湖南衡东早始新世软食中兽
（?非肉齿目，哺乳纲）的头骨

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关键词　　湖南衡东　早始新世　中兽　软食中兽　头骨

内　容　提　要

本文记述了在湖南衡东下始新统中发现的软食中兽头骨化石——河塘软食中兽 *Hapalodectes hetangensis* sp. nov.，并根据头骨特征对软食中兽的系统分类位置提出修正意见，订 Hapalodectidae 科 (Szalay and Gould, 1966) new rank。对与之有关的中国古新统某些中兽的分类位置进行了讨论。

一、前　　言

软食中兽（*Hapalodectes*）是一属小型的非肉齿目（Acreodi）动物。它的化石原来仅发现于北美下始新统和亚洲中、上始新统中，各有一个种。从早始新世早期开始，到晚始新世，这属动物个体始终较小，形态上变化不大，被认为是一类向着食肉或食鱼方向特化的类型。

该属最早发现的一块化石（一段带有 M_2 的右下颌），是 J. L. Wortman 于 1891 年在北美 Wyoming 州 Big Horn 盆地采到的。由于牙齿结构类似中兽科的 *Dissacus*，而归入该属。1909 年，Matthew 报道了采自 Wind River 盆地的另一块不完整下颌，并创建新属 *Hapalodectes*。此后，该属材料在北美虽偶有发现，但始终较少，而且残破。在亚洲，这属化石采到的更少，只有中美考察团于本世纪二十年代初在内蒙伊尔丁曼哈层中找到几颗零星牙齿，以及近年来我所内蒙考察队在同一地区采到的一段下颌。对于该属已发现的材料，Szalay (1966, 1969) 曾进行过系统的研究，并为它建立一新亚科（Hapalodectinae）；与另两亚科（Mesonychinae 和 Andrewsarchinae）一起归入中兽科（Mesonychidae）。近十多年来，还报道过几个归入这一亚科的亚洲的新属，但各属材料均不完整，分类位置尚有争议。

1982 年，笔者等在湖南衡东下始新统中采到一个十分完整的软食中兽头骨；次年，又在同一地点找到另一头骨的前半部分。这不仅是迄今为止所发现的该属最完整的化石材料，而且是首次在亚洲这样早的地层中的发现。笔者将这批材料的研究结果撰写成本文，

希望它有助于增加我们对这一类动物的了解和认识。本文除对这一保存完好的头骨进行详细描述外，还根据头骨特征对这一亚科的系统分类位置提出了修正意见。文中，我们着重讨论了它与中兽科的关系，对于它（以及中兽科）与鲸类、对锥兽类关系的讨论将另文报道。

笔者十分感谢谢树华同志参加野外工作，并帮助修理化石。在研究过程中，翟人杰同志借给我们尚未研究的标本作对比，并讨论有关问题。齐陶同志借给我们正待发表的手稿和标本作参考。美国自然历史博物馆 McKenna 博士对文章内容提出宝贵建议，并帮助修改英文摘要，还为我们提供该博物馆保存的正型标本模型。周明镇教授和美国亚利桑那大学 Lindsay 博士帮助修改英文摘要。王哲夫先生摄制照片。沈文龙同志绘图。对他们的热忱帮助，笔者在此表示深切的谢意。

二、化 石 记 述

目 ?Acreodi Matthew, 1909

科 Hapalodectidae (Szalay and Gould, 1966), new rank

包括属 *Hapalodectes* Matthew (1909)，唯一的已知属。

分布 北美早始新世；亚洲早、中和晚始新世。

修正特征 个体小。头骨长而窄，矢状嵴和枕嵴较低。眼眶封闭。泪骨几乎没有面区膨大。顶骨向侧方膨大显著。头骨基颅部相对较长。耳区特征原始，耳蜗表面有三条动脉沟。镫骨肌窝大。齿式：$\dfrac{?3 \cdot 1 \cdot 4 \cdot 3}{?3 \cdot 1 \cdot 4 \cdot 3}$。无裂齿。上颊齿齿尖尖锐，次尖大，相邻两上颊齿的舌侧间有脉管孔凹 (vascularized embrasure pits)。下颊齿侧扁，下前臼齿的下前尖极弱或无，下臼齿前表面有凹沟 (re-entrant groove)，具刃状跟座。

属 *Hapalodectes* Matthew, 1909

属型种 *Hapalodectes leptognathus* (Osborn et Wortman, 1892)

归人种 *H. serus, H. hetangensis* sp. nov.

分布 同科的分布。

特征 同科的特征。

种 *Hapalodectes hetangensis* sp. nov.

(图版 I，1a，b，2a，b；II，1a，b，2，3，4)

正型标本 一个完整的头骨及下颌，上有保存齐全的左右 $DP^{3-4}C—M^2$ 和 $DP_3C—M_3$ (V5253)。

归人标本 一个头骨的前半部分，上有残破的左 M^{1-2} 及其余牙齿的齿根和齿槽 (V5254)。
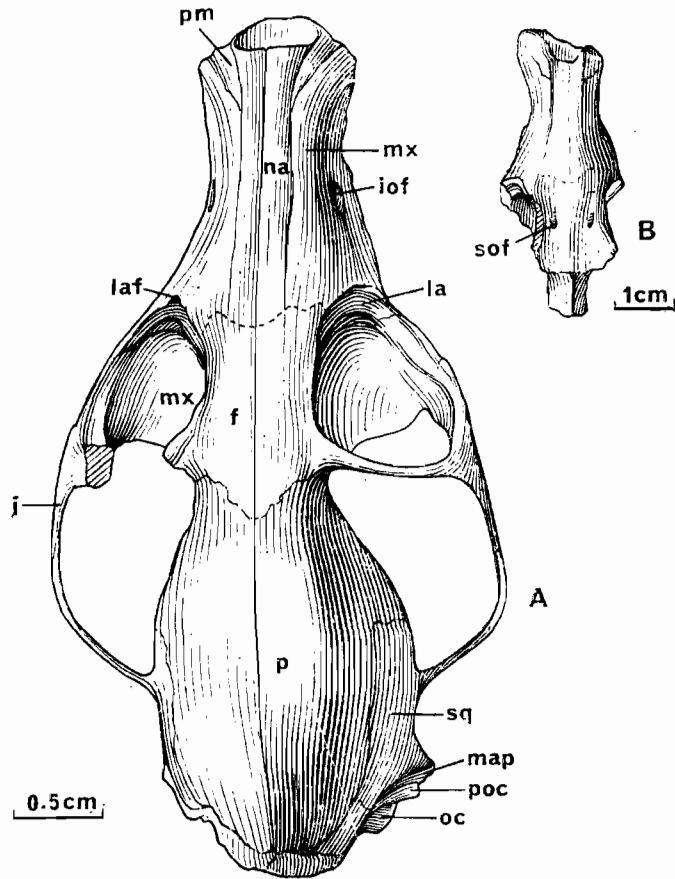
产地 湖南衡东县岭茶河塘村北。

时代及层位 早始新世。岭茶组。

图 1 河塘软食中兽 (*Hapalodectes hetangensis* sp. nov.) 头骨，背面视

Fig. 1 Dorsal view of skull of *Hapalodectes hetangensis* sp. nov. A. V5253 B. V5254

种名由来 以化石产地河塘村为新种种名。

特征 新种以个体小，P_4 无下前尖，下臼齿下后尖发育，区别于属型种 *H. leptogna-thus*；又以上臼齿前附尖和后附尖小，下臼齿下后尖发育区别于 *H. serus*。

描述 V5253 号标本的头骨骨缝清晰易辨，牙齿无明显磨蚀痕迹，DP^{3-4} 和 DP_3 尚未脱落，P_4 和 M_3 未萌出齿槽，M^3 的牙胚尚未形成，它代表一幼年个体。 V5254 号头骨仅保存了前半部分，从矢状嵴较发育和犬齿相当大而粗壮推测，它可能代表一雄性成年个体。

头骨。河塘软食中兽的头骨较长而窄，外形很象某些原始的肉食类(图 1)。

头骨上最显著的特点是眼眶大而封闭。眶前缘及上缘为突出的嵴所围，嵴不连续，被一宽凹分隔。泪骨基本上限于眶内，几乎没有或很小面区膨大，这一点与中兽科有宽的面区膨大区别显著，而接近于 *Vulpavus* 一类的原始肉食类。泪骨孔中等大小，位于泪骨前缘的内侧。鼻骨长而窄，其后缘向后方膨大扩展的很少。前颌骨小，仅限于吻的前面，因而鼻骨在面区主要与上颌骨接触。上颌骨短而深。眶下孔较大，位于 P^3 上方。
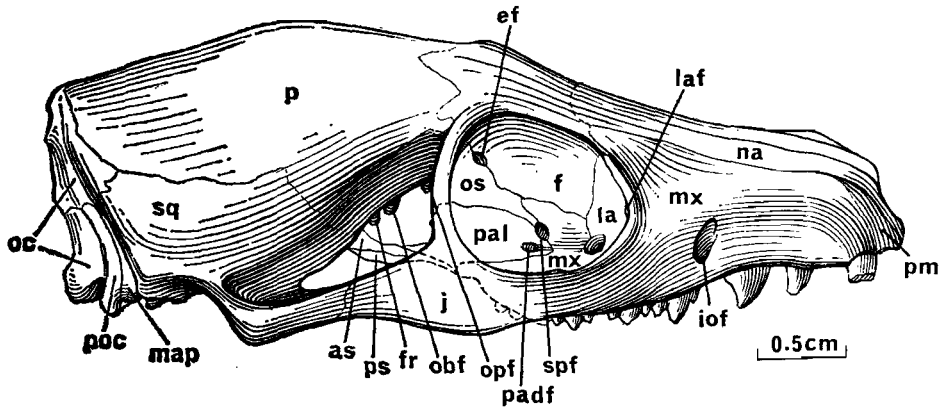
图 2　河塘软食中兽（*Hapalodectes hetangensis* sp. nov.）头骨（V5253），侧面视

Fig. 2　Lateral view of skull of *Hapalodectes hetangensis* sp. nov.

额骨相对较窄，有发育的眶上嵴。眶后收缩强烈。额骨前缘以斜线与上颌骨连结，无突起插入上颌骨和鼻骨之间。额骨的眶后突非常发育，与颧骨的后上支连结，封闭眼眶后缘。在 V5254 号头骨上，额骨背面有两个小眶上孔。

顶骨长，但不太宽，向侧方显著膨大。在 V5253 号头骨上，矢状嵴和枕嵴都非常弱，但在 V5254 号头骨上，保存在额骨后面的部分矢状嵴较发育。枕髁大，两髁分离较远。

鳞骨呈长形，其高度约占头骨后侧部高度的一半。（图 2）

鳞骨的颧突较长而纤细。翼蝶骨较大，是颞窝后壁的主要组成部分。眶蝶骨在颞窝内壁向上伸，接近眶上缘。额骨在眶窝内向下伸至眶窝高的一半处。前蝶骨向侧方延至后鼻孔后壁上。腭骨向上延伸至眶窝内，但不与泪骨接触，它与泪骨被上颌骨分离。视神经孔较大，左右两孔愈合，位于筛孔后下方。眶裂、圆孔和翼蝶管的前开口在 V5253 号标本上未见有骨壁隔开。蝶腭孔及腭孔背口都较大，位于额—上颌骨缝及上颌—腭骨缝的交界处。

颧骨比中兽科相应骨头要大。颧骨的上支又分为两支：一支向前伸，在眶下缘与上颌骨接触；另一支向后上方伸，与额骨的眶后突连结，将眶后缘封闭。颧骨的下支向后下方伸，与鳞骨的颧突连结。眼眶大，眶前缘伸至 P^4 上方，比中兽及 *Vulpavus* 属的眼眶要靠前。

腭骨较短。腹面视呈三角形，其前缘位于 P^3 和 P^4 之间（图 3）。后鼻孔位置较靠前，位于第二上臼齿的后缘。腭孔位于腭—上颌缝的前缘。在与 M^2 后缘相对的腭—上颌缝内侧处，有两个小的腭后孔。上颌骨的腭突窄而长，其前缘有两个小的门齿孔。基蝶骨与前蝶骨均较窄，二者长度相近。

基颅部比中兽科相对较长。基枕骨长度约与基蝶骨相等。乳突小而纤细，它距关节后突的距离比中兽科的相应距离长。副枕突中等大小、纤细，向下后方伸。未保存骨质听泡。下颌窝横向伸长，窝前缘有一低嵴。关节后突粗壮，横向伸长。卵圆孔较大，位于关节窝内侧，其前方距此孔不远有一非常小的孔，为翼蝶管的后开口，翼蝶管较长而细。关
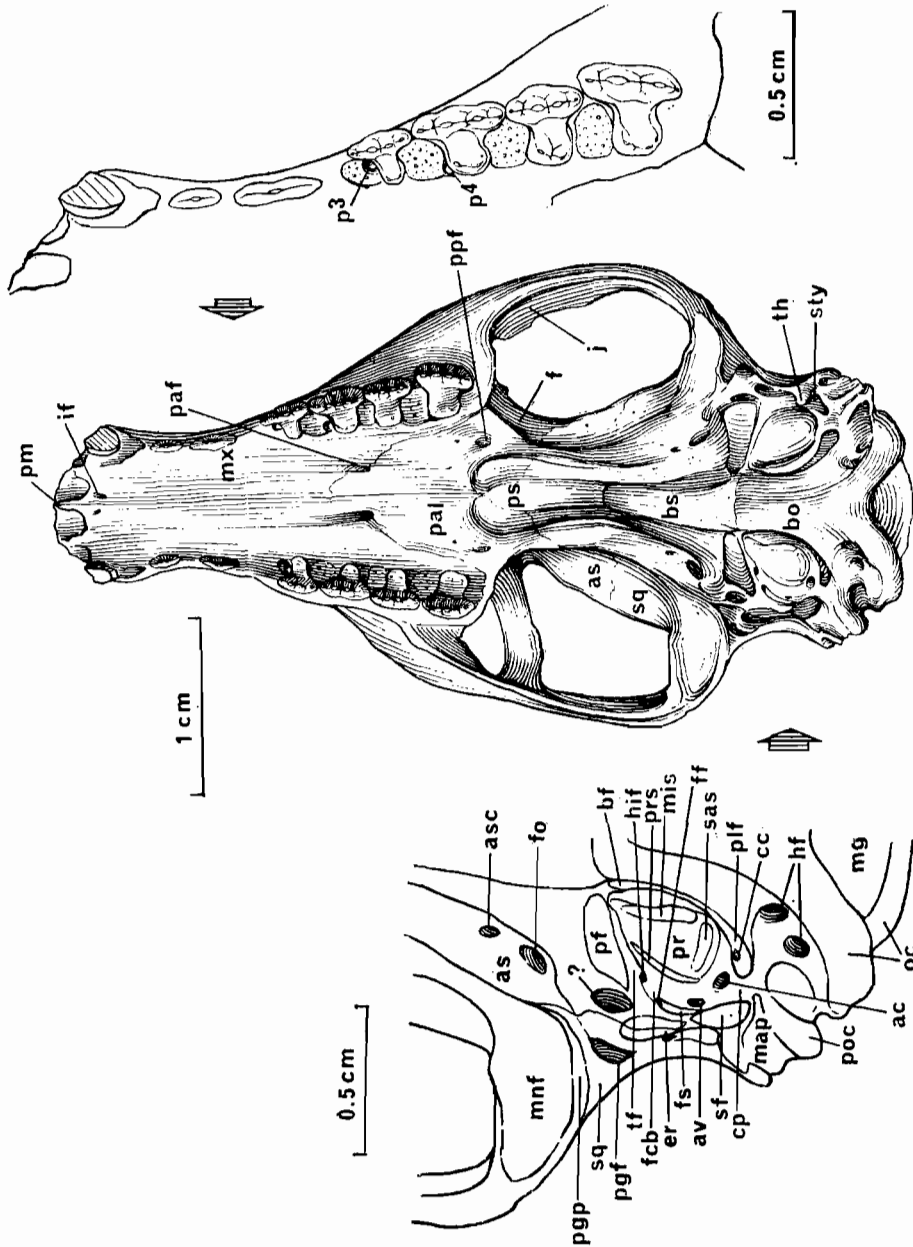
图 3　河塘软食中兽 (*Hapalodectes hetangensis* sp. nov.) 头骨 (V5253)，腹面视

Fig. 3　Ventral view of skull of *Hapalodectes hetangensis* sp. nov.

节后孔较大，紧贴在关节后突的后壁上。鼓室上隐窝较大，位于关节后孔后面，二者距离很近。耳蜗大，但不明显突出，呈杏仁状，其表面有三条清楚的沟。 Presley (1979) 根据胚胎研究结果认为，现生哺乳动物的内颈动脉在听区附近的位置有两种，一种位于基囊裂 (basicapsular fissure) 的内侧 (称为内颈动脉内侧沟, (MICA))，另一种位于耳蜗表面的
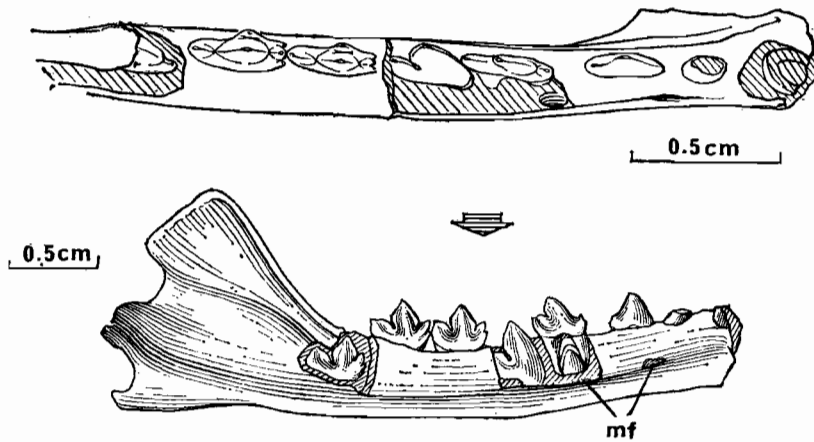
图 4　河塘软食中兽 (*Hapalodectes hetangensis* sp. nov.) 下颌骨 (V5253)

Fig. 4　Mandible of *Hapalodectes hetangensis* sp. nov.

上 (above): 嚼面视 (occlusal view)

下 (below): 唇面视 (lateral view)

外侧(即通常所认为的岬动脉的位置（PICA))。他认为，在耳蜗表面，不可能有内颈动脉和岬动脉同时出现的情况。也就是说，如果加上无论在哪种情况下都可能出现的镫骨动脉，在耳蜗表面不可能同时出现三条动脉沟。但依据 Matthew (1909) 研究肉食类和 MacIntyre (1972) 对晚白垩世原始哺乳动物的报道，在耳蜗表面均有三条动脉沟出现。在 V5253 号标本的耳蜗表面清晰可见三条沟，内侧一条紧靠耳蜗的内缘，较宽而深，与 Matthew 和 MacIntyre 描述的内颈动脉的位置一致，本文采用他们的命名，将此沟命名为内颈动脉内侧沟。另一条较细，位于耳蜗的中间，自蜗窗的前方向前伸至梨形裂（piriform fenestra），为岬动脉沟。镫骨动脉沟在三条沟中是最不明显的，较浅，横向位于蜗窗之前。在耳蜗的外侧，有一圆形前庭窗。蜗窗比前庭窗（卵圆窗）略大，位于耳蜗的后缘，开口向后。在前庭窗前方，有两小孔，前内侧向前开口者为面神经岩支（hiatus Fallopii）的出口，前外侧向后开口者为面神经在岩骨上的出口，两孔之间为一较宽的骨板（面神经桥）隔开。在面神经孔后面，有一窄而深的面神经沟，向后外方伸至茎乳孔。在面神经岩支出口的前方，有一浅窝，为鼓膜张肌窝。镫骨肌窝为一大的椭圆形深窝，位于蜗窗后外侧。基蝶骨和耳蜗之间，有一不太宽的裂隙，本文称为基囊裂（basicapsular fenestra）（McPhee, 1981)。岩骨的后鼓突（caudal tympanic process）在蜗窗后面与乳突连结。乳突内侧前方有一小骨突，可能为鼓舌突（tympanohyal)。

　　下颌骨纤细（图4）。水平支非常浅，其最深处位于 M_{2-3} 下。下颌内侧在 P_3 至 M_3 下有一长而浅的沟。下颌冠状突高而宽大。下颌髁大，横向伸长，位置较低（几与齿列等高)。下颌角小而纤细。咬肌窝大但不太深。有两个颏孔，前面一个位于 P_1 下，后面一个位于 P_{2-3} 下。下颌联合长，由吻前端伸至 P_2 后缘，但连结不牢固。

　　牙齿。齿式：$\frac{?3\cdot1\cdot4\cdot3}{?3\cdot1\cdot4\cdot3}$。V5253 及 V5254 号标本的吻部保存都不够好，门齿的

齿根及齿槽均不清楚，因此，无法准确地鉴定门齿数目及其结构。V5253 号标本保留了左右犬齿的残留部分。从保留部分看，上犬齿较大，横切面为椭圆形，前后各有一条上下延伸的锐利的刃状嵴。 V5254 号标本保留了左右上犬齿齿槽，从齿槽判断，上犬齿非常大而粗壮。P¹ 是前臼齿中最小的一个，单根，横向侧扁，侧面视呈三角形，只有一个大的尖，竖直指向下方。P² 比 P¹ 略大，双根，仅有一个大尖，稍向后指。DP³ 臼齿化，齿冠呈三角形，原尖低；前尖比后尖大；前附尖及后附尖小而低。在 DP³ 齿槽内，修理出一个大的尖，应为 P³ 的牙胚，但 P³ 其余部分的牙胚尚未育出。DP⁴ 臼齿化，比 DP³ 大，齿冠结构与 M¹ 相同，有一大的次尖架，牙齿内缘呈方形。M¹ 为方形，前尖比后尖大，两尖并立，相距较近；原尖呈锥状，高；次尖低；前、后附尖发育，有一弱的前齿缘。M² 是上臼齿中最大者，横向较宽，前尖比后尖大得多；前后附尖比 M¹ 相应的尖发育；原尖高而大；次尖发育；无前齿缘。在 V5253 号标本上，M³ 牙胚尚未形成。 在 V5254 号标本左 M² 的后面残留了一小的齿根，应为 M³ 外侧前面的齿根，比 M² 相应齿根小的多，说明 M³ 可能比 M² 小。上颊齿从 P³ 至 M³ 每相邻两颊齿间都有明显的脉管孔凹(vascularized embrasure pits)。

　　下颊齿仅在 V5253 号标本上保存。犬齿较大，但纤细，略向前倾。P₁ 横向较扁，单根，仅有一个大的尖竖直指向上方。P₂ 比 P₁ 大，双根，横向扁，侧视呈三角形，仅有一个尖。DP₃ 在右下颌上保存完好，臼齿化，双根；有清楚的三角座和跟座；下原尖后倾，下前尖低而小；跟座相对较长，刃状，其前部有一小突起。在 DP₃ 的齿槽中修理出一个大的尖，应为 P₃ 的下原尖，比 P₂ 的相应尖大，但未见 P₃ 其余部分的牙胚形成。P₄ 尚未完全萌出齿槽，是下颊齿中最大者；三角座高，仅由一大的下原尖组成，略向后倾；无下前尖和下后尖的痕迹；跟座低，呈刃状。 P₁ 和 P₂，P₂ 和 P₃ 间有小的齿隙。 三个下臼齿的形态及大小比较相近。 M₁ 横向侧扁，下后尖小但发育很好；下原尖非常大而突出；下前尖比下后尖显著；在下前尖下缘，有两个小尖；牙齿前表面有凹沟(re-entrant groove)；跟座呈刃状，前部有非常小的小突起。 M₂ 比 M₁ 稍大，结构相同，下后尖比 M₁ 的相应尖稍发育。 M₃ 比 M₁、M₂ 略大些，下后尖不清楚；下前尖前下方的两个小尖清楚可见；跟座呈刃状。

　　测量数据：见173—174页。

　　讨论

　　1. 河塘软食中兽最显著的特点是个体小(表 1，Table 1)。 V5254 号标本的上颊齿列比北美属型种 H. leptognathus 的下颊齿列至少短1/4。除个体小外，河塘软食中兽与北美种的区别还有： P₄ 无下前尖，下臼齿下后尖及 M₁₋₂ 下前尖下方的两个小尖更为发育，M₁₋₂ 跟座上有小而清楚的小突起。 它与亚洲晚期的种 H. serus 之间存在如下变

表 1　河塘软食中兽与其他类型臼齿比较

Table 1　Comparisons of length of lower molars of *Hapalodectes hetangensis* and other species

牙齿长度 length of tooth (mm)	*H. leptognathus*	*H. serus*	*H. hetangensis*
M₂	5.5—5.7	?4.5—4.6	3.4
M₃	6	5.5	3.1

化：上臼齿前后附尖逐渐增大，牙齿前后长度逐渐增长；下臼齿下后尖逐渐退化。

河塘软食中兽的个体小，下臼齿下后尖比晚期的种发育，可能是它比 *H. leptognathus* 和 *H. serus* 原始的特点。

2. 在中兽科原有的三个亚科中，Hapalodectinae 的牙齿结构与其他两亚科明显不同的是：上臼齿有一大的次尖，上颊齿相邻牙齿间有脉管孔凹，下臼齿牙齿前表面有凹沟。

本文报道的 *Hapalodectes* 的头骨比牙齿更清楚地反映了这一亚科与其他两亚科的显著区别。现将它们的头骨特征列于表 2；其中，重要的区别摘述如下：

(1) Hapalodectids 眼眶大而封闭，位置较靠前；Mesonychids 眼眶较小，不封闭，位置靠后。

(2) Hapalodectids 泪骨几乎没有面区膨大；Mesonychids 泪骨有相当宽的面区膨大。

(3) Hapalodectids 额骨与上颌骨在背面接触；Mesonychids 额骨与上颌骨不接触。

(4) Hapalodectids 顶骨的侧方膨大显著；Mesonychids 顶骨扁平，不向侧方膨大。

(5) Hapalodectids 基颅部（关节后突至枕髁的长度）相对较长；Mesonychids 的相应部分相对较短。

上述 (1)，大而封闭的眼眶，可以说是软食中兽一个十分特化的特点。就我们所知，这样的眼眶还未见于其他同时代的陆生哺乳动物中。上述 (2)—(5) 显示了软食中兽与中兽科的另两亚科均明显不同，而与某些原始肉食类（如 *Vulpavus*）相似的特点。对于原始肉食类及中兽的头骨，Matthew (1909) 曾作过较详细的阐述。他从大脑发展的角度，解释头骨形态的变化；并指出，在进步类型中，脑颅较长，顶骨向侧方膨大，基颅部较长，泪骨面区膨大较小等；较原始的类型，脑颅较短，顶骨不向侧方膨大，基颅部较短，泪骨有大的面区膨大等。尽管目前对头骨特征的分析还存在着不同意见 (Radinsky, 1977, Novacek, 1980, 1985)，但前述两种不同类型的头骨区别是存在的。将软食中兽头骨与其他类型比较后发现，软食中兽的头骨具有一些进步类型的特点，中兽类的头骨具有更多原始类型的特点。它们头骨的区别进一步表明二者是朝着不同的生活方向特化的，反映出，软食中兽代表了一独立的新科。

河塘软食中兽的耳区与头骨的其他特征相反，十分保守地保留了一些原始特征，它与中兽科其他类型耳区的区别也很明显，如：

(1) Hapalodectids 无骨质听泡；某些 Mesonychids 有骨质听泡。

(2) Hapalodectids 有关节后孔；Mesonychids 无关节后孔。

(3) Hapalodectids 耳蜗表面有三条沟；Mesonychids 无三条沟。

(4) Hapalodectids 的鼓壁上有镫骨动脉上支的出口；Mesonychids 无此出口。

(5) Hapalodectids 耳蜗大而扁平；Mesonychids 较突出。

3. 近十多年来，在亚洲曾报道过几个归入 Hapalodectidae 的新属、种，计有：*Lohoodon, Plagiocristodon* 等。

Lohoodon 属（属型种 *L. lushiensis*）是依据采自河南卢氏上始新统的一个右 M_3 订立的。最初被描述为 *Hapalodectes lushiensis* (Chow, 1965)，后改订 *Lohoodon* (Chow et al., 1975)。Szalay (1969) 曾依据这块标本比北美的属型种个体大的特点，认为 *Hapalodectes* 属除小种外，还包括个体大的种。

　　Metahapalodectes 是 Dashzeveg（1976）依据采自蒙古人民共和国南戈壁 Ингэни-Хобурская 盆地上始新统的几个零星牙齿订立的（属型种 *M. makhchinus*）。这个属下臼齿的形态结构及大小与 *Lohoodon* 非常相似，它们有可能代表了同一个属。这两个属除个体比 *Hapalodectes* 大得多以外，它们与后者最重要的区别是，下臼齿前面没有后者所特有的凹沟。而如果将 *Lohoodon* 的下臼齿与 *Pachyaena* 的相应牙齿比较，它们除个体大小不同外，牙齿结构是基本相似的。从这一点考虑，*Lohoodon* 和 *Metahapalodectes* 更象是 Mesonychidae 科的成员。

　　?*Hapalodectes* sp. 是依据采自江西池江盆地上古新统的一段带有 ?P_3 的残破右下颌订立的（Zhang et al.，1979），是目前已报道的 *Hapalodectes* 属最早的代表。这一下颌骨体的深度与北美 *H. leptognathus* 的相近，但所保存的唯一的一枚前臼齿却比后者相应的牙齿大得多。下前尖比后者相应牙齿的下前尖发育得多。依原作者，将 ?*H.* sp. 归入该属的基本根据是牙齿侧扁的特点。但将 ?*H.* sp. 与属型种仔细比较可以看出，二者牙齿侧扁的情况是不同的。*Hapalodectes* 的下前臼齿是跟座相对比三角座侧扁，刃状跟座嵴相对靠外侧，无齿缘；而 ?*H.* sp. 下前臼齿是三角座相对比跟座侧扁，刃状跟座嵴相对靠内，有内、外齿缘。这些特点恰恰与 *Dissacus* 属下前臼齿相似。另外，我们再将 *Dissacus* 与 *Pachyaena* 的下前臼齿比较，可看出二者牙齿都是三角座比跟座相对侧扁，刃状跟座嵴相对靠内些。因此，从下前臼齿的结构看，下前尖无或小，以及跟座相对比三角座窄是 Hapalodectidae 科下前臼齿区别于 Mesonychidae 科的特点。从这一点考虑，与其将 ?*H.* sp. 归入 ?*Hapalodectes* 属还不如将其归入 ?*Dissacus* 属更合适些。

　　产自内蒙上古新统的 *Plagiocristodon* 属，其下前臼齿结构也有与 ?*H.* sp. 类似的情况。对其分类位置的讨论见后。

三、对 Hapalodectidae 科系统位置的讨论

　　在本文中，我们采用了 Acreodi（非肉齿目）暂作为 Hapalodectidae（软食中兽科）目一级分类单元的名称。这一名称最早是 Matthew（1909）为中兽科取的；他认为中兽是一种古老而特殊的肉齿类，将其列在他所划分的肉齿目 'Inadaptive' 这一类型中。Van Valen（1966）从中兽可能起源于踝节目的 triisodont 考虑，将其随后者移至踝节目。近年来，一些学者倾向于将中兽科从踝节目移出，单独成立一目（Acreodi），作为鲸目的姐妹类群（McKenna，1975；West，1980；Savage 和 Russell，1983）。这一建议是有道理的，也是笔者在本文采用 Acreodi 作为目一级分类单元名称的原因之一。

　　在中兽科原有的三个亚科中，软食中兽是一个分类位置有争议的类群。开始，有些学者认为它是介于 *Dissacus* 和 *Pachyaena* 之间的类型（Osborn 和 Wortman，1892）。不久，Matthew（1909）就指出，这一属仅仅根据下臼齿结构，就看出了与其他中兽的明显不同，说明它很可能代表了该科的另一不同支系。Szalay（1969）对这一类群的起源曾作过三种推测，认为最可能还是从早或中古新世的比目前已知中兽还原始的类型中分化出来。

表 2　河塘软食中兽与其他类型头骨特征比较

Table 2　Cranial features of *H. hetangensis* and selected forms

	Hapalodectes hetangensis	Mesonychids	Creodonts, compared with *Limnocyon* etc.	Miacids, compared with *Vulpavus* etc.
1. 脑颅 Braincase	大 large (d)	小 small (p)	小 small (p)	大 large (d)
2. 基颅部 Basicranium	中等 moderate long (d)	短 short (p)	中等 moderate long (d)	长 long (d)
3. 矢状嵴 Sagittal crest	低或中等 low or moderate (d)	非常高 very high (p)	高 high (p)	低 low (d)
4. 前颌骨 Premaxilla	限于吻前端 restricted to anterior portion of snout (p)	延至不到吻区长的一半 extending to less than half surface of snout (p)	延至不到吻区长的一半 extending to less than half surface of snout (p)	延至不到吻区长的一半 extending to less than half surface (p)
5. 眶下孔(管) Infraorbital foramen (and canal)	P³ 上方,长 above P³ long (p)	p³⁻⁴ 之间,长 between p³⁻⁴ (long) (p)	P³ 上方,长 above P³ (long) (p)	P³ 上方,长 above P³ (long) (p)
6. 眼眶 Orbit	前缘在 M¹ 上方 anterior border above M¹ (d)	前缘在 M²⁻³ 上方 anterior border above M²⁻³ (p)	前缘在 P⁴ 上方 anterior border above P⁴ (d)	前缘在 M¹ 上方 anterior border above M¹ (d)
7. 鼻骨 Nasal	稍向后膨大 slightly expanding posteriorly (d)	向后膨大较宽 widely expanding posteriorly (p)	适度向后膨大 moderate expanding posteriorly (p)	稍向后膨大 slightly expanding posteriorly (d)
8. 额骨(背面视) Frontal (dorsal view)	与上颌骨接触 contact with maxilla (d)	几乎不与上颌骨接触 "excluded, or nearly so, from contact with maxilla" (p)	与上颌骨接触 contact with maxilla (d)	与上颌骨接触 contact with maxilla (d)
9. 额骨的眶后突 Postorbital process of frontal	大,与颧骨连接,封闭眼眶后缘 large, forming complete postorbital bar (d)	无 absent (p)	无 absent (p)	小 small (d)
10. 眶上孔 Supraorbital foramen	有 present (d)	无 absent (p)	无 absent (p)	无 absent (p)
11. 顶骨 Parietal	明显向侧方膨大 lateral expansion (d)	无侧方膨大 no lateral expansion (p)	略向侧方膨大 less lateral expansion (p)	明显向侧方膨大 lateral expansion (d)
12. 泪骨 Lachrinal	限于眶内 confined to orbit (d)	有大的面区膨大 large facial expansion (p)	适度面区膨大 moderate facial expansion (p)	较小面区膨大 less facial expansion (d)
13. 泪骨孔 Lachrinal foramen	小,位于眶内 small, internal to orbit (p)	小,位于眶内 small, internal to orbit (p)	小,位于眶边缘 small, almost marginal (p)	小,位于眶内 small, internal to orbit (p)
14. 上颌骨 Maxilla	大,将泪骨-腭骨分开 large, excluding lachrinal-palatine contact (d)	不明 unknown	不明 unknown	不明 unknown

特征 Character	列1	列2	列3	列4
15. 眶蝶骨 Orbitosphenoid	大，伸至眶内高处 large, high in orbit (p)	不明 unknown	不明 unknown	不明 unknown
16. 腭骨 Palatine	窄，在眶内不与泪骨接触 narrow at base of orbital wall, no lachrinal-palatine contact (d)	不明 unknown	不明 unknown	不明 unknown
17. 颧弓 Zygomatic arch	完全，颧骨纤细 complete, with slender jugal (d)	完全，颧骨中等 complete, with moderate jugal (p)	完全，颧骨中等 complete, with moderate jugal (p)	完全，颧骨中等 complete, with moderate jugal (p)
18. 蝶腭孔 Sphenopalatine foramen	位于上颌骨-腭骨缝上 at maxillary-palatine suture (d)	不明 unknown	不明 unknown	不明 unknown
19. 腭孔背口 Palatine dorsal foramen	清楚，位于蝶腭孔后方 distinct, behind sphenopalatine foramen (p)	不明 unknown	不明 unknown	不明 unknown
20. 视神经孔 Optic foramen	左右两孔愈合为一大开口 Optic foramina confluent between orbits (d)	不明 unknown	不明 unknown	不明 unknown
21. 颞窝 Temporal fossa	不宽 not extensive (d)	宽 extensive (p)	宽 extensive (p)	不宽 not extensive (d)
22. 翼蝶管 Alisphenoid canal	长，开口于前破裂孔 long, anterior opening confluent with sphenoidal fissure (p)	长 long (p)	长 long (p)	长 long (p)
23. 前、后关节突 Antero- and post-glenoid process	有，发育 present, well developed (p)	有，发育 present, well developed (p)	缺前关节突，后关节突发育 anterior process absent, posterior one well developed (p)	有，发育 present, well developed (p)
24. 关节后孔 Postglenoid foramen	大 large (p)	无或小 absent or small (d)	中等 present (p)	中等 present (p)
25. 听泡 Auditory bulla	缺 absent (p)	出现在某些种类 present in some forms (d)	缺 absent (p)	缺 absent (p)
26. 镫骨动脉上枝在鼓壁出口 Exit in tympanic wall for superior ramus of stapedial artery	未定 ?present	不明 unknown	不明 unknown	不明 unknown
27. 外耳道顶部 Roof of external auditory meatus	有清楚的鼓室上隐窝 with distinct depression for epitympanic recess (d)	不明 unknown	不明 unknown	不明 unknown
28. 内颈动脉内枝 Medial internal carotid artery	可能由耳蜗表面内侧沟穿过 may conveyed in a sulcus on medial side of promontory (p)	不明 unknown	通过鼓泡与基枕骨间的沟 does not enter tympanic chamber, lies between bulla and basioccipital (p)	可能通过基枕骨前方进入听区 pass into otic depression over lip of basioccipital a little in front of jugular foramen (p)
29. 岬动脉 Promontory artery	小 small (p)	小 small (p)	小 small (p)	小 small (p)
30. 镫骨动脉 Stapedial artery	有 present	不明 unknown	小 small (p)	清楚 distinct (p)

d: 代表进步特征或可能的进步特征 derived character　　　p: 代表原始特征或可能的原始特征 primitive character

从目前已有的包括头骨在内的 Hapalodectid 的全部材料看,如本文前一节所述,它代表了一个独立的科 (Hapalodectidae)。 它与 Mesonychidae 科从头骨到颊齿都有许多显著区别,但是,两个科的下臼齿结构又是相似的;它们的下臼齿的特点,尚未见于已知的其他陆生哺乳动物中。有意义的是,古鲸类的下臼齿结构,与已知陆生哺乳动物相比,也相似于 Mesonychids 和 Hapalodectids。 但在这三个类群中,古鲸类的牙齿和头骨与中兽科的更相似;如果这二者确实有较近的关系,那么, Hapalodectidae 和 Mesonychidae 的关系可能会比原来所认为的要远些。也就是说,把 Hapalodectidae[1] 归入为 Mesonychidae 所设立的目 (Acreodi),从系统发育关系上就会成为问题,这也是笔者在本文中于目的名称前增加问号的原因。

附记　对我国古新世某些中兽分类位置的讨论

1.在我国古新统发现的一些中兽新属中, Yantanglestes 是最引人注目的属;已知包括四个种： Y. conexus, Y. datangensis, Y. feiganensis, Y. rotundus。 其中, 属型种 Y. conexus 被认为是已知最老和最原始的中兽 (Gingerich, 1981)。

Y. rotundus 原来被描述为 ?Dissacus rotundus (Wang, 1976)。 这个种依据的材料包括不完整的下颌及零散的右 P_{2-4} 和左 M_3。该种与属型种 Y. connexus 的主要区别：下臼齿下后尖不发育,跟座峰不位于正中间,正是 Dissacus 属相应牙齿的特点。因此,该种如原鉴定归入 Dissacus 属是合适的。

Yantanglestes 属颊齿最显著的特点是,上臼齿宽度大于长度;后尖大,与前尖几乎等大,两尖呈圆锥形,紧密联结。 下臼齿的下后尖特别发育,与下原尖几乎等大,并生;下前尖相对较大;由于三个尖大小相近,使下臼齿三角座呈正三角形。 Yantanglestes 上颊齿的上述特征还见于另一早一中古新世的属 Dissacusium 中,这属所依据的唯一一枚上臼齿比 Yantanglestes 更加横宽,前、后尖等大,锥形, 使其牙齿形态显得与中兽很不相同,倒与对锥兽相似。与 Dissacusium 产自同一地点的 Hukoutherium 的上臼齿也有与 Yantanglestes 和 Dissacusium 同样的特点。 这三个属牙齿的上述特征是与中兽科已知类型都不相同的。值得考虑的是,它们是否代表了中兽科的一个新的亚科。

2.根据现有资料,我国 Dissacus 属包括两个晚古新世的种： Dissacus magushanensis 和 ?D. sp. 及一个中古新世的种 D. rotundus。 D. magushanensis 的正型标本为一带有 M_2 和 M_1 跟座的残破左下颌。 这个种的大小与 ?D. sp. 非常接近,M_2 的形态结构与后者相应牙齿几乎完全相同, 两者有可能代表了同一个种,或至少是非常接近的种。如原作者指出, 它们与属型种北美中古新世的 D. navajovius 以及欧洲晚古新世的 D. europaeus 都是非常相似的。 Dissacus rotundus 在该属中是唯一 M_3 不退化的种,它的个体比其他各种都小,齿尖呈锥状。这些特点说明,它代表了 Dissacus 属目前已知最原始的种。

3.与 ?D. sp. 产自同一地点和层位的,还有 Plagiocristodon (周、齐, 1978)。 属型种 P. serratus。该种的正型标本是一段带有 P_{3-4} 和 M_1 跟座的残破左下颌。其下前臼齿三角座相对侧扁, 跟座相对较宽,有内齿缘和发育的下前尖。类似前述江西晚古新世 ?H. sp. 的情况,这些特点与 Dissacus 的下

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1) Hapalodectes 的另两特征： 上颊齿相邻牙齿间有脉管孔凹和颧弓在根部向腹侧伸, 曾作为中兽与古鲸类所共有的特征,为鲸类的中兽起源观点提供的证据 (Szalay, 1969)。 根据已发表的资料,脉管孔凹不仅存在于 Hapalodectes 和古鲸类中,还出现在一些其他化石类型 (Wyolestes, Archaeoryctes, Hsiangolestes[2], Hunanictis) 以及现生有袋类中。颧弓的特点,从 V5253 号头骨上看,是不向腹侧延伸的,因此这两特点不足以作为中兽与鲸类起源有关的证据。

2) 与河塘软食中兽产于同一地点的对锥兽新属 (Hsiangolestes Zheng and Huang, 1984) 的牙齿结构及头骨形态与对锥兽已知各属均不同。新发现的材料表明, Hsiangolestes 的牙齿结构与蒙古发现的 Bogdia, Dashzeveg and Russell, 1985 相似;它代表一早始新世的食虫类。

齿列 Denition:（接 p.174 测量数据）

Upper Dentition:

Upper dentition（上齿列）		C	P¹	P²	P³	P⁴	DP³	DP⁴	M¹	M²	M³
V5253-right	L（长）	2.0	1.3	2.8	—	—	3.0	3.0	3.0	3.0	—
（右侧）	W（宽）	1.1	0.8	0.8	—	—	2.0	2.4	3.0	3.0	—
left	L（长）	1.8	1.3	3.0	—	—	2.7	3.0	3.0	3.1	—
（左侧）	W（宽）	1.3	0.8	0.9	—	—	1.7	2.5	3.0	3.1	—
V5254-right	L（长）	—	1.8	3.8	—	—	—	—	—	—	—
（右侧）	W（宽）	—	0.8(R)	1.4(R)	—	—	—	—	—	—	—
left	L（长）	5.0	2.5	4.0	—	4.2	—	—	3.5	3.5	—
（左侧）	W（宽）	4.0(A)	1.5(A)	1.3(R)	—	3.5(R)	—	—	3.5(C)	4.4(C)	—

Lower dentition（下齿列）		C	P₁	P₂	P₃	P₄	DP₃	M₁	M₂	M₃
V5253-right	L（长）	1.5	1.3	2.5	—	3.7	3.0	3.3	3.4	3.1
（右侧）	W（宽）	1.4(R)	1.0	0.9	—	0.7	0.5	1.0	1.1	—
-left	L（长）	1.5	1.2	2.4	…	—	2.5(B)	3.0	3.1	—
（左侧）	W（宽）	1.5	0.8	0.8	—	—	0.7	1.1	1.1	—

R: 测自齿根　　measured from the root of the tooth
A: 测自齿槽　　measured from the alveolus of the tooth
C: 测自齿冠　　measured from the crown of the tooth
B: 测自齿冠基部　measured from the base of the tooth
L: 长度　　length
W: 宽度　　width

前臼齿相似,而与 *Hapalodectes* 不同。有趣的是,这块标本上残存的 M_1 的大小及跟座形态与同一地点 $?D.$ sp. M_2 的相应结构几乎完全相同(后者未保存 M_1,仅有 M_{2-3})。 因此, *P. serratus* 和 $?D.$ sp. 是否代表了同一种动物是值得注意的。 （1986 年 11 月 11 日收稿）

测量数据 单位：毫米 (Measurements, in mm)

头骨 Skull（V5253）

SL: 全长(吻前端-枕骨),Skull length (from the back of the occipital to the anterior tip of the premaxilla)
··48.5

ZAW: 颧弓宽(两颧弓间最大宽,即头骨最大宽度),Zygomatic arch width (across the widest portion of the zygomatic arches) ················ 26.2

POCW: 眶后收缩处宽, Width at the postorbital constriction ················ 7.3

TFW: 颞窝宽(颧弓宽减去眶后收缩处宽),Temporal fossa width (calculated by subtracting width at the postorbital constriction from width across the zygomatic arches)················ 18.9

TFL: 颞窝长(项嵴后端一眶上突后端), Temporal fossa length (from the most posterior point of the lambdoidal crest to the back of the supraorbital process) ················ 23.6

OCPH: 枕部高(枕骨大孔下中缘一枕骨背缘), Occipital height (from the midventral border of the foramen magnum to the dorsal rim of the occiput) ················11.7

OCPW: 枕部宽(两乳突间宽), Occipital width (at the width point of the occiput, across the mastoid)······15.0

TRL: 上齿列长(平行腭中线,最后一牙(M^2)后缘至前颌骨前缘), Tooth row length (parallel to the palatine midline, from the posterior rim of M^2 to the front of the premaxilla) ················ 23.4

ORBA: 眼眶面积,(由公式 $A=C^2/12.5664$ 求得, A: 面积, C: 圆周长) Orbit area (estimated from the circumference (C) as measured around the orbital rim)················$C=31.9$
················ $A=77.5 mm^2$

PGPCL: 关节后突至枕髁长度, Length from the back of the postglenoid process to the condyle ················11.0

下颌(右), Right mandible（V5253）

JL: 颌长(下颌髁后缘至下颌前缘), Jaw length (from the back of the condyle to the anterior tip of the mandible) ················ 35.2

COM_1: 下颌髁至 M_1 的长度, Length from the back of the mandibular condyle to the M_1 ················21.2

MAM: 下颌髁背缘至下颌角长度,Length from the dorsal surface of the condyle to the ventral border of the angular process ················5.3

MAT: 下颌髁至冠状突顶端长度, Length from the condyle to the coronoid process ················ 9.4

MFL: 咬肌窝长度(下颌髁后缘至咬肌窝最前端), Masseteric fossa length (from the back of the condyle to the most anterior point of the masseteric fossa) ················ 12.5

JH: 下颌高(在 M_1 下的骨体高) (height beneath M_1)················ 3.8

JW: 下颌宽(在 M_1 下的骨体宽) (width beneath M_1)················ 2.7

插 图 简 字 说 明

(Abbreviation for figures)

ac	aperture of cochlear fenestra	圆窗(蜗窗)
as	alisphenoid	翼蝶骨
asc	alisphenoid canal	翼蝶管
av	aperture of vestibular fenestra	卵圆窗(前庭窗)
bf	?basicapsular fenestra	基囊裂
bo	basioccipital	基枕骨
bs	basisphenoid	基蝶骨
cc	?cochlear canaliculus	?蜗水管孔
cp	caudal tympanic process of petrosal	岩骨后鼓突

ef	ethmoid foramen	筛孔
er	epitympanic recess	鼓室上隐窝
f	frontal	额骨
fcb	facial nerve canal bridge	面神经管桥
ff	foramen of facial nerve	面神经孔
fo	foramen ovale	卵圆孔
fr	foramen rotundum	圆孔
fs	facial nerve sulcus	面神经沟
hf	hypoglossal foramen	舌下神经孔
hif	hiatus fallopii	面神经岩枝裂
if	incisive foramen	门齿孔
iof	infraorbital foramen	眶下孔
j	jugal	颧骨
la	lachrymal	泪骨
laf	lachrymal foramen	泪骨孔
map	mastoid process	乳突
mf	mental foramen	颏孔
mg	magnum	枕骨大孔
mis	medial internal carotid artery sulcus	内颈动脉内侧沟
mnf	mandibular fossa	下颌窝
mx	maxilla	上颌骨
na	nasal	鼻骨
obf	orbital fissure	眶裂
oc	occipital	枕骨
opf	optic foramen	视神经孔
os	orbitosphenoid	眶蝶骨
p	parietal	顶骨
padf	palatine dorsal foramen	腭孔背口
paf	palatine foramen	腭孔
pal	palatine	腭骨
pf	piriform fenestra	梨形裂
pgf	postglenoid foramen	关节后孔
pgp	postglenoid process	关节后突
plf	posterior lacerate foramen	后破裂孔
pm	premaxilla	前颌骨
poc	paraoccipital process	副枕突
ppf	posterior palatine foramen	后腭孔
pr	promontory of cochlear	蜗岬
prs	promontory artery sulcus	岬动脉沟
ps	presphenoid	前蝶骨
sas	stapedial artery sulcus	镫骨动脉沟
sof	supraorbital foramen	眶上孔

spf	sphenopalatine foramen	蝶腭孔
sf	stapedius fossa	镫骨肌窝
sq	squamosal	鳞骨
sty	stylomastoid foramen	茎乳孔
tf	tensor tympani fossa	鼓膜张肌窝
th	tympanohyal	鼓舌突
?	foramen for superior ramus of stapedial artery	?镫骨动脉上枝孔

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THE SKULL OF *HAPALODECTES* (?ACREODI, MAMMALIA), WITH NOTES ON SOME CHINESE PALEOCENE MESONYCHIDS

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Key words   Hengdong Hunan; Early Eocene; Mesonychids; Hapalodectids Skull

Summary

Hapalodectes has long been considered as a small mesonychid specialized toward a carnivorous and piscivorous mode of life. Its rare fossil record was known from the early Eocene of North America and middle and upper Eocene of Asia. Knowledge of this genus is still restricted to two species based mainly on some fragmentary materials.

A part of the right mandible of the type species, *H. leptognathus,* was first described by Osborn and Wortman (1892), but was referred by them to *Dissacus,* and renamed as *Hapalodectes* by Matthew (1909). Szalay and Gould (1966) erected a new subfamily, Hapalodectinae, and then all known material were restudied by the former author (Szalay, 1969). No additional material of the genus has been reported since then.

The newly discovered specimens described in this paper are the first, and so far the only, cranial evidence of *Hapalodectes.* The fossils were collected from early Eocene (Ling-cha Formation), Hengdong, Hunan, during two field seasons of 1982—1983. The purpose of the present paper is to place on record the morphology of this well-preserved cranial material and to discuss briefly its significance. It is hoped that the information about the cranial morphology of *Hapalodectes* will increase our understanding of its relationship with Mesonychidae.

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SYSTEMATICS

Order ?Acreodi Matthew, 1909

   Family Hapalodectidae (Szalay and Gould, 1966), new rank

Included Genera   *Hapalodectes* Matthew, 1909, the only known genus.

Distribution   Early Eocene of North America; Early, Middle, and Late Eocene of Asia.

Emended Diagnosis   Distinctly small size; skull moderately long and narrow, with lower

sagittal and occipital crests; orbit closed; lachrimal with nearly no facial expansion; braincase large; parietal long with lateral expansion; basicranial region relatively long; three arteries (promontory, stapedial and medial internal carotid) probably present; stapedial fossa large; dental formula: $?I_3^3$, C_1^1, P_4^4, M_3^3: upper molars with acute cusps, large hypocone, and no shear; vascularized embrasure pits between the lingual parts of the upper cheek teeth; lower teeth greatly compressed transversely, with trenchant talonid heel and re-entrant groove on the anterior surface.

Hapalodectes Matthew, 1909

Type species *Hapalodectes leptognathus* (Osborn and Wortman, 1892)
Included species *H. leptognathus, H. serus,* and *H. hetangensis* sp. nov.
Distribution Same as for family.
Diagnosis Same as for family.

Hapalodectes hetangensis sp. nov.

Holotype A complete sub-adult skull and mandible, with well-preserved right and left DP^3-DP^4 and C-M^2 and left and right DP_3 and C-M_3 (IVPP cat. no. V 5253).

Hypodigm Holotype and anterior part of a skull with deep worn left M^{1-2} and roots or alveoli of the remaining cheek teeth (V 5254), from same locality as the holotype.

Locality He-tang village, Ling-cha, Hengdong county, Hunan province.

Horizon Early Eoccne, Ling-cha Formation.

Etymology Species named for He-tang village, where the fossils were found.

Specific Diagnosis Differs from the type species, *H. leptognathus* in having much smaller size, no paraconid on P_4, more developed metaconid on the lower teeth; differs from *H. serus* in having reduced parastyle and metastyle, retaining well-developed metaconid on the lower molars.

Description
Skull

The skull of *Hapalodectes* is most like that of certain primitive carnivores. It is moderately long and narrow (fig. 1). The anterior margin of the orbit is well defined by a semicircular ridge. A gap separates the semicircular ridge into upper and anterior parts. The lachrimal has nearly no expansion on the face, so that the frontal can approach the maxilla closely, which differs from the broad facial expansion of mesonychids and is much more like that in certain miacids such as Vulpayus. The lachrimal foramen is moderate sized and internal. The nasal is long, narrow and somewhat expanded posteriorly. It is less expanded than that in Mesonychidae. The premaxilla is small and restricted to the anterior part of the snout, so that the nasal is in contact with maxilla for most of the facial region. There are a pair of tiny incisive foramina behind the alveolae of the upper incisors. The maxilla is short and high, with a large infraorbital foramen above P^3, considerably in advance of the anterior border of the orbit, indicating a long infraorbital canal. The jugal bone is relatively larger and heavier than that in either miacid carnivores or mesonychids, very similar to that of recent cats. The superior branch of jugal subdivides into two branches: a posterior branch unites with the postorbital process of the frontal, closing the orbit posteriorly and separating the orbital fossa from the temporal fossa; an anterior branch extends forward, reaching the zygomatic process of the maxilla.

The inferior branch of the jugal diminishes in width to the lower border of the zygomatic process of the squamosal. The orbital fossa is large, although slightly smaller than the temporal fossa. The anterior border of the orbit is above P⁴, not behind P⁴ as in *Vulpavus,* and is more similar to that of *Viverravus* and *Felis* in this aspect.

The frontal is relatively narrow, slightly concave between superorbital crests. The postorbital process of the frontal is strongly developed and connects with the posterior superior branch of the jugal. Anteriorly, the frontal surrounds the posterior end of the nasal and extends a little forward lateral to the nasal to meet the maxilla in a transverse suture; it is not splinted between the nasals and maxillae as in modern carnivores. There are two foramina, located at the inner side, in dorsal view, of the superorbital edges of the frontal respectively in the adult individual V 5254, and continuous with a foramina above the ethmoid foramen in the orbital region. The postorbital constriction is near the posterior border of the frontal. Judged from the skull V 5253, the frontals cover the olfactory lobes and probably the anterior end of the cerebrum.

The parietal is long, comparatively narrow, and covers most of the braincase (cerebrum). The sagittal crest is very low in the sub-adult individual and moderately high in the adult, judged from the anterior end of the crest preserved in the front in V5254. The occipital crest is weak in the sub-adult. The condyles are large and well separated, with no deep fossa above and external to the condyles in V 5253 indicating an expansion of the brain. The paroccipital process is moderately slender, and projects posteroventrally.

The squamosal is large, narrow, and expands laterally to give great width of the posterior part of the skull (fig. 2). The zygomatic process of the squamosal is long, slender and meets the inferior branch of jugal in an oblique suture. The alisphenoid is large with a large expansion to give a great width to the posterior part of the temporal fossa. The orbitosphenoid is of moderate size and high in the orbital fossa. Both the basisphenoid and the presphenoid are of moderate size. The presphenoid expands laterally to form the wall of the internal nares. The orbital fissure and the foramen rotunda are at the lower border of the alisphenoid-orbitosphenoid suture. The optic foramen is large and confluent with the small ethmoid foramina in front of and above it. The frontal expands widely in the orbital fossa, forming the internal wall of the fossa. The sphenopalatine foramen and the palatine dorsal foramen lie below the point where the frontalmaxilla suture and the maxilla-palatine suture meet. The palatine has a moderate expansion in the orbital region and does not contact the lachrimal.

In the ventral view, the palatine is short and triangular-shaped. Its anterior edge extends to the position between DP³ and DP⁴. The internal nares opening are slightly anterior to the level of the posterior end of the second molar. The anterior palatine foramina are located in the palatine-maxilla suture at the level of the embrasure between DP⁴ and M¹. The posterior palatine foramina lie oppsite the posterior side of M².

The basicranial region is relatively longer than in Mesonychidae and more similar to certain creodonts and miacids (fig. 3). The glenoid fossa is transversely elongate; it is limited by a prominent postglenoid process and by a low ridge anteriorly. The hypoglossal foramina, one in left side and two in right side, are well separated from the posterior lacerate foramen. The mastoid process is slender and projects laterally. The tympanic bullae are not if any preserved in V 5253. The postglenoid foramen is large, located posterior to and close to the postglenoid process. The foramen ovale lies medial to the glenoid fossa, and the posterior opening of the rather long alisphenoid canal lies a little anterior to the foramen ovale. The epitympanic recess

is large, posteromedial to the postglenoid foramen. The promontory of the petrosal is large, and projects a little ventral to basicranial surface. Three arteries may have gone through this region. However, according to the embryological evidence proposed by Presley (1979), the internal carotid artery of modern mammals in the vicinity of the auditory capsule, lies either in a medial position (MICA) in the basicapsular groove (or fissure) or upon or lateral to the cochlear promontory (PICA). In other words, according to Presley, it is impossible to have both the medial internal carotid artery and the promontory artery present on the surface of the promontory simultaneously. However, there are apparently three grooves present on the surface of the promontory of V 5253, which is the same as that described by Matthew (1909) for the Carnivora and illustrated by McIntyre (1979, fig. 7, 8) for a restored Late Cretaceous mammal. Therefore, we temporarily keep the same interpretation for the internal carotid artery in the present paper as Matthew and MacIntyre did. The sulcus for the medial internal carotid artery is deep, rather wide, and close to the medial rim of the promontory of the petrosal. The promontory artery sulcus is narrow, extending anterior to the cochlear fenestra, thence the groove curves forward toward the piriform fenestra, but vanishe before it reaches that point. The stapedial artery sulcus is very shallow and oriented transversely; it lies in front of the cochlear fenestra. The fenestra vestibuli is small, located on the lateral side of the promontory. The fenestra cochlea is a little bigger than the fenestra vestibuli in size and is located on the posterior edge of the promontory. Lateral to the fenestra vestibuli is the facial nerve foramen and the hiatus Fallopii, which are covered by the facial canal bridge. The facial nerve sulcus is moderately deep and narrow. In front of the hiatus Fallopii, there is a shallow and small tensor tympani fossa. Posterolateral to the cochlear fenestra is the stapedial fossa, which is rather big, oval, and deep. There is a basicapsular fenestra between the basisphenoid and the promontory. Posterior to the cochlear fenestra, the caudal tympanic process of the petrosal is in contact with the mastoid process. The tympanohyal is internal and anterior to the mastoid process.

Mandible

The mandibular body is slender in V 5253 (fig. 4). The horizontal ramus of the mandible is very shallow and deepest under M_{2-3}. There is a long horizontal groove extending from under P_3 to M_3 on the medial side of the dentary. The coronoid process is large and high. The condyle is big, transversely elongated. The angular process is slender and small. The masseteric fossa is big and moderately deep. There are two mental foramina below P_1 and between, P_{2-3} respectively. The symphysis is long and loose, extending from the anterior end of the jaw to below P_2.

Dentition

The upper teeth of *Hapalodectes hetangensis* are well preserved in the holotype-a subadult individual, and fragmentary left M^{1-2} are present on V 5254, an adult individual.

There is no clear evidence of the number of roots or alveoli of the incisors in either the holotype or V 5254. The upper canine is big and oval-shaped in cross section, with a prominent anteroposterior ridge on the both sides of the crown, judged from the canine remnants. P^1 is smallest among the premolars, single-rooted and transversely compressed. It is triangular in shape in lateral view, with a single cusp. P^2 is larger than P^1 and two-rooted, with the protocone directed slightly posteriorly. DP^3 is molariform. The protocone is much lower than the paracone and metacone. The paracone is larger than the metacone and they are both transversely compressed. The parastyle and metastyle are small and low. P^3 is preserved in the holotype with only one cusp erupted from the alveolus. It is conical and big. DP^4

is molariform and bigger than DP³. The paracone and metacone are well-developed and the protocone is acute. The hypocone is well developed and crest-shaped. Both the parastyle and metastyle are the same as in the molars but a little smaller. M¹ is T-shaped, with the paracone larger than the metacone, connate and acute. The protocone is conical and high. The hypocone is lower. The parastyle and the metastyle are strongly developed, with a weak anterior cingulum present at the anteromedial side of the tooth. M² is larger than M¹. Its paracone is large and the metacone is distinct and small. Both metastyle and parastyle are more developed than in M¹. The lingual half of M² is square, with a well developed protocone and large hypocone; there is no trace of a paraconule or metaconule, and no anterior cingulum. The crown of M³ is unknown, but it is smaller than M² in size, judged from the anterior root preserved posterior to M² on the maxilla of V 5254. There are deep vascularized embrasure pits between P³ and P⁴, P⁴ and M¹, and M¹ and M², respectively.

The lower teeth are preserved only in the holotype. The canine is relatively large, slender, and is directed slightly anteriorly. The crown of P₁ is transversely compressed, single rooted. The protoconid is directed upward. P₂ is larger than P₁, double-rooted. The crown of P₂ is triangular in lateral view and transversely compressed. The protoconid is directed upward, with a low heel cusp. DP₃ is well preserved in the right mandible. It is larger than P₂, double-rooted, and molariform. The trigonid and talonid are well-developed. The protoconid is inclined posteriorly. The paraconid is lower and smaller. The talonid is relatively long, with a rudimentary cusp in the middle of the trenchant ridge of the talonid. There are small diastema on either sides of P₂. P₃, judged from the only cusps, which are formed in the alveolus, is larger than P₂. P₄, with the tip of its protoconid just erupted from the alveolus, is a huge tooth and the biggest among the lower cheek teeth. The trigonid is the highest of all of those teeth, composed of only inclined posteriorly protoconid, with no trace of a paraconid or metaconid. The talonid, with a trenchant heel, is much lower than the trigonid. The lower molars are very similar in both morphology and size. M₁ is transversely compressed. The protoconid is dominant. There is a well-preserved, small, distinct metaconid anteromedial to the protoconid. The paraconid is lower and bigger than the metaconid. There are two small tubercles below the paraconid, one is medial, the other is lateral, forming a triangular shape with the paraconid. There is a well-defined re-entrant groove on the anterior surface of the tooth. The talonid has a rudimentary cusp in the middle of the trenchant ridge. M₂ is slightly larger than and morphologically the same as M₁. The metaconid is better developed on M₂ than M₁. M₃ is bigger than either M₁ or M₂. The metaconid of M₃ is much more reduced, barely distinct. Two small tubercles below the paraconid are also reduced in M₃ and there is no distinct cusp on the trenchant talonid.

The measurements are listed in page 173—174.

DISCUSSION

1. *Hapalodectes hetangensis* is clearly smaller than the North American species, *H. leptognathus* and the Asiatic species, *H. serus*. It is especially smaller than the North American species (table 1). Besides, it is different from *H. leptognathus* in having no paraconid on P₄ (incipient development of the paraconid occurs on P₄ of *H. leptognathus*), the two small tubercles under the paraconid of the lower molars more developed, and the metaconid on the lower molars more developed, and a small cusp developed on the trenchant talonid on M₁₋₂. *H. hetangesis* is slightly smaller than *H. serus* in size, but differs from the latter in having a more developed

metaconid on the lower molars and a smaller parastyle and metastyle, the upper molars transversely wider and longitudinally narrower.

The better developed metaconid on the lower molars and better developed two small tubercles below the paraconid of the molars of *H. hetangensis* are primitive features compared with those of both *H. leptognathus* and *H. serus*.

2. The dentition of *Hapalodectes* differs apparently from those of mesonychids in having a big hypocone on the upper molars and a re-entrant groove on the lower molars. The cranial features of *Hapalodectes* show greater differences from those of Mesonychidae as listed in table 2. The major differences are summarized as following:

(1) The orbit is closed and located more anteriorly in Hapalodectidae; it is open, and more posterior in Mesonychidae;

(2) The lachrimal has nearly no facial expansion in Hapalodectidae; it has a large area of facial expansion in Mesonychidae;

(3) The frontal is in contact with the maxilla in Hapalodectidae; it is excluded, or nearly so, from contact with the maxilla in Mesonychidae;

(4) The braincase is large with lateral expansion of the parietal in Hapalodectidae; it is small, with a flat parietal in Mesonychidae;

(5) The basicranium region is relatively longer in Hapalodectidae; it is shorter in Mesonychidae.

Among the above differences, (1) has not been seen in Mesonychids or archaeocetes. Differences (2)—(5) of Hapalodectidae are very similar to those of certain primitive carnivores, such as *Vulpavus*; this suggests that Hapalodectids had a more progressive miacid-like skull. Matthew (1909) noted that the increase in brain size is the underlying cause of numerous changes in the proportions and the arrangement of bones of the entire skull, and suggested that the early carnivores had a more elongate braincase. On the contrary, mesonychids had a short braincase. More recent synthesis (Novacek, 1980, 1985; Radinsky, 1977) of cranial characters of the eutherian mammals has advanced our understanding of evolution of the nervous system; certain conclusions support some of Matthew's earlier interpretations. Whether or not Matthew's interpretation will eventually be proved correct, it is quite clear that the proportions and arrangement of bones of the elongate skull are very different from those of the short skull of mesonychids. In terms of the same features of the skull that are shared by the ancient carnivores and hapalodectids, it is clear that hapalodectids had an elongate type of skull, more progressive than that of mesonychids. The palatine and maxilla in the orbital fossa of hapalodectids also show more progressive characters, as shown in table 2, which may also be correlated with brain expansion.

Based on the dentition and the cranial characters of the Hapalodectidae, it is apparent that Hapalodectidae is specialized toward a very different mode of life from the Mesonychidae and should represent a distinct family.

In contrast with the more progressive braincase of the primitive carnivores, the ear region of Hapalodectidae retains a much more primitive condition. The main differences of the ear region between Hapalodectidae and Mesonychidae are:

(1) The tympanic bulla is absent (or loosely contact with the petrosal in young animal) in Hapalodectidae and present in some Mesonychids;

(2) The postglenoid foramen is still present in Hapalodectidae and absent in Mesonychidae;

(3) Three arteries are preserved in Hapalodectidae and not in Mesonychidae;

(4) Exit in the tympanic wall for the superior ramus of the stapedial artery is probobly present in Hapalodectidae and absent in Mesonychidae;

(5) Promontory is large but flat in Hapalodectidae and convex in Mesonychidae.

3. There have been several newly described hapalodectids since the first genus, *Hapalodectes*, was reported; these include *Lohoodon, Plagiocristodon, Metahapalodectes* and *?Hapalodectes* sp.

Lohoodon from the early late Eocene of Lushi, Henan province, was first described as *Hapalodectes lushiensis*, based on an isolated right M₃ (Chow, 1965); it was considered as an unnamed new genus of Hapalodectine by Szalay (1969); and erected a new genus later on (Chow et al., 1975).

Metahapalodectes was based on several isolated teeth, from the upper Eocene of Mongolia (Dashzeveg, 1976) (type species *M. makhchinus*); It is very close to *Lohoodon lushiensis* both in morphology and size, according to the original description and illustration and it may be referred to the same genus with the latter.

These two genera are much bigger in size than *Hapalodectes* and were assigned to the Hapalodectidae mainly based on dental characters, i.e., transversely compressed lower molars. However, it seems that the re-entrant groove of the lower molars in more significant character for Hapalodectidae, which does not occur in Mesonychidae. Only use of compressed transversely teeth as a generic character for *Hapalodectes* (or other genera) is in fact an unstable base of the classification because the degree of the compression of the teeth is always relative and change with the size. The lower molars of the both *Lohoodon* and *Metahapalodectes* do not have the re-entrant groove in the anterior surface of the lower molars. From this point of view, they might be assigned to Mesonychidae.

?Hapalodectes sp. from the upper Paleocene of Jiangxi province (Zhang et al., 1979) was based on a fragmentary mandible with ?P₃ This mandible is close in size to that of *Hapalodectes leptognathus*. However, the only preserved tooth, which looks more like a P₄, of this tiny species is much bigger than that of *H. leptognathus* and has a fully developed paraconid, which is a character present in the premolars of Mesonychidae. Besides, it is necessary to point out here that *?H.* sp., as well as *Plagiocristodon, vere* originally assigned to the Hapalodectidae primarily to emphasize the small size compared with other mesonychids, plus the transversely compressed teeth. However, in comparing in detail the premolars of these two species with the type species of *Hapalodectes*, it is found that the teeth transversely compressed in *?H.* sp. and *Plagiocristodon* are compressed in a different way than in *Hapalodectes*. The lower premolars of the former two were more compressed in the trigonid and relatively wider in the talonid, with a distinct cingulum on both the lateral and medial side, which is characteristic of *Dissacus*. The lower premolar of *Hapalodectes* was compressed in the talonid, with no any trace of a cingulum, and is relatively wider in the trigonid. Therefore, it seems *?H* sp. should not be considered a large *Hapalodectes*, but rather a small mesonychid.

THE SYSTEMATIC POSITION OF HAPALODECTIDAE

Hapalodectes has a re-entrant groove on the front surface of the lower molars and a prominent hypocone on the upper molars, which do not occur in mesonychids. The cranial morphology of a young animal of *Hapalodectes*, described in this paper, shows certain important differences from mesonychids, indicating they are specialized toward a very different mode of

life and representing a distinct family.   However, the lower molars of *Hapalodectes* are similar to those of mesonychids, the only character shared by Hapalodectidae and Mesonychidae.   It is more significant that this character also appears in the lower molars (with "simple keeled talonid", Gingerich, 1983) of the archaeocete whales, which so far as we know, does not occur in other mammals.   Recent research suggests that the teeth and skull of the archaeocetes (such as *Pakicetus, Protocetus* etc.) resemble those of mesonychids.   From the view of this point, the terrestrial ancestral form of the whale might have more close relationship to Mesonychidae than to Hapalode ctidae".   If so, the relationships between Hapalodectide and Mesonychidae should be more remote than originally thought.

NOTES ON SOME CHINESE PALEOCENE MESONYCHIDS

1.   *Yantanglestes* Ideker and Yan, 1980, is one of the most notable Paleocene mesonychids from China.   It includes four species: *Y. connexus* (Yan and Tang, 1976), *Y. dantangensis* (Wang. 1976), *Y. feiganensis* (Chow et al., 1973), and *Y. rotundus* (Wang, 1975).   The type species of the genus, *Y. connexus,* was considered the oldest and the most primitive mesonychid (Gingerich, 1981).   *Y. rotundus* was originally described by Wang (1975) as ?*Dissacus rotundus,* based on the incomplete lower jaw and separated right P_{2-4} and left M_3.   It differs from the type species, *Y. connexus,* in having a much more reduced metaconid, laterally located trenchant edge of the talonid and compressed teeth, and is similar to *Dissacus* in these aspects.   Therefore, *Y. rotundus* should be re-assigned to the genus *Dissacus* (Li and Ting, 1983).

Yantanglestes, as well as *Hukoutherium* and *Dissacusium,* are different from all known mesonychids in having a very connate, conical paracone and metacone, the width of upper molars greater than the length, and the metaconid of lowers much more developed.   The characters mentioned above are shared only by these three genera among all known mesonychids.   So, it might be worth notice if possible they represent a different group from the mesonychines at the subfamily level.

2.   The genus *Dissacus* from China known by us includes two late Paleocene forms (*D. magushanensis* from the Shuang-ta-si Formation, Anhui province and ?*D.* sp. from Nao-mu-gen Formation, Inner Mongolia) and one middle Paleocene form, *D. rotundus,* from the Zao-shi Formation, Hunan province.   The two late Paleocene species are very close in both morphology and size.   They are close to *D. navajovius* and *D. europaeus* as originally described.   *D. rotundus* differs from those species in having smaller size, unreduced M_3, and more conical cusps; it may

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1) The family Hapalodectidae has been thought to represent descendents of an aquatic group of mesonychids that gave rise to the archaeocete whales, based on the deeply vascularized embrasure pits between the upper cheek teeth, and the zygomatic arches turned ventrally at their point of origin on the maxilla, a character shared by hapalodectid and the ealiest archaeocete whales (Szalay, 1969). It was found recently that the vascularized embrasure pits appeared not only in these two forms, but also in some other forms, e.g. *Wyolestes. Archaeoryctes, Hunanictis, Hsiangolestes*[2] and even the living oppossum.   The zygomatic arches do not turn ventrally in the specimen V5253. Therefore, it seems that these two characters are questionable as derived characters shared by Hapalodectidae and archaeocete whales.

2) The recently published new genus of Didymoconidae, *Hsiangolestes* Zheng and Huang. 1984, differs from Didymoconids in both teeth and cranial morphology. Judged from newly collected materials, it is slighly similar morphologically to *Bogdia* Dashzeveg and Russell, 1985 from the middle Eocene of Mongolia and represents an early Eocene insectivore.

represent the most primitive *Dissacus* known.

3. The genus *Plagiocristodon* was first described by Chow and Qi (1979), based on the left mandible with P_{3-4} and the talonid of M_1 from the same quarry where ?*D.* sp. was found. The size and talonid of M_1 of *Plagiocristodon serratus* are the same as (or nearly so) those of M_2 of ?*D.* sp; it is possible that *Plagiocristodon serratus* and ?*D.* sp. represent the same animal.
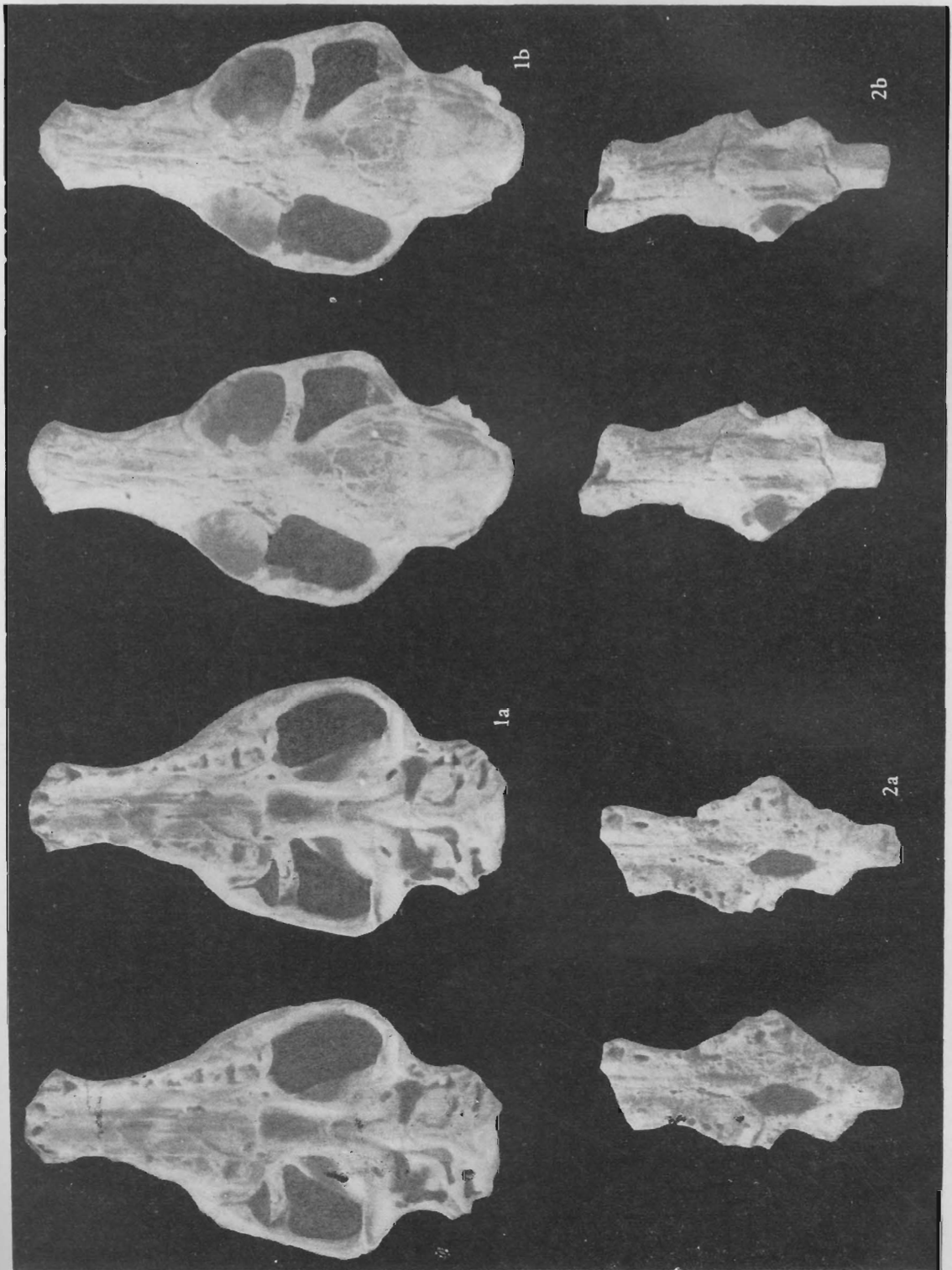
河塘软食中兽 (*Hapalodectes hetangensis* sp. nov.)

1a. 头骨腹面 Ventral view of skull, 1b. 头骨背面 Dorsal view of skull, V5253, ×1.5;　2a. 头骨腹
面 Ventral view of skull, 2b. 头骨背面 Dorsal view of skull V5254, ×1
均为立体照片 All stereophotographs
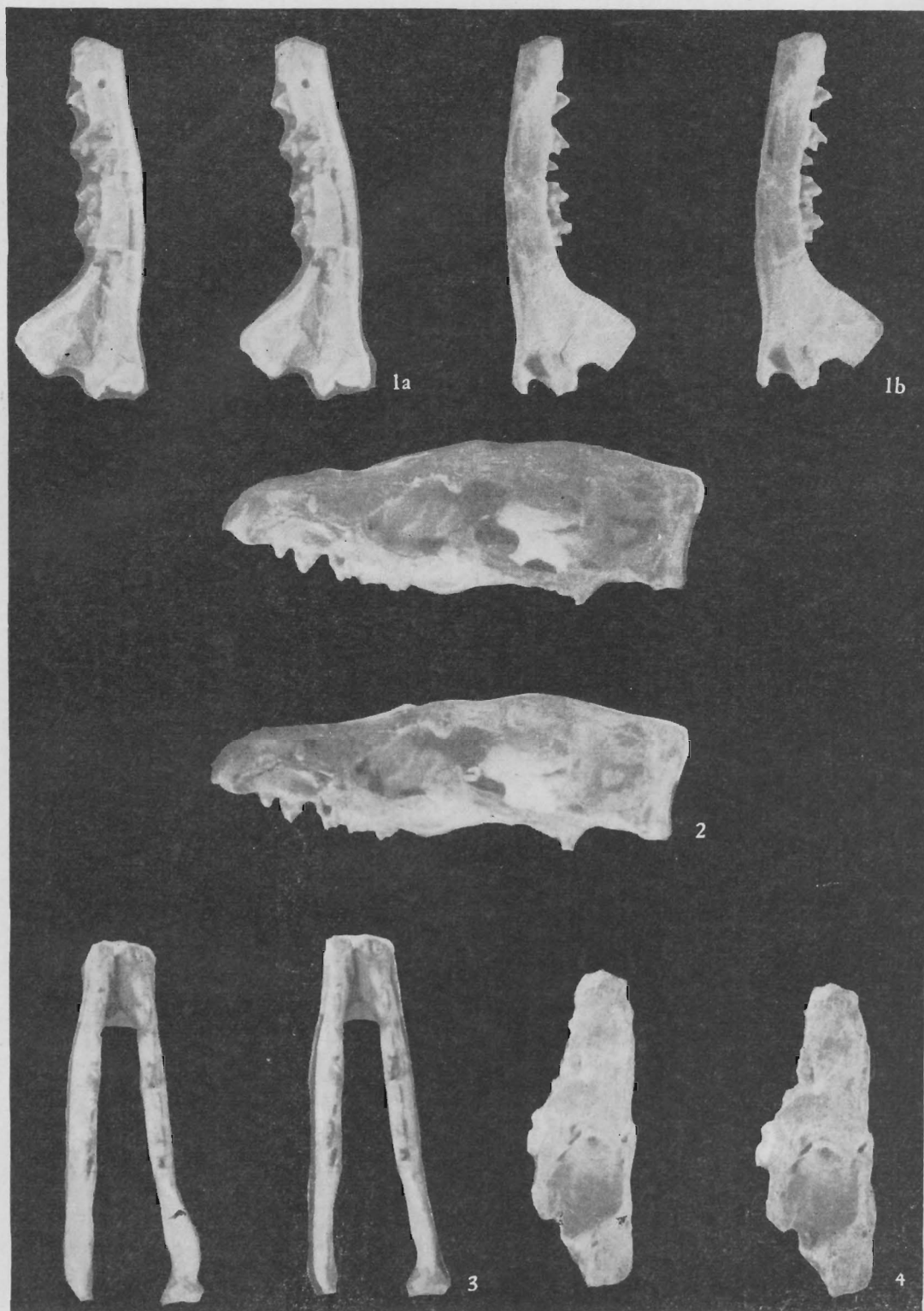
河塘软食中兽 (*Hapalodectes hetangensis* sp. nov.)

1a. 右下颌外侧 Labial view of right mandible, 1b. 右下颌内侧 Lingual view of right mandible;
2. 头骨侧面 Lateral view of skull; 3. 下颌嚼面 Occlusal view of mandible, V5253, × 1.5; 4.
头骨侧面 Lateral view of skull, V5254, ×1
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