

早期哺乳动物三尖齿兽类牙齿的超微结构

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关键词 三尖齿兽 牙齿 超微结构

内 容 提 要

本文用扫描电镜研究了中国云南禄丰盆地禄丰组发现的以及英国威尔士晚三迭世的三尖齿兽类牙齿的超微结构。其釉质具有准釉柱结构，它们呈并行排列从釉牙质界延伸到釉质外表面。这种准釉柱结构由很多羽支状排列的磷灰石微晶组成。微晶的C轴与准釉柱的长轴形成交叉的角度大约为10—20度。早期哺乳动物牙齿釉质的准釉柱结构，很可能是从爬行动物无釉柱结构向哺乳动物真釉柱结构进化过程中的标志。

一、前 言

近年来，应用扫描电镜研究哺乳动物牙齿的超微结构，探讨它们的演化关系已经获得了很多重要的资料，其中最引人注意的就是关于早期哺乳动物牙齿结构的研究。

一般说来，哺乳动物牙齿釉质的特征就是具有釉柱构造，釉柱是构成釉质的基本结构单位。但是 Moss (1969) 认为，有釉柱结构的釉质只出现在早白垩世以后的兽亚纲中，至于那些更早期的哺乳动物，如三尖齿兽类，多瘤齿兽类等，它们的牙齿的釉质则是无釉柱构造，其中的磷灰石微晶呈锯齿状排列。然而，Osborn 等 (1979) 和 Fosse 等 (1973) 分别报告，具有釉柱结构的釉质不仅出现于白垩纪的兽亚纲中，而且也见于多瘤齿兽类中；与此同时，Grine 等 (1979) 报告，在三迭纪晚期的三尖齿兽类 (*Eozostrodon*、*Morganucodon*) 的牙齿釉质中，不但发现有釉柱构造，而且还呈现出交叉排列的特征。最近，Frank 等 (1984) 描述了来自法国晚三迭世的多瘤齿兽类(?) *Haramiyids* 牙齿的超微结构，认为这类釉质是由一种叫做“准釉柱” (Pre-prismatic) 的结构所组成，是介于那些无釉柱构造的爬行类釉质和有真正的釉柱结构的哺乳类釉质之间的一种结构形态。接着 Sigogneau-Russell 等 (1984) 和 Frank 等 (1986) 先后报告了早侏罗世的对齿兽类 *Kuehneotherium* 和晚三迭世三尖齿兽的釉质也显示出“准釉柱”结构的特征。

鉴于 Grine 等 (1979) 和上述其他学者对三尖齿兽类的研究结果有很大的不同，进一步研究这一类群的牙齿超微结构可能具有重要的意义。在孙艾玲教授的支持下，我们用扫描电镜研究了我国云南省禄丰盆地禄丰组出产的原始哺乳类以及来自英国威尔士的

Eozostrodon (*Morganucodon*)¹⁾ 的牙齿超微结构。

二、材料和方法

到目前为止,已报道的从云南禄丰盆地采集的原始哺乳动物共有 6 个种,它们是欧氏摩尔根兽 (*Morganucodon oehleri*), 黑果棚始带齿兽 (*Eozostrodon hekuopengensis*), 芮氏中国尖齿兽 (*Sinoconodon rigneyi*), 帕氏中国尖齿兽 (*Sinoconodon parringtoni*), 张家洼中国尖齿兽 (*Sinoconodon changchiawaensis*), 杨氏中国尖齿兽 (*Sinoconodon yangi*) 和禄丰尖齿兽 (*Lufengconodon*)。

最近,孙艾玲等(1985)同意,摩尔根兽和始带齿兽应为同属异名;禄丰尖齿兽也应当是中国尖齿兽。由此看来,在禄丰盆地下禄丰组发现的原始哺乳动物实际上只有中国尖齿兽和摩尔根兽两个属。至于中国尖齿兽内的四个种是否都能成立,也还有待于今后进一步的研究。目前,由于就始带齿兽和摩尔根兽的命名还是否有效未曾得出一致看法,不同学者仍坚持使用不同名称。因此,在本文中使用的中国材料,仍采用摩尔根兽这一名称。选择的研究材料如下。

三尖齿兽目 (Triconodonta), 摩尔根兽科 (Morganucodontidae), 摩尔根兽 (*Morganucodon* sp.): 一个带有 2 个前臼齿和一个臼齿的残破下颌骨,来自云南禄丰。

中国尖齿兽科 (Sinoconodontidae), 中国尖齿兽 (*Sinoconodon* sp.): 一个牙齿碎片,来自云南禄丰。

此外,我们还研究了 Parrington 生前赠送的英国威尔士晚三迭世 *Eozostrodon* (*Morganucodon*) 的一个犬齿和一个臼齿。

在用扫描电镜观察样品之前,需对这些标本处理。先将标本洗净,用环氧树脂包埋。然后在放有 M3.5 号金刚砂的玻璃上,用手将标本牙尖顶以及沿唇颊面磨成一平面,超声波清洗二分钟,用抛光机抛光,再次用超声波清洗后用 0.1M 的磷酸溶液蚀刻标本的磨面约 50—70 秒钟,接着用清水洗净并在干燥器内放置二天。最后将这些样品放在真空镀膜机内喷镀约 400A 的黄金,之后,便可将样品放在扫描电镜中进行观察。用于本文研究的扫描电镜为 JSM—T200,加速电压为 25KV。

三、观察结果

1. 摩尔根兽

牙齿釉质的厚度在 15—60 微米之间。一般说来,牙尖处的釉质层比较厚,向牙颈区则逐渐变薄。在扫描电镜下,可以见到釉质是由磷灰石微晶集成柱状的结构所组成。这些柱状结构呈并行排列,从釉牙质界面延伸至釉质外表面。每个柱状结构的宽度大约为 4—5 微米;柱状结构之间,未见有柱鞘或柱间质的形态存在。在每个柱状结构中,可以清楚地见到磷灰石微晶呈现出羽支状排列形式。它们的 C 轴与柱状结构的长轴形成约

1) 始带齿兽 (*Eozostrodon*) 最初发现于英国威尔士,后来 Kühne (1979) 根据从那里发现的一个下臼齿,建立了一个新属 *Morganucodon*。然而, Parrington (1967, 1971, 1974, 1978) 认为,这两个属应为同物异名。

10—20 度的夹角,因此,在每个柱状结构中,磷灰石微晶有规则的分叉,其夹角约为 20—40 度(图版 I, 1)。

上述结果,与 Frank 等(1986)描述的来自法国和英国晚三叠世三尖齿兽牙齿釉质(属种未定)的结论是一致的,或相当于 Frank 等(1984)所描述的准釉柱结构的釉质;也与 Osborn 和 Hillman (1979)用偏光显微镜观察的 *Eozostrodon* 的牙齿釉质特征很相似(标本可能来自英国威尔士)。

此外,从我们的标本上,还可见到一些不很规则的细缝分布于釉质层中。这种细裂缝可能是石化过程所致,也可能是样品制作过程中,受机械作用而成。因此可以排除禄丰盆地摩尔根兽的牙齿釉质中有釉质小管存在。这与 Osborn 和 Hillman (1979)的研究结果刚好相反,他们发现,在 *Eozostrodon* 的釉质中,分布有很多釉质小管。

在扫描电镜下,还可见到摩尔根兽牙齿的牙质中分布有很多牙质小管。它们从靠近牙髓腔处向外周牙质延伸,终止在近牙质釉质界。这些牙质小管的横切面一般都呈圆形(图版 I, 2)在被观察的牙质切面中,几乎所有的牙质小管都是中空的。这表明这些牙齿在石化过程中,存留在牙质小管中的牙质纤维被腐蚀掉以后,牙质小管并没有被次生矿物所充填。此外还可以发现,牙质小管并不是均匀分布于牙质中,在靠近髓腔处的牙质中,牙质小管的密度较大,而在外周牙质中,小管的分布很少。

2. 中国尖齿兽

牙齿釉质的厚度约为 15—35 微米。在扫描电镜下观察,釉质的结构与上述摩尔根兽的很相似,由准釉柱结构并行排列组成,大体上与釉质表面垂直。在准釉柱之间,未见有柱间质存在。每个准釉柱的宽度约为 4—5 微米。在每个准釉柱中,羟磷灰石微晶以 15—20 度倾斜排列于中轴两侧,从而构成了约呈 30—40 度的角(图版 I, 3)。此外,在所观察的釉质切面中,未见有釉质小管。

对中国尖齿兽牙齿切面的观察,牙本质中显示有很多牙质小管从靠近牙髓腔处延伸到牙质外周。牙质小管的横切面约呈圆形。与上述摩尔根兽的牙质一样,牙质小管的分布也是不均匀的:近牙髓腔处牙质小管的密度比外周牙质中的要多得多(图版 II, 1)。值得注意的是,绝大多数靠近牙髓腔处的牙质小管被一些看来似乎比牙质小管间牙质更致密的、呈白色无定形的钙化物所充填。在较高倍数下,可以见到在有的牙质小管口上,这些白色的钙化物呈现为环形结构。它们似乎具有较强的抗酸性能,很类似于成牙细胞突的残存物。Fosse 等(1981)在化石哺乳类牙齿中也见到同样现象。

3. 英国始带齿兽

在我们所观察的英国威尔士晚三叠世始带齿兽的一个犬齿和一个臼齿的切面中,可以发现:犬齿釉质的厚度以唇侧侧最厚,约 20 微米;舌侧釉质层则很薄,约 2 微米(见图 1A),臼齿的颊侧和舌侧釉质厚度基本相等,约 25—40 微米(见图 1B)。

扫描电镜下,在这两个牙齿釉质的切面上,磷灰石微晶都显示出准釉柱结构的排列特征,与上述禄丰盆地的摩尔根兽和中国尖齿兽的釉质结构很相似。每个准釉柱的宽度约 4—5 微米,其间未见有柱间质存在。在每个准釉柱中,磷灰石微晶的 C 轴偏离柱的中轴

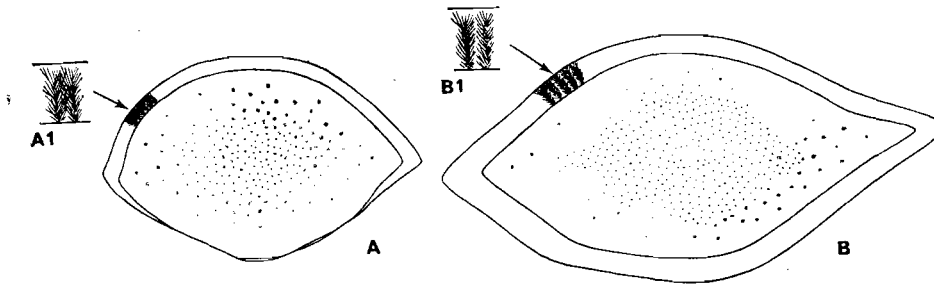


图1 A. 始带齿兽犬齿横切面, A1 是 A 中釉质结构部位的局部放大;
B. 始带齿兽白齿横切面, B1 是 B 中釉质结构部位的局部放大

约 15—20 度,形成了朝向釉质表面约呈 30—40 度的角。这些特征在准釉柱的纵切面(图版 II, 3)和斜切面(图版 II, 4)上都可见到。这种结构与 Grine 等(1979)的研究结果恰恰相反。他们的报告指出,所有被观察的始带齿兽,其牙齿釉质都具有真正的釉柱结构。应当注意的是,在我们所观察的白齿釉质中,还可见到釉质小管,它们一般与釉牙质界面垂直。这些釉质小管,有的分布在准釉柱之间,有的则很清楚地显示出位于准釉柱的中心(图版 II, 3)。而在犬齿的釉质中,看来似乎没有釉质小管。

和上述禄丰盆地的摩尔根兽及中国尖齿兽的牙质特征一样,始带齿兽的犬齿和白齿中的牙质小管不均匀地分布在牙质中,这些牙质小管绝大多数都是中空的(图版 II, 2)。此外,在牙质的横切面上,还可见到大小不一的细管与一些形状不规则的腔隙连接在一起,这些不规则的管腔很可能是动物死后的一种腐生损害现象。

四、讨 论

从上述的研究结果可以看出:

1. 在我们所观察的上述标本中,牙质中存在的大量牙质小管与在爬行类和哺乳类中所发现的很一致。Grine (1979) 所观察的始带齿兽牙质中没有发现牙质小管,他们认为这可能是在制作镜检标本时产生的一种膺象。

另一方面,上述标本中,牙质小管的分布不是均匀的,它们多集中在靠近牙髓腔的牙质中,而在外周牙质则显得稀疏。这种现象在人的牙质中也可见到。据计算,在人类的外周牙质中,每平方毫米内约含 15,000 根牙质小管,而在靠近牙髓腔处的牙质中,每平方毫米内约有 75,000 根牙小管。

2. 上述禄丰盆地发现的摩尔根兽和中国尖齿兽的釉质内没有釉质小管,这与 Frank 等(1986)所观察法国南锡附近及英国威尔士的三尖齿兽(属种未定)的结果相吻合。但本文观察的始带齿兽的釉质具有釉质小管与 Osborn 等(1979)对始带齿兽观察的结果相同。这表明了在三尖齿兽目中,始带齿兽与上述其它类群之间有明显差别。然而,这种差别是否可以作为它们之间分类的标志,由于目前从电子显微镜的研究中得到的资料比较少,尤其是在“科”的分类等级上尚没有建立起稳定的釉质结构特征,因此要把上述研究的

釉质结构特征应用于三尖齿兽类中还需作系统的研究。

3. 釉质系由准釉柱结构组成,它们呈并行排列,从釉牙质界延伸到釉质外表面。每个准釉柱的宽度约4—5微米;在每个釉柱中,磷灰石微晶C轴以10—20度的角偏离柱的中轴。这些特征与 Frank 等(1986)描述的三尖齿兽牙齿(属种未定)的构造是很一致的,也与 Osborn 等(1979)所描述的始带齿兽的特征相似。

到目前为止,晚三迭世和侏罗纪地层中已经发现的哺乳动物有5个目,它们是柱齿兽类(Docodonta),三尖齿兽类(Triconodonta),多瘤齿兽类(Multituberculata),对齿兽类(Symmetrodonta)和古兽类(Pantotheria)。除南美洲、澳洲和南极洲外,各洲都有发现。从已发表的资料看,除本文研究的三尖齿兽类外,准釉柱结构也见于原始的多瘤齿兽类的 Haramiyidae (Frank 等, 1984) 和 plagiaulacoid (Fosse 等, 1985), 柱齿兽(Fosse 等 1985) 和对齿兽类的 *Kuehneotherium* (Sigogneau-Russell 等, 1984)。不难看出,从三迭纪晚期到侏罗纪的哺乳类,釉质超微结构的基本特征是相似的,均为准釉柱结构。而具有真正釉柱结构的釉质只出现在早白垩世以后的多瘤齿兽和兽亚纲中 (Osborn 等, 1979; Fosse 等, 1985)。目前,对于晚三迭世和侏罗纪的这些早期哺乳动物目之间的相互关系仍存在着许多争论。然而,似乎有理由认为,这些早期哺乳动物的牙齿釉质所具有的准釉柱结构特征可能与牙齿形态的分化及咀嚼功能的发生有关,是介于爬行类的无釉柱结构釉质和后来的哺乳动物所具有的真正釉柱结构釉质之间的过渡类型。而这一过渡极可能是沿着一条广阔的适应辐射线而发生的。

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参 考 文 献

- 孙文玲、崔贵海、李雨和、吴肖春, 1985: 禄丰蜥龙动物群的组成及初步分析。古脊椎动物学报, 23(1), 1—11。
- Fosse, G., S. Risnes and N. Holmbakken, 1973: Prisms and tubules in multituberculate enamel. *Calcif. Tiss. Res.* 11, 133—150.
- Fosse, G., B. P. B. Justesen and G. B. R. Wesenberg, 1981: Microstructure and chemical composition of fossil mammalian teeth. *Calcif. Tiss. Int.*, 33, 521—528.
- Fosse, G., Z. Kielan-Jaworowska and S. G. Skaale, 1985: The microstructure of tooth enamel in multituberculate mammals. *Palaeontology*, 28(3), 435—449.
- Frank, R. M., D. Sigogneau-Russell and J. C. Voegel, 1984: Tooth ultrastructure of late Triassic Haramiyidae. *J. Dent. Res.*, 63(5), 661—664.
- Frank, R. M., D. Sigogneau-Russell and Hemmerlé, J. 1986: Ultrastructural study of triconodont (Prototheria, Mammalia) teeth from the Rhaeto-Liassic. *Mem. Mus. natn. Hist. nat., Paris, (série C)*, 53, 101—108.
- Grine, F. E., E. S. Vrba and A. R. I. Cruickshank, 1979: Enamel prisms and Diphyodonty: Linked apomorphies of Mammalia. *S. Afr. J. Sci.*, 75, 114—120.
- Moss, M. L. 1969: Evolution of dental enamel. *Am. Mus. Novit.*, 2360, 1—39.
- Osborn, J. W. and J. Hillman, 1979: Enamel structure in some therapsids and Mesozoic mammals. *Calcif. Tiss. Int.*, 29, 47—61.
- Sigogneau-Russell, D., R. M. Frank and Hemmerlé, J. 1984: Enamel and dentine ultrastructure in the early Jurassic therian *Kuehneotherium*. *Zool. J. Linn. Soc.*, 82, 207—215.
- Sognnaes, R. F. 1963: Dental hard tissue destruction with special reference to idiopathic erosions. IN: Mechanisms of hard tissue destruction, Sognnaes R. F. Ed., *Ann. Ass. Adv. Sci.*, 75, 91—153.

ULTRASTRUCTURE OF TRICONODONT TEETH

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Key words Triconodont; Teeth; Ultrastructure

Summary

The enamel ultrastructure studies of the fossil and extant mammalian teeth have furnished invaluable information for the clarification of evolutionary relationships, and in recent years great attention has been paid to the subject of studying the ultrastructure of the teeth of early mammals.

There is general agreement that the enamel of all recent mammals is characterized by a prismatic structure. The prisms constitute the basic structural units of such enamel. Moss (1969) believed that true prismatic enamel appeared only in the early Cretaceous Theria, and that the enamel of all earliest mammals, such as *Morganucodon*, was non-prismatic and continuous with a sawtoothed pattern of the apatite crystals, whereas Osborn and Hillman (1979) and Fosse et al. (1973) described prismatic enamel in non-therian multituberculates from Cretaceous, and Grine et al. (1979) found it in primitive mammal *Eozostrodon* (*Morganucodon*) from the Rhaeto-Liassic age. Recently, the enamel structure of certain late Triassic mammals: the Theria Symmetrodonta (Kuehneotheriidae), the Prototheria Multituberculata (Haramiyidae) and the Eotheria Triconodonta (Morganucodontidae) has been investigated (Frank et al., 1984; Sigogneau-Russell et al., 1984; Frank et al., 1986) and these studies have reached the conclusion that the enamel in these early mammals possesses a structural pattern defined as "preprismatic".

In view of the differences between the results obtained by Grine et al. (1979) and by other authors mentioned above, concerning Triconodonta, it would be significant to study the enamel structure of the teeth in this group. Through courtesy of Professor Sun Ai-lin we were able to examine with SEM the structure of the teeth in some triconodont. In this instance we used for this study the following material: *Morganucodon* and *Sinoconodon* from lower Lufeng Formation, Yunnan Province, and *Eozostrodon* (*Morganucodon*) from Wales, England. The results are summarized below.

1. Ultrastructure of the teeth in *Morganucodon*

The material consisted of two premolars and a molar *in situ* in a fragment mandible. The enamel layer of the teeth, which is in general thicker in the cusp area and becomes progressively thinner along the cervical region, is 15 to 60 μm thick. SEM examination of the teeth showed that the enamel consists of columns formed by hydroxyapatite crystallites. These columns are juxtaposed one next to the other, extending from the enamel-dentine junction to the external enamel surface, and not separated by an interprismatic substance or by a sheath. The diameter of the columns changes from 4 to 5 μm . In each column, a repetitive orientation pattern of the c-axes of the apatite crystallites with a pinnate disposition was observed (Plate, I, 1).

They diverge the main longitudinal axis of the column at an angle of 10° to 20° , opening towards the external enamel surface.

By comparing with the other known early mammals, it is obvious that the features of the enamel structure in our specimens are very similar to those of unidentified triconodont teeth from Rhaetic or lower Liassic age sediments in France and England, which were described by Frank et al. (1986), and are also consistent with that of *Eozostrodon* observed by Osborn and Hillman (1979) in the polarizing microscope. Such a description corresponds to one referred to the "preprismatic" enamel by Frank et al. (1984), based on their studies of the tooth ultrastructure of late Triassic Haramiyidae.

No enamel tubules have been observed in our specimen. However, the dentine contains numerous dentinal tubules, running from the pulp cavity towards the periphery. And the empty tubules are seen in transverse planes (Plate I, 2).

2. Ultrastructure of a *Sinoconodon* tooth

The thickness of the enamel covering this tooth is 15 to 35 μm . In the SEM preprismatic enamel in *Sinoconodon*, which is similar to that of *Morganucodon* mentioned above, can be observed (Plate I, 3). This structural pattern seemed to consist of 4 to 5 μm wide, closely packed columns of crystals, running again from the enamel-dentine junction to the outer enamel surface. These preprisms are directly in contact with each other, without the intermediary of an interprismatic phase. In each preprism, the apatite crystallites are diverged on each side of the main longitudinal axis of the preprism with an angle of 10° to 20° open towards the enamel surface. Besides, the absence of enamel tubules in this enamel has also been confirmed.

SEM study of the sections of the tooth showed that there is rich in tubules in dentine, extending from the pulp cavity towards the periphery. On cross-sections, the lumen of these tubules is blocked by amorphous calcified material which appeared to be acidresistant (Plate II, 1).

3. Ultrastructure of the teeth in *Eozostrodon*

The material consisted of a canine and a molar. On the transverse sections, it can be seen that the layer of the enamel covering the canine is thicker in the bucco-labial side and becomes thinner towards the lingual side (Fig. 1A). On the contrary, the thickness of the enamel layer of the molar is almost the same in both sides (Fig. 1B). In the SEM we can see that the enamel in these two teeth is made up of parallel columns referred to preprismatic, about 4 to 5 μm in diameter, extending from the enamel-dentine junction to the outer enamel surface (Plate II, 3 and 4). In each preprism, the hydroxyapatite crystallites are disposed from the main longitudinal axis of the preprism at an angle of 15° to 20° , opening towards the enamel surface.

Our aforementioned observations do not corroborate the results described by Grine et al. (1979). By SEM studies they found prismatic enamel in *Eozostrodon* teeth.

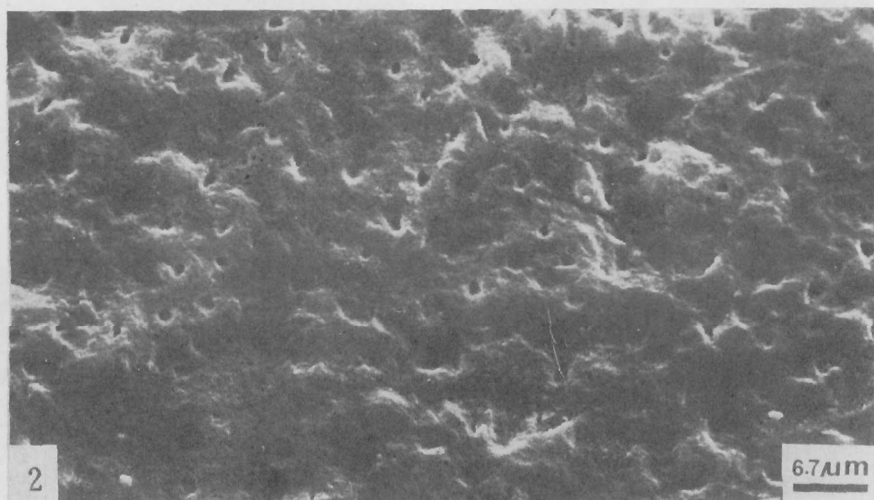
However, it is worth noting that another feature of the enamel in the molar was the presence of tubules running from the enamel-dentine junction. These could be possibly regarded as enamel tubules (Plate II, 3). They appeared fairly straight and parallel with the longitudinal axes of the preprisms. In sections viewed in the SEM, some tubules were located between preprisms, and some in the center of them. Osborn and Hillman (1979) also reported that the enamel tubules were identified in *Eozostrodon*. On the contrary, no tubules were identified in the enamel of the canine in the SEM.

The dentine of *Eozostrodon* teeth examined showed that it has abundant dentine tubules

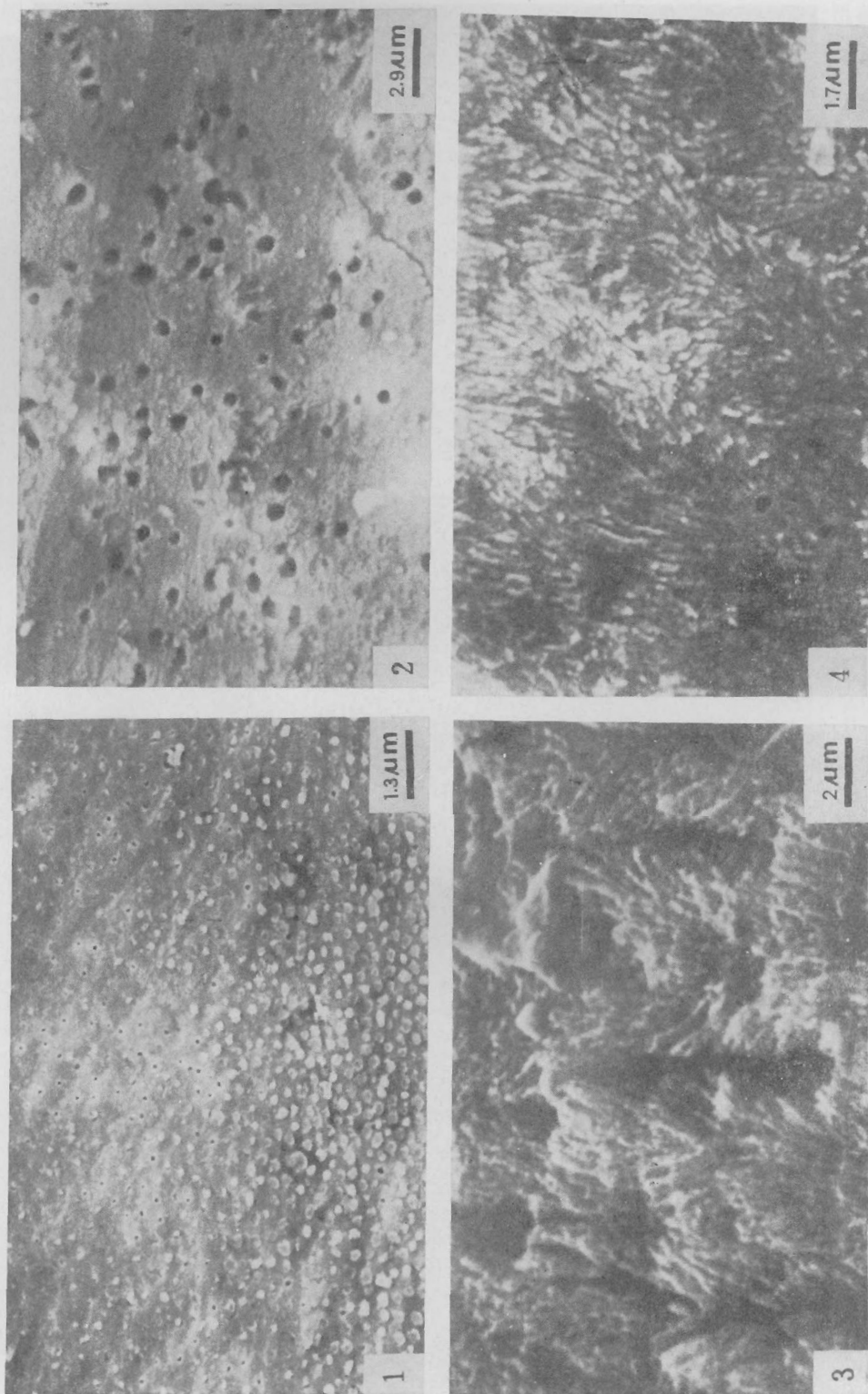
(Plate II, 2), which are similar to that of *Morganucodon* and *Sinoconodon*, mentioned above. However, Grine et al. (1979) reported that the absence of dentine tubules in their observations of *Eozostrodon* may be an artefact of preparation techniques.

On the basis of the foregoing results, we can see that the enamel of triconodont teeth from the lower Lufeng Formation, Yunnan Province, China and from the Rhaeto-Liassic age sediments in Wales, England is non-prismatic, but consists of 4 to 5 μ m in diameter, closely packed columns of crystals, which diverge from the main longitudinal axes of the columns with an angle of 10° to 20° towards the outer enamel surface. This prismatic structure is consistent with that described by Frank et al. (1986) in the unidentified triconodont material from France and England, and is also similar to that of *Eozostrodon* reported by Osborn and Hillman (1979).

So far, five orders of mammals are known from sediments of late Triassic and Jurassic age, and are represented by fossils discovered in Europe, Asia, Africa and North America. These are the Docodonta, the Triconodonta, the Multituberculata, the Symmetrodonta, and the Pantotheria. In the existing literature, the same preprismatic structure is also found in primitive multituberculates, Haramiyid (Frank et al., 1984) and plagiulacoid (Fosse et al., 1985), in docodont (Fosse et al., 1985), and in symmetrodont, *Kuehneotherium* (Sigogneau-Russell et al., 1984). Thus, it may be concluded at present from the reports mentioned above that the preprismatic structure is present in non-therian and therian mammals from late Triassic and Jurassic. And our own observations in triconodont teeth added evidence supporting the presumption that the preprismatic enamel represents an intermediate structural stage between the aprismatic enamel of reptiles and the true prismatic enamel of later mammals.



1. 摩尔根兽白齿釉质颊舌侧切面；2. 摩尔根兽牙质横切面；3. 中国尖齿兽釉质纵切面



1. 中国尖齿兽牙质横切面； 2. 始带齿兽牙质横切面； 3. 始带齿兽白齿釉质颊舌侧切面；
4. 始带齿兽犬齿釉质斜切面