enamel of both tyrannosaurid and mosasaurid did not show prismatic structures. However, most crystals, forming indistinct bundles, run parallel and radiate from the pits nearly at right angles to the flat dentino–enamel junction. They show histology similar to the atypical prismatic enamel described in extant crocodiles of the Archosauromorpha subclass, with clear boundaries between the enamel and dentine (plate 1–7). The dentino–enamel junction is quite flat except at the inner (lingual) and outer (buccal) aspects of the basal portion of the teeth. In the apical portion of the teeth crown, only a few invaginations of dentinal tubules form enamel spindles and clubs.

SEM study on the serrated margin of tyrannosaurid teeth shows the surfaces of the fissures and pits are covered by 1–2 μm thin layer which seems to represent the calcified soft tissue covering the tooth surface. We postulate that most of the recessive enamel epithelium is abraded by mastication, but the membranous cuticle and food debris that remained in the fissures and pits were fossilized, as observed in the specimens. A few enamel lamellae derived from the superficial dentine running vertically towards the tooth surface. Two to three layers of crystals paving the outermost enamel and forming continuous parallel bands with 0.4 μm intervals intersecting the enamel crystals, seem to correspond to the incremental lines of Retzius in the enamel (plate II–8. a, b).

3. Dentine

The dentine of tyrannosaurid and mosasaurid is orthodentine containing many regular dentinal tubules. paralleled dentinal tubules measuring 2 μm in diameter in the deep layer are arranged in regular intervals. In addition, fine structure study shows that dentinal tubules of tyrannosaurid tooth send out two or three terminal branches, measuring from 0.3 to 0.5 μm, which pass through the dentino–enamel junction to form some tubular structures in the thin enamel layer (plate II–9). In contrast, many complicated multiple branchings from the dentinal tubules are characteristic in the
middle and superficial layers of the mosasaurid dentine (plate II–10).

In both tyrannosaurid and mosasaurid teeth, SEM of the non-etched surface of fractured dentinal tubules reveals many waves of circular matrical fibers in the tubular wall, with the crystals precipitated on the dentinal matrix mainly running parallel to the tooth surface (plate II–11). We suppose that the calcified cylindrical masses filling the dentinal tubules represent casts of the odontoblast processes (plate II–9).

Structural differences between the superficial and deep dentine layers are not evident in the ground sections. By etching the ground surface, the superficial 2–3 μm layer characteristically shows an accumulation of many fine (3 to 4 μm) granules (calcospherules) and belt-like depressions along the incremental lines of the dentine (plate I–6). We postulate that diagenesis of the collagen in interglobular dentine and hypocalcified dentine was followed by fossilization to form many loci containing more minerals which were etched to leave cavities in this layer.

The interglobular dentine composed of arrays of large calcospherules (measuring about 8 to 10 μm) and interglobular spaces arranged parallel to dentinal tubules are particularly distinct in the middle layer and pulpal aspect of the mosasaurid dentine (plate II–12a). Continuous dentinal tubules, passing through the interglobular spaces penetrate the calcospherules (plate II–12b). No collagen fibers are found in the large interglobular spaces, however, both a number of smooth-surface and rough-surface calcospherules paved with needle-like crystals are distinct (plate II–12b).

4. Pulp chamber

Pulp chamber of tyrannosaurid teeth is not studied because the basal portion was poorly preserved. In contrast, fine structures on the pulp wall of mosasaurid teeth could be clearly identified, because the teeth are always fractured showing distinct demarcations between the chamber wall and pulp cavity.

The shape of the pulp chamber of mosasaurid resembles the external configuration of tooth in that, from the apical 5 mm portion, the pulp chamber curves towards the posterior aspect. In particular, the pulp wall of the basal portion shows deep depressions containing many continuous absorption (Howship’s) lacunae and dispersive spaces for enclosed osteoclasts measuring about 100 to 150 μm in diameter (plate III–1a–c). High magnification of absorption lacunae clearly shows openings of dental tubules (plate III–1c).

Discussion

Observation of the surfaces of tyrannosaurid teeth reveals serrated margins on the mesial and distal cutting edges similar to some crocodiles; the morphology of the cutting edges is supposed to be characteristic for carnivorous reptiles. Although the present study also finds serrated cutting edges on the basal part of the lepidosaurian
mosasaurid tooth crown, but tubercles and invaginations of the serration are not well-developed. In contrast, many long and deep grooves running parallel to the long axis of the teeth are distinct on mosasaurid teeth, versus. only a few short, shallow and irregular grooves are found on archosauromorphan tyrannosaurid teeth. Further, we suppose that mosasaurid teeth, used in the present study are teeth from the shell-enameled mosasaurid which evolved during the Late Mesozoic.

Regular dentinal tubules without well-developed peritubular dentine are evident in dentine of both tyrannosaurid and mosasaurid. SEM study of tyrannosaurid teeth shows that dentinal tubules branch in the superficial dentine, sending out many terminal branches. In contrast, the branches of dentinal tubules form a complicated network in the middle and superficial layers of the mosasaurid dentine. Furthermore, the present study clearly demonstrates interglobular dentine in both reptiles. Their dentine is composed of many small calcificules and interglobular areas arranged parallel to the dentinal tubules.

Orthodentine is classified into three types according to the structures and arrangement of dentinal tubules (Komada, 1986). The first type contains tubules of different diameters and many irregular branches. The second type contains regular parallel tubules traveling through the whole dentine layer. The third type has highly calcified peritubular dentine. Further, they are termed the primitive—intermediate and progressive—type dentine, respectively. The fossil teeth, of both the dinosauromorphan tyrannosaurid and snakes-like lepidosaurian mosasaurid, observed in our study shows dentine of the intermediate type. Additionally, the mosasaurid orthodentine is histologically more primitive than that of the tyrannosaurid. On the other hand, the fine structure of aprismatic enamel (100 μm in maximal thickness) of both the tyrannosaurid and mosasaurid shows some indistinct bundles as what has been described in the extant crocodile (Yamaiita et al., 1991). The present comparative odontological study indicates histological similarity and dissimilarity of enamel and dentine in both the reptiles of different infraorders.

Concerning the occurrence of Howship’s lacunae and spaces for enclosed osteoclasts in the markedly absorbed pulpal wall of the basal portion of the mosasaurid teeth, we postulate the samples used in the present study might be deciduous in nature. Histology of the samples showing active dentine formation and absorption suggests that life circle of the mosasaurid teeth is considerably short.
References


Explanations of plates

Plate I

1. A fossil tooth of a Tyrannosaurus

Arrows indicate the serrated cutting edges

2. Fossil tooth of a Monosaurus

Arrows show cervical endings of enamel

3. Magnified serrated margin of a Tyrannosaurus tooth

An arrow indicates basal portion of the small tubercle

4. Irregular tubercles on a cutting edge of the basal coronal portion

An asterisk indicates the exposed dentine

5. Middle portion of tooth crown of a Monosaurus

Grooves running parallel to the long axis of the tooth is characteristic

6. Lateral view of a Tyrannosaurus tooth

Serration cutting edge and many shallow longitudinal grooves are observed

7. Cross section of a Tyrannosaurus tooth

Apertetric enamel showing indistinct bundles are found. Interglobular dentine is clearly seen in the superficial dentine (beneath the arrow).
Plate II

8a. SEM picture showing the transitional region of two tubules of the serrated cutting edge.
   A layer of dentin-osteoid-like structure (arrow) measuring about 1 μm is evident.
8b. Higher magnification of 8a.

9. Superficial layer of Dromaeosaurus dentine
   Branches of dentinal tubules and their containing spaces for enclosed odontoblast processes are observed.

10. The middle-dentine of the Mosasaurus tooth
    Completely divided dentinal tubules are characteristic.

11. The Dromaeosaurus dentine is fractured showing its tubular wall and traces of matrical fibrils.
12a. The middle layer of Mosasaurus dentine
    Interglobular areas arranged parallel to the dentinal tubules are observed. An arrow indicates the
    apatitic enamel measuring about 60 μm thick.
12b. Higher magnification of interglobular dentine
    Dentinal tubules penetrating odontophores and odontophores paved with many needle-like crystals are distinct.

Plate III

13a. The basal portion of pulp chamber wall of a Mosasaurus tooth.
    Many absorption lacunae (lower part of the photo) and spaces for enclosed osteoclasts are found.
13b. SEM of a Howship’s lacuna (asterisk)
13c. Photo showing cross sectioned dentinal tubules in the Howship’s lacuna.
    Lower part: Samples used in the present study.