

# 山东早始新世五图组的一种古有蹄类 *Olbitherium millenarium* gen. et sp. nov. (哺乳动物纲,“伪齿兽集目”)<sup>1)</sup>

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**摘要:** 记述了在山东省五图盆地下始新统发现的一种“伪齿兽集目”化石:千禧福兽 (*Olbitherium millenarium* gen. et sp. nov.)。千禧福兽其颊齿形态基本上与原始奇蹄类相似,同时也具有伪齿兽类的一些特征,如 m1 ~ 2 下次尖没有与下内尖直接连接的下次脊。千禧福兽的 M3 次尖具前、后棱,这一点似与原始的蹄兔 *Seggeurius* 相似。因此,新种在目一级的归类有困难,暂置于 Mc Kenna (1975) 创立的“伪齿兽集目”(“Mirorder Phenacodonta”)。千禧福兽的发现进一步证明了奇蹄类可能起源于亚洲和北非类似伪齿兽类(phenacodontids)的古有蹄类,福兽仅是类似伪齿兽类的古新世古有蹄类向奇蹄类进化过程中的一支的代表。

**关键词:** 山东五图,始新世早期,“伪齿兽集目”

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近年来,包括现生的马科(Equidae)、獐科(Tapiridae)和犀科(Rhinocerotidae)在内的奇蹄类的起源问题备受重视。早在 100 多年前,Cope (1881a) 就认为“踝节目”(“Condylarthra”)是已知的奇蹄类的祖先类型。Radinsky (1966, 1969) 从咀嚼和运动器官分析,也提出了踝节类是奇蹄类的祖先类型,奇蹄类可能起源于 *Tetraclaenodon* (一种伪齿兽类)。而近 20 年来,由于广东南雄盆地上古新统中玉萍兰氏兽(*Radinskya yupingae*)的发现,人们相信兰氏兽更有可能是奇蹄类的姐妹群。但有人认为兰氏兽是一种重脚兽类(arsinothere) (Domning et al., 1986; Mc Kenna et al., 1989; Prothero and Schoch, 1989), 就提出古地中海兽类(tethytherians)可能与奇蹄类起源有关。与此相反,在近期的形态分析中,虽然没有明确说明 phenacodontids 是奇蹄类的姐妹群,但大多将 phenacodontids 作为外类群(outgroup), 或者认同 phenacodontids 和奇蹄类之间密切的亲缘关系(Prothero and Schoch, 1989; Court, 1992; Thewissen, 1990; Thewissen and Domning, 1992; Hooker, 1989, 1994; Froehlich, 1999, 2001, 2002; Holbrook, 2001; Ekdale, 2002)。这里报道的产自山东五图盆地早始新世地层的一种古有蹄类 *Olbitherium millenarium* gen. et sp. nov., 其上臼齿形态比 *R. yupingae* 更近似原始奇蹄类。但其 m1 ~ 2 形态却类似 phenacodontids, 似乎又把 phenacodontids 和奇蹄类起源联系在一起。五图标本的发现,相信将对奇蹄类起源问题讨论带来新信息。在早

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始新世五图动物群中有许多古新世哺乳类残余种(Tong and Wang, 1998), *O. millenariusum* 可能是其中之一, 类似的化石在内蒙古古新世最晚期的 Bayan Ulan 动物群也有发现(Meng et al., 1998)。

“伪齿兽集目” “**Mirorder Phenacodonta**” Mc Kenna, 1975 (sensu Mc Kenna, 1975)

目未定 **Order** incertae sedis

福兽(新属) **Olbitherium** gen. nov.

属型种 *Olbitherium millenariusum* gen. et sp. nov.。

特征 同属型种。

词源 Olbi, 希腊语, olbios, 意为有福的, 快乐的; therium, 为兽类常用后缀。

千禧福兽(新属、新种) **Olbitherium millenariusum** gen. et sp. nov.

(图 1, 2)

正模 存 p1 ~ m3 三角座的右下颌骨(IVPP V 10758. 1)。

归入标本 同一个体的存 P2 ~ M1 和 P1、C 齿槽的左上颌骨(V10758. 2)和存 p2 ~ p4 和 p1 齿槽的左下颌骨(V 10758. 3), 零散的左 M1 (V 10758. 4), 右 P2 (V 10758. 5)、P4 (V 10758. 6)和 M2 (V 10758. 7), 右 M3 (V 10758. 8), 存 p4 ~ m3 左下颌骨(V 10758. 9), 存 dp2 ~ m2 的左下颌骨(V 10758. 10)和右 dp4 跟座 ~ m2 三角座(V 10758. 11)。

产地和时代 山东省昌乐县煤矿; 五图组, 早始新世。

特征 齿式: ? 1. 4. 3/ ? 1. 4. 3。C 和 P1 之间齿隙长; P4 无后小尖; 上臼齿为三根齿, 原脊长, 与前尖棱相连; M1 ~ 2 后小尖小, 在次尖的前外方, 后小尖有向后外方延伸的棱脊伸向后尖; 前附尖大, 无中附尖; 舌侧齿带包围原尖和次尖; M3 后小尖很退化, 次尖具前、后棱。p1 无后跟, p2 后跟尖小, p4 下后附尖显著, 无下内尖; m1 ~ 2 下次小尖在牙齿后缘的内侧, 靠近下内尖, 下次尖后棱与下次小尖连接, 下内尖和下次小尖相连, 未形成下次尖和下内尖直接相连的下次脊, 下后附尖弱; m3 延长, 下次小尖大, 并形成下次小尖叶, 下内尖近于孤立。

词源 millenariusum, 拉丁语, 一千年的, 意思是对新千年的祝福。

描述 V 10758. 2 ~ 3 为咬合在一起的上、下颌骨, 可认为是同一个体。根据这两个标本, 将正模和其他标本归为同一个种看来没有问题。颊齿低冠, 但较健壮。

上犬齿未发现, 在 V 10758. 2 上存有齿槽, 齿槽前后长度约 7 mm, 犬齿后的齿隙相当大, 长约 13.4 mm。P1 未保存, 从齿槽观察, P1 可能为双根齿, P1 和 P2 之间似无齿隙。

P2 为双根齿, 冠面呈三角形, 前窄后宽, 2 个标本在形态上有些变化, 在 V 10758. 2 标本上牙齿唇侧只有一个齿尖, 但在 V 10758. 5 标本中的 P2 唇侧似乎分裂成两个小尖。两个 P2 标本的舌侧齿带连续, 在牙齿后内角增大, 使牙齿基部向后内方突出。在舌侧齿带的中部有一或弱(V 10758. 2)或强(V 10758. 5)的突起。在牙齿的前端有或隐(V 10758. 2)或显(V 10758. 5)的前附尖。

P3 为 3 根齿, 横宽, 前尖和后尖已很清楚地分开, 前尖明显地比后尖大。前附尖相对发育, 后附尖弱。虽在 V 10758. 2 标本上 P3 ~ 4 磨蚀比较严重, 但还能看出在 P3 内侧有一近于纵向的磨蚀面, 可能是由原尖和原尖后棱磨蚀而成的。根据牙齿前缘的磨蚀面, 存在

原尖前棱,可能还有前小尖。在 V 10758.2 标本上,齿带断断续续出现,缺少舌侧齿带。

在 V 10758.2 和 V 10758.6 标本上存有 P4, V 10758.6 标本的 P4 磨蚀轻微。前尖和后尖大小相近,原尖居中,原尖前棱伸向前尖前侧基部,中部有小的前小尖。原尖后棱伸达后尖内侧基部,无后小尖。前、后齿带连续,唇侧齿带断续,无舌侧齿带。

M1 和 M2 形态相近, M2 稍大(图 1, D、F)。前尖和后尖大小相近,但后尖位置向舌侧位移,两尖之间由低弱的中央脊相连。前尖有些向外倾斜,前棱向前外方伸至前附尖。无中附尖,后附尖弱,而前附尖发育,向前外方突出。原尖比次尖稍大,原脊和后脊分别斜向伸到前尖前棱和后尖前内侧基部。原尖后棱消失,次尖无后棱,其前棱与后小尖相连。前小尖明显比后小尖大,后小尖有向后外方延伸的弱棱,伸达后尖前内侧基部,这一弱棱相当于 Hooker (1989)的牙齿术语图解中的后小尖前棱(premetaconule crista),后小尖前棱在 M2 上比较清楚。虽然前小尖和后小尖比较明显,但原脊和后脊基本连续,呈所谓的次脊状(sublophoid)。齿带基本连续,舌侧齿带包围原尖和次尖。

M3 基本上与前面臼齿相同,但牙齿后半部分收缩,后尖明显向舌侧位移,次尖比原尖稍小,并具前、后棱,呈 V 字形,次尖前棱伸至原尖基部。后小尖很退化(测量见表 1)。

在 V 10758.3 的下颌骨标本上清楚地保存了 p1 的齿槽,下犬齿齿槽保存不好。p1 之前有一段齿隙, p1 和 p2 之间有较长的齿隙(10.4 mm)(图 1, G)。在正模上 p1 已从齿槽中脱落(图 1, A),为单根齿,但齿根下部已分裂。齿冠侧扁、简单,为单尖齿,主尖前缘较陡直,后缘较斜(p1 长:4.3 mm)。p2 为双根齿,齿冠形态如 p1,但有一小跟尖。

p3 三角座侧扁,带有一宽短的跟座,使牙齿嚼面呈等腰三角形(V 10758.1)。下原尖高大,下前尖小,位于下原尖前棱的基部。下后尖比较明显,位于下原尖后棱中部,下原尖外后棱伸达牙齿的后外角。跟座低、宽短,下次尖发育,位于牙齿后缘中部,有斜脊直指下原尖后棱。无下内尖,齿带不发育。在归入标本(V 10758.3)上, p3 跟座较窄。

p4 嚼面轮廓近似矩形,三角座有几乎与下原尖等高的下后尖,下原脊强,下原尖前棱向前内方延伸到牙齿前缘中部后向内拐。跟座与三角座等宽,但低矮。下后附尖显著,紧挨下后尖,两尖几乎等高。斜脊伸至下原脊中部,下内尖无,齿带不发育。

表 1 千禧福兽(新属、新种)颊齿测量

Table 1 Measurements of cheek teeth of *Olbitherium millenariusum* gen. et sp. nov. (mm)

	P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W
V 10758.2	7.25	5.4	8.15	9.0	8.7	11.3						
V 10758.4~7	8.75	6.95			>10.0	11.5	>12.1		12.9	13.5		
V 10758.8											11.7	12.85
	p2		p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W
V 10758.1	7.8	4.0	8.8	5.6	9.5	6.2	11.4	7.9	13.5	9.75		
V 10758.3	7.6	3.95	9.25	6.0	9.35	7.15						
V 10758.9					8.75	6.7	8.75	>7.6	12.05	9.1	16.85	10.45
V 10758.10							12.2	8.7	14.1	10.3		

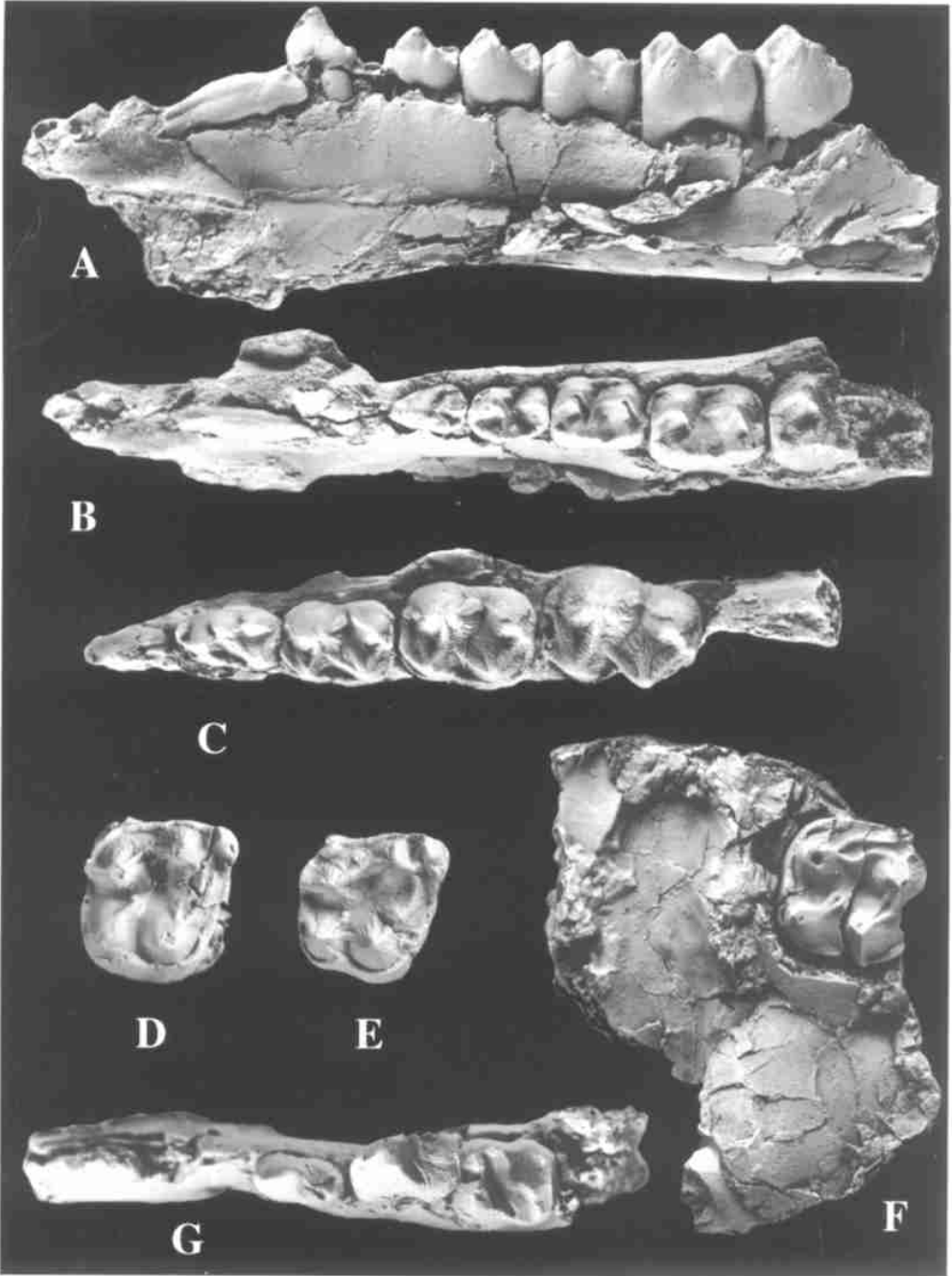


图1 千禧福兽(新属、新种) ,上、下颊齿,冠面视和侧面视

Fig. 1 Upper and lower cheek teeth of *Olbitherium millenariusum* gen. et sp. nov. , occlusal and lateral views  
 A, B. right mandible with p1 ~ m3 (V 10758. 1) , lateral and occlusal views ,  $\times 1.3$  ; C. left mandible with  
 dp2 ~ m2 (V 10758. 10) , occlusal view ,  $\times 1.6$  ; D. right M2 (V 10758. 7) , occlusal view ,  $\times 1.6$  ; E. right M3  
 (V 10758. 8) , occlusal view ,  $\times 1.6$  ; F. fragmentary left maxilla with M1 (V 10758. 4) , occlusal view ,  $\times 1.6$  ;  
 G. left mandible with p2 ~ 4 (V 10758. 3) , occlusal view ,  $\times 1.6$

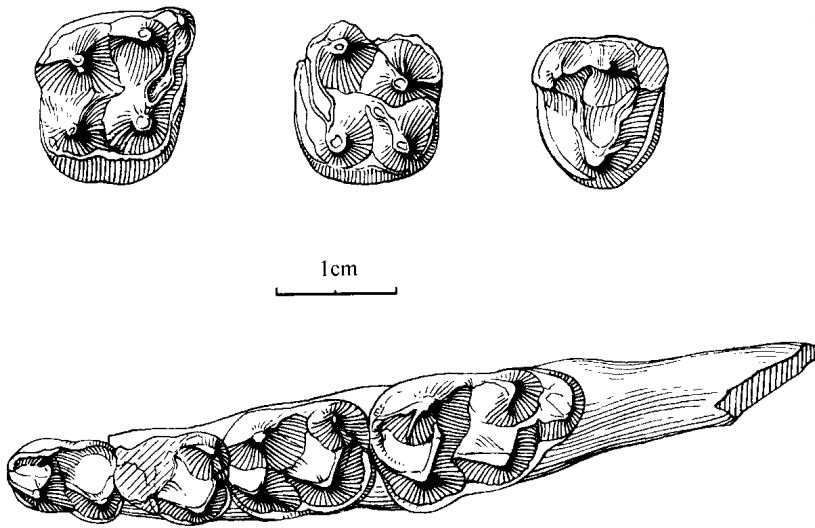


图2 千禧福兽(新属、新种),右 M2(V 10758.7)、左 M1(V 10758.4)、  
右 P4(V 10758.6)和左 p4~m3 (V 10758.9),冠面视  
Fig.2 *Olbitherium millenariusum* gen. et sp. nov., right M2, left M1,  
right P4, and left p4~m3, occlusal view

有三个标本保存了下臼齿,其中 V 10758.10 的 m1 和 m2 尚未磨蚀,V 10758.9 的 m1 三角座已损坏,但还能看得出比正模和 V 10758.10 标本的 m1 小。m1 三角座和跟座高差不明显,牙齿次脊齿化,主要的齿尖仍相当清楚,三角凹和跟凹较浅。三角座前后不大收缩,几乎与跟座等长,下原脊较完全,下前脊伸至牙齿前缘中部后向内拐,在冠面的前内角有一小突起(下前尖)。下后附尖较小,紧挨下后尖。斜脊指向下原脊中部。在未磨蚀的标本(V 10758.10)(图 1,C)上,下次尖与下次小尖由唇侧后棱(buccal postcristid branch, *sensu* Hooker, 1989)相连。下次小尖小,位于牙齿后缘的内侧,靠近下内尖,两尖由短的舌侧后棱(lingual postcristid branch, *sensu* Hooker, 1989)联结。但在磨蚀后的牙齿(V 10758.1)(图 1,B)上,看起来像是下次尖和下内尖直接连接成下次脊,实际上,还是下次尖—下次小尖—下内尖的连线。唇侧齿带相对发育,无舌侧齿带。

m2 如 m1,尺寸稍大,下前尖更弱。

m3 具下次小尖叶,位置靠内侧。三角座形态如前面的臼齿,跟座相差较大。下次尖大,下内尖发育,近于孤立,未与下次尖和下次小尖直接连接,但有弱棱伸向下次尖后棱。下次小尖低壮,向后突出,形成窄长的下次小尖叶。下次小尖有与下次尖相连的棱脊,似乎未与下内尖相连。

在 V 10758.10 标本上带有 dp2~dp4(图 1,C)。dp2 侧扁,在主尖前棱基部有一小突起,主尖后棱分成两支,斜向基部延伸,形成小的跟盆。跟盆中有一小跟尖(dp2 长:7.3 mm,宽:3.4 mm)。dp2 的形态有些类似 *Tetraclaenodon puercensis* 的 dp2 (Butler, 1952),也有些类似成年个体的 P3,但尺寸较小。dp3 前后延长,下前尖低小,位于牙齿的前内角。下后尖大小与下原尖相近,齿尖高度也大致等同,位置在下原尖的后内方。下原尖有一明显的棱脊向后外方下延至下次尖基部。无下后附尖,下次尖前棱伸达下后尖,后棱伸至牙

齿的后内角,无下次小尖。下内尖发育,与下次尖相对(dp3长:9.45 mm,宽:5.45 mm)。dp3的形态与Butler (1952)图示的*Plagiolophus annectens*的dp3有些相似,不过五图标本的三角座更加延长,侧扁,下内尖发育,下次尖后棱伸向牙齿后内角,不与下内尖直接相连。dp4形态如m1,具有小的下后附尖和下次小尖(dp4长:9.9 mm,宽:7.2 mm)。

**比较和讨论** Hooker (1989)曾指出,原始奇蹄类的上臼齿区别于phenacodontids在于奇蹄类上臼齿具有稍微向外倾斜的前尖;原尖和前尖之间的齿脊增强,形成次脊化构造;前小尖的窄的磨蚀面2A (facet 2A)变弱;前附尖延长;原尖后棱缺失,代之连接次尖和向前位移的后小尖的齿脊,并由向后外方延伸的后小尖棱与后尖相连;M3后尖和次尖较大,并分别与前尖和原尖隔离。从上面记述可以看出,福兽的上臼齿基本上与原始奇蹄类很相似,与phenacodonts不同。福兽的上臼齿前尖也有些向外倾斜,原脊长,延伸到前尖棱,前附尖向前外方突出,缺少原尖后棱,后小尖向前位移,后小尖有棱脊向后伸达后尖的基部,这些特征与原始奇蹄类是一致的。福兽的M3比较特殊,其后尖和次尖并不退化,次尖具有前、后棱,使次尖呈V字形,后小尖退化,与已知的原始奇蹄类*Hyracotherium*, *Cymbalophus*, *Cardiophus*和*Homogalax*的M3形态不同。

晚古新世的玉萍兰氏兽(*Radinskya yupingae*)其上颊齿是与原始奇蹄类很相似的古有蹄类,最初怀疑可归入伪脊齿兽科(Phenacolophidae)(McKenna et al., 1989),最近被归入狭义的高等有蹄目(Mirorder Altungulata s. s.)(McKenna and Bell, 1997)。但就上臼齿形态而言,新种*Olbitherium millenariusum*比*R. yupingae*在上颊齿形态上更加接近原始奇蹄类。McKenna et al. (1989)曾提到*R. yupingae*不同于奇蹄类在于上臼齿的前小尖大,后小尖极强,原脊和后脊短且强,次尖、后小尖和后尖排列成一直线,还有缺少围绕原尖和次尖的舌侧齿带。与*R. yupingae*相比较,*O. millenariusum*和原始奇蹄类具有更多的共同特征:前小尖不大,后小尖明显比后尖和次尖小,后小尖位置在后尖和次尖连线的前方,因此后尖、后小尖和次尖不在同一直线上,并有围绕原尖和次尖的舌侧齿带。*O. millenariusum*与*R. yupingae*不同还在于*O. millenariusum*的C和P1之间齿隙长(*R. yupingae*的齿隙短),P1和P2之间无齿隙(*R. yupingae*有短齿隙),P4无后小尖(*R. yupingae*有小的后小尖),上臼齿为三根齿(*R. yupingae*的M1为四根齿),无中附尖(*R. yupingae*的中附尖极弱),具后小尖棱(*R. yupingae*缺少后小尖前、后棱),M3后小尖很退化(*R. yupingae*的后小尖大,但孤立),次尖具前、后棱。*R. yupingae*和可能与其有关的phenacolophids的M3不退化,次尖存在,缺少次尖前、后棱,也容易与福兽区别。

虽然福兽与原始奇蹄类的上臼齿形态大体上相似,但下臼齿则很难直接与奇蹄类相比较,尤其是m1~2,与phenacodontids的m1~2更近似。*O. millenariusum*的m1~2与原始奇蹄类主要区别在于三角凹和跟凹浅,下次小尖的位置在牙齿后缘的内侧,靠近下内尖,与下次尖后棱连接,并与下内尖相连,即存在唇侧后棱和舌侧后棱。通常,原始奇蹄类的m1~2三角凹和跟凹较深,下次小尖在牙齿后缘的中部,下次尖和下内尖直接连接成下次脊,下次小尖紧靠下次脊,无唇侧后棱和舌侧后棱。而某些phenacodontids的m1~2形态与*O. millenariusum*相似,如*Ectocion*、*Phenacodus*和*Copecion*,三角凹和跟凹较浅,下次小尖有时靠近下内尖,分别与下次尖和下内尖连接,虽然这些动物齿脊化程度不如*O. millenariusum*。虽然*O. millenariusum*的m1~2与phenacodontids的相似,但其m3不同于phenacodontids,却与原始奇蹄类相近。phenacodontids的m3通常比较短宽,不如原始奇

蹄类那样延长,并由下次尖、下次小尖和下内尖围成跟凹,无下次小尖叶。而 *O. millenarium* 与原始奇蹄类一样,m<sub>3</sub> 相对延长,下内尖大,下次小尖发育,并向后突出,形成下次小尖叶。但 *O. millenarium* 的 m<sub>3</sub> 下内尖近于孤立,未直接与下次尖连接,形成下次脊,这与常见的原始奇蹄类不同。

从上述比较中可以看出,*Olbitherium millenarium* 的 M1~2 形态比 *Radinskya yupingae* 更像原始奇蹄类,但 m<sub>1</sub>~2 的形态却接近 phenacodontids。此外,还有一些特征似乎可在蹄兔类(Hyracoidea)中出现,如 *O. millenarium* 的 M3 的次尖呈 V 形脊,后小尖很退化,这有点类似原始的蹄兔类 *Seggeurius* (Mahboubi et al., 1986)。虽然蹄兔类 M3 的后面的舌侧齿尖被解释为是后小尖(Sudre, 1979),在奇蹄类中相对应的齿尖被称为次尖,但位置相同。与 *O. millenarium* 一样,*Seggeurius* 的 M3 后舌侧齿尖呈 V 字形。蹄兔类在真兽类中的系统位置一直有争议,前一段时间曾认为它是奇蹄类的姐妹群,极端的意见是将其归入奇蹄目(如 Fischer, 1989; Fischer and Tassy, 1993; Prothero and Schoch, 1989),而分子生物学者将其与 Proboscidea, Sirenia, Tubulidentata, Macroscelidea 和 Afrosoricida 一起归入非洲兽超目(Superorder Afrotheria)(如 Hedges, 2001; Madsen et al., 2001; Helgen, 2003 等)。虽然 *O. millenarium* 的 M3 与原始蹄兔类的后舌侧齿尖呈 V 形脊,但仅有这一特点不足以将新属归入蹄兔目。不过,或许显示了 *O. millenarium* 与蹄兔类在某种程度上相关。

最近, Maas et al. (2001) 记述了在土耳其始新统中发现的“谜一般”的古有蹄类 *Hilalia*, 被置于“踝节目”(“Condylarthra”)。土耳其属的上、下臼齿有些类似雷兽类(brontotheres)和原始爪兽类(chalicotherioidea),上臼齿中附尖发育,外脊呈 W 形,前小尖发达,后小尖小或缺失,下臼齿下后附尖大小如同下后尖,斜脊终于下后附尖。但这个属也有不同于雷兽类、爪兽类和其他奇蹄类的重要区别特征,m<sub>1</sub>~3 下次小尖缺失或很不清晰,m<sub>3</sub> 更无下次小尖叶。原作者将 *Hilalia* 与北美的踝节类 *Meniscotherium* 和法国的踝节类 *Pleuraspidotherium*、*Orthaspidotherium* 比较,并归入“踝节目”。不过,土耳其标本在某些方面似可与王原(1995)记述的丹江兽(*Danjiangia*)比较,可能是与 *Danjiangia* 不在同一进化支系上的爪兽类或雷兽类动物。*Hilalia* 明显地与这里描述的 *Olbitherium* 不同,后者上臼齿外脊不呈 W 形脊,下臼齿的后脊是由下次尖、下次小尖和下内尖连接而成的,有下后附尖,斜脊向前延伸,m<sub>3</sub> 有下次小尖叶。

Gheerbrant et al. (2001) 描述了两种产自摩洛哥 Ouled Abdoun 盆地早始新世地层的古有蹄类。其中,*Abdounodus hamdii* 被归入 Miocleanidae 科,这种古有蹄动物以前只在南、北美洲的古近纪早期地层中发现。在 Ouled Abdoun 盆地发现的另一种古有蹄类是 *Ocepeia daouiensis*, 它被归入 Taxeopoda (Archibald, 1998), 认为可能与“Phenacodonta”有关。不过原作者的“Phenacodonta”的含义与 McKenna (1975) 的原来内涵不一样,与 Thewissen 和 Domning (1992) 以及 Archibald (1998) 的含义相近,“Phenacodonta”仅包含伪齿兽科(Phenacodontidae)(包括 Meniscotheriinae)。*O. daouiensis* 的下臼齿有下内尖脊(entolophid),有下中尖(mesoconid),m<sub>3</sub> 无下次小尖叶,p<sub>4</sub> 简单,成切割状的齿脊,无明显的下后尖。这些特点与这里记述的 *Olbitherium millenarium* 有区别,也与原始奇蹄类和伪齿兽科的成员不同。

从以上对比中可以发现,五图标本不同于已知的古有蹄类和早期奇蹄类,但兼有早期奇蹄类、伪齿兽类和蹄兔类的一些特征。下面简述 *Olbitherium millenarium* 的归类和奇蹄类起源的一些问题。

在历史上,踝节类和蹄兔类都曾经被归入奇蹄目。Owen 于 1848 年将蹄兔 (*Hyrax*) 归入他所定义的奇蹄目中(见 Fischer, 1989), Cope (1881b) 也曾将踝节类 (*Condylarthra*) 作为奇蹄目的次一级分类单元 (subunit)。Mc Kenna (1975) 也将“踝节目”、奇蹄目和蹄兔目归入“伪齿兽集目”(“Mirorder Phenacodonta”), 但在他后来的分类中将“踝节目”、奇蹄目和蹄兔目分别归入不同的集目: 上熊犬集目 (Mirorder Eparctocyona Mc Kenna, 1975) 和高等有蹄集目 (Mirorder Altungulata s. s.) (Mc Kenna and Bell, 1997)。而 Thewissen 和 Domning (1992) 将“Phenacodonta”降为目级分类单元, 仅包括 Phenacodontidae 和 Meniscotheriidae 两科。正如前面所述, *Olbitherium millenariusum* 的上、下颊齿具有奇蹄类、伪齿兽类和蹄兔类的一些特点, 似与这三目有关, 但难以归入上述的目级分类单元, 只能暂置放在 Mc Kenna (1975) 原来提出的包括伪齿兽目、奇蹄目和蹄兔目在内的“伪齿兽集目”。

奇蹄类在欧洲、北美和亚洲的早始新世几乎同时出现 (Ting, 1993; Bowen et al., 2002 等), 原始马形和獭形动物常在同一层位中存在, 显示出奇蹄类已出现分化。奇蹄类起源于何种动物成了古哺乳动物学者关心的问题。总的来说, 奇蹄类起源有两种设想, 一是起源于“*Condylarthra*”中的 phenacodontids (Cope, 1881a; Radinsky, 1966, 1969; Prothero et al., 1988 等), 这是较早期的假设, 在近期的研究者中虽也有持同样的观点, 如 Hooker (1989), Rose (1996) 等, 但 *Radinskya yupingae* 的发现改变了人们对奇蹄类起源的看法, 认为奇蹄类的起源与所谓的古地中海兽有关。古新世的 *R. yupingae* 的上颊齿形态一方面与原始奇蹄类接近, 另一方面 *R. yupingae* 显示出某些伪脊齿兽类 (phenacolophids) 的性质 (Mc Kenna et al., 1989)。而 Phenacolophidae 可能与 tethytherians 有关 (Mc Kenna and Manning, 1977; Domnig et al., 1986)。但这里需要指出的是, 认为可作为伪脊齿兽 *Phenacolophus* (Phenacolophidae) 和古地中海兽类中的重脚兽类的 *Arsinoitherium* 之间过渡的 *Crivadiatherium mackennai*, 其材料只有 p4、m2 和 m3 的前半部。按照 Russell et al. (1982) 的意见, 其时代为渐新世。*C. mackennai* 的材料太少, 不足以说明是 *Phenacolophus*-*Crivadiatherium*-*Arsinoitherium* 之间的形态梯变 (morphocline) 的过渡物种。而且作为过渡的物种, *C. mackennai* 的时代也显得太晚, 作为中间环节不一定合适。因此, 认为 *Phenacolophus* 和 *Radinskya* 有可能与 tethytherians 有关的设想, 其证据尚不充分。相反, 这里记述的 *Olbitherium millenariusum*, 其上、下颊齿兼有原始奇蹄类和古有蹄类 phenacodontids 的特征, 更能反映出奇蹄类起源于类似 phenacodontids 的古有蹄类的可能性更大。亚洲的新发现, 结合近来北非和近东的古有蹄类的发现 (Maas et al., 2001; Gheerbrant et al., 2001), 说明了奇蹄类的起源与亚洲和非洲古近纪早期的类似 phenacodontid 的古有蹄类密切相关, 而 *O. millenariusum* 是这些古有蹄类中的一支系。

五图动物群的时代有争论 (童永生、王景文, 待刊), 但近期湖南衡阳盆地的碳同位素研究 (Bowen et al., 2002; Ting et al., 2003) 确立了亚洲古新统/始新统的界线位置, 支持了五图动物群的时代为早始新世。与其他亚洲早始新世化石地点不同的是, 在五图动物群中存在许多的古新世哺乳动物的残余种, 包括新斜沟齿兽类型的多瘤齿类 (neoplagiulacid multituberculate), 侏兽类型的古乏齿兽类 (epicotherid palaeodont), 食果猴和更猴类型的更猴形类 (carpolestid and paromyid plesiadapiformes), 丽 狓 和 假 古 狓 类 型 的 狓 兽 类 (astigalid and pseudictopid anagalidans), 豕齿兽和伪齿兽类型的“踝节类” (hyposodontid and phenacodontid “condylarths”) 等 (Tong and Wang, 1998), 这里记述的 *Olbitherium millenariusum* 也



可能是一古新世动物的残余种。在 Meng et al. (1998) 研究的中国内蒙古古新世最晚期 Bayan Ulan 动物群中也发现有类似 *Olbitherium millenariusum* 的化石,两个不完全的上臼齿 (IVPP V 11149.2 和 V 11149.5) 在形态上与五图的上臼齿很接近,只是稍小一些。也就是说,在亚洲晚古新世已经出现与早始新世奇蹄类上臼齿很接近的哺乳动物。

简而言之,*Olbitherium millenariusum* 的发现说明奇蹄类可能起源于亚洲和北非古新世 phenacodontids 或 phenacodontid 类型的古有蹄类,而 *Olbitherium millenariusum* 是古老的 phenacodontid 类型的古有蹄类向奇蹄类演化过程中的一支。

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## OLBITHERIUM MILL ENARIUSUM , A NEW PERISSODACTYL-LIKE ARCHAIC UNGULATE (MAMMALIA) FROM THE EARLY EOCENE WUTU FORMATION, SHANDONG

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**Key words** Wutu, Shandong, Early Eocene, “Phenacodonta”

### Summary

A unique mammal was found from the Early Eocene of the Wutu Basin, Shandong Province, China. The upper molars of the species are similar to those of early perissodactyls in general morphology, but the m1 ~ 2 are much like those of phenacodontids in having an incomplete hypoploids, and the M3 has a hypocone with prehypocrista and posthypocrista, which is similar to that of primitive hyraxes. It is difficult to assign the new species to the order Perissodactyla or other definite orders. It seems advisable to refer the new species to “Mirorder Phenacodonta”, including Condylarthra, Perissodactyla and Hyracoidea (*sensu* McKenna, 1975).

“Mirorder Phenacodonta” McKenna, 1975 (*sensu* McKenna, 1975)

**Order** incertae sedis

*Olbitherium millenariusum* gen. et sp. nov.

(Fig. 1, 2)

**Holotype** A right mandible with p1 ~ m3 (IVPP V 10758.1).

**Referred specimens** A fragmentary left maxilla with P2 ~ M1 and alveoli of C and P1 (V 10758.2), and associated left mandible with p2 ~ p4 and alveolus of p1 (V 10758.3); isolated left M1 (V 10758.4), and right P2 (V 10758.5), P4 (V 10758.6), and M2 (V 10758.7); a right M3 (V 10758.8); a fragmentary left mandible with p4 ~ m3 (V 10758.9); and left dp2 ~ m2 (V 10758.10), and right dp4 trigonid and m2 trigonid (V 10758.11).

**Locality and age** Early Eocene Wutu Formation, the coal mine of Changle County, Shangdong Province, China.

**Diagnosis** Dental formula:  $? 1. 4. 3 / ? 1. 4. 3$ ; diastema significant between C and P1; P4 without metaconule; upper molar with three roots, long protoloph connecting to the paracrista; M1 ~ 2 metaconule small, anterolateral to the hypocone, and connecting to the metacone by a posterolaterally oriented ridge; parastyle large; mesostyle absent; lingual cingulum surrounding protocone and hypocone; M3 metaconule greatly reduced, hypocone bearing anterior and posterior crests; talonid absent on p1 and small on p2; p4 metastylid distinct, and entoconid absent; m1 ~ 2 hypoconulid more linguallly positioned and close to entoconid; and connecting to the hypoconid by buccal postcrisid branch (Hooker, 1989), metastylid weak, no hypolophid connecting the hypoconid and entoconid; m3 elongated, entoconid nearly isolated, hypoconulid large and formed third lobe.

**Remarks** *Radinskya yupingae* from the Late Paleocene of the Nanxiong basin, Guangdong Province, China, is similar to early perissodactyls in the upper cheek tooth morphology (McKenna et al., 1989) and was called as a "Chinese Paleocene perissodactyl" (see Froehlich, 1999). The lower cheek teeth of *R. yupingae* are unknown. As recognized by McKenna et al. (1989), *R. yupingae* differs from the primitive perissodactyls in having a large protoconule, a strong metaconule, strong and short protoloph and metaloph, alignment of the hypocone, metaconule, and metacone in a line, and lacking lingual cingulum surrounding the protocone and hypocone. In comparison, *Olbitherium millenariusum* shares more derived features with early perissodactyls, such as a relatively small paraconule, the metaconule being considerably smaller than the metacone and hypocone, the metaconule anterior to both the metacone and hypocone so that the three cusps are not aligned in a line, and the well-developed lingual cingulum surrounding the protocone and hypocone. *O. millenariusum* further differs from *R. yupingae* in having a longer diastema between the canine and the P1 but lacking gap between the P1 and P2, absence of P4 metaconule (small metaconule in *R. yupingae*), upper molars with three roots (M1 with four roots in *R. yupingae*), absence of the mesostyle (an extremely weak mesostyle in *R. yupingae*), presence of the postmetaconule crista (lacking both pre- and postmetaconule cristae in *R. yupingae*), the M3 metaconule reduced (distinct, isolated metaconule in *R. yupingae*), and having hypocone cristae. Moreover, in *R. yupingae* and related phenacodolophids the M3 is little reduced and have the hypocone but lack cristae of the hypocone, which are also distinctive from *O. millenariusum*.

In contrast, the lower cheek teeth of *O. millenariusum*, particularly the m1 and m2, are hardly comparable with those of perissodactyls. Instead, they show more similarities with those of phenacodontids. *O. millenariusum* differs from early perissodactyls in the following features: the trigonid and talonid basins are shallow; the hypoconulid is more linguallly positioned and is closer to the entoconid; and the hypoconulid connects to both the entoconid and hypoconid by the lingual postcrisid branch and the buccal postcrisid brach, respectively. In primitive perissodactyls, the trigonid and talonid of basins of the m1 and m2 are deep; the hypoconulid rides on the posterior cingulid, and is usually at the longitudinal axis of the tooth; the entoconid directly connects the hypoconid by the hypolophid; the hypoconulid lacks the lingual and the buccal postcrisid branches (*sensu* Hooker, 1989). The lower cheek teeth, particularly the m1 and m2, of *O. millenariusum* are similar to those of some phenacodontids, such as *Ectocion*, *Phenacodus*, and *Copecion* in the following characters: the trigonid and talonid basins are shallow; the hypoconulid in some cases is closer to the entoconid; and the hypoconulid connects to both the entoconid and hypoconid, although these taxa differ from *O. millenariusum* in having less developed lophids. However, the m3 of phenacodontids is different from that of *O. millenariusum* in being shorter, and lacking the hypoconulid lobe. In phenacodontids, the m3 is relatively shorter, has a talonid formed by the hypoconid, hypoconulid, and entoconid, and lacks a hypoconulid lobe. Similar to primitive perissodactyls, the m3 of *O. millenariusum* is relatively long and has the hypoconulid lobe. The m3 entoconid of *O. millenariusum* is nearly isolated and is not connected by the hypolophid to the hypoconid, which

differs from the condition in perissodactyls. In sum, *O. millenarium* is more similar to primitive perissodactyls than is *R. yepingae* in the upper molar morphology, but the m1 and m2 are more comparable to those of phenacodontids.

*O. millenarium* is also comparable to early hyracoids in some features. For instance, the V-shaped hypocone on the M3 and reduction of the hypoconule in *O. millenarium* are similar to those of the hyracoid *Seggeurius* (Mahboubi et al., 1986).

Cope (1881a) first proposed that the Condylarthra are the ancestral type of the known perissodactyls; the proposal has been influential since then. Based on his study on structures of the mastication and locomotion, Radinsky (1966, 1969) specifically pointed out that perissodactyls originated from the phenacodont genus *Tetraclaenodon*. McKenna (1975) further grouped the orders Condylarthra, Perissodactyla, and Hyracoidea to the “Mirorder Phenacodonta”, although Hyracoidea is transferred to the Superorder Afrotheria based on molecular data (Hedges, 2001; Madsen et al., 2001; Helgen, 2003). The cheek teeth of *O. millenarium* concurrently possess some characters of perissodactyls, phenacodontids and hyracoids, and make it difficult to assign a definite order. Therefore, the new taxon from the Early Eocene of Wutu Basin is tentatively referred to the “Mirorder Phenacodonta” (McKenna, 1975).

The similarity of *O. millenarium* to the primitive perissodactyls and phenacodontids suggests that perissodactyls derived from phenacodonts or *Phenacodus*-like archaic ungulates. And the new taxon, *Olbitherium millenarium*, represents an offshoot when the Paleocene *Phenacodus*-like archaic ungulates evolved to perissodactyl-like mammals.

Some archaic ungulates were reported recently, *Abdounodu hamdii* (Miocleanidae), *Ocepeia daouiensis* (cf. “Phenacodonta”), and *Hilalia* (“Condylarthra”) were found from the early Paleogene of Morocco and Turkey (Mass et al., 2001; Gheerbrant et al., 2001). These suggest that origin of perissodactyls is possibly related to Asian and North African archaic ungulates.

*Olbitherium millenarium* is probably one of many Eocene relic forms of archaic mammals in the Wutu fauna (Tong and Wang, 1998). Fossils similar to *O. millenarium* were also found in the latest Paleocene Bayan Ulan fauna (Meng et al., 1998).

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