

蜥臀目霸王龙及有鳞目沧龙牙齿 组织的微细结构

石川嘉三 岩井康智 东义景

(大阪齿科大学口腔解剖学讲座 日本 大阪 540)

本文是利用扫描电子显微镜对陆栖恐龙 tyrannosaurid 与海栖蜥蜴 mosasaurid 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 Horseshoe Canyon 组。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,可以了解动物为了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 mosasaurid 都拥有锥状的同形齿,牙齿侧向扁平,且略向后弯曲。研究结果确认了 tyrannosaurid 的牙齿由于薄层的无柱釉质 (aprismatic enamel) 向齿质的侵入而造成许多的凹凸构造,此锯齿状构造沿着牙齿的前后缘,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。但是类似的锯齿状构造只能在齿冠呈钝圆状的 mosasaurid 牙齿的基部附近观察到。我们以扫描电子显微镜 (SEM) 检索,确认两爬行类的齿质皆是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—釉质相接处 (dentino-enamel junction) 附近放散出规则性的分歧与末枝。但 mosasaurid 的真性齿质的齿质小管,在齿质的中间层与表层中,呈现着由复杂的侧枝与联络枝来形成的网状构造。微细结构的观察显示,这两种古爬行类的真性齿质都只有少数的齿质小管侵入了釉质,并且管周齿质 (peritubular dentine) 皆不甚发达。在非薄的无柱釉质之下,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,讨论了鳞龙下纲与初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

Yoshizou ISHIKAWA Yasutomo IWZI-LIAO Yoshikage HIGASHI

(Department of Oral Anatomy, Osaka Dental University Osaka, Japan 540)

Abstract Teeth of saurischian tyrannosaurid and squamate mosasaurid are studied mainly by scanning electron microscopy. The teeth of both diapsids are cone-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 aprismatic enamel layer. Fissures and pits of the invaginations are packed with what is possibly a layer of fossilized 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 orthodentine (tubular dentine) with ill-developed peritubular 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 tubular 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 elucidates 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). *Mosasaurus*, which evolved during the Cretaceous has been reported to be a shell-eating reptile with dentition similar to the extant Delphinoidea in having cone-shaped teeth with a blunt cusp (Williston, 1898; Osborn, 1899; Ijiri, 1981; Tasumi, 1984; Hewitt and Westermann, 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 radial plane passing through the anterior and posterior cutting edges. We preserve the precious 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 I-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 I-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 I-1,3).

On the contrary, continuous tubercles showing similar configuration are only observed on the basal portion of mosasaurid teeth (plate I-2,4). On the basal portion of the teeth, many characteristic longitudinal grooves of 400 to 500 μ m intervals are present and running along the long axis of the teeth (plate I-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 I-5,6).

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 135 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 Archosauria subclass, with clear boundaries between the enamel and dentine (plate I-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 invasions 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- 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 wakes of circular matricial 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 (calco-sphericles) 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 calcosphericles (measuring about 8 to 10 μm) and interglobular spaces arranging 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 calcosphericles (plate II-12b). No collagen fibers are found in the large interglobular spaces, however, both a number of smooth-surface and rough-surface calcosphericles 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-13a-c). High magnification of absorption lacunae clearly shows openings of dental tubules (plate III-13c).

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 archosaurian tyrannosaurid teeth. Further, we suppose that mosasaurid teeth, used in the present study are teeth from the shell-eaten 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 calcosphericles 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 dinosaurian tyrannosaurid and snake-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 (Yamasita *et al.*, 1991). The present comparative odontological study indicates histological similarity and dis-similarity of enamel and dentine in both the reptiles of different infraclasses.

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.

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Explanations of plates

Plate I

1. A fossil tooth of a *Tyrannosaurus*
Arrows indicate the serrated cutting edges
2. Fossil teeth of a *Mosasaurus*
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 *Mosasaurus*
Grooves running parallel to the long axis of the tooth is characteristic
6. Lateral view of a *Tyrannosaurus* tooth
Serrated cutting edge and many shallow longitudinal grooves are observed
7. Cross section of a *Tyrannosaurus* tooth
Aprismatic enamel showing indistinct bundles are found. Interglobular dentine is clearly seen in the superficial dentine (beneath the arrows).

Plate II

- 8a. SEM picture showing the transitional region of two tubercles of the serrated cutting edge
A layer of dental-cuticle-like structure (arrow) measuring about $1\ \mu\text{m}$ is evident
- 8b. Higher magnification of 8a
Notice some incremental lines in the enamel
9. Superficial layer of *Tyrannosaurus* dentine
Branchings of dentinal tubules and their containing spaces for enclosed odontoblast processes are observed
10. The middle-layer dentine of the *Mosasaurus* tooth
Complicatedly branched dentinal tubules are characteristic
11. The *Tyrannosaurus* dentine is fractured showing its tubular wall and traces of matricial fibrils
- 12a. The middle layer of *Mosasaurus* dentine
Interglobular areas arranged parallel to the dentinal tubules are observed. An arrow indicates the aprismatic enamel measuring about $60\ \mu\text{m}$ thick
- 12b. Higher magnification of interglobular dentine
Dentinal tubules penetrating calcosphericles and calcosphericles 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 lacunae
Lower part: Samples used in the present study





