

内蒙古梳趾鼠类一新科——双柱鼠科

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关键词 内蒙古 中中新统 上渐新统 梳趾鼠超科 双柱鼠科

内 容 摘 要

本文记述了采自内蒙古中中新统和上渐新统啮齿动物一新属——双柱鼠属 (*Distylomys*) 的两个新种 *D. tedfordi* 和 *D. qianlishanensis*。它们是一类很特别的鼠类,可能代表了梳趾鼠超科中的一个新科: 双柱鼠科 *Distylomyidae*。文中讨论了梳趾鼠超科中各科之间,以及它与 *hystricognaths* 的关系。

1978年笔者在内蒙古自治区伊克昭盟千里山地区考察时,在上渐新统伊克布拉格组中发现了可能为同一个体的啮齿动物的左、右下颌骨。它的颊齿形态很特别,虽经多方对比,始终未能确定它的分类位置。它的颊齿数目和形态很象南美的一种豚鼠 *Cephalomys*。遗憾的是内蒙古的这两件标本未保存下颌角部分,笔者无法进一步判定它们和有关豚鼠之间的关系。1984年,笔者访问纽约美国自然历史博物馆时,发现在美国第三中亚考察团1928年采集的标本中,也有类似形态的一枚下颌骨。它采自内蒙古通古尔地区中中新统通古尔组。这件标本由于保存了下颌角基部,为我们认识这类啮齿动物的系统位置提供了关键的特征。这证明这类啮齿动物与 *Cephalomys* 属于不同的支系。我们还切片观察了它们的门齿珐琅质的微细结构。研究表明,内蒙古这些材料可能代表 *Ctenodactyloidea* 超科的一个独特的分支。这一发现表明 *Ctenodactyloidea* 在系统发育和分类上远比目前已知的要复杂。

美国自然历史博物馆的 R. H. Tedford 博士给予笔者多方面的帮助,并将该馆所藏的,尚未研究的标本借给笔者研究。美国哈佛大学的 L. J. Flynn 博士帮助做 *Cephalomys* 的门齿切片和电镜照片,美国 Amherst 学院 M. C. Coombs 博士和阿根廷 Platina 国立大学的 M. G. Vucetich 博士及时寄来有关的标本和模型。乌拉圭国家自然历史博物馆的 A. Mores 博士提供了有益的信息,胡惠清同志绘图,欧阳莲同志磨制门齿切片和照相,杜治同志照相,著者一并表示感谢!

一、系统描述

? 梳趾鼠超科 ?*Ctenodactyloidea* Simpson, 1945

双柱鼠科(新科) *Distylomyidae* fam. nov.

双柱鼠属(新属) *Distylomys* gen. nov.

属型种 *Distylomys tedfordi* 新种。

属的特征 中小型梳趾鼠类。下颌骨较粗壮, 颞孔位于齿隙中部近上缘处; 咬肌嵴很发达, 伸达 P_4 下方, 具松鼠型下颌角。齿式 $\overline{I013}$ 。 P_4 臼齿化, 与臼齿几乎等大, 跟座宽于三角座。颊齿高冠, 无齿根; 颊齿呈双三角柱形; 三角座柱与跟座柱连接处很窄, 位于齿的中部; 下中折和下外折都很发达, 深而开阔, 彼此相对, 中有白垩质填充; 牙齿嚼面双叶型, 磨蚀后光滑而凹入; 珐琅质在齿后缘变薄或完全消失。门齿珐琅质为复系结构。

包括种 *Distylomys qianlishanensis* 新种。

时代和地理分布 中国内蒙古晚渐新世—中中新世。

名称来源 Di+stylo+mys (希): 双+柱+鼠, 表示该动物具双棱柱形的颊齿。

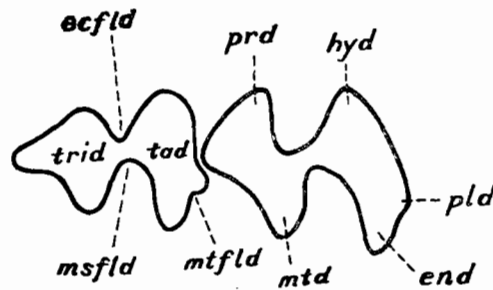


图1 *Distylomys* 下颊齿结构名称

Fig. 1 Terminology of the lower cheek teeth of *Distylomys*

ecfld. ectoflexid 下外折; end. entoconid 下内尖; hyd. hypoconid 下次尖; msfld. mesoflexid 下中折; mtd. metaconid 下后尖; mtfld. metaflexid 下后折; pld. posterolophid 下后边脊; prd. protoconid 下原尖; tad. talonid 下跟座; trid. trigonid 下三角座

特氏双柱鼠(新种) *Distylomys tedfordi* sp. nov.

(图版 I, 3—6, 图 2)

正型标本 右下颌骨具 I 和 P_4-M_2 (美国自然历史博物馆编号: AMNH no. 114262)

产地和层位 内蒙古锡林浩特苏尼特左旗通古尔地区 Tairum Nor 盆地; 中中新统, 通古尔组。

特征 下颌骨粗壮; 颊齿跟座比例上较宽短; P_4 前端较尖; 下后折在 P_4 明显, 但很浅, 在 M_1 有残留痕迹, 在 M_2 完全消失。

名称来源 Tedford, 人名, 用以向 R. H. Tedford 博士致意。

描述 下颌骨体唇面凸, 舌面稍凹, 下缘呈 S 形弯曲。颞孔位于齿隙中部近上缘处。咬肌窝下咬肌嵴非常发达, 明显突出, 从 P_4 下方斜向后下方伸达下颌角。无明显的咬肌窝上缘。下颌角大部分破损, 仅保存了下颌角基部。下颌角位于门齿齿槽下方, 属于松鼠型下颌角。

下门齿向后伸达 M_2 下方。门齿横切面为三角形。珐琅质表面光滑, 无明显纹饰。

颊齿为高冠齿, 无齿根。每个颊齿均由两个前凸的三角柱组成。跟座柱的前边棱与三角柱的后面中部相连, 连接处很窄。下中折和下外折彼此相对, 都很深, 均有白垩质充填。颊齿嚼面双叶型。AMNH no. 114262 颊齿嚼面经磨蚀后呈光滑微凹的面, 未见嚼面结构。珐琅质在三角座和跟座前缘较厚, 在跟座后缘明显变薄, 甚至完全消失。

P_4 : 三角座窄于跟座, 约呈等边三角形, 前端较窄, 舌面明显凹入, 唇面稍凹。跟座宽扁, 唇端浑圆, 舌端下内尖处前后压缩, 后面有一向后内方的突起, 可能为下后边脊的内端。有明显的下后折, 但很浅。

M_1 和 M_2 的大小和形状相近。三角座明显变宽, 其宽度和形状与跟座的相近, 均呈前后压扁的三角形, 但跟座唇端较尖锐。下后折在 M_1 很弱, 在 M_2 完全消失。

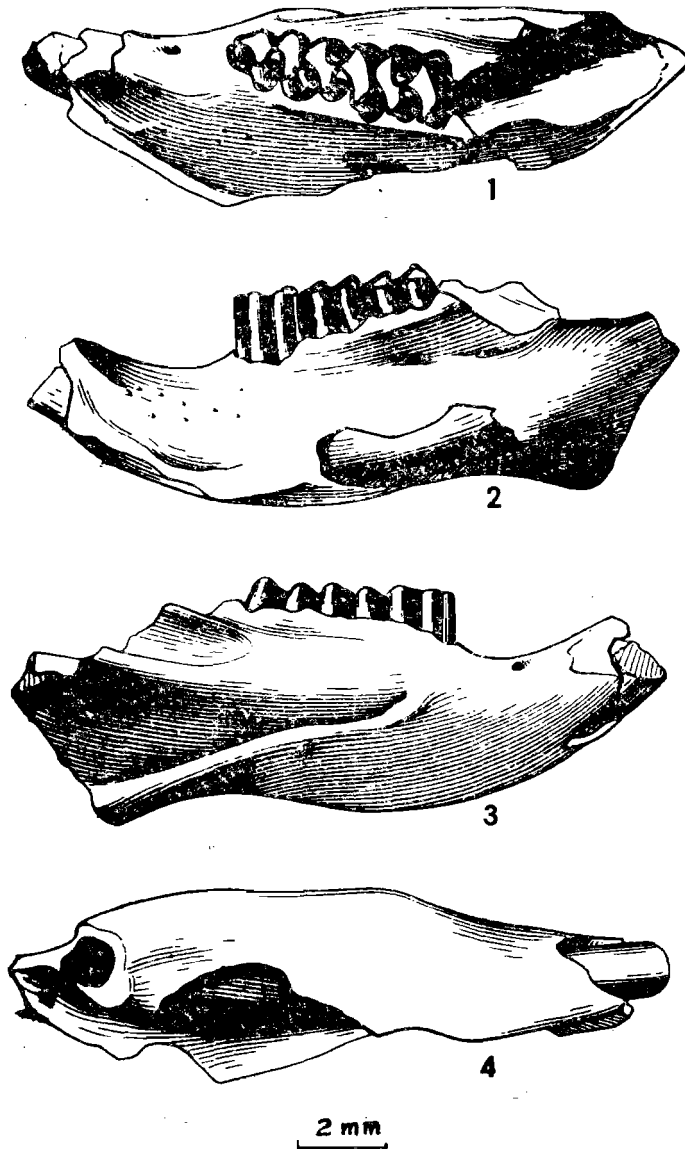


图 2 *Distylomys tedfordi* 新属、新种 正型标本: 右下颌具 P_4-M_2 , (AMNH no. 114262)
1. 嚼面观, 2. 舌面观, 3. 唇面观和 4. 腹面观

Fig. 2 *Distylomys tedfordi* gen. et sp. nov. Holotype: right lower jaw with P_4-M_2 (AMNH no. 114262) 1. occlusal view, 2. lingual view, 3. labial view and 4. ventral view

千里山双柱鼠(新种) *Distylomys qianlishanensis* sp. nov.

(图版 I, 1-2, 图版 II; 图 3)

正型标本 可能为同一个体的具 P_4-M_2 和 M_3 三角座的左下颌骨和具 P_4-M_3 的右下颌骨(古脊椎动物与古人类研究所化石编号: V 7961)。

产地和层位 内蒙古伊克昭盟鄂托克旗伊克布拉格, 中国科学院古脊椎动物与古人类研究所野外地点编号: 79017 地点; 上新新统, 伊克布拉格组。

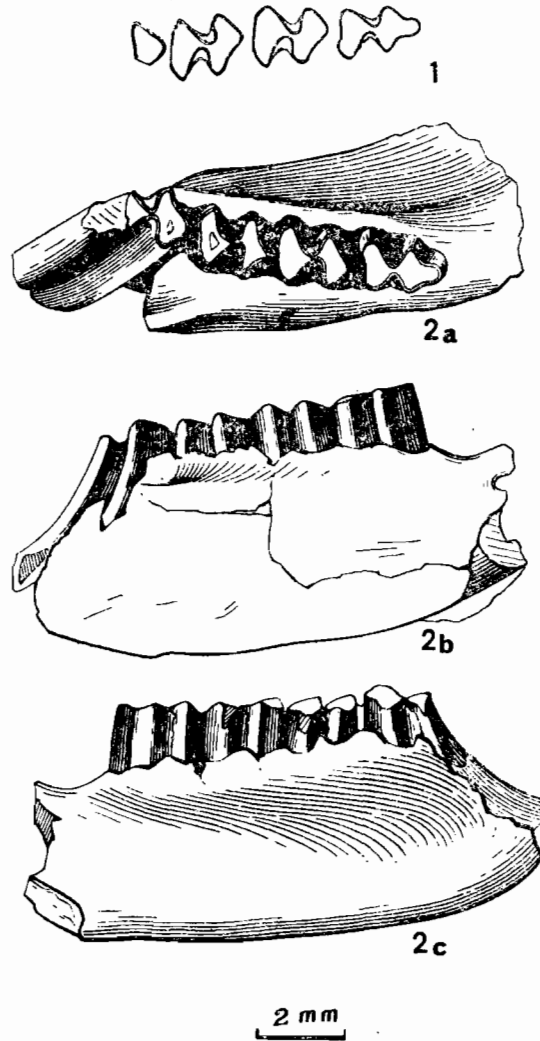


图 3 *Distylomys qianlishanensis* 新种

正型标本: 可能为同一个体的左、右下颌骨 (V 7961)。1. 左 P_4-M_2 和 M_3 三角座嚼面; 2. 右下颌骨具 P_4-M_3 , 2a. 嚼面观, 2b. 唇面观, 2c. 舌面观

Fig. 3 *Distylomys qianlishanensis* sp. nov.

Holotype: right and left lower jaws which may be the same individual (V 7961).
1. left P_4-M_2 and trigonid of M_3 , occlusal view; 2. right lower jaw with P_4-M_3 ,
2a. occlusal view, 2b. labial view and 3c. lingual view

特征 尺寸较 *D. tedfordi* 约大 $\frac{1}{4}$ 。下颌骨较粗壮。门齿相对较窄。颊齿, 特别是跟座相对较窄长。P₄ 三角座前端较钝圆。颊齿无任何下后折的痕迹。

名称来源 Qianlishan 千里山, 化石地点名称。

描述与比较 下颌骨体比 *Distylomys tedfordi* 的粗壮。唇面更凸, 舌面凹入明显。颊孔位置较 *D. tedfordi* 的低。

门齿伸达 M₂ 下方, 横切面为次长方形, 舌唇向较长, 横向较窄。珐琅质表面光滑。珐琅质的微细结构为复系 (multiserial)。珐琅质层厚约 0.132 毫米, 由两层珐琅质层组成。外珐琅质层较薄, 仅为珐琅质层总厚的 12%。内珐琅质层的带约呈 55° 倾斜。每条带平均宽约 0.0168 毫米, 由 3—5 根柱组成。

颊齿比 *D. tedfordi* 的大, 跟座相对较窄长。P₄ 和下臼齿均无任何下后折的痕迹。P₄ 前端较钝圆。臼齿跟座与三角座相连接的窄颈部相对较短。M₃ 跟座比三角座窄。

表 1 *Distylomys* 牙齿测量(单位: 毫米)

| | | <i>D. tedfordi</i> AMNH no. 114262 | <i>D. qianlishanensis</i> V 7961 | |
|---------------------------------------|--------------------|--|-------------------------------------|--------|
| | | | (right) | (left) |
| P ₄ -M ₂ 长 (L.) | | 4.64 | 6.24 | 6.32 |
| P ₄ | 长 (L.) | 1.6 | 2.16 | 2.16 |
| | 三角座宽 (W. of trid.) | 0.88 | 1.28 | 1.28 |
| | 跟座宽 (W. of tad.) | 1.12 | 1.44 | 1.44 |
| M ₁ | 长 (L.) | 1.76 | 2.08 | 2.08 |
| | 三角座宽 (W. of trid.) | 1.2 | 1.76 | 1.6 |
| | 跟座宽 (W. of tad.) | 1.36 | 1.76 | 1.76 |
| M ₂ | 长 (L.) | 1.68 | 1.92 | 2.0 |
| | 三角座宽 (W. of trid.) | 1.36 | 1.76 | 1.76 |
| | 跟座宽 (W. of tad.) | 1.44 | 1.76 | 1.6 |
| M ₃ | 三角座宽 (W. of trid.) | | 1.76 | |
| | 跟座宽 (W. of tad.) | | 1.6 | |
| I | 唇舌向长 (L.) | 1.28 | 1.68 | |
| | 横宽 (W.) | 1.2 | 1.28 | |

二、讨 论

(一) 关于 *Distylomys* 的系统位置

Distylomys 的颊齿形态很特别。初看起来, 它的颊齿形态结构与南美豚鼠类的很相似。豚鼠 (Caviomorpha) 的分布仅限于南美, 具有豪猪型咬肌结构和豪猪型下颌角, 最早的代表出现于早渐新世。*Distylomys* 的颊齿形态与产于阿根廷早渐新世的豚鼠 *Cephalomys* (Wood, 1959, 339 页, 图 19) 特别相似, 如两者的下牙的齿式为 $\overline{1013}$; 下颊齿均由

两齿柱组成,三角座柱与跟座柱连接处很窄,位于纵轴附近,下中折和下外折彼此相对; P_4 臼齿化,三角座呈尖端向前的三角形,跟座宽于三角座;门齿珐琅质为复系等。但是, *Distylomys* 的下颌角从下门齿齿槽下方伸出,应属松鼠型下颌角。而 *Cephalomys* 具豪猪型下颌角,它的下颌角从下门齿齿槽外侧伸出。这一区别不但将 *Distylomys* 与 *Cephalomys* 从根本上分开了,而且也使 *Distylomys* 不能归入 Caviomorpha 这一大类。这样, *Distylomys* 与 *Cephalomys* 在颊齿上的相似只能用平行进化来解释了。

在具松鼠型下颌骨的啮齿动物中,下颌具 $\overline{I013}$ 齿式和高冠齿的有 Aplodontoidea, Theridomyoidea, Heteromyidae, Geomyidae, Anomaluridae, Pedetidae 和 Ctenodactyloidea 等。但前五类的门齿珐琅质结构为单系 (uniserial) 或散系 (pauciserial), 而且颊齿的形态和结构特征与 *Distylomys* 的区别也很明显。只有 Pedetidae 和 Ctenodactyloidea 具复系 (multiserial) 珐琅质结构的门齿。 *Distylomys* 在 P_4 臼齿化和颊齿为双叶型的特点与 Pedetidae 的相似,但两者的颊齿的其他结构都明显不同。

Distylomys 与 Ctenodactyloidea 比较,情况比较复杂。Ctenodactyloidea 目前包括四科: Ctenodactylidae Zittel, 1893, Cocomyidae Dawson et al., 1984, Yuomyidae Dawson et al., 1984 和 Chapattimyidae Hussain et al., 1978。关于 Ctenodactyloidea 中各科的相互关系, Dawson 等 (1984, 149 页) 认为 Ctenodactyloidea 在始新世时已分成两支。Cocomyidae 代表一支,这一支的主要特点是 P_4 非臼齿化。Ctenodactylidae 可能代表 Cocomyidae 的后裔。Yuomyidae 代表另一支。笔者 (1984, 46 页) 曾进一步指出 Chapattimyidae 与 Yuomyidae 属同一支,它们的共近裔特征是 P_4 次臼齿化。Flynn 等 (1986, 42 页) 也认为 Chapattimyidae 和 Yuomyidae 是姐妹组。不过他倾向于将 Cocomyidae 从 Ctenodactyloidea 中排除或作为单系科归入 Ctenodactyloidea 超科。

将 *Distylomys* 与 Ctenodactyloidea 各科比较, *Distylomys* 在下颌骨和颊齿的一些特点上与某些 ctenodactylids 的较相似。如它的咬肌窝较向前伸,咬肌嵴很发达,明显向前伸和无明显的咬肌上缘等特点与某些渐新世的 ctenodactylids 如 *Woodomys*、*Karakorumys*、*Tatāromys* 和 *Leptotataromys* 的相似。但它的颊齿却比这些属的进步得多。与此相反, *Distylomys* 的颊齿形态,如双叶型高冠齿,下中折和下外折同等发达,彼此相对,有时有下后折存在,嚼面磨蚀后光滑,无尖和脊的结构等特点与某些较晚期的、或现生的 ctenodactylids, 如 *Pectinator*、*Ctenodactylus*、*Felovia*、*Massouteria*、*Irhoudia* 和 *Pellegrinia* 的相似,然而 *Distylomys* 的下颌骨的形态却与这些属的不同。前者的咬肌嵴与下颌角相连,而后者的与下颌髁相连等。此外, Ctenodactyloidea 的 P_4 非臼齿化,而且有逐渐退化变小,甚至完全消失的趋势,而 *Distylomys* 的 P_4 臼齿化,尺寸与臼齿的相近。在这一点上, *Distylomys* 显然与 Chapattimyidae 和 Yuomyidae 的一致。但是后两科的下颌骨和颊齿的其他特点都与 *Distylomys* 的不相同,显得原始得多。 *Distylomys* 与 Cocomyidae 的区别更加明显。由上面的比较可以看出,即使将 *Distylomys* 归入 Ctenodactyloidea, 它也代表一独立的科,我们称之为双柱鼠科 Distylomyidae。

假若把 Distylomyidae 归入 Ctenodactyloidea 的意见是正确的话,那么它与该超科中其他各科的关系,根据现有的材料看,似乎存在两种可能性: 如果根据 P_4 臼齿化的特

点, *Distylomyidae* 与 *Chapattimyidae* 和 *Yuomyidae* 这一支有较近的关系; 如果强调下颌骨和颊齿形态上的相似, *Distylomyidae* 则与 *Cocomyidae* 和 *Ctenodactylidae* 属于同一支系。

在权衡这两种可能性的时候, 我们特别注意了 P4 臼齿化的意义。过去通常认为 P4 非臼齿化是啮齿类的原始特点之一。Wood (1962, 139—147 页) 曾假设啮齿类祖先的 P4 都是非臼齿化的。Dawson 等 (1984, 146—147 页) 和李等 (待刊) 根据 *Heomys* 和 *Cocomys* 的 P4 的特点也认为非臼齿化的第四前臼齿是啮齿类的原始特点之一。但是 Butler (1941, 444 页) 曾指出: “在颊齿的进化过程中, 功能上最重要的牙齿是最进步的, 而功能上最不重要的前面的前臼齿和乳齿趋向于保持古老的特征。” 我们发现 *Cocomys* 这一亚洲目前已知最早的啮齿类虽具非臼齿化的 P4, 但它的 DP⁴ 是臼齿化的。而且 *Ctenodactylidae* 也有类似的现象, 它们的 DP⁴ 和 DP₄ 均臼齿化。此外, *Chapattimyidae*、*Yuomyidae* 和 *Paramyidae* 目前已知的 DP₄ 也都是臼齿化的。如果 Butler 上述的看法是正确的话, 上述情况表明 P4 臼齿化代表啮齿类的原始特征。而非臼齿化的 P4 并不代表啮齿类的原始特征, 而是一种进步特征。事实上, *Cocomys* 的 P₄ 的三角座仅稍宽于跟座, 跟座仅稍退化, 似乎表示 P4 非臼齿化的开始。此外, 从啮齿类颊齿的总的进化趋势和目前已知最早的啮齿类, 北美晚古新世的 *Acritoparamys* 的 P⁴ 也是臼齿化来看, 这一推论也是合理的。

如果臼齿化的 P4 代表啮齿类的原始特征的看法是正确的话, *Cocomyidae* 和 *Ctenodactylidae* 的非臼齿化的 P4 不是原始特征, 而是进步特征。相反地, *Distylomyidae*、*Chapattimyidae* 和 *Yuomyidae* 却保留了原始的、臼齿化的 P4。这样 *Cocomyidae* 和 *Ctenodactylidae* 以非臼齿化的 P4 作为其近裔共性而与后三科从较基部分开了。这样一来, *Distylomyidae* 与 *Ctenodactylidae* 在颊齿和下颌骨上的相似可能是平行进化的结果。因此, 笔者考虑 *Distylomyidae* 可能是 *Chapattimyidae*-*Yuomyidae* 的姐妹群。但是 *Chapattimyidae*-*Yuomyidae* 这一组总的来说变化较少, 在颊齿和下颌骨形态上都保持了许多原始特征。而 *Distylomyidae* 则偏离较远, 获得了许多特化特征, 如高冠的双柱型齿, 前伸的咬肌窝和发达的咬肌嵴等。根据 P4 臼齿化等特点, *Pedetidae* 有可能也和 *Distylomyidae* 等科属同一支系。

在 *Distylomys* 属中, *D. tedfordi* 的个体较小, 而且 P₄ 和 M₁ 都保留下后折。而 *D. qianlishanensis* 的个体较大, 颊齿未保留下后折的任何痕迹。在这些特点上, *D. tedfordi* 显得比 *D. qianlishanensis* 更原始。但 *D. tedfordi* 产出的时代为中中新世, 较 *D. qianlishanensis* (晚渐新世) 产出的时代晚。很可能这两个种代表不同的支系。

(二) 关于具豪猪型下颌骨的啮齿动物的起源和相互关系

豪猪型下颌骨的特点是下颌角从下门齿齿槽外侧伸出。具豪猪型下颌骨的啮齿动物 (*Hystricognathi*) 目前至少包括 *Hystricidae*、*Caviomorpha*、*Thryonomyoidea* 和 *Bathyergoidea*。关于它们的起源和相互关系一直是人们关注的问题。尽管有关学者一致认为南美的 *Caviomorpha* 与非洲的 *Thryonomyoidea* 在形态上很相似, 但关于它们的起源、相互关系和迁徙等问题都存在不同的看法, 而且争论很激烈。归纳起来大致有三种看

法。以 Wood 为代表的观点是 Hystricognathi 还包括他认为具原始豪猪型下颌角的啮齿动物——Framomorpha。他认为 hystricognaths 是由 franimorphs 起源的。但是它的各分支的起源地不同。如南美的 Caviomorpha 是由中美的 franimorphs 起源的,旧大陆的 Hystricidae 和非洲的 Thryonomyoidea 是独立地由亚洲目前尚不知的某种 franimorphs 起源的等。它们彼此的相似是平行进化的结果。他认为 ctenodactylids 与 hystricognaths 没有直接的亲缘关系。Lavocat 的观点与 Wood 的截然不同。他认为 hystricognaths 是由非洲起源的。原始的 Phiomorpha 分化成三支:一支是非洲的 Phiomorpha (包括 Thryonomyoidea 和 Bathyergoidea 两超科);另一支为旧大陆的 Hystricidae;而第三支飘过大西洋,进入南美,发展为 Caviomorpha。第三种观点是 Hussain 等(1978)首先提出的。他们认为亚洲的 Chapattimyidae 可能代表 Caviomorpha 和 Phiomorpha 等的共同的祖先类型。随后,Jaeger (1985)根据在西北非阿尔及利亚上始新统发现的最原始的 Phiomysidae 化石 *Protophiomys*,认为非洲的 Phiomysidae 是亚洲 Chapattimyidae 的一支迁入非洲发展成的,它与 Chapattimyidae 组成姐妹组。Flynn 等(1986, 48 页, 24 图)则表明 ctenodactylids 和 hystricognaths 是姐妹组。这第三种观点与 Wood 所提出的 Hystricognathi 从北半球起源的观点很接近,而与 Lavocat 的 hystricognaths 由北非起源的观点不同。但是他们普遍认为非洲的 Phiomorpha 与南美的 Caviomorpha 有更近的亲缘关系。在这一点上,他们又与 Lavocat 的一致。

笔者认为 Chapattimyidae 的颊齿与 Thryonomyoidea 的的确很相似。特别是在非洲始新统中发现的 *Protophiomys* 的牙齿特征进一步证明了 Thryonomyoidea 可能是由 Chapattimyidae 中产生的。此外,Chapattimyidae 与某些 caviomorphs 和 hystricids 在颊齿上也很相似,有些脊形的 caviomorphs 有可能由像 chapattimyids 的丘形齿发展而来。根据它们在颊齿上的相似似乎可以考虑 thryonomyoids、caviomorphs 和 hystricids 等 hystricognaths 构成了 chapattimyids 的姐妹组。但是这样的结论仍存在一些问题。其关键是下颌角的形态问题。hystricognaths 具豪猪型下颌角,而已知的 chapattimyids 的下颌角是与其他的 ctenodactylids 的一样,都是松鼠型下颌角。笔者认为松鼠型下颌角代表较原始类型,豪猪型下颌角代表较进步的类型。后者可能由前者进化发展来。问题是豪猪型下颌角产生的时间,是先于具非臼齿化的 P4 的 *Cocomys* 的分化,还是更晚些?假如 *Cocomys* 的 P4 非臼齿化的分化早于豪猪形下颌角的形成,而且上述类型的豪猪型下颌角是由类似于 chapattimyids 的一支发展来的,很可能 chapattimyids 就是上述那些 hystricognaths 的姐妹组。在这种情况下,仍将 Chapattimyidae 包括在 Ctenodactyloidea 中,那么 Ctenodactyloidea 就是并系发生了。因此,只能将 Chapattimyidae 从 Ctenodactyloidea 中排除。如果豪猪型下颌角产生的时间更早些,例如早于具非臼齿化 P4 的 *Cocomys* 分化,这样,作为分类特征,下颌角的区别则显得比牙齿上的相似更重要。倘若以下颌角的结构为其基本分类特征,不应是单个的 Chapattimyidae,而至少应是包括 Chapattimyidae 在内的整个 Ctenodactyloidea 超科与 hystricognaths 构成姐妹组。

在 Distylomyidae 与 *Cephalomys* 的关系上也存在类似的问题。如果豪猪型下颌角发生的时间较晚,Distylomyidae 与 *Cephalomys* 在颊齿上的如此相似也应表明它们有较近的亲缘关系,可能有较近的共同祖先。要是情况果真如此,那么也得将 Distylomyidae 从

Ctenodactyloidea 中排除。特别是目前发现 Distylomyidae 的地理位置也值得进一步考虑。chapattimyids 主要发现于南亚印度次大陆(最早出现于中始新世), 而 distylomyids 是在我国内蒙古发现的(目前最早出现于晚渐新世)。这说明在亚洲北方大陆上也有类似于南方大陆的 hystricognaths (如南美的 *Cephalomys*) 的啮齿动物存在。这是否说明 hystricognaths 就是由亚洲大陆起源的? 更进一步, 已知最早出现于晚渐新世的 distylomyids 在亚洲大陆的出现是由于印度板块与亚洲大陆板块相撞后由印度次大陆上类似于 chapattimyids 类型发展迁到北方的, 还是它本身就起源于北方? 这些问题尽管目前还不能解决, 但的确是耐人寻味, 值得探索的。

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DISTYLOMYIDAE FAM. NOV. (?CTENODACTYLOIDEA, RODENTIA) FROM NEI MONGOL, CHINA

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Key words Nei Mongol; Upper Oligocene; Middle Miocene; Ctenodactyloidea; Distylomyidae

Summary

Introduction

A pair of rodent lower jaws believed belonging to one and the same individual were collected by the present author from Upper Oligocene Yikebulage Formation in Qianlishan district, Ih Ju League (=Yih Ju Meng), Nei Mongol, in 1978. The affinity searching of the lower jaws has really been a brain-racking one. At first glance I was struck by the similarity between their teeth and those of *Cephalomys*, a caviomorph of Deseadan Oligocene of Patagonia, South America. However, the lack of angular process in the Mongolian specimens hindered the author from drawing any conclusion as to the phylogenetic relationships between the two. During her visit to the American Museum of Natural History in 1984, the author found unexpectedly a similar lower jaw in the museum's collection of the third Central Asiatic Expedition. The latter was collected from Middle Miocene Tunggur Formation, Nei Mongol. The sciurognathous angular process of the Tunggur specimen enabled the author finally to separate the Chinese form from the South American *Cephalomys* on subordinal level and set up a new family for the former: Distylomyidae, which are arranged in the Ctenodactyloidea temporarily.

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Systematics

?Ctenodactyloidea Simpson, 1945

Distylomyidae fam. nov.

Distylomys gen. nov.

Type species *Distylomys tedfordi* sp. nov.

Diagnosis of genus Middle sized ctenodactyloid, lower jaw thick, mental foramen

near upper margin of middle of diastem, distinct masseteric crest extends anteriorly to below P_4 , sciurognathous angular process; dental formula $\overline{1013}$; P_4 molariform, with wide talonid; cheek teeth hypsodont, root-less and composed of two prisms; the bridge connecting the two prisms narrow; mesoflexid and ectoflexid deep and wide, opposite to each other and covered by cement; worn occlusal surface of cheek teeth smooth and concave; on posterior side enamel thin or interrupted.

Included species *Distylomys qianlishanensis* nov. sp.

Etymology di + stylo + mys, Greek, referring to two-prism pattern of its cheek teeth.

Distylomys tedfordi sp. nov.

Holotype Right lower jaw with I and P_4 — M_2 (AMNH, no. 114262).

Locality and horizon Tairum Nor Basin, Tunggur district, Sonid Left Banner, Xilin Gol League, Nei Mongol, China; Middle Miocene, Tunggur Formation.

Diagnosis Lower jaw thick, talonid of cheek teeth relatively wide and short, anterior end of P_4 pointed, metaflexid distinct on P_4 , vestigial on M_1 and disappears on M_2 .

Etymology In honour of Dr. R. H. Tedford, an eminent vertebrate palaeontologist of USA.

Description The horizontal part of the lower jaw is concave lingually and convex labially. The ventral border is S-shaped. The mental foramen is located near the upper margin of the middle of the diastem. The masseteric crest is very developed and extends from angular to below P_4 . The basal part of angular process rises anteriorly from the ventral part of the alveolus. Therefore it is sciurognathous.

Incisor extends below M_2 . The cross section is triangular. The surface of the enamel is smooth and does not show any ornament.

Cheek teeth are hypsodont and rootless, and composed of two prisms of triangular-shape. The bridge connecting trigonid with talonid is very narrow. The mesoflexid and ectoflexid are deep and wide, and opposite to each other. Both are covered by cement. Their occlusal surface are bi-lophed. After wearing they are smooth and slight concave, without any structure. The enamel on the posterior wall is thinner than that on the anterior wall or interrupted.

P_4 : The trigonid is roughly equilaterally triangular in form, with a anterior apex pointed, but lingual and labial sides concave. The talonid is wide and short, with compressed lingual end and a round labial one. The metaflexid is distinct, but shallow.

M_1 and M_2 are about the same in size and shape. The trigonid is as wide as the talonid. Both trigonid and talonid are flat triangular. The metaflexid is vestigial on M_1 and disappears on M_2 .

Distylomys qianlishanensis sp. nov.

Holotype A left lower jaw with P_4 — M_2 and anterior part of M_3 and a right lower jaw with P_4 — M_3 , which may belong to an individual. (IVPP: 7961).

Locality and horizon Loc. 79017, Yikebulage Otog Banner, Ih Ju League (=Yih Ju Meng), Nei Mongol, China; Upper Oligocene, Yikebulage Formation.

Diagnosis About one-fourth larger than *D. tedfordi*; lower jaw thick; incisor narrow; cheek teeth with narrower talonid but without any vestige of metaflexid, anterior end of P_4 is ro-

unded.

Etymology The name of the district where the fossils were collected.

Description and comparison The lower jaw is thicker than that of *D. tedfordi*. The mental foramen is located near the upper margin of the middle of the diastem and a little lower than that in *D. tedfordi*.

Incisor extends below M_2 . Its cross section is rectangular. The enamel surface smooth and multiserial in microstructure. The total enamel thickness is 0.132 mm. The external enamel layer is very thin. The external index is 12%. The band of the inner enamel layer is composed of 3—5 prisms. The mean band width is 0.0168 mm. Inclination of bands is about 55° .

Cheek teeth are larger than those of *D. tedfordi*. Talonid is relatively narrow and long, and without any vestige of metaflexid. The bridge connecting trigonid and talonid is short. On M_3 talonid is narrower than trigonid.

Discussion

1. Phylogenetic status of *Distylomys*

At the first glance, *Distylomys* seemed similar to *Cephalomys*, a caviomorph of Deseadan Oligocene of Patagonia, South America. They share a series of features in tooth structure: both have the same dental formula $\overline{1013}$; cheek teeth are composed of two prisms, possess developed and opposite situated mesoflexid and ectoflexid and smooth occlusal surface; P_4 is molariform; incisor has a multiserial enamel layer. However, *Cephalomys* has hystriognathous angular process, while *Distylomys* has a sciurognathous one. It shows that the above listed similarities could only be evolved by parallelism.

Among the rodents with sciurognathous lower jaw, $\overline{1013}$ dental formula and hypsodonty, only Pedetidae and Ctenodactyloidea have incisors with multiserial enamels. Although *Distylomys* is similar to Pedetidae in having molariform P_4 and bi-lobed cheek teeth, the other dental features of *Distylomys* are quite different from those in Pedetidae.

The comparison of *Distylomys* with the Ctenodactyloidea is rather complicated. The Ctenodactyloidea are now composed of four families: Ctenodactylidae Zittle, 1893, Cocomyidae Dawson et al., 1984, Yuomyidae Dawson et al., 1984 and Chapattimyidae Hussain et al., 1978. Based on the structure of P_4 the Ctenodactyloidea can be divided into two distinct groups. One is represented by Cocomyidae and Ctenodactylidae. Its main characteristic is a non-molariform P_4 . The other group includes Yuomyidae and Chapattimyidae, which are characterized by having molariform P_4 . *Distylomys* resembles some Oligocene ctenodactylids, such as *Woodomys*, *Karakoromys*, *Tataromys* and *Lepiotataromys* in its mandible morphology: having heavy ventral masseteric crest, but lacking dorsal masseteric crest, while in its dental features, such as hypsodont and bi-lobed cheek teeth, opposite situated and equally developed mesoflexid and ectoflexid and smooth occlusal surface, *Distylomys* is more similar to the late ctenodactylids: *Pectinator*, *Ctenodactylus*, *Felovia*, *Massoutiera*, *Pellegrinia* and *Irhoudia*. However, P_4 in Ctenodactylidae is non-molariform and tends to be reduced or even lost, while *Distylomys* has a molariform P_4 . Meanwhile, Chapattimyidae and Yuomyidae have molariform P_4 . However, in other characteristics *Distylomys* is different from the latter. The foregoing comparison seems to show that *Distylomys* is distinctive enough to warrant a family separation. We will call it Distylomyidae and temporarily arrange it in the Ctenodactyloidea.

As far as phylogenetical status of the Distylomyidae concerned there might be two possibilities, if it is true that the Distylomyidae is a member of the Ctenodactyloidea. According to its molariform P₄, Distylomyidae are likely to be linked with Yuomyidae and Chapattimyidae, while the other dental and mandible features seem to support a close affinity between Distylomyidae and Ctenodactylidae.

It seems to the author that the key problem here is the correct interpretation of the molariform P₄ versus non-molariform P₄ in the rodent phylogeny. Wood (1962, p. 139—147) considered non-molariform P⁴ of *Franimys amberstensis* as primitive for rodents and hypothesized that P₄ of the ancestral rodent must be non-molariform. Dawson et al. (1984, 146—147) concurred with Wood, saying "The evidence from *Heomys* and *Cocomys* suggests that primitive dental characters for rodents include non-molariform premolars..." Li et al. (in press) seem to favor this viewpoint as well. However, Butler (1941, p. 444) stated: "In the evolution of the dentition the teeth that are functionally the most important have been the most progressive, while the anterior premolars and milk molars, which are functionally the least important, have tended to retain archaic characters." It is known that *Cocomys* possesses molariform DP⁴, although the P⁴ is non-molariform. The other ctenodactyloids, such as Ctenodactylidae, Chapattimyidae and Yuomyidae, all have molariform DP₄⁴. Moreover, all known DP₄⁴ of the Paramyidae are molariform as well. According to Butler's view it seems that molariform P₄ represents a primitive character in the rodent evolution, while non-molariform P₄ may be advanced. In fact, in *Cocomys* the trigonid of P₄ is only slightly wider than its talonid. It seems to mean that the *Cocomys*' P₄ represent the very beginning of the non-molariform process. It is interesting that the earliest known Paleocene rodent, *Acritoparamys*, has a molariform P⁴ indeed. Besides, the dental evolutionary tendency of the rodents coincides with this inference as well.

If the inference is true, non-molariform P₄ of the Cocomyidae and Ctenodactylidae must be an advanced rather than a primitive character. On the contrary, Distylomyidae, Chapattimyidae and Yuomyidae retain a primitive molariform P₄. Sharing non-molariform P₄ Cocomyidae and Ctenodactylidae may split from Distylomyidae, Chapattimyidae and Yuomyidae earlier than we have so far expected. In this case, it is better to consider Distylomyidae the sister group of Chapattimyidae-Yuomyidae. Comparison with known forms of Chapattimyidae-Yuomyidae made it clear that Distylomyidae are further deviated from their common ancestor. Based on molariform P₄ Pedetidae may be included in the same group as Distylomyidae.

By the dental features, such as smaller size and retaining metaflexid on P₄—M₁, *Distylomys tedfordi* seems more primitive than *D. qianlishanensis*. However, the former is found in later deposits (Middle Miocene) than the latter (Upper Oligocene). The discrepancy could only be dispelled if we consider the two species belong to different branches.

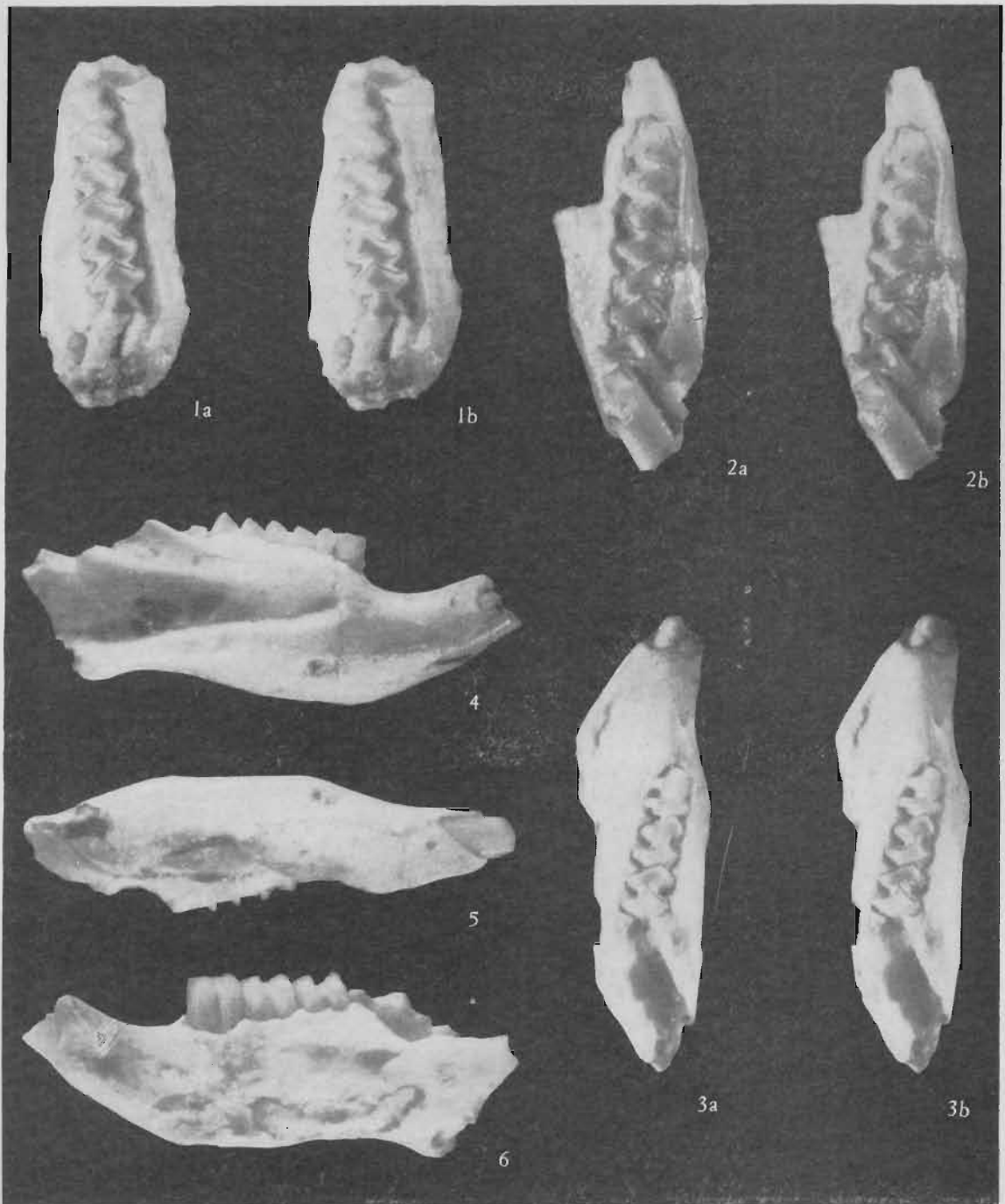
2. Affinity of Hystricognathi

The Hystricognathi are a group of rodents in which the angular process of the lower jaw rises from the lateral surface of the incisor alveolus. Concerning their origin and relation with other rodent groups there has been heated debate among paleontologists. Wood thought that the Hystricognathi included five groups: Hystricidae, Thryonomyoidea, Bathyergoidea, Caviomorpha and Franimorpha. He believes that hystricids and thryonomyoids were derived from still unknown Asian franimorphs, while caviomorphs originated from Middle American Eo-

cene franimorphs and bathyergoids were derived from Asian cylindrodontids. According to him, "Ctenodactyloidea are members of sciurognathous that have retained many ancestral rodent characteristics from a time prior to the hystricognath-sciurognath split" (Wood, 1986, p. 496). In contrast to Wood's opinion Lavocat thought the Hystricognathi composed of African Phiomorpha (including Thryonomyoidea and Bathyergoidea), Asian Hystricidae and South American Caviomorpha. They were all derived from African primitive Phiomorpha. The third opinion was first proposed by Hussain et al. in 1978. According to theirs the Chapattimyidae may represent a candidate of the common ancestor of the hystricognaths. Jeager et al. (1985) supported that Chapattimyidae may be the sister group to Phiomidae. Flynn et al. (1986, p. 48, fig. 24) suggested that Ctenodactyloidea and Pedetidae constitute the sister group of the Hystricognathi (including Bathyergoidea).

It is obvious that the chapattimyid cheek teeth resemble those of the thryonomyoids. The evidence of the dental features of *Protophiomys* from Eocene of Africa suggests further that thryonomyoids may be derived from chapattimyids. Besides, in the dental features chapattimyids are also similar to some caviomorphs and hystricids. The lophodont caviomorphs could be derived from the chapattimyid cusp pattern. It is possible that the hystricognaths (including thryonomyoids, caviomorphs and hystricids, at least,) may constitute the sister group of the chapattimyids in the light of their dental similarities. The problem is that they have different kinds of angular process. It is known that hystricognaths possess hystricognathous angular process, while chapattimyids as well as other ctenodactyloids have sciurognathous one. It is believed that the sciurognathous lower jaw is primitive for rodents and the hystricognathous is advanced and the latter may be derived from the former. Then, when did the hystricognathous-sciurognathous split take place? Is it prior to the time when *Cocomys* possessing non-molariform P4 split from ancestral rodent stem? Or later? If the hystricognathous originated from the chapattimyid-like animals, chapattimyids may be the sister group of the hystricognaths. However, Chapattimyidae are considered belonging to the Ctenodactyloidea. Recognition of the sister-group relationships between chapattimyids and hystricognaths would inevitably mean paraphyletic composition of the Ctenodactyloidea. In accordance with the foregoing arguments the Chapattimyidae are to be excluded from the Ctenodactyloidea. If the separation of the hystricognathous is earlier, say, earlier than the split of *Cocomys*, then the difference in the angular morphology would be much more important than the tooth similarities. Based on the morphology of the lower jaw it occurs that Ctenodactyloidea including Chapattimyidae as a whole are to be taken as a sister group of the hystricognaths.

The same holds true for the relationships between Distylomyidae and *Cephalomys*. If the hystricognathous occurs later, the dental similarities may show that Distylomyidae and *Cephalomys* have close relationships. They may have close common ancestry. However, the conclusion will give rise a series of bio-geographical problems to be solved. It is known that the Chapattimyidae were mainly found in the Indian subcontinent. While the Distylomyidae were discovered in Nei Mongol, China. It seems that in East Asia existed once a group of rodents which resembled hystricognaths of the southern continent. In this case, is it possible that hystricognaths directly originated from Asia continent? Furthermore, where did Distylomyidae come from? Were distylomyids derived from chapattimyid-like animals and immigrated from the Indian subcontinent? Or did distylomyids originate in Eastern Asia?... Of course, it is impossible to solve those problems right now. However, they are very interesting and give one much food for thought.

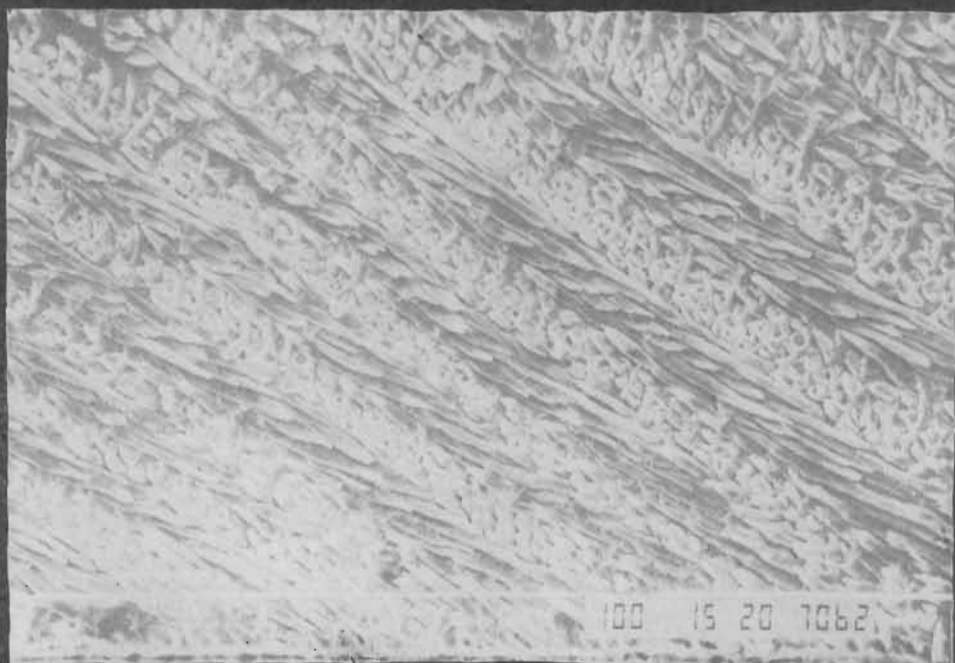
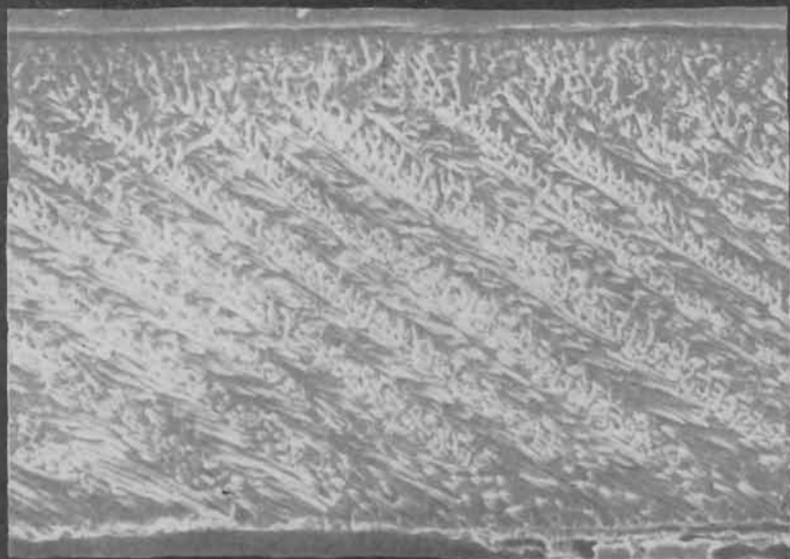


双柱鼠(新属) *Distylomys* gen. nov. $\times 5$

- 1—2. 千里山双柱鼠(新种) *D. qianlishanensis* sp. nov. 正型标本: 可能为同一个体的左、右下颌骨(V 7961)。1a, 1b. 左下颌骨具 P_4-M_2 和 M_3 三角座, 嚼面观(立体照片); 2a, 2b. 右下颌骨具 P_4-M_3 , 嚼面观(立体照片);
 3—6. 特氏双柱鼠(新种) *D. tedfordi* sp. nov. 正型标本: 右下颌骨具 P_4-M_2 , AMNH no. 114262。3a, 3b. 嚼面观(立体照片); 4. 唇面观; 5. 腹面观; 6. 舌面观

Distylomys gen. nov. all $\times 5$

- 1—2. *D. qianlishanensis* sp. nov. Holotype: right and left lower jaws which may be the same individual (V 7961)。1a, 1b. left P_4-M_2 and trigonid of M_3 , occlusal view (stereoscope); 2a, 2b. right lower jaw with P_4-M_3 , occlusal view (stereoscope);
 3—6. *D. tedfordi* sp. nov. Holotype: right lower jaw with P_4-M_2 , AMNH no. 114262。3a, 3b. occlusal view (stereoscope); 4. labial view; 5. ventral view and 6. lingual view



千里山双柱鼠(新属、新种) *Distylomys qianlishanensis* gen. et sp. nov.

正型标本 V 7961 右下颌齿纵剖面(左侧为门齿前端)。上: $\times 500$, 下: $\times 750$

Sagittal section of enamel in right lower incisor of holotype (V 7961) of *Distylomys qianlishanensis* gen. et sp. nov. Tips of incisors are to the left, upper: $\times 500$, left: $\times 750$