

钝脚目全棱齿兽科的分类

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摘要 本文在重新观察某些亚洲土著钝脚类的基础上,结合前人研究成果,将原全棱齿兽科、古脊齿兽科和牧兽科合并成一个科——全棱齿兽科,分全棱齿兽和牧兽两个亚科,并对其组成做了分析。

关键词 亚洲, 早第三纪, 钝脚目, 全棱齿兽科

钝脚目是个庞杂的类群。从在法国首次发现冠齿兽化石起,至今已有一百八十多年的研究历史,先后建过十多个科——冠齿兽科 (*Coryphodontidae* Marsh, 1876)、全脊兽科 (*Pantolambdidae* Cope, 1883)、全棱齿兽科 (*Pantolambdodontidae* Granger et Gregory, 1934)、巨脊齿兽科 (*Titanoideidae* Scott, 1937)、厚脊齿兽科 (*Barylambdidae* Patterson, 1939)、古脊齿兽科 (*Archaeolambdidae* Flerov, 1952)、阶齿兽科 (*Bemalambdidae* Chow *et al.*, 1973)、牧兽科 (*Pastoralodontidae* Chow et Qi, 1978)、翼齿兽科 (*Harpyodidae* Wang, 1979)、星期天兽科 (*Cyriacotheridae* Rose et Krause, 1982, 该科已被 Lucas 等排除出钝脚目)、丰齿兽科 (*Plethorodontidae* Huang et Zheng, 1987) 和多尔比尼兽科 (*Alcidedorbignyidae* Muizon et Marshall, 1992)。对于这些科的相互关系已有不少学者做过研究 (Simons, 1960; Kielan-Jaworowska, 1968; Dashzeveg, 1980; Lucas, 1982; Gingerich and Childress, 1983; 黄学诗, 1977, 1978; 周明镇、王伴月, 1979)。本文是在研究安徽贵池动物群中钝脚类的同时,在前人工作的基础上,对亚洲土著类群钝脚目的全棱齿兽科、古脊齿兽科和牧兽科的系统分类和组成进行了初步的探讨。

一、历史的回顾

1. 全棱齿兽科

该科化石最先由美国自然历史博物馆中亚考察队于1925年和1928年在我国内蒙古沙拉木伦地区中始新世乌兰希热组中所采,标本为三块带部分颊齿的不完整的下颌骨,先被归入奇蹄目爪兽类,后经 Granger 和 Gregory (1934) 详细研究,认为应属广义的钝脚目 (*Amblypoda*),订了一新属和两新种——弱全棱齿兽 (*Pantolambdodon inermis*) 和强全棱齿兽 (*P. fortis*),并以此建立了一新科——全棱齿兽科 (*Pantolambdodontidae*)。

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建科后很长一段时间一直未发现全棱齿兽科的新材料。直到 1978 年,童永生报道了采自新疆晚古新世台子村组的一段带 1 个半牙齿 (M_2 和 M_3 的三角座)的右下颌骨,并订了一新属新种——秀丽双脊齿兽 (*Dilambda speciosa*)。同年,周明镇和齐陶在“内蒙古四子王旗晚古新世哺乳类化石”一文的附记中,提到后一作者在与强全棱齿兽和弱全棱齿兽正型标本同一层位中找到了该属完整的上腭板和上颊齿列。Dashzeveg (1980) 记述了在蒙古中始新世地层中发现的新材料,标本为一带 P^4-M^3 的左上颌骨残段和两块带少量颊齿的破碎的下颌骨,并订了一新种——包格德全棱齿兽 (*Pantolambdodon bogdensis*)。丁素因等 (1982) 报道了发现在我国宁夏盐池县大水坑地质时代不明的一残破头骨和少量保存不好的下颊齿,认为在从牙齿特征上,与全棱齿兽可能同属,至少同科。之后,他们 (Ding *et al.*, 1987) 将其命名为翟氏全棱齿兽 (*Pantolambdodon zhaii*)。翟氏种提供了该属的头骨前部和上牙齿的特征。

2. 古脊齿兽科

该科最早的化石是发现在蒙古南戈壁地区奈玛盖特盆地那兰布拉克组晚古新世地层中,标本为两件较完整的下颌骨和一块带右 P^3-M^1 的相当残破的上腭。Flerov (1952) 研究后订了一新属新种——平齿古脊齿兽 (*Archaeolambda planicanina*), 同时建立单型属科——古脊齿兽科 (Archaeolambdidae)。Kielan-Jaworowska (1968) 记述了与平齿古脊齿兽发现在同一地区奈玛盖特盆地的三块下颌骨和一件残破头骨。下颌骨在大小和特征上与平齿古脊齿兽一致,而上颌骨上的牙齿是该种的一倍半大,故被订为属型种的相似种 (*A. cf. planicanina*)。1974 年 Flerov 和 Dashzeveg 记述了在蒙古阿尔泰山乌拉山附近发现的一带 P_4-M_3 的左下颌骨标本,建立新种特氏古脊齿兽 (*Archaeolambda trofimovi*)。1977 年,本文作者研究了在我国安徽潜山晚古新世痘姆组中发现的一基本完整的骨架,建立新种大别古脊齿兽 (*A. tabeiensis*)。目前这是该属乃至整个全棱齿兽科唯一的骨架标本。翌年,作者又根据在安徽宣城晚古新世双塔寺组¹⁾中发现的一带完整 DP^4-M^3 的上颌骨残段和几块破碎的下颌骨,订立另一新种——扬子古脊齿兽 (*A. yangtzeensis*)。同年,童永生 (1978) 记述了发现在新疆吐鲁番盆地晚古新世台子村组中的一带不完全颊齿的残破上颌骨(年轻个体),作为平齿古脊齿兽的相似种。1979 年童永生将发现在江西池江盆地晚古新世地层中的一带颊齿不全的右下颌骨,描述为新属新种——池江南岭兽 (*Nanlingilambda chijiangensis*), 将另一右下颌骨残段(具残破颊齿 P_4-M_2) 和一右 P^4 (残破) 订为新种——大余古脊齿兽 (*A. dayuensis*)。发现在该地的另一些破碎材料被他归到古脊齿兽未定种或属种不定。1980 年, Dashzeveg 根据在蒙古奥洛克诺尔湖 (Orok Nor) 附近的中始新世 Kholboldzhi 组中发现的、带部分颊齿的不完整的下颌骨,建立古脊齿兽科的新属新种——原始奥洛克脊齿兽 (*Oroklambda prima*)。这是古脊齿兽科在地史上的最晚记录。1982 年,童永生根据在广东南雄盆地晚古新世浓山组中发现的一带 M_2-M_3 的右下颌骨断块建立双脊齿兽属新种——竹桂坑双脊兽 (*Dilambda zhuguikengensis*), 在没有阐述理由的情况下,将他建的双脊齿兽属

1) 双塔寺组的时代有争议,有人认为是早始新世,也有人认为是晚古新世。作者倾向于后者。

表 1 钝脚目原全棱齿兽科、古脊齿兽科和牧兽科已被记述之属种
 Table 1 Described species of original Pantolambdodontidae, Archaeolambdidae and Pastoralodontidae

		属种名称 (species)	产地 (location)	时代 (age)
钝脚目 (Pantodonta)	全棱齿兽科 (Pantolambdodontidae)	<i>Pantolambdodon inermis</i> Granger et Gregory, 1934	内蒙古沙拉木伦 (Shara Murun, Nei Mongol)	E ₂
		<i>Pantolambdodon fortis</i> Granger et Gregory, 1934	内蒙古沙拉木伦 (Shara Murun, Nei Mongol)	E ₂
		<i>Dilambda speciosa</i> Tong, 1978	新疆吐鲁番 (Turpan, Xinjiang)	E ₁
		<i>Pantolambdodon bogdensis</i> Dashzeveg, 1980	蒙古奥洛克诺尔 (Orok Nor, Mongolia)	E ₂
		<i>Pantolambdodon zhaisi</i> Ding, Schiebout et Zhou, 1987	宁夏盐池 (Yanchi, Ningxia)	E ₂
	古脊齿兽科 (Archaeolambdidae)	<i>Archaeolambda planicanina</i> Flerov, 1952	蒙古奈玛盖特 (Nemegt, Mongolia)	E ₁
		<i>Archaeolambda trofimovi</i> Flerov et Dashzeveg, 1974	蒙古阿尔泰乌拉山 (Altai Ula, Mongolia)	E ₁
		<i>Archaeolambda zabiensis</i> Huang, 1977	安徽潜山 (Qianshan, Anhui)	E ₁
		<i>Archaeolambda yangizeensis</i> Huang, 1978	安徽宣城 (Xuancheng, Anhui)	E ₁
		<i>Archaeolambda dayuensis</i> Tong, 1979	江西大余 (Dayu, Jiangxi)	E ₁
		<i>Nanlingilambda chijiangensis</i> Tong, 1979	江西大余 (Dayu, Jiangxi)	E ₁
		<i>Oroklambda prima</i> Dashzeveg, 1980	蒙古奥洛克诺尔 (Orok Nor, Mongolia)	E ₂
		<i>Dilambda zhuguikengensis</i> Tong, 1982	广东南雄 (Nanxiong, Guangdong)	E ₁
	牧兽科 (Pastoralodontidae)	<i>Pastoralodon lacustris</i> Chow et Qi, 1978	内蒙古四子王旗 (Siziwang Banner, Nei Mongol)	E ₁ - E ₂
		<i>Convallisodon convexus</i> Chow et Qi, 1978	内蒙古四子王旗 (Siziwang Banner, Nei Mongol)	E ₁
		<i>Convallisodon haliutensis</i> Chow et Qi, 1978	内蒙古四子王旗 (Siziwang Banner, Nei Mongol)	E ₁
		<i>Altilambda pactus</i> Chow et Wang, 1978	安徽怀宁; 广东南雄 (Huaining, Anhui; Nanxiong, Guangdong)	E ₁ ²⁻³
		<i>Altilambda tenuis</i> Chow et Wang, 1978	安徽潜山 (Qianshan, Anhui)	E ₁
		<i>Altilambda minor</i> Tong, 1982	广东南雄 (Nanxiong, Guangdong)	E ₁
		<i>Altilambda yujingensis</i> Wang, Yu et Li, 1992	安徽潜山 (Qianshan, Anhui)	E ₁

从全棱齿兽科移到古脊齿兽科名下。还将在该层位中发现的带残破的 C_1-M_2 的下颌骨处理为南岭兽未定种。

3. 牧兽科

牧兽科是近年来新建科。1978年,周明镇、齐陶根据内蒙古四子王旗晚古新世脑木根组脑木根层中发现的、原先(周明镇等,1976)认为是古脊齿兽科新属新种的几件标本——未完全修好的头骨和带数目不同颊齿的下颌骨,建立了牧兽科(Pastoralodontidae),下辖两个新属和三个新种——湖牧兽(*Pastoralodon lacustris*)、圆谷齿兽(*Convallisodon convexus*)和哈流特谷齿兽(*C. haliutensis*)。同年,周明镇、王伴月根据发现在安徽潜山和怀宁中古新世望虎墩组及广东南雄晚古新世浓山组的一些零星标本,建立一新属——高脊兽(*Altilambda*),也归入牧兽科。该属分两个种:和平高脊兽(*A. pactus*),正型标本为带部分颊齿的一个不完整的下颌骨和一上颌骨,还有一带 M_1-M_2 的下颌骨段块也被归入该种;细高脊兽(*A. tenuis*)标本为带 P_3-M_3 的一段下颌骨和一具乳齿的年轻个体的下颌骨。1982年,童永生根据在广东南雄盆地晚古新世浓山组中发现的一带右 $C-M_3$ 和左 P_1-P_4 的下颌骨,建立高脊兽一新种——小高脊兽(*A. minor*),还将带一个牙齿(M_3)的右下颌骨段块订为高脊兽未定种。最近,王元青、余本爰、李丁生(1992)记述了发现在安徽潜山盆地中古新世望虎墩组中的一齿列基本完全的残破头骨,并建一新种——余井高脊兽(*A. yujingensis*)。

以往发现的全棱齿兽科、古脊齿兽科和牧兽科所建属种、产地、时代可归纳成表1。

二、关于原全棱齿兽科、古脊齿兽科和牧兽科新的分类意见

1. 新的认识

从表1可知,原上述三科动物地史分布时间不长,最古老的属种出现在中古新世,最晚的代表发现在中始新世地层中。此外,它们的地理分布也很局限,仅发现在中国和蒙古,因此,无疑是亚洲特有的土著类群。

半个多世纪来,特别是最近的发现,不仅使它们的标本和种类增多,而且使这些类群的性质也更加清楚。我们在研究安徽贵池的钝脚类标本时,收集了几乎全部现有的资料和标本,通过观察对比,并结合前人的研究成果,提出如下的分类意见,并对调整后科的组成进行了厘定(表2)。

2. 分类简述

全棱齿兽科 *Pantolambdodontidae* Granger et Gregory, 1934

Archaeolambdidae Flerov, 1952

Pastoralodontidae Chow et Qi, 1978

特征 小到中等大小的钝脚类。头骨面、颅两部高差不大,矢状脊弱。犬齿小,呈门齿或前臼齿化(南岭兽可能例外,从齿槽看,它的犬齿似较大)。上颊齿外齿带不很发育,外谷浅而清楚。 M^1 和 M^2 外脊成显著的W形,向内伸超过齿宽之半,具较发育的中附尖。

表 2 钝脚目全棱齿兽科中的亚科和属种

Table 2 The subfamilies and species of Pantolambdodontidae

目	科	亚科	属种名称 (species)	产地 (location)	时代 (age)
目 钝 脚 兽 目 (Pantodonta)	科 全 棱 齿 兽 科 (Pantolambdodontidae)	亚科 全棱齿兽亚科 (Pantolambdodontinae)	<i>Pantolambdodon inermis</i> Granger et Gregory, 1934	内蒙古沙拉木伦 (Shara Murun, Nei Mongol)	E ₂ ²
			<i>Pantolambdodon fortis</i> Granger et Gregory, 1934	内蒙古沙拉木伦 (Shara Murun, Nei Mongol)	E ₂ ²
			<i>Pantolambdodon zhaiti</i> Ding, Schiebout et Zhou, 1987	宁夏盐池 (Yanchi, Ningxia)	E ₂ ²
			<i>Archaeolambda planicanina</i> Flerov, 1952	蒙古奈玛盖特 (Nemegt, Mongolia)	E ₁ ¹
			<i>Archaeolambda tabiensis</i> Huang, 1977	安徽潜山 (Qianshan, Anhui)	E ₁ ¹
			<i>Archaeolambda yangizeensis</i> Huang, 1978	安徽宣城、贵池 (Xuancheng and Guichi, Anhui)	E ₁ ¹
			<i>Archaeolambda speciosa</i> (Tong), 1978	新疆吐鲁番; 广东南雄 (Turpan, Xinjiang; Nanxiong, Guangdong)	E ₁ ¹
			<i>Archaeolambda bogdensis</i> (Dashzeveg), 1980	蒙古奥洛克诺尔 (Orok Nor, Mongolia)	E ₂ ²
			<i>Archaeolambda prima</i> (Dashzeveg), 1980	蒙古奥洛克诺尔 (Orok Nor, Mongolia)	E ₂ ²
		<i>Archaeolambda</i> sp. nov. (Huang et Chen, in press)	安徽贵池 (Guichi, Anhui)	E ₁ ¹	
		<i>Nanlingilambda chijiangensis</i> Tong, 1979	江西大余 (Dayu, Jiangxi)	E ₁ ¹	
		亚科 牧兽亚科 (Pastoralodontinae)	<i>Pastoralodon lacustris</i> Chow et Qi, 1978	内蒙古四子王旗 (Siziwang Banner, Nei Mongol)	E ₁ ¹ -E ₂ ²
			<i>Pastoralodon trofimovi</i> (Flerov et Dashzeveg), 1974	内蒙古四子王旗; 蒙古阿尔泰山乌拉山 (Siziwang banner, Nei Mongol; Mongolia)	E ₁ ¹
			<i>Altilambda pactus</i> Chow et Wang, 1978	安徽怀宁; 广东南雄 (Huaining, Anhui; Nanxiong, Guangdong)	E ₁ ¹⁻³
			<i>Altilambda tenuis</i> Chow et Wang, 1978	安徽潜山 (Qianshan, Anhui)	E ₁ ¹
			<i>Altilambda minor</i> Tong, 1982	广东南雄 (Nanxiong, Guangdong)	E ₁ ¹
			<i>Altilambda yujingensis</i> Wang, Yu et Li, 1992	安徽潜山 (Qianshan, Anhui)	E ₁ ¹

M³ 外脊成 V 形, 一般后尖在后脊上表现不清楚。下颊齿下前尖不退化, 下前臼齿不臼齿化, P₁-P₂ 齿冠成纵向的扁片状, P₃-P₄ 跟座脊状, M₁-M₂ 三角座和跟座成 V 形或 U 形, 后者低小。M₃ 跟座多成杯形或盆形。

关于原全棱齿兽科、古脊齿兽科和牧兽科的分类, 一直存在着不同的意见。自 1952 年弗辽罗夫建立古脊齿兽科以来, 在蒙古、特别是我国不断发现新材料。一些学者

(Kielan-Jaworowska, 1968; 黄学诗, 1978) 根据手中标本的研究, 认为古脊齿兽应是一独立的科, 其讨论的焦点是否定 Simons (1960) 关于 *Archaeolambda* 是北美厚脊齿兽科 (Barylambdidae) 中的 *Haplolambda* 同物异名的说法。不过本文作者(黄学诗, 1977) 首次提出全棱齿兽和古脊齿兽属于同一个科的可能性。1978 年, 周明镇、齐陶根据在内蒙古发现的一全棱齿兽头骨, 明确指出古脊齿兽科是全棱齿兽科的同物异名。翌年, 周明镇、王伴月在“全齿目和裂齿目的关系和分类系统”一文中, 正式将古脊齿兽科归入全棱齿兽科。1980 年, Dashzeveg 将原全棱齿兽科和古脊齿兽科合并成一个全棱齿兽亚科 (Pantolambdodontinae), 并将北美古新世的厚脊齿兽科降级成亚科, 与前一亚科共同组成全棱齿兽科。事实上, 厚脊齿兽科与北美的其他钝脚类科关系更近, 而与包括全棱齿兽和古脊齿兽在内的亚洲类群相差甚远 (黄学诗, 1978)。不过, 他将全棱齿兽科和古脊齿兽科合并成一个亚科的意见是可取的, 本文接受了这个分类。Lucas (1982) 在他的关于钝脚类十九个属系统关系设想图表中, 不仅将全棱齿兽、古脊齿兽和牧兽这三类动物列在一起, 而且认为 *Titanoides* 和 *Harpyodus* 与它们有很近的系统关系。1984 年他又面告笔者, 原全棱齿兽科、古脊齿兽科、牧兽科和翼齿兽科是一个科。事实上, 翼齿兽 (*Harpyodus*) 很特殊, 与前三者似无更近的系统关系 (黄学诗、郑家坚, 1987)。而牧兽与全棱齿兽和古脊齿兽确实有许多重要的共同点, (见前面科的特点), 表明这三者之间比与钝脚类其他类群有更近的关系, 应是同科为宜。但由于牧兽较为特殊, 它与全棱齿兽和古脊齿兽之间要比后两者之间关系要远, 故立为不同亚科。当然, 牧兽有与全棱齿兽相似而与古脊齿兽不同的特点, 如 P^1 的后原尖脊连续等等, 但又有些与古脊齿兽相近而与全棱齿兽不同的特点, 如下臼齿跟座相对低小等等。基于这些相似性, 周明镇和齐陶最初 (1976) 将湖牧兽和“圆谷齿兽”当作古脊齿兽科的新属新种。它们之间特征的交错现象, 进一步反映三者关系密切, 应同科。这样, 原全棱齿兽科、古脊齿兽科和牧兽科的 8 属 20 种动物, 在本文被合并为 1 科 2 亚科 5 属 17 个种 (其中包括 1 个将要记述的新种)。

全棱齿兽亚科 *Pantolambdodontinae* (Granger et Gregory), 1934

亚科型属 全棱齿兽属 *Pantolambdodon* Granger et Gregory, 1934

包括属 亚科型属、古脊齿兽属 (*Archaeolambda* Flerov, 1952) 和南岭兽属 (*Nanlingilambda* Tong, 1979)。

特征 前颌骨鼻突长, 门齿孔大。上颊齿前、后齿带不发育, 无次尖。 M^1 和 M^2 冠面成三角形, 外中凹较深。下颌上升支比较平缓, 与水平支夹角大。下前臼齿齿列长度大于或接近臼齿齿列。

分布及时代 蒙古, 晚古新世和中始新世; 广东和江西, 晚古新世; 安徽, 晚古新世; 湖南, 早始新世; 新疆, 晚古新世; 内蒙古, 晚古新世和中始新世; 宁夏, 始新世(?)。

全棱齿兽属 *Pantolambdodon* Granger et Gregory, 1934

属型种 弱全棱齿兽 *Pantolambdodon inermis* Granger et Gregory, 1934。

包括种 属型种和强全棱齿兽 (*Pantolambdodon fortis* Granger et Gregory, 1934)。

翟氏全棱齿兽 (*P. zhaii* Ding, Schiebout et Zhou, 1987)。

特征 个体较大。头骨面部低平。上颊齿三角形, 齿冠高。 P^4 V形脊后原尖脊连续。上臼齿W形外脊宽度大, 中附尖成脊状。 M^1 后翼长于前翼, M^2 则后翼短于前翼, 前者是最大的上颊齿。下臼齿三角座和跟座都很开阔, 具与下斜脊相连的下后附尖。 M_3 是最长的下臼齿。

分布及时代 内蒙古, 中始新世; 宁夏, 始新世(?)。

弱全棱齿兽 *Pantolambdodon inermis* Granger et Gregory, 1934

特征 个体较小。 M_2 处下颌骨深度为 29—36 毫米。 M_1 长 20 毫米, 宽 9.5—11 毫米。

产地与层位 内蒙古中始新世乌兰希热组。

强全棱齿兽 *Pantolambdodon fortis* Granger et Gregory, 1934

特征 个体大, 下颌骨粗壮。 M_1 长 29 毫米, 宽 13 毫米。

产地与层位 内蒙古中始新世乌兰希热组。

翟氏全棱齿兽 *Pantolambdodon zhaii* Ding, Schiebout et Zhou, 1987

特征 个体小于强全棱齿兽。面部低, 长而平, 鼻切迹大大缩进, 外鼻孔扩大形成长而窄的深沟。眶下孔距眼眶远。上前臼齿V形脊和上臼齿W形外脊开口相对较窄, 颊齿较横宽, 内壁成圆弧形, 不成典型的三角形。 M^2 是最长的上臼齿。

产地与时代 宁夏, 盐池, 大水坑; 始新世(?)。

古脊齿兽属 *Archaeolambda* Flerov, 1952

属型种 平齿古脊齿兽 (*Archaeolambda planicanina* Flerov, 1952)。

包括种 属型种和大别古脊齿兽 (*Archaeolambda tabiensis* Huang, 1977), 扬子古脊齿兽 (*A. yangtzeensis* Huang, 1978), 秀丽古脊齿兽 [*A. speciosa* (Tong), 1978 = *Dilambda speciosa* Tong, 1978], 包格德古脊齿兽 [*A. bogdensis* (Dashzeveg), 1980 = *Pantolambdodon bogdensis* Dashzeveg, 1980], 原始古脊齿兽 [*A. prima* (Dashzeveg), 1980 = *Oroklambda prima* Dashzeveg, 1980] 和古脊齿兽新种 (*Archaeolambda* sp. nov., 黄学诗、陈烈祖, 待刊)。

特征 个体比全棱齿兽属小。 P^4 后原尖脊不连续, 与原尖相接处中断。 M^2 后翼长于或接近前翼, 为上颊齿中最大者。下臼齿跟座较低小, M_1 和 M_2 的三角座和跟座V形夹角近等, 约 60° 。 M_3 跟座圆盆状。颅后骨骼比较轻巧、平直、细长。第三指(趾)节骨呈爪状(此特征可能也是全亚科乃至全科的特征)。

分布与时代 广东南雄, 晚古新世; 江西池江, 晚古新世; 湖南衡东, 早始新世; 安徽潜山, 宣城, 贵池, 晚古新世; 新疆吐鲁番, 晚古新世; 蒙古, 晚古新世和中始新世。

古脊齿兽和全棱齿兽虽有许多共同特征, 同为一亚科, 但两属之间的区别仍是很明显的。全棱齿兽个体较大, 头骨较特化, 面部相当低平, 前颌骨鼻突细长, 眼眶位于 M^3 之后, 眶下孔相对小。下颌骨细长, 牙齿排列较松散。上臼齿W形外脊较开阔, 宽度大, 前、

后附尖与前、后尖高差不大, 无外齿带及前、后齿带。上臼齿大小向后递减, M^1 是最大的上颊齿。下前臼齿臼齿化程度相对较高。下臼齿跟座较大, M_3 跟座向内开口不成封闭的跟盆。而古脊齿兽在有些特征上与之正相反或在程度上有差异。古脊齿兽的个体相对较小, 头骨的面部稍高, 前颌骨鼻突较宽, 眼眶前缘位于 M^2 上方, 眶下孔较大。下颌骨相对较粗壮, 牙齿紧密排列无齿隙。上臼齿的前、后附尖位置低, 有弱的前、后齿带及外齿带。 M^2 是最大的上颊齿。下臼齿三角座和跟座 V 形夹角小, 约 60° , 跟座比三角座低小, M_3 有近于封闭的跟盆。这些差别说明这两个属的界限是清楚的。

平齿古脊齿兽 *Archaeolambda planicanina* Flerov, 1952

特征 P^3-M^1 长约 20 毫米, P_1-M_3 长约 75 毫米, P_1-P_4 长约 39 毫米, M_1-M_3 长约 36 毫米。 M_3 处下颌骨底缘不收缩。

产地和层位 蒙古奈玛格特盆地晚古新世那兰布拉克组; 新疆吐鲁番盆地晚古新世台子村组; 江西大余晚古新世池江组。

大别古脊齿兽 *Archaeolambda tabiensis* Huang, 1977

特征 个体比平齿古脊齿兽小, M_1-M_3 长约 28 毫米。 P^3-P^4 V 形外脊的前、后臂上具小纵肋, M^3 后脊弯曲。 M_3 处下颌骨底缘略有收缩。

产地及层位 安徽潜山晚古新世痘姆组。

大别古脊齿兽是目前全棱齿兽科中唯一发现骨架标本的种。

扬子古脊齿兽 *Archaeolambda yangtzeensis* Huang, 1978

特征 个体较大别古脊齿兽稍小。 M^1 和 M^2 中附尖强大。 M^2 很短宽, 外脊后翼特别伸长, 弱的前、后齿带在内侧相连。 M^3 小, 不对称, 外脊后翼长度是前翼的一半。

产地与层位 安徽宣城、贵池, 晚古新世双塔寺组。

扬子古脊齿兽下臼齿的跟座与三角座比值比在平齿种中更小, 下后脊更平直, 上牙的特征与该种也很不一样。扬子古脊齿兽上臼齿的中附尖特别发育, M^2 外形显著不对称, M^3 小而歪斜等特点可与大别种相区别。

秀丽古脊齿兽 *Archaeolambda speciosa* (Tong), 1978

Dilambda speciosa Tong, 1978

Dilambda zhuguihengensis Tong, 1982

特征 下臼齿齿冠高、齿脊陡, 具发育程度不同的下后附尖。 M_3 具下内尖。

产地与层位 新疆吐鲁番盆地晚古新世台子村组; 广东南雄盆地晚古新世浓山组。

1978 年, 童永生根据在台子村组中发现的一个半下臼齿, 命名新属新种“秀丽双脊齿兽”(*Dilambda speciosa*), 并将其放在原全棱齿兽科。Lucas (1982) 将它移至古脊齿兽属, 作为一个独立的种。该标本除具下后附尖(实际上在古脊齿兽属中有些种, 如平齿种和大别种, 在下后尖的后方也有下后附尖的雏型)外, 其三角座和跟座确是古脊齿兽的性质。1982 年, 童永生又根据南雄盆地的标本建立“双脊齿兽”另一新种——竹桂坑双脊

齿兽 (*Dilambda zhuguiakensis*)。他将该种直接置于原古脊齿兽科名下,这足以说明原放在全棱齿兽科中的“双脊齿兽”,与古脊齿兽的关系多么密切。童永生认为竹桂坑种与秀丽种的区别在于下臼齿下后附尖不显著,V形脊夹角较小,齿带发育,个体稍大。实际上,这些差别很小,有些仅是程度上的差异。如个体大小,秀丽种 M_2 长 9.4 毫米,而竹桂坑种 M_2 长 10.0 毫米,仅差 0.6 毫米,差别实在不大,无法分开。所以把这两个种合并成一个种——秀丽古脊齿兽是适宜的。

包格德古脊齿兽 *Archaeolambda bogdensis* (Dashzeveg), 1980

Pantolambdodon bogdensis Dashzeveg, 1980

特征 上臼齿相对较长。下臼齿具下后附尖。 M_1 长 11.5 毫米,宽 7.5 毫米。

产地与层位 蒙古 Orok Nor 湖附近,中始新世 Kholboldzhi 组。

1980 年, Dashzeveg 根据在蒙古 Orok Nor 湖附近中始新世地层中发现的带牙齿的上颌骨和下颌骨,建立全脊齿兽属一新种——包格德全脊齿兽 (*Pantolambdodon bogdensis*)。这个种的上臼齿的前、后附尖比前、后尖低得多, M^2 是最大的上颊齿。这些都是古脊齿兽的特点。此外,它的大小接近平齿古脊齿兽,而比目前全棱齿兽属中的三个种均小得多。所以它应该是古脊齿兽而不是全棱齿兽。它的下臼齿与秀丽古脊齿兽一样具下后附尖,但个体比后者大。它的上臼齿比目前已知古脊齿兽其他种均较窄长,因此仍不失其是一独立种。

原始古脊齿兽 *Archaeolambda prima* (Dashzeveg), 1980

Oroklambda prima Dashzeveg, 1980

特征 个体大小与扬子种相近,但下前臼齿特别是 P_4 的臼齿化程度高,跟座近半圆形。下臼齿的下原尖比较膨大,三角座稍成 U 形。

产地与层位 蒙古 Orok Nor 湖附近中始新世 Kholboldzhi 组。

1980 年, Dashzeveg 在研究 Orok Nor 湖附近中始新世钝脚类化石时,除命名了一新种——包格德全棱齿兽(现为包格德古脊齿兽)外,还建了一新属新种——原始奥洛克古脊齿兽(*Oroklambda prima*)。这后一个属已被 Lucas (1982) 作为一个独立种归到古脊齿兽,笔者认为适宜的。这个种的标本虽保存不好,磨蚀也重,但下颊齿的基本式样仍相似于古脊齿兽,只是它的下前臼齿臼齿化程度较高, P_4 的跟座略成半圆形或月牙形,下臼齿的三角座由于原尖膨大而成 U 形(其实在平齿古脊齿兽中三角座也多少有点成 U 形),不同于基本上成 V 形的其他种。

南岭兽属 *Nanlingilambda* Tong, 1979

属型种 池江南岭兽 (*Nanlingilambda chijiangensis* Tong, 1979)。

包括种 仅属型种一种。

特征 下颌水平支前浅后深,粗壮。下犬齿断面成圆形,较大,与 P_1 之间有一短的齿隙。下臼齿的下跟座较短宽。 M_3 的下次尖和下次小尖明显。

分布及时代 江西大余和广东南雄,晚古新世。

池江南岭兽 *Nanlingilambda chijiangensis* Tong, 1979

Nanlingilambda chijiangensis Tong, 1979

Archaeolambda tayuensis Tong, 1979

特征 同属。

产地及层位 江西大余晚古新世池江组。

原池江南岭兽已被 Lucas (1982) 并入秀丽古脊齿兽。虽然标本保存得十分不好,但仍可看出该属种的下颌骨较粗壮,下臼齿相对横宽等特点。它的下犬齿断面成圆形,较大,并与 P_1 之间有齿隙,这不仅不同于古脊齿兽,而且也有别于全棱齿兽科中的其他属种,应为一独立属种。此外,童永生(1979)原订大余古脊齿兽(*Archaeolambda tayuensis*)也被 Lucas (1982) 在同一篇文章中并入秀丽古脊齿兽。这种归并似乎不太合适。秀丽古脊齿兽的下臼齿不那么横宽,且具下后附尖。但是,卢卡斯将原大余古脊齿兽和池江南岭兽放在一起的看法是可取的。原大余古脊齿兽的标本也是相当破碎,它的 P_4 跟座斜脊比较平行齿列长轴,这确实比较特殊,但这特征稳定性如何?在分类上意义怎样?原池江南岭兽标本未保存 P_4 ,它是否代表这个种 P_4 的特征?均不得而知。尽管如此,原大余古脊齿兽与池江南岭兽的下臼齿下原尖均较圆隆,下臼齿都较横宽等特点均相似。两者的个体相差不大,又产在同一处(江西大余青龙乡),所以笔者同意卢卡斯关于原大余古脊齿兽与池江南岭兽是同一个种的意见,但不同意他取消池江南岭兽这个属种。

在中国发现的其他一些钝脚类标本,被原作者处理为古脊齿兽相似种、未定种及南岭兽未定种者,由于标本太破碎,难以做进一步鉴定,故未包括在本文研究之中。

牧兽亚科 *Pastoralodontinae* (Chow et Qi), 1978

亚科型属 牧兽属 (*Pastoralodon* Chow et Qi, 1978)

包括属 亚科型属和高脊兽 (*Altilambda* Chow et Wang, 1978)。

特征 个体小到中等。上颌骨鼻突长。门齿、犬齿、前臼齿相对后面的臼齿均显得小。后面的两上前臼齿原尖前脊发育差。前面的两上臼齿前、后齿带很发育,具次尖,冠面成横宽的矩形或方形。下颌垂直支比较陡,与水平支夹角小。下颊齿有单面高冠现象。下前臼齿齿列短于臼齿齿列。

分布及时代 广东、安徽和内蒙古,中、晚古新世;蒙古,晚古新世。

牧兽属 *Pastoralodon* Chow et Qi, 1978

Pastoralodon Chow et Qi, 1978

Convallisodon Chow et Qi, 1978

属型种 湖牧兽 (*Pastoralodon lacustris* Chow et Qi, 1978)。

包括种 属型种和特氏牧兽 [*Pastoralodon trofimovi* (Flerov et Dashzeveg), 1974 = *Archaeolambda trofimovi* Flerov et Dashzeveg, 1974 = *Convallisodon convexus* Chow et Qi, 1978 = *Convallisodon haliutensis* Chow et Qi, 1978]。

特征 个体比高脊兽大。鼻骨前端较宽,与前颌骨和上颌骨接缝较弯曲。牙齿齿冠

相对较高。 M^1 和 M^2 内缘直,次尖特别发育。下臼齿不象高脊兽那样单面高冠,三角座与跟座的长度和V形夹角的角度相差较大。

分布及时代 内蒙古,晚古新世到早始新世;蒙古,晚古新世。

周明镇和齐陶(1978年)在建立牧兽科时,订了两个新属——牧兽和圆谷兽。由于这两个属在一些主要特征(如 M^1 和 M^2 中附尖特别发育,内缘平直,前、后齿带尤其是后齿带发育成强的次尖架。下颌上升支比较陡直,前臼齿齿列短于臼齿齿列,下臼齿单面高冠不显著,个体大等)上相似,所以 Lucas (1982) 已将这两个属归并成一个属——牧兽属,笔者认为适宜的。

湖牧兽 *Pastoralodon lacustris* Chow et Qi, 1978

特征 上前臼齿相对较小。 M^1 和 M^2 近方形,次尖很发育。下臼齿三角座和跟座均成V形脊,三角座比跟座大得多。

产地及层位 内蒙古四子王旗,晚古新世到早始新世脑木根组。

特氏牧兽 *Pastoralodon trofimovi* (Flerov et Dashzeveg), 1974

Archaeolambda trofimovi Flerov et Dashzeveg, 1974

Convallisodon convexus Chow et Qi, 1978

Convallisodon haliutensis Chow et Qi, 1978

特征 下颌骨短而粗壮。 M_1 和 M_2 的三角座大,外壁圆隆,成U形。跟座比三角座短得多。上臼齿横宽, M^1 和 M^2 成矩形。

产地与层位 内蒙古,晚古新世脑木根组脑木根层;蒙古晚古新世。

Flerov 和 Dashzeveg (1974) 根据发现在蒙古阿尔泰乌拉山的一块带 P_4-M_3 的下颌骨标本,建立特氏古脊齿兽 (*Archaeolambda trofimovi*)。这块标本比古脊齿兽成员要大。童永生(1982)认为它的下臼齿三角座V形脊开阔(从图版上看象U形脊),下跟座较高,下斜脊伸达舌面等特征与原“圆谷齿兽” (*Convallisodon convexus*) 相似。笔者同意这种看法,两者无大的差别,应为同一种——特氏牧兽。

此外,周明镇和齐陶(1978)命名的哈流特谷齿兽 (*Convallisodon haliutensis*), 虽个体较大,颊齿也较大且横宽,但总的看其特点与牧兽中已知的两个种差别不大,有些差别是种内变异还是性别的不同也很难说。它与湖牧兽产于同一地点——脑木根哈流特,但牙齿特点更似特氏牧兽,故在本文被归入该种。

高脊兽属 *Altilambda* Chow et Wang, 1978

属型种 和平高脊兽 (*Altilambda pactus* Chow et Wang, 1978)。

包括种 属型种和细高脊兽 (*Altilambda tenuis* Chow et Wang, 1978)、小高脊兽 (*Altilambda minor* Tong, 1982)、余井高脊兽 (*Altilambda yujingensis* Wang, Yu et Li, 1992)。

特征 个体比牧兽小。鼻骨长,后端变宽,与前颌骨和上颌骨接缝较直。颊齿脊形化程度较低。 M^1 和 M^2 成横宽的矩形,前尖、后尖和原尖均成三角锥状。下臼齿冠外壁

陡直,单面高冠现象显著,三角座与跟座的前后长度及V形夹角的大小接近相等,下斜脊高出下后棱,与下后附尖相连。

分布及时代 安徽潜山、怀宁;广东南雄。中、晚古新世。

和平高脊兽 *Altilambda pactus* Chow et Wang, 1978

特征 下颌骨粗壮,肥厚,下颌联合短而浅。下臼齿三角座和跟座V形夹角小,下后附尖明显,下内尖不发育。

产地及层位 安徽怀宁毛安,中古新世望虎墩组;广东南雄大塘,晚古新世浓山组。

细高脊兽 *Altilambda tenuis* Chow et Wang, 1978

特征 个体较小。下颌骨纤细。下臼齿的下内尖很发育,下斜脊伸达下后尖与下后附尖之间沟中。

产地及层位 安徽潜山上下楼,中古新世望虎墩组。

小高脊兽 *Altilambda minor* Tong, 1982

特征 个体很小的一种高脊兽, M_1 仅长 4.9 毫米。下臼齿无下内小尖。

产地及层位 广东南雄大塘圩,晚古新世浓山组。

余井高脊兽 *Altilambda yujingensis* Wang, Yu et Li, 1992

特征 目前所知个体最大的一种高脊兽,头骨较粗壮。

产地及层位 安徽潜山余井,中古新世望虎墩组。

发现在广东南雄盆地,被童永生(1982)处理为高脊兽未定种的标本,由于只保存一个牙齿,性质不明,难以归属。

综上所述,原全棱齿兽科、古脊齿兽科和牧兽科被合并成一个科——全棱齿兽科,分全棱齿兽亚科和牧兽亚科,前者包括全棱齿兽属、古脊齿兽属和南岭兽属共 11 个种,后者由牧兽属和高脊兽属的 6 个种组成。

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CLASSIFICATION OF PANTOLAMBODONTIDAE (PANTODONTA, MAMMALIA)

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Key words Pantolambdodontidae, Pantodontata; Early Tertiary

Summary

Pantodontata is a big mammalian group. The first fossil to be discovered, apparently a specimen of *Coryphodon*, was found more than a hundred and eighty years ago in France. Since then over ten families of the order have been established: Coryphodontidae, Pantolambdidae, Pantolambdodontidae, Titanoididae, Barylambdidae, Archaeolambdidae, Bemalambdidae, Pastoralodontidae, Harpyodidae, Plethorodontidae and Alcidedorbignyiidae. The relationships among these families have been studied by many paleontologists (Simons, 1960; Kielan-Jaworowska, 1968; Huang, 1977, 1978; Chow and Wang, 1979; Dashzeveg, 1980; Lucas, 1982; Gingerich and Childress,

1983). Based upon the previous study and the observation on the materials at hand, brief review about original *Pantolambdodontidae*, *Archaeolambdidae* and *Pastoralodontidae* is made and a new classification is proposed for these Asian endemic pantodonts.

1. Historical review

1) ***Pantolambdodontidae*** Fossils found by the Asian Expedition of American Museum of Natural History in Shara Murun area, Nei Mongol in 1925 and 1928 for the first time were described by Granger and Gregory (1934) as new genus and species, *Pantolambdodon inermis* and *P. fortis*, and for which a new family, *Pantolambdodontidae*, was created at the same time. In 1978 Tong described a fragmentary lower jaw with m2 and trigonid of m3 from the Late Paleocene Taizicun Formation, Xinjiang and established a new genus and species, *Dilambda speciosa*. In the same year Chow and Qi (1978) mentioned that Qi collected an upper jaw with complete tooth row of *Pantolambdodon* in the same horizon with the two known species of *Pantolambdodon*. Dashzeveg (1980) named a new species, *Pantolambdodon bagdensis*, based upon an upper jaw with P4-M3 and two fragmentary lower jaws bearing some teeth from the Middle Eocene of Mongolia. Two years later Ting et al. (1982) reported a broken skull and some lower cheek teeth from Dashuikeng, Yanchi County, Ningxia Hui Autonomous Region, and later (1987) named *Pantolambdodon zhaii*, which provides the characters of the front skull and upper cheek teeth of the genus.

2) ***Archaeolambdidae*** The fossils of the family were first found from the Late Paleocene Naran Bulak formation of Nemget Basin, Mongolia. The specimens are a fragmentary upper jaw with P4-M3 and two broken lower jaws with some teeth. Flerov (1952) created a new genus and species, *Archaeolambda planicanina*, and meantime on which a new family, *Archaeolambdidae*, was established. Kielan-Jaworowska (1968) reported three lower jaws and a broken skull found in the same area with *A. planicanina*. The lower jaws and lower cheek teeth are the same with those of *A. planicanina* both in size and in morphology, while the upper cheek teeth are one and a half times of size of that species. So she treated them as *A. cf. planicanina*. Flerov and Dashzeveg (1974) described a new species, *A. trofimovi*, based on a lower jaw with p4-m3 found from the Late Paleocene of Mongolia. The author of the present paper (Huang 1977) created a new species, *A. tabiensis*, the specimen of which is an almost complete skeleton discovered from the Late Paleocene Doumu Formation, Qianshan Basin, Anhui Province. The next year he (Huang, 1978) named another species, *A. yangtzeensis*, the specimens were found from the Late Paleocene Shuangtasi Formation, Xuancheng Basin, Anhui. In the same year, Tong (1978) described a broken upper jaw (juvenile individual) from the Late Paleocene Taizicun Formation, Turpan Basin, Xinjiang as *A. cf. planicanina*. Tong (1979) studied the pantodont fossils from the Late Paleocene Chijiang Formation, Chijiang Basin, Jiangxi Province. He established a new genus and species, *Nanlingilambda chijiangensis* based on a lower jaw with some teeth. Another lower jaw was named as a new species *Archaeolambda dayuensis*. The remaining materials were treated as *Archaeolambda* sp. or *Archaeolambdidae* gen. et sp. indet. Dashzeveg (1980) established a new genus and species, *Oroklambda prima*, the specimen of which is

a lower jaw with some teeth collected from the Middle Eocene Kholboldzhi Formation near Orok Nor Lake. This species is the youngest one in age in the family fossil record. Tong (1982) named another new species under the genus *Dilambda*, *D. zhuguikegensis*, based on a fragmentary lower jaw with m2-m3 found from the Late Paleocene Nungshan Formation, Nanxiong Basin, Guangdong Province. The other broken lower jaw found in the same stratum was treated as *Nanlingilambda* sp. by him.

3) Pastoralodontidae This family was created more recently. Chow et al. (1976) identified several skulls and lower jaws found from the Late Paleocene to Early Eocene Naomugen Formation, Siziwang Banner, Nei Mongol as *Archaeolambdidae* gen. et sp. nov.. Two years later Chow and Qi (1978) restudied these fossils and established a new family, *Pastoralodontidae*, including two genera and three species, *Pastoralodon lacustris*, *Convallisodon convexus* and *C. haliutensis*. In 1978 Chow and Wang placed their new genus and species, *Altilambda pactus* and *A. tenuis* into family *Pastoralodontidae*. *A. pactus* is represented by two lower jaws with some cheek teeth found from the Middle Paleocene Wanghudun Formation, Huaining County, Anhui Province and from the Late Paleocene Nungshan Formation, Nanxiong Basin, Guangdong Province. *Altilambda tenuis* is based on some lower cheek teeth from the Middle Paleocene Wanghudun Formation, Qianshan Basin, Anhui Province. Tong (1982) created a new species, *A. minor*, based on a lower jaw bearing some teeth from the Late Paleocene Nungshan Formation. Recently Wang et al. (1992) described a fragmentary skull with nearly complete tooth rows from the Middle Paleocene Wanghudun Formation and named it as *Altilambda yujingensis*.

The genera and species described in the past are listed in table 1.

2: New idea about the classification of *Pantolambdodontidae*, *Archaeolambdidae* and *Pastoralodontidae*

As can be seen in table 1, above three families have relatively short geological history ranging from Middle Paleocene to Middle Eocene. Their geographical distribution is also very limited, only in China and Mongolia. So they are endemic or autogeneus forms.

In the past half a century, especially in the recent years, not only specimens and taxa increase rapidly but also the relationships among above families are clearer than before. new classification (see Table 2) is now proposed through observing specimens and analysing data while we study Guichi Fauna (Huang and Chen, in press).

***Pantolambdodontidae* Granger et Gregory, 1934**

Archaeolambdidae Flerov, 1952

Pastoralodontidae Chow et Qi, 1978

Diagnosis Small to medium-sized pantodonts. Facial region and brain region nearly equal in height. Sagittal crest weak. Canine relatively small, usually incisor-or premolar-like. Ectoflêxus of the upper cheek teeth shallow but distinct. Ectoloph of M1 and M2 W-shaped, extending inward over half width of the tooth, and having more developed mesostyle. Ectoloph of M3 V-shaped with metacone not distinct on the metaloph. Paraconid of the lower cheek teeth not reduced. p1 and p2 contra-

ctive transversely. Trigonid and talonid of m1 and m2 V or U-shaped, the latter much smaller than the former. Talonid of m3 cup- or basin-shaped.

Remarks Simons (1960) considered that *Archaeolambda* was the synonym of North American *Haplolambda* of Barylambdidae. Szalay and McKenna (1971) agreed this opinion. Since Archaeolambdidae was established in 1952, abundant materials of the family have been found in Mongolia, especially in China. Some paleontologists (Kielan-Jaworowska, 1968; Huang, 1978) provided new data that Asian *Archaeolambda* was not North American *Haplolambda* and Archaeolambdidae was still a valid family. But Huang (1977) also pointed out the possibility that Archaeolambdidae was the synonym of Pantolambdodontidae for the first time. Chow and Qi (1978) had the same idea. The next year Chow and Wang (1979) placed Archaeolambdidae into Pantolambdodontidae formally. Dashzëveg (1980) combined above two families into Pantolambdodontinae. He also treated Barylambdidae as Barylambdinae. He thought above two subfamilies forming Pantolambdodontidae. In fact Barylambdidae possesses closer relationships with North American forms and differs greatly from Asian pantodonts, including *Pastoralodon* and *Archaeolambda*. Combining Archaeolambdidae and Pantolambdodontidae as Pantolambdodontinae is a good idea and this classification is accepted in the present paper. Lucas (1982) considered the genera not only *Pantolambdodon*, *Archaeolambda* and *Pastoralodon* but also *Titanoides* and *Harpyodus* have closer relationships. In 1984 he told the author that Pantolambdodontidae, Archaeolambdidae, Pastoralodontidae and Harpyodidae were one family. Actually *Harpyodus* is a special animal and has no close relationships with the above first three genera (Huang et Zheng, 1987). *Pastoralodon* indeed has many important common characteristics with *Pantolambdodon* and *Archaeolambda* (see diagnosis of the family), indicating they have closer relationships than the other pantodonts. So they should be placed in the same family. *Pantolambdodon* and *Archaeolambda* are more closer than they are with *Pastoralodon*. So it together with *Altilambda* forms another subfamily Pastoralodontinae under Pantolambdodontidae. Thus, 8 genera and 20 species of the original Pantolambdodontidae, Archaeolambdidae and Pastoralodontidae now become 1 family, 2 subfamilies, 5 genera and 17 species (including a new species, Huang et Chen, in press).

Pantolambdodontinae (Granger et Gregory), 1934

Type genus *Pantolambdodon* Granger et Gregory, 1934

Included genera: Type genus, *Archaeolambda* Flerov, 1952 and *Nanlingilambda* Tong, 1979.

Diagnosis The connection of premaxilla with nasal long. Incisive foramen large. Upper cheek teeth without hypocone, and pre- and postcingulum weak. Crown of M1 and M2 triangular. The angle between vertical and horizontal parts of mandibular ramus large. Lower premolar tooth row longer than or nearly equal with the molar one.

Age and distribution Late Paleocene and Middle Eocene of Mongolia; Late Paleocene of Guangdong, Jiangxi, Xinjiang and Anhui; Late Paleocene and Middle Eocene of Nei Mongol; Early Eocene of Hunan and ?Eocene of Ningxia.

Pantolambdodon Granger et Gregory, 1934

Type species *Pantolambdodon inermis* Granger et Gregory, 1934

Included species Type species, *P. fortis* Granger et Gregory, 1934 and *P. zhaii* Ding, Schiebout et Zhou, 1987

Diagnosis Relatively large in size. Facial region low and flat. P4 has continuing postprotocrista. Ectoloph of M1 and M2 wide and mesostyle crest-like. The posterior wall in M1, largest tooth of the upper cheek teeth, longer than anterior one and it shorter in M2. Both trigonid and talonid of the lower molars relatively broad. Lower molars have metastylids which usually link the cristid obliqua.

Age and Distribution Middle Eocene of Nei Mongol; ?Eocene of Ningxia.

Pantolambdodon inermis Granger et Gregory, 1934

Diagnosis Small-sized *Pantolambdodon*. The height of horizontal part of ramus under m2 29—36 mm, m1 20 mm long and 9.5—11 mm wide.

Locality and horizon Middle Eocene, Ulan Shiereh Formation of Shara Murun Region, Nei Mongol.

Pantolambdodon fortis Granger et Gregory, 1934

Diagnosis Big in size and Mandible robust. m1 29 mm long and 13mm wide.

Locality and horizon Same as for *P. inermis*.

Pantolambdodon zhaii Ding, Schiebout et Zhou, 1987

Diagnosis A moderately large pantodont with a very long and flat facial region and a greatly retracted nasal incision. External nares enlarged to form a long, straight deep canal. Upper cheek teeth relatively wide with somewhat rounded internal wall. M2 the longest of the upper molars.

Locality and age ? Eocene of Dashuikeng, Yanchi, Ningxia.

Archaeolambda Flerov, 1952

Type species *Archaeolambda planicanina* Flerov, 1952

Included species Type species, *A. tabiensis* Huang, 1977, *A. yangtzeensis* Huang, 1978, *A. speciosa* (Tong), 1978, *Archaeolambda* sp. nov (Huang and Chen, in press), *A. bagdensis* (Dashzeveg), 1980 and *A. prima* (Dashzeveg), 1980.

Diagnosis Smaller than *Pantolambdodon* in size. Postprotocrista of P4 not continuing. Posterior wall of M2, the largest of upper cheek teeth, longer than the anterior one. Talonid of lower molars low and small, having same angle (about 60°) as the trigonid on m1 and m2. The postcranial slight-structured and slender. The third phalanx claw-shaped.

Age and distribution Late Paleocene of Nanxiong, Guangdong; Dayu, Jiangxi; Turpan, Xinjiang and Qianshan, Xuancheng, and Guichi, Anhui; Late Paleocene and Middle Eocene of Mongolia.

The difference between *Pantolambdodon* and *Archaeolambda* is distinct though

they have many common characters (see diagnosis of the subfamily). *Pantolambdodon* has big size, specialized skull, relatively low and flat facial region and rather slender mandible. Whereas *Archaeolambda* possesses relatively small size, somewhat high facial region and comparatively robust mandible. The former upper molars reduce in size from M1 to M3. The parastyle and metastyle are nearly as high as paracone and metacone. The talonids of lower molars are relatively large. While in *Archaeolambda* M2 is the largest of the upper cheek teeth. The parastyle and metastyle are much lower than the paracone and metacone. The angle of the trigonid and talonid of the lower molars are nearly equal, about 60° , and the talonids are much lower and smaller than the trigonids. So the two genera are easy to be distinguished.

Archaeolambda planicanina Flerov, 1952

Diagnosis The length for P3—M1 20 mm, p1—m3 75 mm, p—p4 39 mm and m1—m3 36 mm. Mandible not contractive under m3.

Locality and horizon Late Paleocene, Naran Bulak Formation, Nemegt Basin, Mongolia; Late Paleocene Taizicun Formation, Turpan Basin, Xinjiang; Late Paleocene Chijiang Formation, Chijiang Basin, Jiangxi.

Archaeolambda tabiensis Huang, 1977

Diagnosis Smaller than *P. planicanina* in size. There are small vertical ridges on the external side of V-ectoloph in P3 and P4. Mandible slightly contractive under m3.

Locality and horizon Late Paleocene, Doumu Formation, Qianshan Basin, Anhui Province.

A. tabiensis is the only species in *Pantolambdodontidae* found skeleton.

Archaeolambda yangtzeensis Huang, 1978

Diagnosis Size smaller than that of *A. tabiensis*. Mesostyle strong in M1 and M2. M2 very wide with much longer posterior wall, weak pre- and postcingulum connecting inside. M3 small and asymmetric, the length of posterior wall only half of anterior one.

Locality and horizon Late Paleocene Shuangtasi Formation, Xuancheng and Tongning Basins, Anhui.

Archaeolambda speciosa (Tong), 1978

Dilambda speciosa Tong, 1978

Dilambda zhuguikengensis Tong, 1982

Diagnosis Lower molars more hypsodont with steep crests and metastylids. m3 with entoconid.

Locality and horizon Late Paleocene, Taizicun Formation, Turpan Basin, Xinjiang; Late Paleocene, Nungshan Formation, Nanxiong Basin, Guangdong Province.

In 1978 Tong named a new genus and species, *Dilambda speciosa*, under *Panto-*

lambdodontidae. Lucas (1982) removed this species to *Archaeolambda*. The material of the species is one and a half lower molars from the Taizicun Formation. The morphology of both trigonid and talonid of the lower molars is indeed the same as that of *Archaeolambda*. He (Tong, 1982) described another species, *Dilambda zhuguiakensis*, under Archaeolambdidae, which indicates that *Dilambda* is the synonym of *Archaeolambda*. This species is not different greatly in tooth structure and size from the former.

***Archaeolambda bagdensis* (Dashzeveg), 1980**

Pantolambdodon bagdensis Dashzeveg, 1980

Diagnosis Upper molars relatively long. Lower molars have metastylids. ml 11.5mm long and 7.5mm wide.

Locality and horizon Middle Eocene, Kholboldzhi Formation, Near Orok Nor Lake, Mongolia.

This species originally was created by Dashzeveg (1980) as *Pantolambdodon bagdensis*. It is the smallest of all species of *Pantolambdodon*. The parastyle and metastyle of the upper molars are much lower than paracone and metacone, and M2 is the largest of the upper cheek teeth. It should be referred to *Archaeolambda* and is a species with metastylid but bigger than *A. speciosa*.

***Archaeolambda prima* (Dashzeveg), 1980**

Oroklambda prima Dashzeveg, 1980

Diagnosis Almost same-sized as *A. yangtzeensis*. Lower premolars more molariform and p4 with semicircle talonid. Trigonid of lower molars somewhat U-shaped.

Locality and horizon Same as for *A. bagdensis*.

Dashzeveg (1980) created a new genus and species, *Oroklambda prima*, apart from "*Pantolambdodon bagdensis*" while he studied the pantodont materials from Mongolia. This taxon was already removed to *Archaeolambda* by Lucas (1982) and we think it is reasonable. But its lower premolars are more molariform and the trigonid of the lower molars is somewhat U-shaped, differing from the other species of the genus.

***Nanlingilambda* Tong, 1979**

Type species *Nanlingilambda chijiangensis* Tong, 1979

Included species Type species only.

Diagnosis Mandible robust, higher from front to rear. Root of lower canine relatively large and rounded, having a short diastema with pl. Trigonids of lower molars wide and m3 having distinct hypoconid and hypoconulid.

Age and distribution Late Paleocene, Nanxiong, Guangdong; Dayu, Jiangxi.

***Nanlingilambda chijiangensis* Tong, 1979**

Nanlingilambda chijiangensis Tong, 1979

Archaeolambda dayuensis Tong, 1979

Diagnosis As for the genus.

Locality and horizon Late Paleocene, Chijiang Formation, Chijiang, Dayu County, Jiangxi Province.

Lucas (1982) considered this genus was *Archaeolambda speciosa*. It can be seen that the mandible is robust and the lower molars are wide though the specimen is not in good preservation. The root of lower canine is big and rounded, and having diastema with pl, which differ from the other species of *Archaeolambda* and even the other genera of *Pantolambdodontidae*. So it should be treated as a valid genus. "*Archaeolambda dayuensis*" was also thought by Lucas (1982) as *Archaeolambda speciosa* in the same paper. This species has wide lower molars and is nearly the same in size as *Nanlingilambda chijiangensis*.

Pastoralodontinae (Chow et Qi), 1978

Type genus *Pastoralodon* Chow et Qi, 1978.

Included genera Type genus and *Altilambda* Chow et Wang, 1978.

Diagnosis Small to medium-sized pantodonts. The connection between maxilla and nasal long. Incisor, canine and premolar are relatively small in comparison with the molars. Preprotocrista of P3 and P4 weak. Pre- and postcingulum of M1 and M2 rather developed, making transversely rectangular or square crown of the two teeth which have hypocone. Vertical ramus of mandible more steep and has relatively small angle with horizontal one. The length of premolar row shorter than the molar one.

Age and distribution Middle and Late Paleocene of Guangdong, Anhui and Late Paleocene to Early Eocene of Nei Mongol; Late Paleocene of Mongolia.

***Pastoralodon* Chow et Qi, 1978**

Pastoralodon Chow et Qi, 1978

Convallisodon Chow et Qi, 1978

Type species *Pastoralodon lacustris* Chow et Qi, 1978.

Included species Tyhe species and *Pastoralodon trofimovi* (Flerov et Dashzeveg), 1974.

Diagnosis Bigger size than *Altilambda*. The suture between premaxilla, maxilla and nasal slightly curved and wider anteriorly. Cheek teeth more hypsodont. M1 and M2 have strong hypocone with straight internal wall. Lower molars not as unilaterally hypsodont as those of *Altilambda*.

Age and distribution Late Paleocene to Early Eocene of Nei Mongol; Late Paleocene of Mongolia.

Pastoralodontidae included *Pastoralodon* and *Convallisodon* when Chow and Qi (1978) established the family. Owing to the similarities in main morphology between above two genera Lucas (1982) combined them into one genus, *Pastoralodon*, which seems reasonable.

***Pastoralodon lacustris* Chow et Qi, 1978**

Diagnosis Upper premolars relatively small. Crown of M1 and M2 square with more developed hypocone. Both trigonid and talonid of m1 and m2 V-shaped.

Locality and horizon Late Paleocene to Early Eocene Nomogen Formation, Nomogen, Siziwang Banner, Nei Mongol.

***Pastoralodon trofimovi* (Flerov et Dashzeveg), 1974**

Archaeolambda trofimovi Flerov et Dashzeveg, 1974

Convallisodon convexus Chow et Qi, 1978

Convallisodon haliutensis Chow et Qi, 1978

Diagnosis Mandible short and robust. Trigonid of m1 and m2 big and U-shaped with somewhat rounded external wall. M1 and M2 transversely rectangular in outline.

Locality and horizon Late Paleocene Naran Bulak Formation, Mongolia; Late Paleocene, Nomogen Member of Nomogen Formation, Siziwang Banner, Nei Mongol.

Flerov and Dashzeveg (1974) named "*Archaeolambda trofimovi*" which was removed to *Pastoralodon* in the present paper. As early as 1982 Tong already pointed out this species resembles "*Convallisodon convexus*" in big size, nearly U-shaped trigonid of the lower molars and cristid obliqua extending more internally. It is likely that they are the same species.

The specimens of "*Convallisodon haliutensis*" named by Chow and Qi (1978) are not different greatly from those of two species of the genus. Here tentatively placed it in *P. trofimovi*.

***Altilambda* Chow et Wang, 1978**

Type species *Altilambda pactus* Chow et Wang, 1978.

Included species Type species, *A. tenuis* Chow et wang, 1978, *A. minor* Tong, 1982 and *A. yujingensis* Wang, Yu et Li, 1992.

Diagnosis Smaller than *Pastoralodon* in size. Nasal long and wider posteriorly, the suture with premaxilla and maxilla rather straight. M1 and M2 transversely rectangular in outline. Lower molars unilaterally hypsodont distinctly with steep external wall. The angle and size of trigonid and talonid of lower molars nearly equal.

Age and distribution Middle and Late Paleocene of Anhui and Guangdong.

***Altilambda pactus* Chow et Wang, 1978**

Diagnosis Mandible thick and robust with short and shallow symphysis. The V-shaped angle of trigonid and talonid relatively small. Metastylid distinct and entoconid weak.

Locality and horizon Middle Paleocene, Wanghudun Formation, Maoan, Huaining County, Anhui Province; Late Paleocene, Nungshan Formation, Datang, Nanxiong, Guangdong.

***Altilambda tenuis* Chow et Wang, 1978**

Diagnosis Size small and mandible narrow. Cristid obliqua extends the place between metaconid and metastylid. Entoconid more developed.

Locality and horizon Middle Paleocene, Wanghudun Formation, Shangxialou, Qianshan, Anhui.

***Altilambda minor* Tong, 1982**

Diagnosis Smallest *Altilambda*, m1 4.9 mm long. Lower molars without entocoid.

Locality and horizon Late Paleocene, Nungshan Formation, Datang, Nanxiong, Guangdong.

***Altilambda yujingensis* Wang, Yu et Li, 1992**

Diagnosis Largest *Altilambda* with robust skull.

Locality and horizon Middle Paleocene, Wanghudun Formation, Yujing, Qianshan, Anhui.

To sum up, according to the present study the family Pantolambdodontidae contains two subfamilies: Pantolambdodontinae which includes three genera (*Pantolambdodon*, *Archaeolambda* and *Nanlingilambda*) and eleven species; Pastoralodontinae includes two genera (*Pastoralodon* and *Altilambda*) and about six species.