

山东昌乐早始新世五图组伪齿兽类 (哺乳纲, 踝节目)一新属¹⁾

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摘要 记述了在山东早始新世地层中发现的一种伪齿兽类——亚洲脊兽(新属、新种) (*Lophocion asiaticus* gen. et sp. nov.), 肯定了伪齿兽类在亚洲的存在。新种在牙齿形态上与北美的 *Ectocion* 接近, 但脊齿化程度较高, 表现在上臼齿上有初始的后脊, 从次尖向不同方向伸出三条清晰的棱脊。这些特征使新属容易与其他已知伪齿兽类相区别。

关键词 山东昌乐, 早始新世, 踝节目

中图法分类号 Q915.873

踝节目 (Condylarthra) 是一类古老的有蹄动物, 是老第三纪早期在北半球广泛分布的哺乳动物类群之一。踝节目各科之间的亲缘关系有待进一步研究, 从目前材料来看, 这一古老的目可能是复系, 但某些种类可能与现生类群 (如偶蹄目、奇蹄目) 起源有关。其中伪齿兽科 (Phenacodontidae) 除欧洲有少量的发现外, 主要出现在北美。北美伪齿兽相当丰富, 收进数据库的已超过 6000 件标本 (Thewissen, 1990)。在某些北美化石地点很富集, 有时占总标本数的四分之三 (Matthew and Granger, 1915)。在亚洲, 伪齿兽类虽有报道, 或因材料不足而不能确定, 或因鉴定上失误而未被承认。因此, 亚洲至今未有确切的伪齿兽类的记录。

1993 年春, 在山东五图盆地早始新世地层中采到两件标本, 其牙齿形态与北美古新世晚期—始新世早期常见的 *Ectocion* 非常接近, 无疑可归入伪齿兽科。与其共生的约有三十种哺乳动物, 已报道的有多瘤齿兽类、古乏齿兽类、食虫形类、啮齿类 (Tong and Dawson, 1995)、食果猴类 (Beard and Wang, 1995) 和脊齿猿类? (王景文、童永生, 1996)。

踝节目 *Condylarthra* Cope, 1881

伪齿兽科 *Phenacodontidae* Cope, 1881

亚洲脊兽 (新属、新种) *Lophocion asiaticus* gen. et sp. nov.

(图 1; 图版 I)

正型标本 存有 M1-3 的破残的左上颌骨 (IVPP V10707)。

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归入标本 存有 DP3-4的右上颌骨(V10707.1)。

地点和层位 山东昌乐五图盆地县矿;五图组,始新世早期。

特征 上臼齿形态与 *Ectocion* 相近,但更脊齿化。具伸向前尖的原小尖前棱,形成较完整的前脊,次尖前棱伸至后小尖,与斜向拉长的后小尖一起形成不完全的后脊;舌侧齿带明显,出现在原尖和次尖之间。

名称由来 属名: *loph*: 出自希腊文 *lophodos*, 意为脊状的; *cion*, 出自希腊文 *chione*, 意为半神半人的女神,常作为兽类名称的后缀。种名为产地名,意为此类动物在亚洲肯定存在。

描述 正型标本和归入标本都是从一块 4cm(长) × 3cm(宽) × 2cm(高)的岩石中修理出来的。两块标本似乎不大可能是同一个体,但同一个体的可能性也不能排除。归入标本上的 DP4 和 DP3 磨蚀轻微,而正型标本上 M3 已经萌出,并已磨蚀,这在现生的和绝大部分化石哺乳动物中不可能出现在同一个体中,但在个别的化石种类中这种情况是否出现在同一个体中就难以确定。就伪齿兽类而言,在归入到 *Phenacodus primaevus* 的 USNM 20070 标本上,保存了磨蚀程度轻微的 DP3-M3 (West, 1971, Fig. 13B)。由此,在 West 推测的伪齿兽类颊齿萌出次序中, P3 和 P4 的萌出晚于 M3。因此,五图的两块标本是属于同一个体的可能性不能排除。这里暂按一般规律将这两块标本编成两个号。

DP3, 外形近似直角三角形, 牙齿后缘几乎与外侧缘垂直。前附尖大, 远离前尖, 但有低脊伸至前尖基部。无中附尖和后附尖。后尖发育, 几乎与前尖等大, 两尖接近, 仅由窄沟将两者分开。前尖高瘦, 稍高于后尖。原尖位置靠后, 与后尖相对, 虽比前尖和后尖粗壮, 但齿尖低于后两者。原小尖明显, 斜向拉长, 有向前外方延伸的短棱与前尖前侧相连, 并有向后内方伸长的棱脊与原尖连接。无后小尖。在原尖和外脊之间形成向后开放的宽谷。外齿带弱, 后齿带较发育, 从后尖后壁基部一直延伸到原尖, 前内侧齿带仅存于原小尖和原尖之间。

DP4, 完全臼齿化, 近于方形。四个主尖(前尖、后尖、原尖和次尖)的大小相近, 其间有低脊相连。前附尖贴近前尖, 中附尖发育, 无后附尖。前尖有低的前、后棱分别与前附尖、中附尖连接, 后尖前棱与中附尖相接, 形成近于 W 形的外脊。前尖和后尖之间有宽谷相隔。原小尖和后小尖明显。原尖基本上与前尖相对, 具前、后棱。原尖前棱与原小尖前棱一起形成清楚的前脊。原尖后棱较低, 伸向后小尖前内侧。位于原尖后方的次尖相对较小, 其前棱伸至后小尖, 与低弱的后小尖前棱一起组成初始的后脊。次尖后棱与后齿带相接。外齿带、前、后齿带基本连续, 内齿带短, 由次尖前壁降至原尖后壁基部。

M1, 近似长方形, 宽大于长。牙齿形态类似 DP4, 但前附尖更发育, 更加靠近前尖, 中附尖相对发育, 原小尖似较突出, 后小尖较小, 近于孤立, 无伸向后尖的后小尖前棱, 次尖相对较大。

M2 大于 M1, 形态似 M1, 但中附尖和次尖相对不如 M1 发育, 原尖后棱较弱, 后小尖斜向延长, 但不与后尖连结。

测 量(单位: 毫米)

DP3		DP4		M1		M2		M3	
L.	W.	L.	W.	L.	W.	L.	W.	L.	W.
5.80	4.88	6.15	6.50	6.20	8.52	6.02	8.70	5.36	7.00

M3 明显地小于前面两个臼齿和 DP4, 大小与 DP3 相近, 外形近似卵圆形。前半部类

似前面的两个上臼齿, 后半部分明显退化。无次尖, 后小尖小且孤立, 原尖与中附尖相对, 齿带发育, 除原尖基部外, 基本连续。

比较和讨论 现有的伪齿兽类标本大部分出自北美的早第三纪早期的陆相地层, 最早出现在古新世 Torrejonian 中期 *Tetraclaenodon*/*Pantolambda* 带。伪齿兽在北美早第三纪相当繁盛, *Tetraclaenodon* 是中古新世化石点的最常见的标本, *Phenacodus* 和 *Ectocion* 出现在晚古新世的 Tiffanian 期, 延续到始新世中期。*Tetraclaenodon* 的消失和 *Phenacodus* 的出现是北美 Torrejonian 期和 Tiffanian 期分期的重要依据。伪齿兽类在某些 Clarkforkian 地点很富集, 有时占标本总量的 45%。在始新世早期, 伪齿兽类也是常见的化石, 有时被作为带化石。在欧洲也有伪齿兽类的发现, 但数量不多。

亚洲曾有伪齿兽类的报道, 但不能肯定。Gabunia(1971) 记叙了产自斋桑盆地始新世中期 Obayla 层的两颗下颊齿, 命名为 *Paraphenacodus solivagus*, 并归入伪齿兽科。Russell 和 Zhai(1987) 认为这是一种偶蹄类, Thewissen(1990) 在整理北美伪齿兽科时也将其排斥在伪齿兽科之外。周明镇等(1977) 怀疑广东南雄盆地上湖组发现的一个破残的右下颌骨(IVPP V4237) 是一种伪齿兽类。这块下颌骨仅存一完整的 p2, p2 具有不完全的三角座和初始的跟座, 在中文的描述中还提到有一小的下后尖。而在北美的伪脊齿类中 p2 比较简单, 无下后尖。因此, 正如作者指出的那样, 这块标本的分类位置有待新增标本再确定。童永生等(1976) 也曾提到在南雄盆地浓山组中找到一块类似伪齿兽科的标本, 因为标本不多也难以肯定。Van Valen(1978) 曾将印巴次大陆中始新世的 *Pilgrimella* 归入伪齿兽科, 但未提出理由。*Pilgrimella* 属是由 Dehm 和 Oettinge-Spielberg(1958) 建立的, 随着新材料的增加, 发现 *Pilgrimella* 是 *Anthracobune* 的同物异名(West, 1980)。而 *Anthracobune* 现在认为是一种原始的长鼻类。因此, 在五图标本发现之前, 亚洲早第三纪地层中还没有肯定的伪齿兽科的记录。

自 Cope 在 1881 建立伪齿兽科以来, 已提出十一个属名, 根据 Thewissen(1990) 系统研究, 只有四个有效属: *Tetraclaenodon*、*Phenacodus*、*Ectocion* 和 *Copecion*。这一归类与 Matthew 和 Granger(1915) 的意见是一致的。在这四个有效属中, 除 *Ectocion* 颊齿有些脊齿化外, 其他三个属都为丘形齿。五图标本最接近 *Ectocion*, 但更加脊齿化。

五图标本上臼齿在齿尖、齿脊的配置上与北美的 *Ectocion* 很接近, 因而将五图标本归

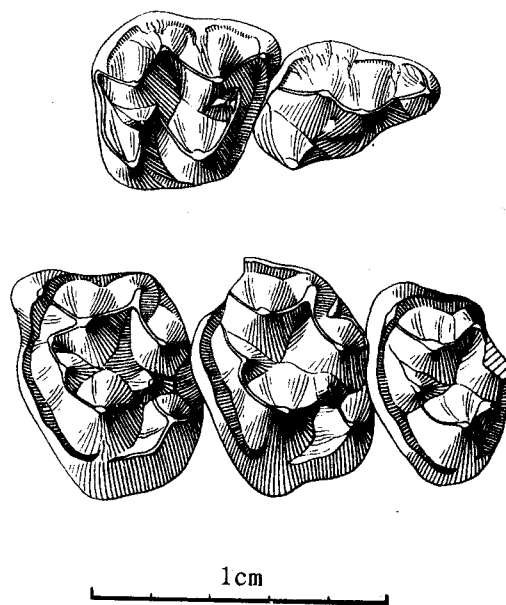


图 1 亚洲脊兽(新属、新种), 左 M1-3 和右 DP3-4, 嚼面视

Fig.1 *Lophocion asiaticus* gen. et sp. nov., LM1-3 (type, IVPP V10707), and RDP3-4 (IVPP V10707.1), occlusal views

入伪齿兽科。与北美属的主要区别在于五图种上臼齿的齿脊更加发育,表现在原小尖有伸向前尖的短棱,与原尖前棱一起形成相对明显的前脊,次尖前棱伸达后小尖,与斜向拉长的后小尖(M2)或弱的后小尖前棱(DP4)一起形成初始的后脊。在 *Ectocion* 的上臼齿上,原小尖和后小尖与前尖、后尖之间有较深的谷相隔,原尖前棱也较弱,次尖伸向后小尖的棱脊低弱,或者缺少伸向后小尖的棱脊。五图种臼齿的脊齿化程度与 *Ectocion* 的 DP4 更相近,而五图种 DP4 的齿脊似乎更发育一些,后小尖有伸向后尖舌侧基部的弱棱。由于五图上臼齿相对于伪齿兽科已知属有更发育的前脊和后脊,故称脊兽。虽在北美的 *Ectocion* 标本中,大部分上臼齿的后小尖不与次尖相连,但在某些标本上具有微弱的次尖前棱,如卡内基自然历史博物馆收藏的 CM 12287 号标本。即使如此,与五图标本仍有明显的差异。另外,五图种 M1-2 的原尖和次尖间有发育的舌侧齿带,北美标本则缺乏。这些差异可将五图属与北美属分开。在已知的伪齿兽科四个属中, *Ectocion* 齿脊相对发育,其他三属都是丘形齿,所以五图属与其他已知属容易区分。

五图上乳齿标本与奇蹄类乳齿不同。奇蹄类乳臼齿已有系统论述(Bulter, 1952),五图的 DP3-4 标本容易与之区分,不再赘述。五图的 DP3 前附尖强烈地向前突出,原尖后移,与伪齿兽类的相应牙齿很相似。五图种 DP3 后尖几乎与前尖等高,DP4 齿脊发育,说明更接近这一科的 *Ectocion* 属,然而,DP3 前尖和后尖部分相连,却与 *Phenacodus* 相似。

北美伪齿兽类四个属特征清楚,容易区分,而且标本量也相当丰富,但其系统关系目前还不很清楚。虽然五图属明显地与北美四属不同,但在上颊齿形态与 *Ectocion* 相似性,或许说明它与后一属有关,齿脊化进一步加强。传统上认为伪齿兽类可能与奇蹄类有关,现在有人认为蹄兔类(Hyracoidea)也是伪齿兽类的姐妹群(Prothero *et al.*, 1988 等)。五图标本的发现虽然无助于解决伪齿兽类的系统关系和与其他类群之间的关系,但表明了伪齿兽类诸多问题的解决可能有待于亚洲的新发现。

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A NEW PHENACODONTID CONDYLARTH (MAMMALIA) FROM THE EARLY EOCENE OF THE WUTU BASIN, SHANDONG

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Key words Wutu, Shandong, Early Eocene, phenacodontid condylarths

Summary

This paper describes a new genus of Phenacodontidae, *Lophocion*. Although phenacodontids are important elements from Torrejonian (M. Paleocene) through Wasatchian (Early Eocene) of North America, only a few specimens have been found in Europe, and definite phenacodontid has never been recorded in Asia until the discovery of the Wutu specimens.

The *Ectocion*-like upper cheek teeth were collected from the Wutu Formation in 1993, along with *Mesodmops dawsonae* (Multituberculata), *Changlelestes dissetiformis* (Insectivora), palaeonodonts, carpolesiid plesiadapoids (Beard and Wang, 1995), rodents (Tong and Dawson, 1995), hyoposodontid condylarths, creodonts, carnivores, tillodonts, and primitive perissodactyls.

Condylarthra Cope, 1881**Phenacodontidae Cope, 1881*****Lophocion asiaticus* gen. et sp. nov.**

(Fig. 1; Pl. I)

Type A fragmentary left maxilla with M1-3 (IVPP V10707).

Referred specimen A fragmentary right maxilla with DP3-4 (IVPP V10707.1).

Locality and horizon County Coal Mine, about 2km east of Wutu Village of Changle County, Shandong Province; Wutu Formation, Early Eocene.

Diagnosis An *Ectocion*-like phenacodont, but somewhat more lophodont. On DP4 and upper molars paraconule distinct, with preparaconule crista extending to paracone, to constitute a clear paraloph together with preprotocrista; hypocone with a distinct prehypocrista run to metaconule, to form an incipient metaloph along with obliquely elongated metaconule; lingual cingulum developed at valley between protocone and hypocone.

Description The specimens, V10707 and V10707.1, repaired from a small coal may be the same individual.

DP3 is triangular in outline. The parastyle projects forwards at the anterior end of tooth. The protocone is posteriorly displaced. The metacone is well developed, although it is partly united with the paracone, and separated from the latter by a narrow valley. The protoconule is distinct, and the metaconule is absent.

DP4 is molariform. The parastyle and mesostyle are relatively large, and the former does not project forward as in DP3. The anterior and posterior crests of the paracone extend to the parastyle and mesostyle, respectively. The metacone separates from the paracone by a wide valley. The anterior crest of the metacone connects with the mesostyle, which forms W-shaped ectoloph. Paraconule and metaconule are present. The protocone is situated lingual to the paracone. The preprotocrista run to the paraconule, and constitutes a relatively complete paraloph with the preparaconule crista. The postprotocrista is clear, and extends to the metaconule. The hypocone is subequal in size with the protocone, and is separated from the latter by a deep valley. The prehypocrista reaches to the metaconule, forming an incipient metaloph with a weak premetaconule crista. The metaconule is disconnected with the metacone. The pre-, post-, and ectocingulum are basically continued, and the lingual cingulum is short, descends from the apex of the hypocone to the posterior base of the protocone.

M1 is wider, and rectangular in outline. It is similar to DP4 in dental morphology, but the parastyle is closer to the paracone, the mesostyle relatively developed, the metaconule smaller, the premetaconule crista absent, and the hypocone larger.

M2 is larger than M1. The mesostyle and hypocone are somewhat reduced related to the counterparts of M1, the postprotocrista is weaker, and the metaconule is obliquely elongated.

M3 is much smaller than the anterior molars. The protocone is lingual to mesostyle, and the hypocone is absent. The metaconule is decreased, and separates from the metacone and protocone. The cingula are basically continuous, except at lingual base of the protocone.

Comparison and discussion Phenacodontids are abundant and diverse in the early Paleogene of North America, only a few specimens have been recorded from Europe. It is uncertain in Asia, although several taxa from Asia have been assigned to the family. Two lower molars from the Obaila beds of the Zaysan Basin were named *Paraphenacodus solivagus*, and were referred to the Phenacodontidae by Gabunia (1971). Russell and Zhai (1987) considered this taxon an artiodactyl, and Thewissen (1990) also did not regard it as a phenacodontid based on newly discovered material from the same basin. Zhou *et al.* (1977) doubted that a lower jaw (IVPP V4237) from the Paleocene of the Nanxiong Basin is a phenacodontid. The lower jaw only preserves a complete p2, which has a small metaconid, as mentioned in their Chinese text. It is not a typical character in the known phenacodontids. Van Valen (1978) allocated an Asian Eocene genus, *Pilgrimella*, to the Phenacodontidae, but did not give an explanation. Generally the genus is considered a synonym with *Anthracobune*, which is suggested to have a closer affinities with the moeritheriids.

In known phenacodontids, *Tetraclaenodon*, *Phenacodus*, and *Copecion* have bunodont molars, but *Ectocion* somewhat lophodont. The Wutu upper cheek teeth are the closest to those of *Ectocion* morphologically, but more lophodont. The paraconules of Dp4 and M1-3 possess a short crest extending to paracone, which forms a clear paraloph with the distinct preprotocrista. The nascent metaloph is present on the Wutu specimen, which is made of a prehypocrista run to metaconule and a feeble premetaconule crista (on DP4) or an obliquely elongated metaconule (on M2). On the upper molars of *Ectocion* the metaconule is isolated, separated from the hypocone and metacone by transverse valleys, and the preparaconule crista is absent. Therefore, the Wutu specimens are different from the known phenacodontids.

图版 I 说明 (Explanations of Plate I)

亚洲脊兽(新属、新种), 上颊齿, 嚼面视(立体)

(*Lophocion asiaticus* gen. et sp. nov., upper cheek teeth, occlusal stereo pair)

A. Left maxilla with M1-3 (IVPP V10707) $\times 2.5$

B. Right maxilla with DP3-4 (IVPP V10707.1) $\times 3.5$

