第37卷 第1期
1999年 1 月
古脊椎动物学报
VERTEBRATA PALASIATICA
pp.40～47
fig.1, pls.I～II

争胜鼠(*Zelomys*)的门齿釉质结构和分类位置[1)]

王伴月 欧阳涟
(中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要 争胜鼠的上门齿釉质结构分为两层。内层施氏明暗带界线清楚，呈横向延伸，带宽不规则，主要为1个釉柱宽。釉柱间质很发育，围绕釉柱，其微晶方向与釉柱平行，属单系。争胜鼠与始鼠科共有单系门齿微细结构，而与先松鼠科共有始啮型头骨的特征，因前者为较进特征而后者为近祖的原始特征，故争胜鼠与始鼠科有较近的系统关系。

关键词 门齿釉质微细结构，中始新世，始鼠科，先松鼠科
中图法分类号 Q915.873

1 前 言

门齿是啮齿动物生活的重要工具之一。它们的外观形态比较单一，但其釉质的微细结构比较复杂。啮齿动物的门齿釉质主要由内、外两层组成(图1)。外层(PE: portio externa)由彼此近于平行的釉柱组成。内层(PI: portio interna)由交叉的釉柱组成，此交叉的釉柱在纵切面上以施氏明暗带的形式表现。基于施氏明暗带中釉柱的数量和排列方式等的不同，啮齿动物门齿釉质微细结构可分为三种类型：散系(pauciserial)[2)]、单系(uniserial)和多系(或复系，multiserial)(Korvenkontio, 1934; Wahlert, 1968; Martin, 1992, 1993)。散系为较原始的釉质结构，其内层的釉柱的排列是无序的，主要出现在古新世和始新世早期的较原始的啮齿类中。单系的施氏明暗带的每带主要为一个釉柱宽，发现于松鼠类、鼠形类、河狸类和兽鼠类等啮齿动物。多系的施氏明暗带为3～7个釉柱宽，发现于梳趾鼠和具豪猪形下颌骨的啮齿类。因此，啮齿类的釉质微细结构是确定其系统分类位置的有意义的证据之一。

争胜鼠(*Zelomys*)是产于我国中始新世地层中的一类啮齿动物。关于它的系统分类位置，存在不同的看法：有人将它归入先松鼠科(Sciuravidae)(王伴月和李春田，1990; McKenna & Bell, 1997)；也有人认为它应属始鼠科(Eomyidae)(Korth, 1994; Chiment

---

1) 本课题得到中国科学院古生物学与古人类学科基础研究特别支持基金资助(编号：9708)。

2) pauciserial中的pauci原意为"少"，但近年来关于pauciserial的含义有了较大的变化，根据其形态结构，拟翻译为散系。

收稿日期：1998-03-25

& Korth, 1996；童永生，1997)。为了对该属的特征有更多的了解，以便对它的系统分类位置的进一步确认提供更多的信息，我们对 *Zelomys* 的门齿釉质结构作了切片观察。

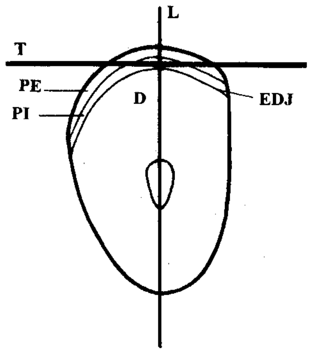


图 1　门齿横切面
(依 Martin，1992，稍修改)
Fig. 1　Cross section of incisor
图中缩写(Abbreviations)：D，齿质(dentine)；EDJ，釉齿质界(enamel dentine junction)；L，纵切面线(longitudinal section)；PE，外层(portio externa)；PI，内层(portio interna)；T，弦切面(tangent section)

文中所用的有关釉质微细结构的术语主要根据 Wahlert(1968)和 Martin(1992，1993)的。现将啮齿动物门齿的釉质微细结构的常用术语列述如下：

釉柱(或珐琅质柱，prismas)：由成束的羟磷灰石微晶组成的棒状物，为釉质最重要的单元。

釉质类型(enamel type)：釉柱具相同方向的釉质单位。

放射釉质(radial enamel)：釉柱近于平行排列的釉质类型，在纵切面上呈放射状排列。

施氏明暗带(HSB：Hunter-Schreger bands)：由釉柱组成的层，在纵、横切面上表现为带。每带由一个或数个釉柱组成。在同一带中，釉柱彼此平行；在相邻的带中的釉柱彼此呈高角度相交。

釉柱间质(IPM：Interprismatic matrix)：填充于釉柱间区的羟磷灰石微晶，具有一定方向，但不捆扎成釉柱。

釉质结构(Schmelzmuster)：釉质类型的三维排列。

釉齿质界(或釉牙本质界、珐琅质齿质界，EDJ：enamel dentine junction)：牙齿的釉质和齿质之间的界线。

釉质层总厚度(total enamel thickness)：由釉齿质界面到釉质最外层外面的间距。

釉质内层厚度(PI thickness)：从釉齿质界面到釉质内、外层界面的间距。

釉质外层厚度(PE thickness)：从釉质内、外层界面到釉质最外层外面的间距。

釉质外层厚度比率(external index)：釉质外层厚度与釉质总厚度之比。

施氏明暗带宽(band width)：在纵切面上施氏明暗带中单条带的宽度。它是用单条带中与带间界线垂直线上所包含的釉柱的数量计算的。

施氏明暗带的倾斜度(inclination of bands)：在纵切面上施氏明暗带与釉齿质界面的垂线的夹角。

无釉柱的最外层(PLEX：prismless external layer)：釉质的最外层，无釉柱，全部由釉柱间质的微晶融合而成。

2　材料和方法

由于 *Zelomys* 已知的材料很少，而且为了尽可能少地损坏已知的标本，我们只观察了它的上门齿。材料为东方争胜鼠(*Zelomys orientalis*)V8799(部分头骨)的上门齿。该标本产自吉林省桦甸县原公吉屯大勃吉公社油母页岩矿的中始新世桦甸组第三岩性段。我们将右门齿取出一段，首先用胶包埋，根据在上颌上的位置将其定向，作纵向切割，用 M5 号金刚砂细磨，用三氧化二铬抛光，后用 0.1mol 磷酸蚀刻 50 秒左右，在冲洗凉干后镀金，最

后在 JSM-6100 扫描电镜下观察。我们用同样的仪器和材料将其左上门齿前端直接细磨、抛光、蚀刻、镀金后，用电镜观察其横断面。

3 *Zelomys* 门齿的形态结构

Zelomys 的上门齿的横切面约呈卵圆形，唇面较平。釉质覆盖其唇面和外侧面唇侧的1/4 处，几乎不伸达内侧面。釉质唇面具不规则的纵向纹饰，但无明显的沟或棱。

***Zelomys* 上门齿的横切面**（图版 I） 釉质层厚度较均匀，只是在唇外侧稍厚（图版 I，1）。由于只有一枚门齿，为了避免破坏，只能简单制样处理，电镜图片上所显示的釉质微细结构不清晰。特别是在唇面平直部位的釉质的微细结构似乎显得很混乱（图版 I，2）。但稍仔细观察我们就会发现，釉质仍然分两层，只是两层的界线不清楚。内层仍然可区分出施氏明暗带。带宽为 1～3 个釉柱宽。相邻的带的釉柱的交角近于 90°。外层的釉柱切面呈卵圆形，其长轴约与外表面垂直。釉柱间质发育，微晶方向也与外面垂直。在唇面外侧至外面唇侧的图像要清晰些（图版 I，3）。釉质结构明显分为内、外两层。施氏明暗带的宽度不一，由于釉柱的界线不清，其宽度范围估计为 1～3 根釉柱。外层釉柱切面呈卵圆形，其长轴稍倾斜，均被很厚的釉柱间质包围。上述图像不清晰很可能与切片的方向有关，即该图像并不是垂直门齿纵轴的真正的横切面，而代表与纵轴稍斜交的横切面。也可能代表较原始的特征。

***Zelomys* 上门齿的纵切面**（图版 II） 釉质层的总厚度约为 98μ。其釉质层明显分成两层。内层厚约 62μ。施氏明暗带界线清楚，但带本身的形状不很规则。有时各釉柱间的界线也不清楚。带宽主要为单柱宽，但也有由 2～3 根釉柱组成者。其中单釉柱宽者约占 65%，1～2 釉柱宽者为 13%，2 根釉柱宽者为 13%，2～3 釉柱宽者为 4.5%，3 根釉柱宽者为 4.5%，而且有时出现分叉现象。不同带宽所占的百分比在同一纵剖面上的不同位置会稍有差异，与上述比率相比，2～3 根釉柱宽者比率会稍有增加，而单根柱宽者比率有所减少。但单根柱宽者总是占多数，超过 50%，而且单根和 1～2 根宽者之和总是 80% 左右。施氏明暗带的倾斜度为 0°～5°。釉柱截面形状不规则。釉柱间质很厚，围绕釉柱，其微晶的方向与釉柱平行。外层釉质厚约 36μ，其厚度比率为 37%。釉柱很小，倾角很大。角度由内向外逐渐增大，在近外面处几乎与外面平行。其倾角可由 40°增至近 80°。釉柱间质非常发育，很厚。其微晶方向几乎与外表面垂直，即倾角几乎等于零。无釉柱的最外层很薄。综合来看，*Zelomys* 门齿的釉质微细结构虽属单系，但很原始，似乎是正处在由散系向典型的单系转变过程中。

4 关于 *Zelomys* 的分类位置

争胜鼠 *Zelomys* 是王伴月和李春田（1990）根据在吉林省桦甸县桦甸组中所产的标本建立的。该属共包括两个种：东方争胜鼠（*Zelomys orientalis*）和纤细争胜鼠（*Zelomys gracilis*）。但它们的标本主要是下颌骨和下颊齿，只有一保存有上门齿的部分头骨。该属的下颌骨和下颊齿的形态与先松鼠科（Sciuravidae）的先松鼠（*Sciuravus*）和始鼠科

(Eomyidae)的 *Namatomys* 两者都很相似，而头骨属始啮型。目前已知的先松鼠科的头骨属始啮型，始鼠科的头骨都是松鼠型的，而 *Namatomys* 是根据单个的颊齿建立的，不知其头骨形态。在这种情况下，原作者主要根据头骨形态将 *Zelomys* 归入了 Sciuravidae。但后来，有些古生物学家(Korth, 1994; Chiment & Korth, 1996; 童永生，1997)根据 *Zelomys* 在下颊齿形态上与 *Namatomys* 的相似，认为 *Zelomys* 应归入 Eomyidae。

由上面的描述可以看出，*Zelomys* 的门齿的釉质微细结构属单系。从目前已知的门齿釉质微细结构看，Sciuravidae 的已知门齿都属散系，而 Eomyidae 的为单系 (Wahlert, 1968; Wahlert & Koenigswald, 1985)。单系代表较散系进步的类型，是由散系进化而来的(Wahlert, 1968, Koenigswald, 1985; Martin, 1992, 1993)。由于 *Zelomys* 与 Eomyidae 共有的单系釉质结构为较进步的特征，而 *Zelomys* 与 Sciuravidae 相似的始啮型头骨为较原始的近祖特征，很可能 *Zelomys* 与 Eomyidae 有较近的关系。

在具单系的门齿微细结构的啮齿类中，又可根据釉柱的分布以及其与釉柱间质的关系的不同分为松鼠型和鼠形型两类(Boyde, 1978; Wahlert & Koenigswald, 1985)。在松鼠型单系中，釉柱与釉齿质界面近于垂直，釉柱间质微晶与釉柱平行。在鼠形型的单系中，釉柱与釉齿质界面斜交，釉柱间质微晶与釉柱垂直。与此同时，Wahlert 和 Koenigswald (1985)对已知的 Eomyidae 的门齿釉质微细结构进行了专门研究。他们发现 Eomyidae 的门齿釉质微细结构很特殊。与其他的啮齿类的单系不同，它们的釉质内层又分为两部分，即其釉质可分为三层。其内层外部与松鼠型的单系相似。内层内部则和鼠形型的单系相似。更加特别的是，他们的下门齿的内层外部的施氏明暗带不呈横向，而主要呈纵向排列。尽管如此，Eomyidae 较原始的代表，*Eomys zitteli* 的门齿内层内、外部的釉柱的方向上的差异仍很小。而且，Eomyidae 的上门齿的施氏明暗带仍为横向排列，内层内部釉柱间质的微晶与釉柱仅呈锐角相交。很可能三层珐琅质是由两层的进化来的，而纵向的施氏明暗带是由横向的进化来的。他们认为始鼠所特有的釉质结构是由鼠形类单系进化来的(Wahlert & Koenigswald, 1985, p.11)。然而，Martin(1992, p.29)明确指出，具平行于釉柱的釉柱间质微晶的单系(松鼠型)是由散系直接进化来的，而且比具垂直于釉柱的釉柱间质的单系(鼠形型)的要原始。这样，始鼠科特有的三层门齿也有可能是由松鼠型的单系进化来的。

Zelomys 的门齿的釉质微细结构属最原始的单系。它的施氏明暗带几乎与釉齿质界垂直，釉柱间质围绕釉柱，与釉柱平行，与始鼠科的 *Paradjiaomo* 上门齿的很相似，只是较原始些。这些特点都表明，*Zelomys* 的单系可能属松鼠型。由它向 eomyid 型的门齿进化的可能性是存在的。这也进一步论证了 Martin(1992)的推论。

最近，在我国江苏省溧阳县发现了一些象 *Zelomys* 的啮齿类。其下颊齿与 *Zelomys* 的很相似，可归入该属。其上颊齿很象 Eomyidae 的，而与 Sciuravidae 的区别明显。这些都表明，*Zelomys* 有可能属 Eomyidae 而不属 Sciuravidae。但是，*Zelomys* 的门齿和头骨形态结构都比较原始，如果将它归入 Eomyidae，它显然代表较原始的一类。联系到它的下颊齿的下次脊为横向，与下外脊相连，这些都表明它可能不同于已知的 Eomyinae，它至少代表与目前已知的 Eomyinae 不同的支系。

致谢　在本文撰写过程中曾与李传夔、吴文裕研究员讨论过，获益匪浅；古哺乳动物研究

室的同仁审阅手稿，并提出宝贵意见，杨明婉绘制插图，诚致谢意。

INCISOR ENAMEL MICROSTRUCTURE AND PHYLOGENETIC POSITION OF *ZELOMYS*

WANG Ban-Yue OUYANG Lian

(*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044)

Key words enamel microstructure, Middle Eocene, Eomyidae, Sciuravidae

Summary

Zelomys, known from Middle Eocene of China, was first referred to the Sciuravidae (Wang and Li, 1990). The main reason of the above referral was that it had a protrogomorphous skull, although the lower cheek teeth were similar to both *Sciuravus* (Sciuravidae) and *Namatomys* (Eomyidae). Recently *Zelomys* has been suggested to belong to the Eomyidae (Korth, 1994; Chiment and Korth, 1996; Tong, 1997) based on the similarities of the lower cheek teeth between *Zelomys* and *Namatomys*. To know more precisely the phylogenetic position of *Zelomys* among Rodentia, we examined its incisor enamel structure.

We sectioned only the upper incisors of *Zelomys orientalis* because the material of *Zelomys* was rare. The upper incisors are from V8799 (part of skull) from Middle Eocene Huadian Formation, Huadian County, Jilin Province, China.

We observed the cross section of the left upper incisor after abrading and polishing. Meantime, we cut a segment of the right upper incisor. It was imbedded in artificial resin, then abraded, polished and etched briefly with 0.1mol phosphoric acid. After rinsing and drying, the specimen was coated with gold, and examined with a scanning electronic microscope (JSM-6100).

The upper incisor is oval in cross section, with a slightly flat labial side. The enamel covers the labial side and 1/4 labial part of the lateral side, but does not extend to the medial side. The buccal surface has fine dendritic veins but no distinct groove or ridge.

The incisor enamel consists of two layers: an inner portion (PI: portio interna) and an outer portion (PE: portio externa).

For some reason, in the cross section the picture of the enamel microstructure is not very clear, especially in the straight labial part, where it looks rather obscure. However, a careful observation revealed that the enamel included two layers, with an obscure boundary (Pl. I, 2). In PI the Hunter-Schreger bands (HSB) are clear, and

1～3 prisms wide. In adjacent bands they decussate at nearly 90°. In PE the prisms are oval in section, with major axis perpendicular to the external surface. The developed IPM crystallites are almost perpendicular to the external surface. In the lateral part of the labial side and the labial part of the lateral side the picture of the microstructure is clearer. The boundary of the two layers is distinct. However, the boundary of the HSB in PI is blurred. The width of the HSB varies from one to three prisms. The prisms of PE are oval in section and surrounded by thick interprismatic matrix (IPM). They are of radial enamel type.

In the longitudinal section the total thickness is about 98μ. Two layers of the enamel are distinct. The PI thickness is about 62μ. The HSB are distinct, but irregular in shape, and variable in width. The band is usually 1 or 1～2 prism wide (near 80%), occasionally 1～3 or 3 prisms wide (near 20%). Most of them are one prism wide (50%～65%). Occasionally a forked band can be observed. The bands are nearly perpendicular to the enamel dentine junction (EDJ), with 0°～5° inclination. The prisms are irregular in shape. The IPM is distinct, and surrounds the prisms. The IPM crystallites run parallel to the prisms. The PE is nearly 36μ thick. The radial enamel is composed of small prisms, which run nearly parallel to each other, but the inclinations increase from near the boundary between the PI and PE (near 40°) to the most outer side (near 80°) gradually. The IPM is very developed and thick. The IPM crystallites run perpendicularly to the EDJ. It seems that the enamel microstructure of *Zelomys* belongs to uniserial type, but represents a relatively primitive stage (see below for further discussion).

The known enamel microstructures of Sciuravidae are all of pauciserial and those of Eomyidae are of uniserial. The uniserial is known to be derived from the pauciserial and represent a more advanced enamel type than the latter (Wahlert, 1968; Koenigswald, 1985; Martin, 1992, 1993). Thus, we infer that *Zelomys* has closer relationship with the Eomyidae than with the Sciuravidae.

The uniserial is known to be divided into two subtypes: sciurid type and myomorph type (Boyde, 1978; Wahlert and Koenigswald, 1985). In the former the HSB are perpendicular to the EDJ and the IPM crystallites are parallel to the prisms in the PI; whereas in the latter the HSB is inclined to the EDJ and the IPM crystallites run across the prisms at 90°. Wahlert and Koenigswald (1985) stated that the eomyid enamel was very special: the PI enamel was divided into two parts, the HSB in the outer part of PI were longitudinal rather than transverse as is common in rodents, the PI outer part was similar to the uniserial bands in sciurids, and the PI inner part resembled those in myomorphs. They supposed "the special eomyid Schmelzmuster is derived from the myomorph type of uniserial enamel." However, in the same paper they described two specimens. One was the lower incisor of *Eomys* *zitteli*, in which the orientation of the longitudinal HSB between the inner and outer parts of PI showed no difference in cross section. Another was the upper incisor of *Paradjidaumo*, of which the HSB were oriented transversely and inclined apically, and the difference between the inner and outer parts of PI was showed only in the different relationships of matrix to prisms. In the outer part crystallites of both IMP and prisms were parallel. In the inner part crystallites of IMP radiated from the EDJ, whereas prisms and their crystallites ascended apically and those of adjacent bands decussated. Thus the crystallites of IPM were across the prisms in acute angle. Both specimens show more primitive cases of the eomyid enamel. Martin (1992) believed that the uniserial enamel of sciurid type was directly derived from the pauciserial enamel and more primitive than those of myomorph type. It seems that the three layers of the enamel of the eomyid uniserial can derived from two layers of the sciurid type uniserial.

The uniserial enamel of *Zelomys* is similar to that of *Paradjidaumo*, but more primitive. Possibly the special enamel of eomyid uniserial can be derived from that of *Zelomys*.

Recently some *Zelomys*-like rodents have been discovered in the Middle Eocene of Liyang County, Jiangsu Province, China. The lower cheek teeth are similar to those of *Zelomys* and the upper ones resemble those of the Eomyidae and differ from those of the Sciuravidae. This indicates that probably *Zelomys* belongs to the Eomyidae rather than the Sciuravidae. As mentioned above, *Zelomys* possesses some primitive features, more primitive incisor enamel structure and protrogomorphous skull. *Zelomys* may represent a primitive taxon if it is referred to the Eomyidae. In addition, *Zelomys* is also different from the Eomyinae in having transverse hypolophid joining the ectolophid in the lower cheek teeth. It appears that *Zelomys* may represent a primitive lineage distinct from the Eomyinae.

References

Boyde A, 1978. Development of the structure of the enamel of the incisor teeth in the three classical subordinal groups of Rodentia. In: Butler P M, Josey K A eds. Development, function and evolution of teeth. London: Academic Press. 43～58

Chiment J J, Korth W W, 1996. A new genus of eomyid rodent (Mammalia) from the Eocene (Uintan-Duchesnean) of southern California. J Paleont, **16**(1): 116～124

Korth W W, 1994. The Tertiary record of rodents in North America. New York: Plenum Press. 1～319

Korvenkontio V A, 1934. Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmelzstruktur der Backenzähne. Ann Zool Soc Zool-Bot Fennicae Vanamo, **2**: 1～274

Martin T, 1992. Schmelzmikrostruktur in den Inzisiven alt- und neuweltlicher hystricognather Nagetiere. Palaeovertebrata, Mem Extra: 1～168

Martin T, 1993. Early rodent incisor enamel evolution: phylogenetic implications. J Mammal Evol, **1**(4): 227～254

McKenna M C, Bell S K, 1997. Classification of mammals above the species level. New York: Columbia Univ.

Press. 1～631

Tong Y S (童永生), 1997. Middle Eocene small mammals from Liguanqiao Basin of Henan Province and Yuanqu Basin of Shanxi Province, central China. Palaeontol Sin (中国古生物志), New Ser C, **26**: 1～256 (in Chinese with English summary)

von Koenigswald W, 1985. Evolutionary trends in the enamel or rodent incisors. In: Luckett W P, Hartenberger J -L eds. Evolutionary relationships among rodents. New York: Plenum Press. 403～422

Wahlert J H, 1968. Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and recent rodent groups. Breviora, (309): 1～18

Wahlert J H, von Koenigswald W, 1985. Specialized enamel in incisors of eomyid rodents. Am Mus Novit, (2832): 1～12

Wang B Y (王伴月), Li C T (李春田), 1990. First Paleogene mammalian fauna from Northeast China. Vert PalAsiat (古脊椎动物学报), **28**(3): 165～205 (in Chinese with English summary)

图版说明 (Explanations of plates)

图版 I (Plate I)

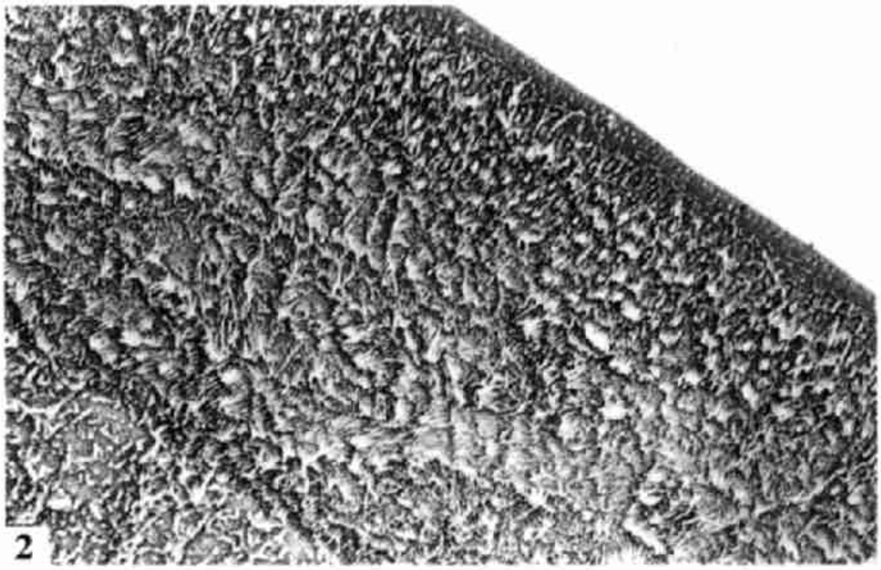
东方争胜鼠(V8799)左上门齿横切面 [Cross section of left upper incisor of *Zelomys orientalis* (V8799)]

1. 左上门齿横切面的形状，并标明所观察的微细结构的位置 (Cross section showing the position of two parts observed): a: 唇侧平直部位 (straight part of labial side); b. 唇侧外部 (lateral part of labial side), ×35
2. 唇侧平直部(1a)釉质微细结构 (microstructure of 1a), ×1000
3. 唇侧外部(1b)釉质微细结构 (microstructure of 1b), ×1000

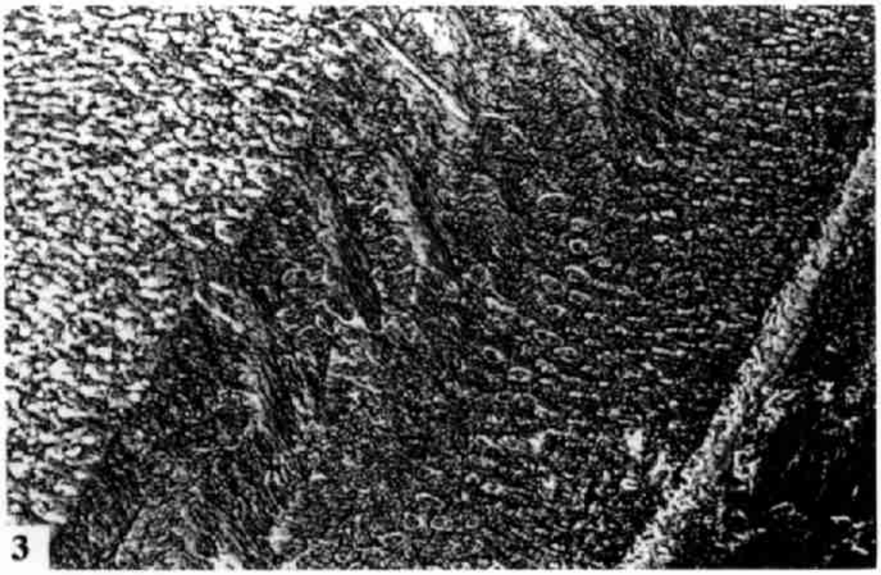
图版 II (Plate II)

东方争胜鼠(V8799)右上门齿纵切面微细结构 [Microstructure of longitudinal section of right upper incisor of *Zelomys orientalis* (V8799)] 1. ×500; 2. 图1的部分放大 (part of fig. 1) ×1600。图中文字缩写 (Abbreviations): D, 齿质 (dentine); EDJ, 釉齿质界 (enamel dentine junction); IPM, 釉柱间质 (interprismatic matrix); P, 釉柱 (prismas); PE, 外层 (portio externa); PI, 内层 (portio interna); PLEX, 无釉柱的最外层 (prismless external layer)

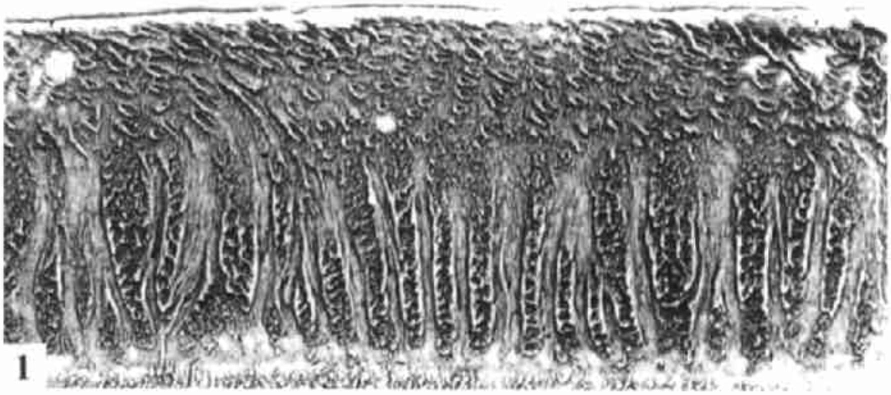
1



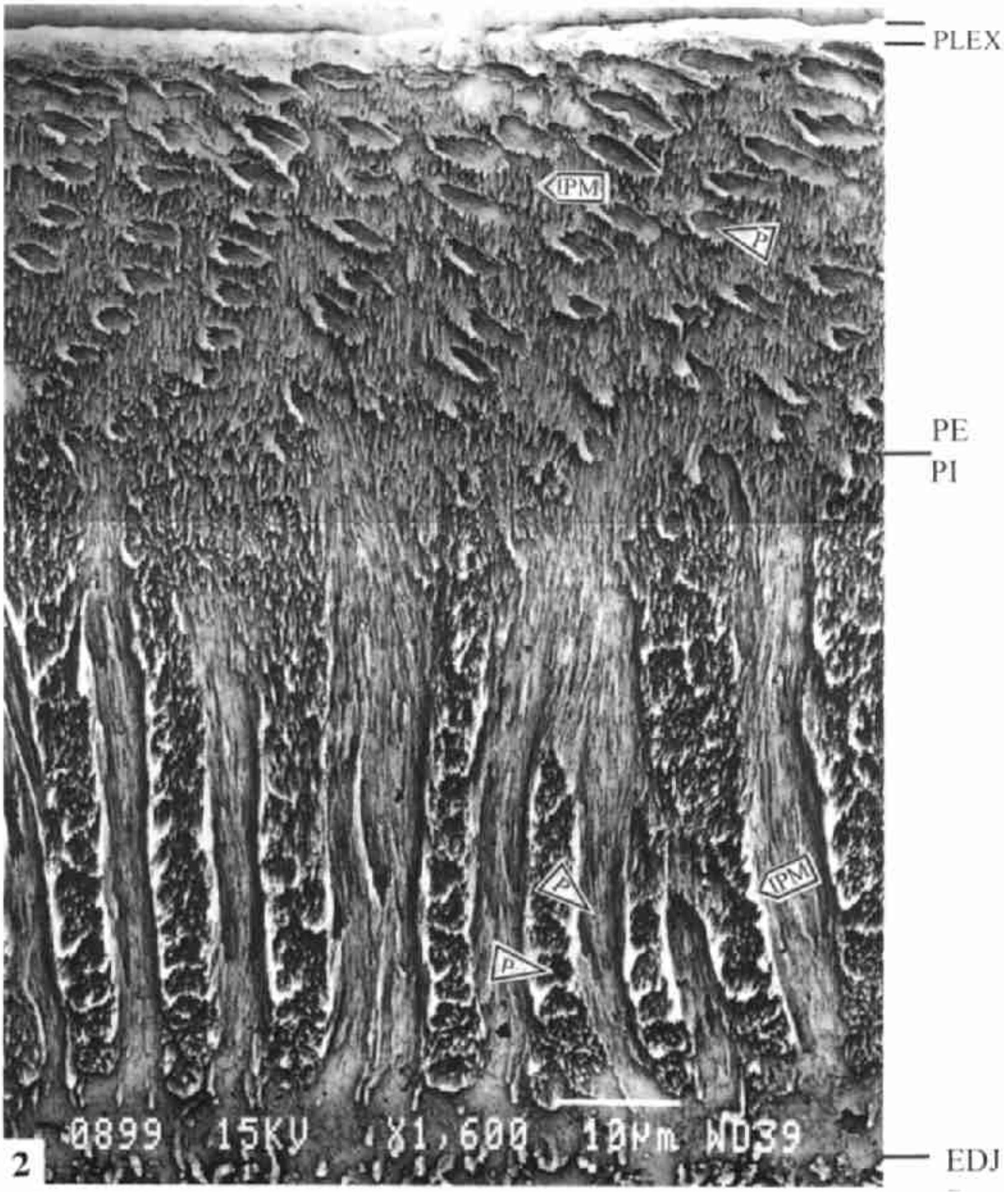
2



3



1



2