

湖北早始新世爪兽新发现及其意义

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摘要 文章描述了中国湖北李官桥盆地早始新世一奇蹄类新材料, 建立了一个新属新种: 秉志丹江兽 (*Danjiangia pingi* gen. et sp. nov.), 经过系统分析将其归入了爪兽类群。秉志丹江兽是迄今发现的时代最早的爪兽。该文对爪兽的早期形态演化、爪兽类与古马类可能存在的亲缘关系以及爪兽类的起源等问题也进行了探讨。

关键词 湖北, 李官桥盆地, 早始新世, 爪兽

1992 年 11 月, 我所王元青博士在湖北李官桥盆地采到了一副保存很好的奇蹄类头骨及下颌骨化石, 该化石产自玉皇顶组中段中部的褐红色砂质泥岩层的钙泥质团块中。玉皇顶组中段产出的哺乳动物化石有: cf. *Heptodon* sp., *Rhombomylus* cf. *turpanensis*, *Advenimus hubeiensis*, *Hohomys lii*, *Asiocoryphodon conicus*, *Heterocoryphodon flerowi* 等, 根据前人的研究成果, 其地层时代为早始新世晚期(马安成、程捷, 1991; 徐余瑄等, 1979; Li and Ting, 1983)。

本文将该材料鉴定为爪兽, 标本描述基本采纳了周明镇等(1975)关于原始真兽类牙齿结构的命名建议, 并参照了 Radinsky (1964)、胡长康(1959)等人关于爪兽描述的习惯用语。

一、化石描述

奇蹄目 *Perissodactyla* Owen, 1848

爪兽超科 *Chalicotherioidea* Gill, 1872

? 始爪兽科 ? *Eomoropidae* Viret, 1958

丹江兽属(新属) *Danjiangia* gen. nov.

属型种 秉志丹江兽(新属、新种) *Danjiangia pingi* gen. et sp. nov.

归入种 只有属型种。

特征 原始的小型爪兽 (M/1 长约 8.3 mm)。头骨低, 吻部较长。下颌骨水平支纤细, 联合部浅而窄长。低冠齿, 齿式 3, 1, 4, 3/3, 1, 4, 3。

前臼齿未臼齿化, P2/2 均只有一刃状齿尖; P3—4/发育有中附尖雏形。上臼齿宽大于长, 具“W”型外脊; 前附尖强壮, 偏向前唇侧; 中附尖发育, 呈尖锥状, 与前尖、后尖连接较弱; 前尖、后尖稍向舌侧倾倒; 无后附尖; 横脊低弱, 不与外脊相连; 原尖、次尖向后弯转。下臼齿双“V”形; 下后脊高, 强烈斜向舌侧并与下后附尖相连; 下前脊低, 无明显

下前尖; M/1—2 下次小尖弱, 略偏向舌侧。

该属与其它早期爪兽¹⁾的区别是: 前臼齿结构更原始, 保留 P/1; 上臼齿外脊、横脊较弱; 下臼齿下后脊更加发育, 并斜向舌侧与下后附尖相连。该属保存的头骨部分、下颌骨部分与 *Eomoropus*、*Litolophus* 属相似而与 *Grangeria* 属不同。

属名由来 根据产地丹江口市命名。

秉志丹江兽(新属、新种) *Danjiangia pingi* gen. et sp. nov.

(图 1; 图版 1)

正型标本 一个压扁的眶后缺失的头骨及同一个体的左右下颌骨水平支, 保存几乎全部牙齿。中国科学院古脊椎动物与古人类研究所标本编号 V 10842。

地点与层位 湖北省丹江口市习家店镇东北青塘岭 (E111°12'10", N32°46'30"); 玉皇顶组中段, 早始新世晚期。

特 征 同属征。

种名由来 种名献给李官桥盆地动物化石的早期研究者秉志先生(1886—1965)。

标本描述

头骨: V 10842 的头骨仅保存眼眶以前的部分, 且因上下挤压而破损、变形, 头骨中矢面稍向左偏。

头骨低矮, 吻部窄长; 鼻骨、额骨因受挤压而破裂下陷, 二者间的骨缝不清; 鼻切迹 (narial incision) 较浅, 后端不超过 C1/; 上颌骨在颜面处比较陡立; 眶区破损严重, 右侧保存部分颧弓, 眼眶前缘约在 M1/上方; 左右眶下孔破裂, 大致位于 P3/的上方; 门齿孔前端破损, 后缘不超过 I3/; 腭骨前部未保存, 与上颌骨接缝不清, 后鼻孔的前缘约在 M2/的中央谷处。

下颌骨: 左右下颌骨均只有水平支, 仅左下颌骨保留部分上升支。下颌骨水平支纤细, 向后逐渐加深 (P/2 前下方下颌骨高 11.3mm, M/1 前下方高 13.7mm, M/3 后下方高 19.2mm); 下颌联合部窄长, 其后缘延至 P/2 后端下方; P/2—M/3 齿槽缘稍向下凹, P/4 处最低; 左下颌孔部分保留, 约与 M/3 等高; 颞孔数目不清, 仅左 P/2 唇侧前下方见一明显的颞孔。

牙齿(颊齿测量数据见表 1):

1) 上门齿: 上门齿左右各三个, 稀松地排列成半圆形, 除左 I3/保存较好外, 其余上门齿均较残破, 右侧门齿残破严重。I1/与 I2/形态、大小相似, 伸向前下方, 齿冠均破损, 截面为长椭圆形; I3/比前二者稍大(长约 4mm), 扁锥状, 略向外倾斜, 齿冠顶端的外后侧有一明显的小齿尖磨面。

2) 上犬齿: 左、右 C1/的齿冠顶端破损。C1/中等大小, 为粗壮的稍侧扁的锥形(基部长 7.4mm, 宽 5.8mm); C1/稍后弯并向唇侧倾斜; 它与 I3/之间有一较长的齿隙。

3) 上前臼齿:

P1/: 左、右 P1/仅存齿根。P1/双齿根, 截面长椭圆形(从齿根测量 P1 长 5.8mm, 宽

1) 早期爪兽指所有已知的始新世爪兽属种, 代表较原始的爪兽类型。Viret (1958) 和 Radinsky (1964) 分别用始爪兽亚科 (*Eomoropinae*) 和始爪兽科 (*Eomoropidae*) 表示之。

表 1 秉志丹江兽颊齿测量 (单位: 毫米)

Table 1 Measurement of Check Teeth of *Danjiangia pingi* gen. et sp. nov. (in mm)

上颊齿	P2/	P3/	P4/	M1/	M2/	M3/	P2-4/	M1-3/
长 (length)	6.6	6.4	7.1	9.2	9.8	9.3	20.0	27.0
宽 (width)	4.7	7.2	9.1	11.9	12.8	12.6		
下颊齿	P/2	P/3	P/4	M/1	M/2	M/3	P/2-4	M/1-3
长 (length)	6.0	6.7	6.8	8.3	9.6	13.4	20.0	31.2
宽*(width)	3.7	3.9	5.4	6.0	7.0	6.9		
				6.2	7.1	6.1		

* 上为下三角座宽 (above: trigonid width), 下为下跟座宽 (below: talonid width)。

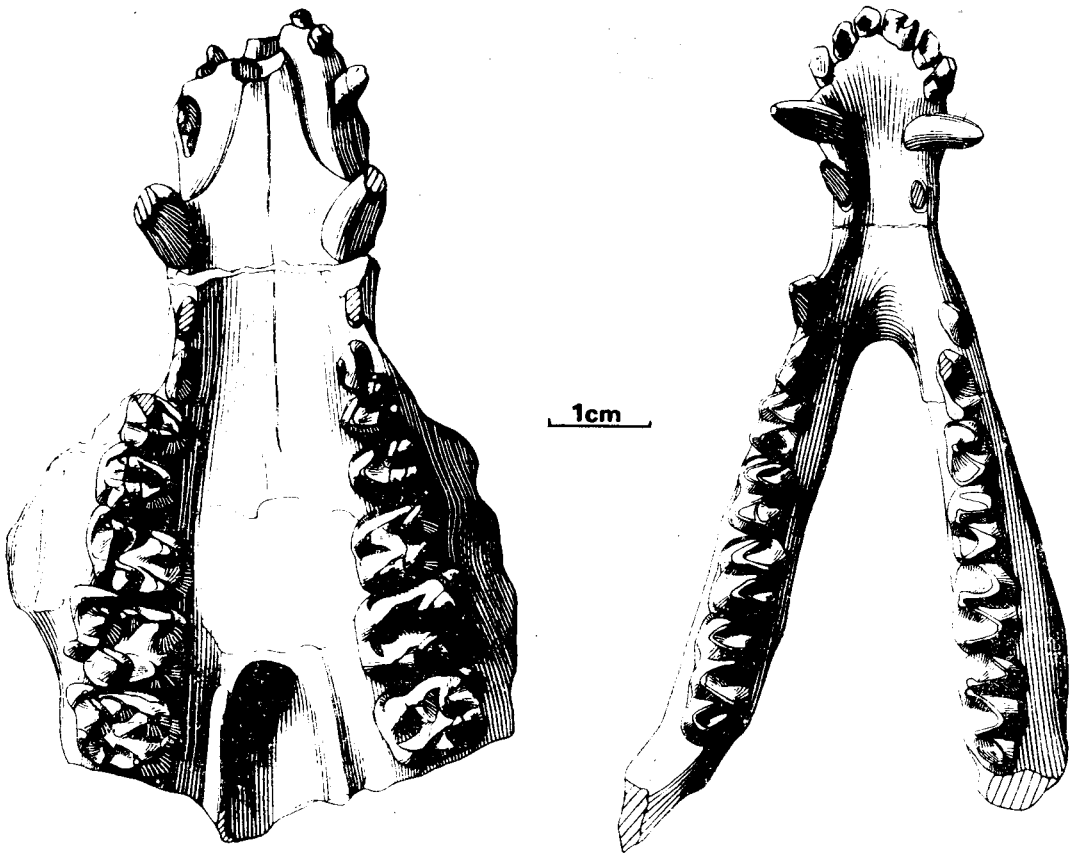


图 1 秉志丹江兽(新属、新种) (V10842) 头骨及下颌骨

Fig. 1 Skull and mandibles of *Danjiangia pingi* gen. et sp. nov.

左图 (left): 头骨腭面观 (palatal view of the skull)

右图 (right): 下颌骨背面视 (dorsal view of the lower jaw)

3.4mm); P1/齿根与 C1/、P2/之间各有一短的齿隙。

P2/: 左 P2/前端稍损,右 P2/完好。P2/前窄后宽,呈三角形;主要由一尖刃状齿尖构成,其舌侧下方有一弱的齿缘突起,从位置判断为原尖的雏形。该标本的 P2/十分原始,没有分化出前、后尖。

P3/: 右 P3/前唇端稍有破损,左 P3/完好。P3/近三角形,有三个明显的主尖:唇侧前尖、后尖和舌侧的原尖。前、后尖已基本分开,锥状,其间有弱棱相连,二者大小相近,前尖略高,后尖相对前尖略偏舌侧;原尖锥状,很发育,远低于前、后尖。从原尖向前尖前下方引出一条弱的原尖前棱,其上有一小的突起,为前小尖,原尖后棱很不明显;前尖前唇侧可见一雏形的前附尖与之以弱棱相连,前附尖位置很低;显微镜下观察会发现在后尖的唇面,齿缘微微突起,与上臼齿比较,这是中附尖开始萌发的标志。P3/的前、后齿带发育,且后齿带较前齿带宽。

P4/: 左、右 P4/保存完好。P4/近方形,与 P3/相比,前、后尖更加分离,前附尖、中附尖和前小尖更大、更明显,但前附尖、中附尖位置仍很低,中附尖与前尖、后尖无明显的齿棱相连;原尖前棱更显著,同时从原尖向后尖下方伸出一条很弱的原尖后棱,从而在 P4/舌侧形成一个不发育的“V”形脊环;无明显后小尖。P4/的前、后齿带十分发育,后齿带非常宽大。

4) 上臼齿: 左、右 M1/的前、后脊略有破损,右 M2/的中附尖有些变形,其他臼齿保存完好。

上臼齿宽略大于长,呈前宽后窄的梯形;“W”型外脊的宽度约占整个臼齿宽的三分之一至五分之二,走向前唇-后舌向,其上齿尖比较孤立,齿尖之间的连棱短而弱,使外脊不甚连续;前附尖大而孤立,位于前尖的前唇侧,其前唇侧壁外凸,后舌侧壁较陡直,从前尖引出的前尖前棱止于前附尖后舌侧壁的中部;中附尖发育,呈锥状,较孤立,它与前尖、后尖以弱棱相连;前尖、后尖为侧扁的三角锥状,唇面扁平,微向舌侧倾倒,其上各有一条弱的棱状突起;后尖比前尖略小且更偏向舌侧,后尖唇侧壁与齿缘之间有一小凹坑,无后附尖;上臼齿的横脊显著低于外脊,脊型程度较低且不与外脊相连;两横脊近平行;前小尖发育,与锥状的原尖之间有弱棱相连;前脊指向前尖与前附尖之间,止于前尖的前基部;后脊由大的锥状次尖以及从上引出的弱棱构成,次尖比原尖更偏唇侧;在后脊中部有一很弱的隆起,可能代表一后小尖,但很不明显;后脊止于后尖前基部,不与外脊相连;上臼齿原尖和次尖均稍向后偏移;在次尖与原尖之间,臼齿中央谷的舌侧开口处有一小的突起,在 M2/上比较明显。

上臼齿的前齿带很发育,后齿带次之,无唇侧和舌侧齿带。

M1—3/无明显形态差异,其中 M2/稍大些。

5) 下门齿: 右 I/1 顶端破裂,其它下门齿保存完好。下门齿铲状,一律平倒指向前方并排列成半圆形;各下门齿间有小的齿隙。舌面视 I/1 与 I/2 近方形,顶端有磨蚀面; I/3 近长方形(长 4.2mm),较 I/1—2 厚些,凿状,外侧有一小齿尖的磨面。

6) 下犬齿: 左、右 C/1 保存较好。下犬齿比上犬齿纤细,呈锐利的锥状,齿冠微侧扁; C/1 长约 10mm,基径 6.8mm × 4.3mm;同上犬齿一样,下犬齿也向唇侧倾斜; C/1 与 I/3 之间存在一短的齿隙。

7) 下前臼齿:

P/1: 左 P/1 保留, 右 P/1 仅余齿槽。P/1 较细长, 单齿根; 齿冠单锥型, 釉质层薄, 顶端有磨面; P/1 大小与下门齿相近 (长约 4.5mm); 比较特别的是, 该前臼齿前倒指向 C/1, 且略向唇侧倾斜; 另外它靠近 C/1 而远离 P/2。

P/2: 保存完整。P/2 为单一尖刃状齿尖, 齿冠侧扁, 后端较前端稍宽厚; P/2 同 P/1、C/1 一样, 向唇侧倾斜, 从而偏离了下颊齿列的主轴线; P/1—2 间存在一个较长的齿隙。

P/3: 右 P/3 前端错裂, 左 P/3 完好。P/3 与 P/2 相似, 有一高的尖刃状主齿尖, 但它的后端拉长、膨大, 从主尖后下方的棱状突起向后唇侧引出一条脊(下后脊的雏形), 并内弯构成一个低的雏形的跟座; 主尖的前棱也略微偏向舌侧, 在前端舌侧壁上出现一凹陷, 这是三角座开始发育的迹象。

P/4: 保存较好。P/4 次臼齿化, 近双“V”型, 三角座高于跟座; 下原尖、下后尖、下次尖十分显著, 其中下后尖最高; 下后附尖已经开始从下后尖分出, 但很不明显; 下原脊高而显著, 中部低凹; 下前脊、下后脊、下次脊已经出现, 但都比较低弱, 下后脊斜向舌侧止于下后附尖的唇侧; 三角凹 (trigonid basin) 呈沟状, 与下前脊走向一致, 后唇-前舌向伸向前下方, 其舌侧开口不封闭; 跟凹 (talonid basin) 凹坑状, 最低点靠近舌侧。

8) 下臼齿: M/1、M/2 的唇侧齿冠磨损, 其中 M/1 较严重; M/3 保存较好。

M/1、M/2 由“V”型的下三角座和下跟座构成, 下跟座略大于下三角座; 下前脊不发育, 向下伸向前舌侧; 下原脊、下后脊、下次脊均高而平直, 其唇侧壁陡立, 下后脊强烈斜向舌侧, 直接与下后附尖相连; 下后附尖与下后尖已明显分离, 它位于下后尖的后舌侧且较之略低, 此二齿尖高于其它齿尖; 下原尖、下次尖构成“V”型脊的唇侧尖角; 舌侧除下后尖、下后附尖外, 还有一明显的下内尖, 但无显著下前尖; 下跟凹、下三角凹的舌侧基本不封闭; M/1、M/2 的下次小尖很不明显, 为后齿缘的一个突起, 位于下次脊的后壁上, 位置较高且偏向舌侧(它与后面臼齿的下前脊前端基本等高); M/1、M/2 均有明显的前齿带和唇侧齿带。

M/3 与 M/1、M/2 相似, 区别在于它有一个十分显著的下次小尖, 从下三角座、下跟座到后面的下次小尖, 齿冠宽度逐渐减小; M/3 的下次小尖唇侧棱指向下内尖, 该棱与舌侧齿缘之间有一明显的条状凹沟, 凹沟的走向与棱的走向一致; M/3 的前、后及唇侧齿带均比较发育。

二、比较与讨论

从前面的描述可以看出, 秉志丹江兽是一种比较原始的小型奇蹄动物。根据它的上臼齿具十分发育的中附尖, 下臼齿下后脊强烈斜向舌侧等特征, 可以明显排除它是始祖马类、獭类以及犀类的可能。秉志丹江兽与欧洲早、中始新世的原始古马类(如原厚脊齿马 *Propachynolophus*、原古马 *Propalaeotherium* 等属), 北美早始新世晚期的雷兽属 *Lambdotherium*¹⁾, 以及中国、北美的早期爪兽(如中始新世的始爪兽属 *Eomoropus*) 都

1) *Lambdotherium* 的分类地位有争议, 后文将予讨论。

有一定的相似之处,下面分别讨论它们的异同。

1. 与原始古马类比较

秉志丹江兽的头骨及下颌骨形态与原始古马类没有大的差别,它们都保留了奇蹄类中的原始特征(包括头骨低,鼻切迹浅,吻部较长,下颌骨纤细,联合部长而浅等)。原始古马类的上臼齿也发育有明显的前附尖和中附尖,也具有低的横脊,其下臼齿下后脊同样斜向舌侧。

Danjiangia 与原始古马类的区别为: 1) 后者的上臼齿前附尖、中附尖不如前者中的发育,且中附尖仅为中央棱的褶曲,与前尖、后尖联系密切;而前者的中附尖相当发育且孤立。2) 后者的上臼齿后脊上具有显著的后小尖,后脊伸向前、后尖之间,止于后尖之前;而前者无明显后小尖,后脊止于后尖基部。3) 后者的下臼齿下原脊、下次脊不发育,中部有凹刻(notched),下后脊指在下后附尖的唇侧;而前者的下臼齿齿脊均高而锐利(下前脊除外),齿脊上无凹刻,下后脊更加斜向舌侧并与下后附尖相连。4) 前者的 M/1—2 下次小尖缩小并偏向舌侧, M/3 下次小尖具有一典型的凹沟形构造,下次小尖的唇侧棱指向下内尖;在后者中,下臼齿的下次小尖不缩小,其下次小尖唇侧棱指向下次脊中部的凹刻。

以上是二者臼齿结构上的差别。在前臼齿上, *Danjiangia* 的前臼齿比较原始而独特,表现为: 1) 它的 C1/与 P1/间的齿隙很窄,而 C1/与上门齿间的齿隙很宽;在原始古马类中,情况正好相反。2) 它的 P/1 为单齿根,靠近 C/1 而与 P/2 间有一很宽的齿隙;在原始古马类中 P/1 为双齿根,靠近 P/2 而远离 C/1 (Savage et al., 1965)。3) 它的 P2/2 结构十分原始,均为单一刃状齿尖,基本无分化;原始古马类的 P2/2 已经分化,结构较之复杂。4) 它的 P3—4/脊环不发育,其上无后小尖,而 P4/上有一显著的较孤立的中附尖;在原始古马类中, P3—4/上的脊环明显,且具后小尖, P4/的中附尖是由中央棱褶曲产生的,很不发育。

以上特征可以明显将 *Danjiangia* 与原始古马类区别开。

2. 与原始雷兽类比较

Eotitanops 是一典型的原始雷兽,它的上臼齿具有“W”型的外脊,下臼齿的下后脊斜向舌侧,这些特征与 *Danjiangia* 相似。不过 *Eotitanops* 与 *Danjiangia* 的区别也比较明显: 1) 前者的外脊十分发育且宽大而连续,后者的外脊不很发育,唇侧各齿尖比较孤立。2) 前者的上臼齿无横脊,舌侧齿尖孤立,而后者横脊虽弱但很显著。3) 前者的下臼齿“W”型,无分离的下后附尖,而后者下臼齿双“V”型,下后附尖发育。上述特征可以把 *Danjiangia* 与 *Eotitanops* 区分开。

Lambdaotherium 过去一直被当作一种原始的雷兽 (Osborn, 1929; Bonillas, 1936)。1980年,北美 Wallace 在一篇未发表的硕士论文中认为该属属于广义的古马类,这一观点当时为许多人所接受,目前对 *Lambdaotherium* 的分类地位尚有分歧 (Mader, 1989)。秉志丹江兽与 *Lambdaotherium* 有许多相似之处,但又有重要的区别,在此讨论如下。二者相似点: 1) 头骨、下颌骨整体形态相似,均保持奇蹄类中的原始特征。2) P4/上均发

育有明显的较孤立的中附尖。3) 上臼齿前附尖发育并强烈伸向前唇侧, 使上臼齿横宽, 形状近梯形; 都具有“W”型外脊和低弱的横脊。4) 下臼齿均具分离的下后附尖, 并且下后脊斜向舌侧。*Danjiangia* 与 *Lambdaotherium* 的区别也很显著: 1) 后者的上臼齿齿尖较粗钝, 横脊也不如前者中的锐利, 且后脊上一般具有明显的后小尖。2) 后者前臼齿的臼齿化程度比前者高, 尤其表现为 P2/2 的齿尖已经分化, P3/上发育有后小尖。3) 后者下臼齿齿脊粗钝, 下后脊止于下后附尖的唇侧, 不似前者齿脊高而锐利, 下后脊直接与下后附尖相连; 另外 *Lambdaotherium* 的 M/3 下次小尖唇侧棱指在下次脊的中部, 这点似与原始古马类相似而与 *Danjiangia* 不同。4) *Lambdaotherium* 无 P/1。5) 后者体型 (M/1 长约 11—12mm) 比前者稍大。

以上特征可以把 *Danjiangia* 和 *Lambdaotherium* 两属区别开。

3. 与已知的早期爪兽类比较

在早期爪兽中有两种头骨及下颌骨形态, 一类以 *Grangeria* 属为代表, 头骨粗壮, 吻部较短, 下颌骨深, 联合部短; 另一类头骨低, 吻部较长, 下颌骨纤细, 联合部长, 如 *Eomoropus*、*Litolophus* 等属 (Radinsky, 1964; Lucas and Schoch, 1989)。*Danjiangia* 的头骨、下颌骨特征属于后一类。以 *Eomoropus* 为例, *Danjiangia* 与早期爪兽属种有以下相同点: 1) 上臼齿都具有“W”型的外脊, 前附尖和中附尖十分发育, 后尖倾向舌侧, 有显著的横脊和发育的前小尖, 无后小尖, 原尖和次尖后移。2) 下臼齿齿脊锐利无凹刻, 具有分离的下后附尖及斜向舌侧的下后脊, M/1—2 下次小尖缩小并偏向舌侧, M/3 下次小尖呈凹沟状。3) 上前臼齿的后尖 (如果存在) 相对前尖偏向舌侧, P4/无后小尖。*Danjiangia* 与其它早期爪兽尽管有以上相似之处, 它们的区别也是很明显的: 1) 前者有一个退化的靠近 C/1 的 P/1, 后者均无 P/1。2) 前者的 P2/2 结构较原始, 为单一刃状齿尖, 基本未分化, P3—4/的“V”型脊环很不发育, 却有显著的中附尖和前小尖; 后者的 P2/2 均已明显分化, P3—4/“V”型脊环发育, 无前小尖和中附尖。3) 前者的上臼齿明显比后者原始, 外形较横宽, 外脊、横脊不如后者中的发育。4) 下臼齿的区别主要在下后脊上, 前者的下后脊更加斜向舌侧, 并与下后附尖直接相连, 而后者的下后脊一般指向下后附尖唇侧; 另外前者的 M/3 下次小尖虽然有缩小趋势, 但仍比后者中的发育。

通过以上比较讨论可以确定, 秉志丹江兽 *Danjiangia pingi* 与其它原始奇蹄动物各属种均不相同, 它应代表一新属新种。

三、系统发育分析及相关问题讨论

1. *Danjiangia* 的系统发育分析

综合前文描述及比较讨论的结果, 秉志丹江兽作为一种早始新世的原始的奇蹄动物包含了以下近祖特征: 1) 头骨低, 鼻切迹浅, 吻部较长。2) 下颌骨水平支纤细, 联合部窄长。3) 齿式完整(3.1.4.3/3.1.4.3), 低冠齿。4) 门齿铲型, I3/3 具外侧小齿尖。5) 前臼齿列长度相对较长 ($P2-4/M1-3 = 0.74$, $P2-4/M1-3 = 0.64$), 前臼齿未臼齿化。

Danjiangia 除了有上述原始特征, 它也表现出一些奇蹄类中的进步特征(近裔性状): 1) 上臼齿前附尖发育并偏向前唇侧; 中附尖十分发育; 后尖向舌侧倾倒; 后脊上无明显后小尖; 原尖、次尖的后端向后弯转。2) 下臼齿齿脊锐利, 无凹刻; 下后脊斜向舌侧; 下次小尖缩小且偏向舌侧。3) 上前臼齿的后尖(如果存在)相对前尖偏向舌侧。4) C1/—P1/间的齿隙缩短。5) P/1 退化。

上述近裔特征中, 从 *Danjiangia* 上臼齿具十分发育的中附尖、下臼齿下后脊强烈斜向舌侧并与下后附尖相连等特点, 可以明显排除它是始祖马类、獐类以及犀类的可能。原始雷兽类(以最早的典型雷兽 *Eotitanops* 为代表)的上臼齿已具有连续而宽大的外脊, 其舌侧齿尖钝锥状, 完全孤立, 无横脊发育。可以认为它是向单一的外脊发育的方向发展, 一开始就没有横脊发育的过程, 而 *Danjiangia* 的上臼齿具有显著的横脊, 所以它也不可能属于雷兽类。

Danjiangia 的上臼齿具有十分发育的前附尖和中附尖(构成“W”型外脊), 横脊上前小尖显著而无明显的后小尖, 这些特征把它与早期爪兽联系起来, 而与原始古马类相区别; 再有它的下臼齿下后脊锐利, 斜向舌侧并与下后附尖相连, 这是进步爪兽所具有的特征; 另外 *Danjiangia* 的下原脊、下次脊高脊型, 中部无凹刻, 这也可与原始古马类区别而与爪兽类相同; 上前臼齿后尖相对前尖偏向舌侧, 以及下臼齿下次小尖缩小并偏向舌侧等特征也表现了 *Danjiangia* 与爪兽类的近裔共性。

根据以上分析, *Danjiangia* 应归入爪兽类群中。为了进一步验证这一观点, 在此为秉志丹江兽及相关类群作一支支图如下。参考 Hooker (1989) 对早期奇蹄类的性状极性分析, 以及 Coombs (1989) 对爪兽科的总结, 笔者归纳出与 *Danjiangia* 系统发育分类相关的性状如下(其中 0 代表原始特征, 1、2 代表衍生特征, 演化方向为 0—1—2, ? 表示该性状情况不清):

- | | | | |
|------------------------------------|----------|--------------|--------------|
| 1) I/3 外侧齿尖 | 0: 有 | 1: 无 | |
| 2) 门齿形状 | 0: 铲形 | 1: I/3 锐利 | 2: 全部锐利 |
| 3) P3/前小尖 | 0: 无 | 1: 有 | |
| 4) P3/原尖后棱 | 0: 无 | 1: 弱, 不与外脊相连 | 2: 脊型, 与外脊相连 |
| 5) P3/后小尖 | 0: 无 | 1: 有 | |
| 6) P4/前小尖 | 0: 有 | 1: 无 | |
| 7) P4/原尖后棱脊状, 与外脊相连 | 0: 否 | 1: 是 | |
| 8) P4/后小尖 | 0: 有 | 1: 无 | |
| 9) P/后尖相对前尖的位置 | 0: 后端 | 1: 后端偏舌侧 | |
| 10) M/前尖、原尖会聚造成前尖前、后棱折曲及/M 下后脊斜向舌侧 | 0: 否 | 1: 轻微 | 2: 强烈 |
| 11) M/中央棱折曲造成/M 下后脊斜向舌侧 | 0: 否 | 1: 轻微 | 2: 强烈 |
| 12) M/前小尖的大小及/M 下后附尖与下后尖的分离 | 0: 小, 紧密 | 1: 大, 分离 | |
| 13) M/3 下次小尖 | 0: 不缩小 | 1: 缩小 | |
| 14) M3/前附尖向唇侧扩展 | 0: 否 | 1: 是 | |
| 15) M/原尖、次尖的后端向后弯转 | 0: 否 | 1: 是 | |

所选择的相关类群是: *Propachynolophus*、*Eotitanops*、*Lambdaotherium* 和

Eomoropus 等四个属。其中 *Propachynolophus* 属于原始的广义古马,与 *Danjiangia* 有一定的相似之处,在此作为古马类群的代表; *Eotitanops* 是一典型的原始雷兽,作为雷兽类的代表; *Lambdaotherium* 的分类地位有争议,它与 *Danjiangia* 有许多相似之处,但又有重要的差别,因此把它也列在其中比较其相互关系。*Eomoropus* 是一个典型的早期爪兽,这里可代表爪兽类群。*Danjiangia* 与以上四个属,再加上一个外类群(outgroup,假定其所有性状都是原始特征,用 0 表示),与上面的 15 个性状结合,可以得到下面的性状分布矩阵:

outgroup	000000000000000
<i>Propachynolophus</i>	??1110000111000
<i>Eotitanops</i>	110000?10220000
<i>Lambdaotherium</i>	101110000111010
<i>Eomoropus</i>	?00201111111111
<i>Danjiangia</i>	001100011221111

将该性状分布矩阵用 Hennig 86 软件处理,即得到如下两个分支图(图 2),这两个分支图是同样简约的。

从图 2 可以看出, *Danjiangia* 与 *Eomoropus* 总在一个分支上,也就是说在上述分类单元中 *Danjiangia* 与 *Eomoropus* 的亲缘关系是最接近的。

综合该图以及前面比较讨论的结果,笔者归纳出 *Danjiangia* 与 *Eomoropus* 具有如下近裔共性:上臼齿具“W”外脊;前附尖强壮,偏向前唇侧;中附尖发育;后尖的唇面向舌侧倒伏;原尖、次尖向后弯转;后脊脊型(或向脊型方向发展),其上无后小尖;上前臼齿的后尖(如果存在)相对前尖偏向舌侧;P/1 退化或消失;下臼齿下后脊斜向舌侧,下原脊、下次脊脊型,无凹刻;下次小尖缩小且偏向舌侧。

由于 *Eomoropus* 是早期爪兽中的典型代表,以上性状实际上反映了秉志丹江兽与其它早期爪兽的近裔特征,即从节点 A、A' 向右划分出爪兽类群。

根据上述秉志丹江兽与爪兽的近裔相似性以及它与其它类群的明显区别,本文将它归在爪兽超科(Chalicotherioidea)中。在科级划分上, *Danjiangia* 作为早始新世的原始爪兽

应与其它早期爪兽一样归在始爪兽科(Eomoropidae)中。需要指出的是, *Danjiangia* 与

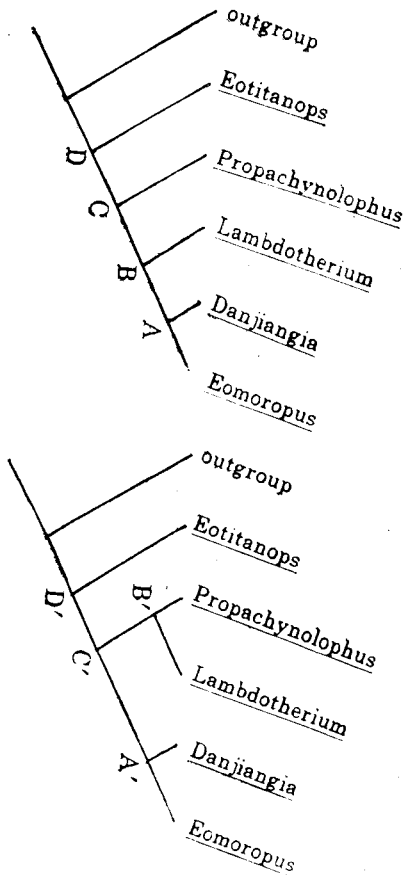


图 2 *Danjiangia pingi* 的系统发育分析
 Fig. 2 Phylogenetic analysis of *Danjiangia pingi* gen. et sp. nov.

支持各节点的近裔共性 (the synapomorphies supporting each node):

上图 (above): A(8,9,13,15);B(14);
 C(3,4,5,12); D(10,11)

下图 (below): A'(8,9,13,14,15);
 B'(5); C'(3,4,12); D'(10,11)

其它早期爪兽也有较大的差别,而且 Lucas 和 Schoch (1989) 曾指出始爪兽科是一个并系的类群,但由于化石材料有限,该科系统发育关系尚不能解决,现有材料又不足以建立新科,因此本文暂时将 *Danjiangia* 归入始爪兽科,并于科名前标一“?”。

2. 对爪兽早期性状演化的探讨

秉志丹江兽的发现为研究爪兽类群的早期性状演化提供了一个很好的材料,因为它是目前发现的爪兽材料中地质时代最早、特征又十分原始的标本。综合前面比较讨论的结果,*Danjiangia* 包含了以下爪兽类群内部的原始特征: 头骨低,吻部较长,鼻切迹很浅;下颌骨纤细,联合部窄长;前臼齿列与臼齿列的长度比大;门齿数目完整且形态原始(铲状,具 $1/3$ 外侧齿尖);保留 P1/和 P/1;前臼齿未臼齿化,P2/无后尖;上臼齿宽大于长,前附尖强大,外脊连棱弱,其上齿尖较孤立,前、后脊低弱,不与外脊相连;下臼齿不拉长,M/3 下次小尖较大。

除了有上述诸多原始特征,*Danjiangia* 也表现出一些爪兽类群内部的进步特征,尤其是它的下臼齿齿脊高而锐利,下后脊高并且强烈地斜向舌侧,直接与下后附尖相连,使下臼齿呈典型的双“V”型,这是始新世以后的较进步的爪兽所共有的特征。

可以看出,在爪兽类群内部比较,*Danjiangia* 的前臼齿和上臼齿表现出了较多的原始特征,而其下臼齿表现出了明显的进步特征,因此 *Danjiangia* 不太可能是爪兽类群中最原始的类型,但我们仍可从其原始特征中找出一些爪兽早期性状演化的特点:

Danjiangia 的上臼齿原尖和次尖均前后向压扁,前小尖横向拉长,连在前脊上;后脊虽然较低,但比较锐利,有向脊型化发展的趋势。中始新世的 *Eomoropus* 属,前、后脊高而发育,并与外脊直接相连,由此我们推测,前、后脊由低到高,由弱变强,从不与外脊相连接到与外脊相连代表早期爪兽横脊进化的方向。

Danjiangia 的上臼齿前附尖、前尖、中附尖和后尖虽然还比较孤立,但齿尖之间已经有弱棱相连,而且前尖、后尖明显呈新月状并微微倒向舌侧,其发展方向应是一个“W”型的连续而强大的外脊,经过 *Eomoropus* 的外脊形态发展为后期爪兽的外脊形态(如 *Moropus*、*Chalicotherium* 等属)。在这个过程中必然伴随前附尖的缩小,因为如此它才能与外脊融合。

Danjiangia 的臼齿咬合主要在舌侧(即内侧),咀嚼食物时下臼齿沿上臼齿的横脊左右移动。由于以横脊剪咬为主,故其横脊部分宽于外脊部分,且上臼齿宽大于长。根据其它爪兽的特点可以推断:随着外脊的发育(包括拉长、加宽),臼齿咬合重点将从横脊转向外脊,而上下臼齿的长度也必然随之拉长。

Danjiangia 中附尖的发育很有特色。其 P3/后尖唇侧齿缘凸起,显示了中附尖的萌芽,P4/上的中附尖已经十分明显,但此时它与前尖、后尖之间尚无齿棱相连,上臼齿中附尖发育,但仍比较孤立,与前尖、后尖之间有弱棱连接;可以看出,这种中附尖的发生方式与早期马类的中央棱折曲产生中附尖的方式有所不同。其它早期爪兽的 P3/、P4/均无中附尖(尽管 P3—4/上已有前附尖发育),所以这种中附尖的发生方式可能代表一种近裔自性。

前文谈到,*Danjiangia* 的下臼齿形态已经相当进化,其齿脊高而锐利,下后脊强烈

斜向舌侧并与下后附尖相连,这在其它早期爪兽中是比较少见的: *Eomoropus*、*Grangeria*、*Lunania* 的下后脊均指在下后附尖的唇侧,只有 *Litolophus gobiensis* 的下后脊与之相似 (Radinsky, 1964; Colbert, 1934)。 *Danjiangia* 的下臼齿形态表明,下后脊逐渐斜向舌侧的性状在爪兽中不是一次进化的,同时也证明 *Danjiangia* 不可能是其它爪兽的祖先。

Danjiangia 的 M/3 下次小尖上有一长条形狭沟,周明镇(1962)在讨论 *Lunania* 的分类地位时就谈到了这一构造,并指出其它早期爪兽的下次小尖也有相似结构。笔者认为,这一特点再次证明了爪兽中 M/3 下次小尖缩小的趋势,正是因为下次小尖的缩小,才使盆形的下次小尖变为狭沟形。因此这种下次小尖可以和早期马类的下次小尖区分开。再有由于下前脊、下后脊的倾斜,造成下三角凹、下跟凹从阔盆状变为舌侧不封闭的凹沟状,这一特点在爪兽中也十分普遍,很可能代表其一种进化趋势。

综上所述, *Danjiangia* 的发现,扩展了早期爪兽的范围,从而在一定程度上填补了爪兽早期演化的空白,对爪兽类群的性状分析很有研究价值。由于化石材料有限,这方面的研究还很不完善,在此仅作为一种尝试性的探讨。

3. 关于爪兽起源的讨论

根据前文的讨论结果,笔者将 *Danjiangia pingi* 与古马类群区别开,而归入了爪兽类群。而 *Danjiangia* 与原始古马类的相似性,表明爪兽类群与古马类群具有某种可能的亲缘关系,即它们可能拥有一共同的祖先,这对我们探讨爪兽的起源提供了一些启示。反映在图 2 中, *Danjiangia* 和 *Lambdotherium* 成为两大类群联系的纽带。值得注意的是,在 Simpson (1945) 的分类方案中,马类、爪兽类和雷兽类被一同归入了马形亚目,然而近年来也有人提出爪兽类群应归入角形亚目 (Prothero and Schoch, 1989a, b), 笔者根据本文材料的研究认为爪兽与马类的亲缘关系还是近于它与獬犀类的关系。

过去一般认为爪兽起源于北美,而后进入亚洲、欧洲和非洲 (Colbert, 1934, 1935; Radinsky, 1964), 如今这一起源观点由于 *Danjiangia* 的发现而面临挑战。北美最早的爪兽是 Uinta "B" (中始新世中期) 的 *Eomoropus amarorum*, 其特征已经相当进步 (Lucas and Schoch, 1989; Radinsky, 1964), 不可能作为爪兽起源的代表,而 *Danjiangia pingi* (时代为早始新世晚期) 则表现出诸多前者没有的原始特征并有向爪兽方向进化的趋势。不过 *Danjiangia* 的下臼齿特征已经比较进步,所以它也不可能代表爪兽起源时的形态,因此还必须向前追溯,寻找爪兽的祖先。根据 *Danjiangia* 的形态特征以及早期爪兽在中国属种分异度较北美大的事实¹⁾, 笔者推测爪兽很可能是起源于亚洲的,我们期待发现更多的材料来给予证实。

致谢 这篇文章是本人硕士论文的一部分,导师周明镇先生给予了全面的辅导;李传夔、童永生、齐陶、王景文等先生审阅了论文初稿并提供了宝贵的意见;王元青博士提供了论文标本,并与胡耀明先生一起给予了重要的帮助;郭建崑先生、周伟先生参加了野外工

1) 中国已报道的早期爪兽有 5 属 9 种(胡长康, 1959; 周明镇, 1962; 周明镇等, 1973; 张玉萍, 1976; 石荣琳, 1989; Chow, 1957; Radinsky, 1964; Colbert, 1934; Zdansky, 1930 等文), 而北美已报道的早期爪兽只有 2 属 2 种 (Osborn, 1913; Lucas and Schoch, 1989; Radinsky, 1964 等文)。

作;谢树华先生修理了标本,张杰先生和杨明婉女士分别制作了图版和插图,王钊先生复制了模型。笔者在此一并表示感谢。

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A NEW PRIMITIVE CHALICOTHERE (PERISSODACTYLA, MAMMALIA) FROM THE EARLY EOCENE OF HUBEI, CHINA

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Key words Liguanqiao Basin, Hubei; Early Eocene; Chalicothere

Summary

A new material of perissodactyl represented by a crushed skull and the same individual's pair of mandibles (both lost their posterior parts) is described in this paper. The specimen was collected in 1992 by Dr. Wang Yuanqing of IVPP from the late Early Eocene of Danjiangkou, Hubei, China. This new material, *Danjiangia pingi* gen. et sp. nov., is here referred to Chalicotherioidea and recognized as the earliest known chalicothere. Several relevant issues, such as the early character evolution of chalicothere group, the possible close relationship between chalicothere and palaeothere group and the origin of chalicotheres, will also be tentatively discussed in the present paper.

I. DESCRIPTION

Order Perissodactyla Owen, 1848

Superfamily Chalicotherioidea Gill, 1872

Family ?Eomoropidae Viret, 1958

Genus *Danjiangia* gen. nov.

Type species *Danjiangia pingi* gen. et sp. nov.

Diagnosis Small primitive chalicothere (length of M/1=8.3mm), skull shallow with cranial rostrum relatively long, mandibular horizontal ramus and mandibular symphysis fairly long and shallow, teeth low-crowned, dentition formula: 3.1.4.3/3.1.4.3.

Premolar nonmolariform, P2/2 trenchant, P4/with incipient mesostyle. M/wider than length with W-shaped ectoloph, parastyle strong and extending anterolabially, developed conoid mesostyle with weak crista respectively to paracone and metacone (which slightly flattened buccally), no metastyle, transverse lophs low and weak bearing a prominent paraconule and no metaconule, protocone and hypocone to some extent distally recurved. /M double V-shaped with metalophid obliqued lingually and connecting with the separate metastylid, paralophid low, no obvious paraconid,

M/1—2 hypoconulid weak and slightly lingually displaced.

Danjiangia distinguished from all other early chalicotheres¹⁾ by its smaller size, more primitive and peculiar premolars, presence of a remnant P/1, relative weak ectoloph and transverse loph and more oblique metalophid. The preserved parts of skull and mandibles of this genus are similar to that of *Eomoropus* and *Litolophus* and different from that of *Grangeria*.

Etymology The genus name comes from "Danjiangkou City" which is the nearest city to the fossil locality

Danjiangia pingi gen. et sp. nov.

(Fig. 1, Plate I)

Holotype A crushed skull (lost its postorbital part) and the same individual's two mandibular horizontal rami, with almost all teeth preserved well. IVPP specimen number: V10842.

Horizon and locality Middle member of Yuhuangding Formation (late Early Eocene), Liguanqiao Basin, Hubei, China.

Diagnosis As for the genus.

Etymology The species name is dedicated to Mr. C. Ping (1886—1965), who is a famous geologist and a early researcher of Liguanqiao Basin.

Description

Skull The skull of V10842 has lost its postorbital part and the nasals and temporals are both broken and pressed downwards. The orbital region is also badly damaged.

The skull is shallow with a relatively long and narrow cranial rostrum. The nasal incision is not marked with its posterior end not beyond C1/. The maxilla is steep at the face, and the anterior edge of the orbital is approximately above M1/. Both infraorbital foramina are broken and roughly above P3/. The incisive foramen is damaged with its posterior edge to I3/. The anterior part of the palatine is not preserved and the front edge of internal nares is corresponding to the middle of M2/.

Mandibles V10842 preserves only the horizontal rami of the lower jaw. The mandible is long and shallow and gradually deepened backwards. The mandibular symphysis is relatively long and narrow while its post end reaches the rear of P2/. The left mandibular foramen is partially preserved and roughly equal in height with M3/. The number of mental foramen are not less than two.

Teeth (measurements of cheek teeth see Table 1.)

1) upper incisors all I/ are badly damaged except left I3/. I/ are sparsely arranged in a semi-circle with short diastema between them. I1/ is similar to I2/ with elliptical cross section. I3/ is a little larger (L = 4mm) and flat conoid like bearing a distinct facet of a distal cusp.

2) upper canines The top of the crown of two C/ are both broken. C1/ is

1) "early chalicotheres" refers to all known Eocene genera of chalicotheres which represent relatively primitive types. Viret (1958) and Radinsky (1964) used respectively Eomoropinae and Eomoropidae to include them.

middle-sized and strong conoid like (measurement at the base: 7.4mm × 5.8mm). It is a little recurved backward and tilting labially with a relatively long diastema to I3/.

3) upper premolars

Two P1/ only preserve their roots. P1/is double-rooted (measurement: 5.8mm × 3.4mm) with very short (or no) diastema to C1/1 and P2/.

P2/ is trigonid in shape and mainly made up of a blade-like cusp. There is a weak cingular projection at the postlingual side of P2/ suggesting an incipient protocone. This P2/ is very primitive with no separate paracone and metacone.

P3/ is roughly trigonid in shape with three main cusps: paracone, metacone and protocone. The first two cusps are already separated and conoid like with weak crista between them. Metacone is a little lower and lingually displaced comparing with paracone. Protocone of P3/ is well-developed and lower than the labial cusps. There is a weak preprotocrista from protocone to anterior base of paracone with a small paraconule on it. Postprotocrista on P3/ is much weak and hardly be seen. An incipient parastyle can be observed anterior to paracone with weak crista connecting them. On the labial side of metacone, the cingulum is slightly projecting as a symbol of incipient mesostyle comparing with M/. The pre-and post-cingula of P3/ are very prominent, and the latter is wider.

P4/ is sub-squared and larger than P3/. The characters on P4/ are more distinct than those on P3/. Besides, a weak postprotocrista is present to construct a low incomplete V-shaped ring on the lingual side. No metaconule is observed on P4/. Something remarkable is that the prominent mesostyle on P4/is to some extent isolated and has no cristae to the labial main cusps. P4/ has well-developed pre-and post-cingula, and the postcingulum is quite wide.

4) upper molars The transverse lophs of two M1/ are slightly broken and the mesostyle of M2/ is a little deformed. Others are preserved well.

M/ is characteristic by its well-developed isolated parastyle and mesostyle, weak transverse lophs and the lost of metaconule. M/ is transversely wide with an anterolabially expanded strong parastyle to form a trapezium in outline. The width of W-shaped ectoloph is about 1/3 to 2/5 of the whole width of tooth. Cusps on ectoloph are relatively isolated with weak cristae between them, so the ectoloph is not strong and continuous but still rather distinct. Mesostyle is well-developed and conoid like with weak cristae to paracone and metacone. The latter two cusps are slightly flattened buccally while metacone is a little smaller and postlingual to paracone. There is a pit at the base of metacone's labial side and no metastyle is present. The transverse lophs of M/ are much lower than the ectoloph and not joining with it. Transverse lophs are weak and low but rather distinct. There is a prominent paraconule on the paraloph and no distinct metaconule on the lophoid metaloph which terminates at the anterior base of metacone. Protocone and hypocone on M/ are slightly distally recurved while the hypocone is more labially displaced. M/has prominent precingulum and less developed postcingulum.

M1-3/ have little differences in structure while M2/ is a little larger among them.

5) lower incisors Right I/1 is a little broken at the top. Other incisors

are preserved well. /I are all spatulate and directing forward. They arrange in a semi-circle with short diastema between them as the upper incisors. There is also a small distal cusp on I/3 (length of I/3 = 4.2mm).

6) lower canines C/1 is more slender than C1/ and be a long pointed cone (10mm long). It tilts labially as C1/ and has a short diastema to I/3.

7) lower premolars

V10842 preserved left P/1 and lost the right one. P/1 has a single root and a slender cusp. The enamel of it is very thin and worn at the top. P/1 is similar in size with /I (length of P/1 = 4.5mm). Specially, this P/1 is distant from P/2 by a long diastema but close to C/1. Furthermore, it falls forwards and points to C/1. Apparently it dose not commit the teeth occlusion.

P/2 is very simple with only a single blade cusp. It is double-rooted and the crown of it is slightly tilting labially and obliqued from the main line of the cheek teeth.

P/3 is similar to P/2 by having a high blade cusp. Besides, its posterior part is lengthened and widened to form a low junior talonid with incipient metaconid and metalophid.

As to P/4, it is W-shaped and submolariform with distinct protoconid, metaconid and hypoconid. Metaconid is the highest cusp from which a metastylid begins to differentiate but not distinct. Protolophid is high and outstanding, while paralophid, metalophid and hypolophid are still low and weak. Metalophid obliques lingually and ends labially to the metastylid. The trigonid and talonid basins are valley-like with their lingual sides opening.

8) lower molars

M/1 and M/2 are double V-shaped and characteristic by their sharp continuous lophes and well oblique metalophid which connects directly with the separated metastylid. Paralophid is not developed, while protolophid, metalophid and hypolophid are all high and straight with steep labial walls. Metastylid is obviously separated from metaconid, and it situates postlingually to the latter. The two cusps are higher than the other ones. A prominent endoconid is also present but no distinct paraconid is observed. Hypoconulid on M/1—2 is reduced representing by a small process (from postcingulum) on the post wall of hypolophid, and it is lingually displaced and relatively high in position. M/1—2 both have distinct pre- and ecto-cingulids.

M/3 is similar to M/1—2 but distinguished by a very prominent hypoconulid. M/3 tapers backwards in width and its hypoconulid has a groove-like structure with the buccal postcristid branch (see Hooker, 1989) directing to endoconid. The pre-, post- and ecto-cingulids of M/3 are all well distinct.

II. COMPARISON AND DISCUSSION

Danjiangia pingi gen. et sp. nov. is a relatively primitive and small-sized perissodactyl. It cannot be hyracotheres, tapiroids and rhinocerotoids judging from its well-developed mesostyle and oblique metalophid. *Danjiangia* has some similarities with European primitive palaeotheres (*Propachynolopus*, Early to Middle Eocene),

North American late Early Eocene brontothere *Lambdaotherium*²⁾ and early chalicotheres (*Eomoropus*, *Grangeria*, etc.) from China and North America. Detailed comparisons will be mainly given to these relevant taxa.

1. with primitive palaeotheres (abbreviated as p.p., the same below)

There is not much differences of cranial and mandibular morphology between *Danjiangia* and p.p. They both preserve primitive characters of perissodactyls (such as shallow skull and narial incision, relatively long cranial rostrum, slender mandibles and long and shallow mandibular symphysis). P. p. also have prominent parastyle and mesostyle, low transverse lophs and oblique metalophid.

Danjiangia is distinguished from p.p. by: 1) more developed parastyle and mesostyle, more isolated mesostyle which has weaker connection with paracone and metacone; 2) no obvious metaconule, metaloph directing to metacone and not to the front of metacone as in p.p.; 3) high and unnotched protolophid and hypolophid, more oblique metalophid which directly connects with metastylid; 4) reduced M/1-2 hypoconulid which lingually displaced and a groove-like structure on M/3 hypoconulid with its buccal postcrisid branch to endoconid (not to the middle notch of hypolophid as in p.p.); 5) more primitive premolar structure (especially on P2/2); 6) no metaconule on P4/; 7) having a singleroot P/1 which is close to C/1 and distant to P/2 (right contrary to p.p.).

2. with primitive brontotheres

Eotitanops is a typical primitive brontothere with broad W-shaped ectoloph and oblique metalophid. *Danjiangia* has obvious distinctions from *Eotitanops* as follows: 1) relatively isolated labial cusps to form a weak and uncontinuous ectoloph; 2) prominent transverse lophs and separate metastylid which are never present in *Eotitanops*.

Lambdaotherium was regarded as primitive brontothere in the past (Osborn, 1929; Bonillas, 1936, etc.). In 1980, S. Wallace argued in his unpublished but widely cited master thesis that *Lambdaotherium* was actually a palaeothere *sensu lato* (Mader, 1989). *Danjiangia* has many similarities with *Lambdaotherium* as well as prominent distinctions. Discussions are given below.

Similarities: 1) both having primitive cranial and mandibular morphology of perissodactyl; 2) both having relatively isolated mesostyle on P4/-M3/; 3) M/having similar outline (transversely wide) and W-shaped ectoloph and low transverse lophs, parastyle strong and expanding anterolabially; 4) both having separate metastylid and oblique metalophid.

Distinctions: in *Lambdaotherium*, 1) M/ cusps blunt, transverse lophs not as sharp as in *Danjiangia* and it usually bearing prominent metaconule on metaloph; 2) premolar structure more complicated by having differentiated P2/2 and metaconule on P3/; 3) /M lophs blunt and metalophid ending at the labial side of metastylid; 4) M/3 hypoconulid's buccal postcrisid branch pointing at the middle of hypolophid, which is similar to primitive palaeothere and different from *Danjiangia*; 5) P/1 not present; 6) body size larger (length of M/1 = 11—12mm).

3. with early chalicotheres

2) *Lambdaotherium*'s classification status is under disputations. Discussions are given below.

Danjiangia's cranial and mandibular morphology are similar to that of *Eomoropus* and *Litolophus* and different from that of *Grangeria*.

The similarities of *Danjiangia* to early chalicotheres include: 1) M/ with W-shaped ectoloph and well developed parastyle and mesostyle, metacone flattened labially, transverse lophs prominent with developed paraconule and no metaconule, protocone and hypocone distally recurved; 2) /M lophs sharp and unnotched, metastylid separated from metaconid, metalophid lingually obliqued, M/1—2 hypoconulid reduced and lingually displaced, M/3 hypoconulid having a groove-like structure; 3) P/ metacone (where present) distolingual to paracone, P4/ with no metaconule.

Danjiangia is distinguished from other known early chalicotheres by: 1) presence of a remnant P/1; 2) more simple P2/2; 3) V-shaped loop on P3—4 undeveloped, prominent paraconule and mesostyle on P4/ (which were not present in other early chalicotheres); 4) more primitive M/, transversely wide in shape with weaker ectoloph and transverse lophs; 5) more oblique metalophid; 6) relatively larger hypoconulid on M/3.

From above discussions, it can be concluded that *Danjiangia pingi* is different from other known perissodactyl genera and it should represent a new genus and species.

III. PHYLOGENETIC ANALYSIS AND SOME RELEVANT QUESTIONS

1. Phylogenetic analysis of *Danjiangia*

Danjiangia has shown the following derived characters (apomorphies) in the perissodactyl group: 1) M/ parastyle strong and labially expanded, mesostyle well-developed, metacone flattened labially, no obvious metaconule, protocone and hypocone distally recurved; 2) /M lophs sharp with no middle notch, metalophid lingually obliqued, hypoconulid reduced and displaced lingually; 3) P/ metacone (where present) position distolingual to paracone; 4) diastema between C1/ and P1/ reduced. 5) P/1 degenerating.

From the above discussions, we have ruled out the possibilities of *Danjiangia* belonging to hyracothere group, tapiroids and rhinocerotoids. M/ on primitive brontotheres (represented by the earliest typical brontothere *Eotitanops*) already have continuous broad ectoloph, and their lingual cusps are blunt and completely isolated with no transverse lophs. It can be inferred that brontotheres are going to the direction of pure ectoloph development and without a course of development of transverse lophs from the beginning. On the contrary, *Danjiangia* has prominent transverse lophs, so it can not be brontothere either.

Concerning the derived characters mentioned above, *Danjiangia's* M/ has well-developed parastyle and mesostyle (forming a W-shaped ectoloph), and its transverse lophs have prominent paraconule and no metaconule. These characters associate *Danjiangia* with early chalicotheres and distinguish it from primitive palaeotheres. /M of *Danjiangia* has sharp metalophid which oblique lingually and connecting with a separate metastylid. This character is also belonging to later advanced chalicotheres. *Danjiangia's* protolophid and hypolophid are high and unnotched, and it is different from primitive palaeotheres and similar to chalicotheres. Besides those

above, the characters of having a lingually displaced P/ metacone and a reducing /M hypoconulid have also shown the synapomorphies between *Danjiangia* and chalicothere group.

After those analyses, *Danjiangia* is likely to be put into chalicothere group. In order to further prove this classification, a cladistic analysis is made to show the relationship between *Danjiangia* and some relevant taxa. Fifteen characters were chosen here after Hooker (1989) and Combs (1989) with some minor revisions. (0:primitive characters; 1,2: derived characters; ?:uncertainty; 0-1-2:character polarity):

- 1) I3/ distal cusp 0:present 1:absent
- 2) Incisor shape 0:spatulate 1:1/3 pointed 2: all pointed
- 3) P3/ paraconule 0: absent 1: present
- 4) P3/ postprotocrista 0: absent 1: weak, not joining ectoloph 2: lophoid, joining ectoloph
- 5) P3/ metaconule 0: absent 1: present
- 6) P4/paraconule 0: present 1: absent
- 7) P4/ postprotocrista lophoid, buccolingually orientated, joining ectoloph 0:no 1: yes
- 8) P4/ metaconule 0: present 1: absent
- 9) P/ metacone (where present) position re paracone 0: distal 1: distolingual
- 10) Convergence of M/ paracone and protocone causing: buccal bending of pre- and postparacristae and obliquity of /M metalophid 0: no 1: incipient 2: advanced
- 11) M/ centrocrista buccal flexing causing oblique /M metalophid 0:no 1: incipient 2: advanced
- 12) M/ paraconule size and /M metaconid-metastylid separation 0: small and close 1: large and distant
- 13) M/3 hypoconulid 0: not reduced 1: reduced
- 14) M3/ parastyle buccally expanded 0: no 1: yes
- 15) M/ protocone and hypocone distally recurved 0: no 1: yes

Four relevant taxa and a outgroup (suppose its all characters are primitive and represented by "0") were selected to form a data matrix. The computer analysis (Hennig86) of this data table resulted in two equally parsimonious trees (see fig. 2). In fig. 2, *Danjiangia* is always on the same clade with *Eomoropus*, which means they are closer related in those selected taxa.

From these cladograms and the previous discussions, the synapomorphies of *Danjiangia* and *Eomoropus* are summarized as follows: M/ parastyle strong and expanding anterolabially, mesostyle well-developed, metacone flattened buccally, protocone and hypocone distally recurved, metaloph lophoid, no metaconule on P4/ and M/, P/ metacone (where present) distolingual to paracone, P/1 degenerated or lost, /M metalophid lingually oblique while protolophid and hypolophid lophoid with no notches, hypoconulid reduced and lingually displaced.

Eomoropus is a typical representative of early chalicotheres, so the above characters are actually regarded as synapomorphies of *Danjiangia* and other early chalicotheres, and also a definition of the chalicothere group in this paper.

Danjiangia is here put into superfamily Chalicotherioidea. As to the division on

family level, it should also be concluded into Eomoropidae as other Eocene early chalicotheres. But it must be pointed out that *Danjiangia* still has many differences with other early chalicotheres, and the family of Eomoropidae is regarded as paraphyletic (Lucas and Schoch, 1989). We are not presently able to complete a phylogenetic analysis of Eomoropidae, and the material of *Danjiangia* is not sufficient to generate a new family, so I tentatively give a “?” before the family name.

2. Discussion on early character evolution of chalicotheres

The discovery of *Danjiangia* has given us a good opportunity to study the early character evolution of chalicotheres group, since it is the earliest known chalicotheres and preserves many primitive characters which were not yet found in other chalicotheres.

The primitive characters of *Danjiangia* in the scope of chalicotheres group include: shallow skull with relatively long cranial rostrum, nasal incision not marked, mandibular horizontal rami and symphysis shallow and slender, length ratio of P/M relatively large, incisors full and primitive in morphology, retaining of P1/1, premolar nonmolariform, P2/2 with single blade-like cusp, M/ wider than length, parastyle very strong, ectoloph still weak with relatively isolated labial cusps, transverse loph low and not joining the ectoloph, /M not lengthened, M/3 hypoconulid still relatively large. From these primitive characters and comparing with later chalicotheres, we can try to find some pattern and tendency in the early evolution of chalicotheres group. For some instances as follows:

Danjiangia's M/ protocone and hypocone are pressed anteroposteriorly and metaloph is very sharp (though low), so the transverse lophs are inclined to a lophoid direction. In Middle Eocene genus *Eomoropus*, the transverse lophs are already high and developed and joining the ectoloph. *Danjiangia*'s molar occlusion emphasized on the lingual side: the lower molars moved transversely along the upper molars' transverse lophs when chewing the food. On account of this, the lingual part are wider than the labial part, and the upper molars are transversely wide. As the ectoloph gradually becoming lengthened and strong, we'll get square upper molar as in *Eomoropus* and more lengthened molars as in advanced forms (*Moropus*, *Chalicotherium*, etc.). So the evolution of M/ ectoloph and transverse lophs in chalicotheres is probably undergoing such a process, that is from low to high, weak to strong, uncontinuous to continuous. *Danjiangia* has given us a example of the primitive condition.

Danjiangia has sharp /M lophs and its metalophid is strongly obliqued and connecting directly with metastylid. This is rare in other early chalicotheres most of which have less oblique metalophid (*Eomoropus*, *Grangeria*, etc.). It seems that the character of metalophid obliquity is not evolved out once-a-time in the chalicotheres group, and *Danjiangia* also can not be the ancestor type of other chalicotheres.

The mesostyle evolution in *Danjiangia* is very special. There is an incipient mesostyle on P4/, and it has no crista to paracone and metacone. On the upper molars, the mesostyle is well-developed but has only weak connections with paracone and metacone. Obviously, this kind of mesostyle evolution is different from the centrocrystal mesostyle in early equioids. Other early chalicotheres haven't any trace

of mesostyle on the P/. *Lambdotherium* has this similar kind of mesostyle, but the significance of such mesostyle is not clear, maybe it represents autapomorphy or parallelism.

Danjiangia has a groove-like structure on M/3 hypoconulid. Chow (1962) has mentioned this structure when he discussed the classification of *Lunania*, and he pointed out other early chalicotheres also have the similar construction. I regard it as a proof of M/3 hypoconulid reducing which makes the original basin-like hypoconulid to a groove-like one. Furthermore, the paralophid and metalophid obliquities have made the trigonid and talonid basins from shallow basins to oblique valleys (which opened lingually). This is also popular in chalicotheres and might represent an evolutionary tendency.

From above discussions, we can see that the discovery of *Danjiangia* has expanded the range of chalicotheres and to some extent filled out the blanks of early evolutions of chalicotheres. This will be very valuable to the character analyses of the chalicothere group. Limited by the materials, this kind of study is still far from satisfaction. It is only a tentative and incomplete discussion here.

3. Discussion on the origin of chalicotheres

Danjiangia shares many similarities both with chalicothere and with palaeothere group. These similarities have given us some clues to the possible close relationship between the two groups. *Danjiangia* is certainly at the base in the family tree of the two groups, and *Danjiangia* and *Lambdotherium* may be the important links between them. This can also be drawn out from fig. 2, in which the presence of metaconule is regarded as a useful distinction. Anyhow, the discovery of *Danjiangia* has thrown a light on the arising of chalicotheres. It is remarkable that in Simpson's classification (1945), equioid, chalicothere and brontothere were put together into Hippomorpha, but recently chalicothere group was regarded as closer related to Ceratomorpha (Prothero and Schoch, 1989a,b). According to the studies of *Danjiangia*, chalicotheres are still closer related to Equioidea than to Ceratomorpha.

In the past, chalicotheres were considered to be derived from *Eomoropus* of North American, and subsequently spread into Asia, Europe and Africa (Colbert, 1934, 1935; Radinsky, 1964), and now this view is challenged by the find of *Danjiangia*. The earliest chalicothere of North America is *Eomoropus amarorum* from Uinta "B" interval middle (Middle Eocene), and most of its characters are rather advanced, so it can not be a representative of the origin of chalicotheres. *Danjiangia* (from late Early Eocene) has shown many primitive features as well as the tendency to later chalicotheres. But it has relatively advanced lower molars and also can not represent the original conditions. But the facts of *Danjiangia*'s primitive morphology and Chinese larger diversity of early chalicotheres (than North America)³⁾ make us suggest a Asian origin of chalicothere group, and we hope to find more evidence to further prove it in the later studies.

3) The published materials of chalicothere in China include 5 genera and 9 species (Hu, 1959; Chow, 1957, 1962; Chow et al., 1973; Zhang, 1976; Shi, 1989; Radinsky, 1964; Colbert, 1934; Zdansky, 1930, etc.), while in North America there are only 2 genera and 2 species (Osborn, 1913; Radinsky, 1964; Lucas and Schoch, 1989, etc).

图版说明 (Explanations of plate)**图版 I (Plate I)**

秉志丹江兽(新属、新种) *Danjiangia pingi* gen. et sp. nov.
V10842, 正型标本 (Holotype), $\times 1$

1. 头骨腹视 (ventral view of the skull)
2. 头骨背视 (dorsal view of the skull)
3. 头骨右唇侧视 (right labial view of the skull)
4. 下颌骨左唇侧视 (left labial view of the lower jaw)
5. 下颌骨背视 (dorsal view of the lower jaw)



1993年6月,中国科学院古脊椎动物与古人类研究所考察队在湖北秭归县两河口镇二甲村孙家岩屋发现一处旧石器洞穴遗址。

洞穴海拔约820米,发育于高出谷底约60米的奥陶系石灰岩中。洞口高约3.5米,往里洞顶逐渐降低。

遗址面积约 4×60 m,文化层至少厚1.5 m,无人工扰动痕迹。石制品含量丰富,在不到1米³的文化层中挖出16件。石制品岩性多为石英砂岩,加工技术简单,具有我国华南中、晚更新世的旧石器文化特征。文化层中伴生的哺乳动物化石系大熊猫剑齿象动物群的常见属种,包括犀牛、獐、大熊猫巴氏亚种、猫类、东方剑齿象、鹿类、牛、青羊等至少8个类别,少数碎骨有明显的砍砸痕迹。

(董明星)

