

斯氏黄河猴(哺乳动物纲, 灵长目)

较完整下颌骨的发现¹⁾

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摘要 新发现的下颌骨说明斯氏黄河猴下齿式为 2?, 1, 3, 3。p2 为双根齿, 其前后有短的齿隙; p3 具有低小的后跟; p4 未臼齿化, 无下前尖, 有初始的下后尖, 在较大的跟盆上, 有明显的下次尖和很小的下内尖?; m1 下前尖小, 有些前后收缩(与 *Rencunius zhowi* 比较), m3 下次小尖不如正模发育。下颌骨联合部倾斜, 不愈合。黄河猴的下臼齿在形态上与西瓦兔猴亚科和原始类人猿——渐新猿亚科有许多共同点, 但上臼齿形态差异显著。黄河猴类可能出自亚洲的 cercamoniine 形的兔猴形灵长类。

关键词 山西垣曲, 始新世, 黄河猴, 下颌骨

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黄河猴是我国最早发现的始新世灵长类, 产于山西省垣曲盆地“河岸剖面”(“River Section”)或第一地点(Lok. 1), 即现在的古城镇寨里村东土桥沟。最初, 由师丹斯基(Zdansky, 1930)研究, 订名为斯氏黄河猴(*Hoanghonius stehlini*), 标本仅为带两个臼齿的一段下颌骨和一单个的上臼齿。他认为其下颊齿与某些假熊猴类中的 *Smilodectes* 相似, 而上臼齿则与始镜猴类的 *Hemiacodon* 和 *Washakius* 相近, 因而以为黄河猴是一类分类位置未定的灵长类(*Primates incertae sedis*)。在此后半个多世纪的研究中, 意见也不一致, 其分类位置一直未能确立。在较早的论文中通常将其归入始镜猴科(Omomyidae)(Hill, 1955; Romer, 1966 等)。吴汝康和周明镇(Woo and Chow, 1957)研究同一盆地河南渑池县任村附近的 4 块标本时, 也将黄河猴及与其形态相近的标本归入始镜猴类。近 20 年来, 黄河猴一般被归入兔猴科(Adapidae, 广义)(Szalay, 1974; Gingerich, 1976, 1977; Rasmussen and Simons, 1988), 也有人认为与马达加斯加现生的侏儒猴类(chirogoleids)有关(Schwartz, 1986)。由于其与早期类人猿(anthropoids)中的渐新猿(*Oligopithecus*)在下颊齿上的某些类似性, 以至有人相信或怀疑黄河猴可能与类人猿起源有关(Gingerich et al., 1994 等)。这样, 黄河猴的研究不再限于其自身的系统位置问题, 而是涉及类人猿起源的重大问题。

对黄河猴的分类位置认识相差这样大, 其主要原因是材料不全。近几年, 我们在垣曲

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盆地连续进行野外考察,找到珍贵的曙猿(*Eosiamis*)和其他哺乳动物标本,其中包括黄河猴的不完整的颌骨及零散的牙齿。幸运的是在最近的发掘中,在斯氏黄河猴正模产地(寨里)发现了一个近于完整的下颌骨标本,这是黄河猴建属以来发现的最好材料。这件标本不仅使我们了解到许多前所不知的黄河猴形态方面的信息,而且对解决黄河猴的分类位置以及它与早期类人猿的关系很有帮助。

1 标本记述

灵长目 Primates Linnaeus, 1758

兔猴形次目 Adapiformes Hoffstetter, 1977(Szalay et Delson, 1979)¹⁾

西瓦兔猴科 Sivaladapidae Thomas et Verma, 1979

黄河猴亚科 Hoanghoniinae Gingerich, Holroyd, et Ciochon, 1994

斯氏黄河猴 *Hoanghonius stehlini* Zdansky, 1930

(图1; 图版I)

正模 具m2~3的左下颌骨(瑞典乌普萨拉大学古生物博物馆,无编号)。

新增标本 左下颌骨,存有c~m3(IVPP V10220)。

产地与层位 山西垣曲古城镇寨里村东土桥沟;河堤组寨里段,中始新世晚期。

描述 在新发现的斯氏黄河猴左下颌骨上,存留c~m3(IVPP V10220)。下颌骨比较细长,m1处高为7.2mm,联合部斜,向后延伸到p2后齿根下方。有两个颏孔,分别在p2和p4前齿根的下方,前颏孔较大。下门齿未保存,推测有2颗门齿,下齿式可能为2?,1,3,3。下犬齿已几乎从齿槽中脱落,呈锥状,稍向后弯曲,外侧面浑圆,内侧面较平坦,但有微突的中隆自顶端向下延伸。犬齿前后侧有纵棱,后侧纵棱较直,前棱则弯向内侧基部。三颗下前臼齿,都为双根齿。p2侧扁,侧面呈三角形,主尖高锐,从顶端分别向前向后伸出棱脊,前棱较短较陡,后棱较长较缓。其后端基部有一小跟尖,与内齿带一起形成很小的后跟,内齿带弱但清楚。p2前后似有短的齿隙。p3与p2相似,但较大,前棱和后棱几乎等长,后跟稍明显,后跟尖清楚。p4三角座由大的下原尖和初始的下后尖组成,下前脊向前下方延伸,与内齿带前面部分连接,形成窄小的盆状构造。下后脊向后内方斜伸,与下后尖相连。下后尖很小,位于下原尖后内方。由后齿带围成的跟盆明显地比p3大,跟盆后缘中部有小尖(下次尖),在后内角有一很小、但比较清晰的小尖(下内尖?)。

下臼齿列(11.8mm)稍长于下前臼齿列(9.7mm),牙齿比较延长(与*Oligopithecus*比较),冠低,下三角座比下跟座稍高,也较窄。m1三角座不如m2和m3那样前后收缩,下前脊先向前内方延伸,后拐向下前尖。下前尖小但清晰,位于下后尖的前外方。下后尖较强,与下前尖之间有一较宽阔的齿谷,使三角凹向内开放。下跟座较延长,斜脊伸达下原尖的后壁,下次凹较浅,但比*Oligopithecus*的深。下次尖后棱延至牙齿的后内角,与下次小尖相连。下次小尖似比下内尖稍大,下内尖也在牙齿的后内角,两尖之间只有很窄但很清楚

1) Adapiformes一词在Szalay和Delson(1979)的著作中写的是新建的分类单元,但在此之前Hoffstetter (1977)文章中已经使用这一词,且内涵相近(Godinot, 1998)。

的齿谷, 有点与云南中新世的 *Sinoadapis* 的相应部位类似。在三角座上唇侧齿带明显, 在跟座上则很弱, 后齿带存在, 从下次小尖后方下降到下次尖的基部。 m_2 跟座与 m_1 相似, 但三角座前后明显收缩, 下前尖退化, 下前脊先向前内方延伸, 后拐向后内方, 使三角座外形呈长方形。下后尖与下前脊之间有齿谷相隔, 三角凹向舌侧开放。唇侧齿带不如 m_1 发育。 m_3 三角座与 m_2 近似, 但下前脊较短。跟座窄长, 下次小尖大, 向后突出, 在新增标本上不如正模上发育。下内尖不大, 呈扁锥状, 与下次小尖之间有弱棱相连。测量见表 1。

表1 测量

Table 1 Measurements of lower teeth of *Hoanghonius stehlini* Zdansky, 1930 (mm)

	c		p2		p3		p4		m1		m2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
V10220	2.2?	2.2	2.1	1.4	3.0	1.9	3.4	2.3	3.9	2.8	4.0	3.0	4.6	2.7
Holotype											4.0	3.4	4.6	2.8

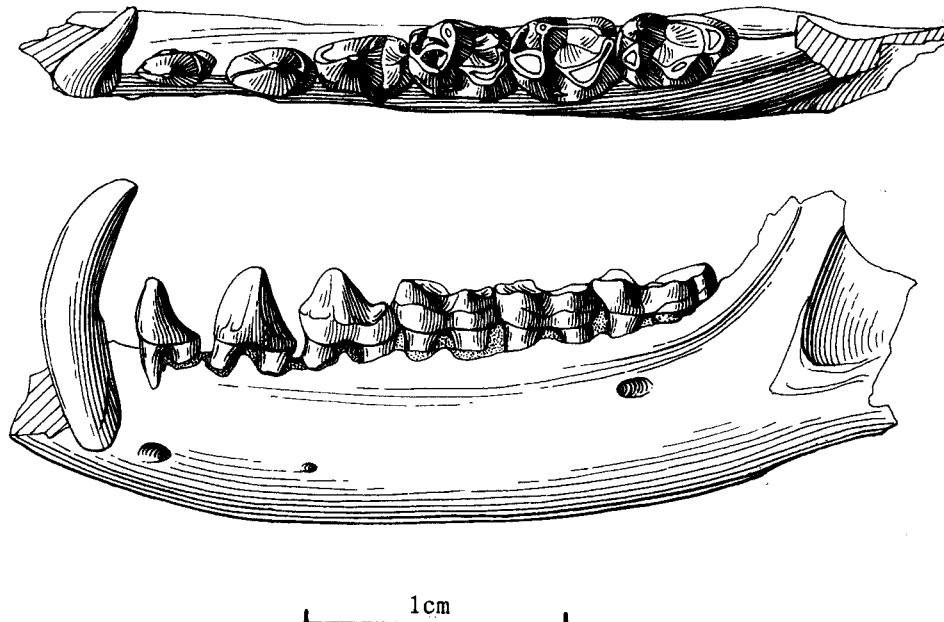


图1 斯氏黄河猴, 存 c~m3 的左下颌骨(IVPP V10220)冠面视和颊面视

Fig.1 *Hoanghonius stehlini* Zdansky, 1930, occlusal and labial views of left lower jaw with c~m3 (IVPP V10220)

2 比较与讨论

新采的下颌骨与斯氏黄河猴的正模出自同一地点, 牙齿尺寸和形态大致相同(见表 1), 应是同一种灵长类。新增的下颌骨标本上的 m_3 下次小尖不如正模发育, 可认为个体差异。同一盆地的任村猴(*Rencunius*), 除层位较低外, 在牙齿形态上也有明显的差别。任村猴 p_4 后跟小, 也较简单, 只有一个后跟尖; m_1 的下前尖较大, 三角座几呈三角形, 下后

脊很弱，斜脊伸向下原尖的中部，形成较深的下次凹； m_2 和 m_3 或有很小的下前尖 (*R. zhoui*)，或有弱棱连接下前尖与下后尖 (*R. wui*)， m_1 和 m_2 跟凹显浅，下次小尖和下内尖呈低钝的丘形，两尖之间的齿谷宽阔； m_3 下次小尖相对于正模较小，第三叶也不大发育。

黄河猴分类位置在历史上有不同看法，但近 20 年来，经过许多学者深入的研究，大多认为它是一种兔猴形灵长类。Gingerich(1976, 1977)率先指出 *Hoanghonius stehlini* 的上臼齿可与兔猴形灵长类 *Periconodon* 和 *Protoadapis* 相比较，其下臼齿则与原始类人猿 *Oligopithecus* 相近。虽然也有人将黄河猴归入始镜猴科 (Omomyidae) 或其他类群 (Szalay and Delson, 1979; Schwartz, 1986 等)，但在 Rasmussen 和 Simons(1988) 将黄河猴上、下臼齿与其他原始灵长类进行对比后，黄河猴分类位置基本得以确立。

Zdansky(1930) 认为黄河猴的上臼齿类似北美始新世的始镜猴 *Washakius* 和 *Hemiacodon*。此后，有些学者将其归入始镜猴科中的始镜猴亚科 (Omomyinae) (Hill, 1955)，或归入悬猴亚科 (Anaptomorphinae) (Woo and Chow, 1957 等)，但都没有很详细的说明。黄河猴的上臼齿相当短宽，不像大部分兔猴类那样窄长，而始镜猴类常具有这样短宽的上臼齿。但黄河猴和始镜猴类形成上臼齿短宽的原因是不同的。黄河猴是由于次尖和围尖的发育形成横宽的上臼齿，但其三角凹呈半圆形，原尖并不向舌侧位移；而始镜猴类的原尖向舌侧位移，形成三角形的三角凹，使牙齿显得横宽。因此，横宽的上臼齿不能作为将黄河猴归入始镜猴科的依据，相反，窄长的三角座，原尖的位置，完全的内齿带以及整个牙齿的结构，尤其是下颊齿形态，可认为是一种兔猴形灵长类，并可与亚洲中新世的西瓦兔猴类联系在一起，归入西瓦兔猴科。

黄河猴亚科 (*Hoanghoninae*) 是由 Gingerich 等 (1994) 建立，仅包括 *Hoanghonius* 和 *Rencunius* (吴汝康、周明镇, 1957; Gingerich *et al.*, 1994; 童永生, 1997) 两属。Gingerich 等在建立亚科时指出，黄河猴类不同于其他兔猴形灵长类在于上臼齿舌侧齿带上有发育的次尖和围尖，下臼齿后内角下次小尖和下内尖很发育，并呈孪生状。新材料的发现增加了一些可区别同时期的兔猴形灵长类的性状： p_1 缺失（与狭义的兔猴科和大部分假熊猴类 (notharctids) 不同）， P_4 和 p_4 未臼齿化（与狭义的兔猴科不同）， m_1 下前尖清晰， $m_2 \sim 3$ 下前尖退化，三角座前后收缩，呈长方形（与 Northarctidae 科区别）。另外，上臼齿舌侧齿带连续，无后原尖褶 (postprotocone-fold, 也有人称 *Nannopithex*-fold)，也可用来区别同时期的假熊猴。上臼齿中附尖的出现，也与狭义的兔猴科不同。

近来，Ducrocq 等 (1995) 记述了产于泰国 Krabi 盆地始新统中的一种灵长类化石——*Waileka orientale*，认为是一种类似 *Oligopithecus* 的原始类人猿。原作者所指出的与 *Oligopithecus* 的类似性，其实也可在黄河猴和西瓦兔猴类 (sivaladapines) 的下臼齿上见到，这一点在 Godinot(1998) 和齐陶、毕丛山 (Qi and Beard, 1998) 的文章中已经指出。从 $m_2 \sim 3$ 的三角座和跟座较浅来看，更像始新世的黄河猴类的下臼齿，因此，*Waileka* 似可归入黄河猴亚科或可认为是与黄河猴类密切相关的种类。Qi 和 Beard(1998) 最近记述了广西百色盆地一种始新世广西猴 (*Guangxilemur*)，也归入到西瓦兔猴科，其上臼齿也具有与黄河猴相似的次尖和围尖。现在看来，牙齿形态和黄河猴类似的灵长类在亚洲始新世分布相当广泛，也很分化，除黄河猴外，还有 3 属：*Rencunius*、*Waileka* 和 *Guangxilemur*。其实，在泰国 Krabi 盆地始新统中还发现一颗类似 *Hoanghonius* 的 m_2 的下臼齿 (Suteethorn *et al.*,

1988), 这颗牙齿虽然比较大, 从形态看有可能亦是一种类似 *Hoanghonius* 的灵长类。

南亚中新世发现的 *sivaladapis* 和 *Indroloris* 以前曾归入懒猴科 (Lorisidae), 现在都认为是兔猴科 (Adapidae) 的成员。80年代记述的 *Sinoadapis* (吴汝康、潘悦容, 1985; 潘悦容、吴汝康, 1986) 也被归入兔猴科。Thomas 和 Verma (1979) 曾为南亚的两个属建立了西瓦兔猴亚科, 以此与欧亚和北美大陆早第三纪的兔猴化石相区别。近年, 这个亚科又被提升为科——Sivaladapidae (Groves, 1989; Tattersall *et al.*, 1988; 童永生, 1997; Godinot, 1998; Qi and Beard, 1998), 并认为亚洲始新世的黄河猴亚科是西瓦兔猴亚科 (包括 *Sivaladapis*、*Indroloris* 和 *Sinoadapis*) 的祖先类型, 但不是后者的直接祖先 (童永生, 1997)。垣曲盆地始新世中期的 *Rencunius* 和 *Hoanghonius* 之间的某些进化趋势, 在中新世的西瓦兔猴亚科也有反映, 如下三角凹、下跟凹和三角凹增深, 下次小尖增大, 上臼齿附尖进一步发育, 下次小尖和下内尖之间的齿谷增深等。*Guangxilemur* 的上臼齿的形态介于黄河猴和西瓦兔猴之间, 进一步说明黄河猴类和西瓦兔猴类 (*sivaladapines*) 之间有着较密切的亲缘关系。黄河猴类和西瓦兔猴类的区别还在于下颌骨联合部不愈合 (在西瓦兔猴类中出现愈合), 上臼齿有次尖和围尖, 前脊和后脊直接与前尖和后尖舌面相连; 小尖清楚; p2 为双根齿, p4 臼齿化程度较低, 下臼齿下次小尖与下内尖间的齿谷相对浅 (*Rencunius*), m1 三角座相对延长。西瓦兔猴科的定义还没有正式描述过。当初, Thomas 和 Verma 建立西瓦兔猴亚科时定义如下: 小型的亚洲裸鼻猴类 (*Strepsirhini*), 齿式为 2133/ 2133。P4/ 4 很臼齿化, 门齿和犬齿不呈梳状齿; 上臼齿缺少次尖, 下臼齿的下次小尖发育显著, 齿尖锐, 但不高。至今, 西瓦兔猴科未发现头骨和头后骨骼, 以前只在 *Sivaladapis* 和 *Sinoadapis* 中有比较完整的下颌骨, 现在 *Hoanghonius stehlini* 较完整的下颌骨的发现似可进一步了解西瓦兔猴科的一些特征: 颊齿低冠或适度高冠; 门齿呈抹刀状 (Gingerich and Sahni, 1984), 犬齿大, P1/ 1 缺失, p2 在中新世种类中为单根齿, 在始新世种类中为双根齿; 在黄河猴亚科中 P4/ 4 未臼齿化, 但在西瓦兔猴亚科中则臼齿化; m1 三角座相对延长, 下前尖比较清楚, 而 m2~3 的下前尖退化, 三角座前后收缩, 常形成封闭的长方形凹盆; m1~2 下次小尖舌位, 与下内尖孪生。上臼齿三角凹呈半圆形, 附尖从弱 (*Rencunius*) 变强 (*sivaladapines*), 舌侧齿带完全。下颌骨细长, 吻部向前倾斜, 在始新世属中联合部不愈合, 在中新世属中出现愈合。

黄河猴在下颊齿上与埃及早期类人猿的相似性早在 20 多年前已引起人们的注意。Gingerich (1977) 虽然没有详细讨论黄河猴与渐新世早期 *Oligopithecus* 相类似的性状, 但图示了两者下臼齿之间的相似性。Szalay 和 Delson (1979) 也指出了其下臼齿与埃及标本和南亚中新世西瓦兔猴之间的相似之处。详细列举了这两种动物下臼齿间的相似点的学者是 Rasmussen 和 Simons (1988), 他们列表说明渐新猿与其他灵长类异同时, 其中列举了下臼齿 7 项性状 (m1~2 有下次小尖, 下次小尖与下内尖孪生, m2~3 下三角座前后收缩, m2 缺少下前尖, 下后尖前棱明显, 无下后附尖, 臼齿釉质层不粗糙), 在与之相比较的早期灵长类中只有黄河猴与渐新猿完全相同。Gingerich 等 (1994) 也就此得出结论: “黄河猴在形态上和时间上不得不和与类人猿起源相关的始新世祖先联系在一起”。

近年, 非洲及其邻近地区的始新世和渐新世哺乳动物群调查广泛展开。北至阿尔及利亚, 南达安哥拉, 东起阿曼, 西临大西洋的塞内加尔的广大地区内已发现十多处早第三

纪早期类人猿化石地点(Simons 等, 1994; Godinot, 1994 等)。当然, 最具代表性的、研究程度最高的还是埃及的 Fayum 地区, 除采集到早渐新世哺乳动物化石外, 还发现始新世晚期的类人猿化石(L-41地点)¹⁾: *Catopithecus browni*, *Proteopithecus sylviae*²⁾ (Propriopithecidae), *Serapia eocaena* (Parapithecidae) 和分类位置难以确定的 *Plesiopithecus teras*³⁾ 和 *Arsinoea kallimos*⁴⁾ (Simons, 1989, 1990, 1992, 1995)。其中, *Catopithecus browni* 只有两个前臼齿, 下臼齿形态与渐新猿的下臼齿很相似, Simons(1989)将 *Oligopithecus* 和 *Catopithecus* 归入新亚科——渐新猿亚科(Oligopitheciniae)。*Catopithecus* 与渐新猿一样, 在下颊齿形态上与黄河猴有相似点, 在上臼齿上的区别则比较明显。黄河猴新材料的发现似乎进一步说明了其与非洲原始类人猿之间的差异。黄河猴具有 p2(渐新猿类则无), p3 后跟盆小(与 *Catopithecus* 比较), p4 跟盆不大, 但有明显的后跟尖, m3 下次小尖增大, 下颌骨联合部不愈合, 水平支较浅等。而非洲原始类人猿在下颊齿上与黄河猴和其他西瓦兔猴类的相似性, 即下三角座前后收缩和下次小尖与下内尖孪生, 也不能不引起注意。

对黄河猴与渐新猿亚科下臼齿之间的相似性可以有两种解释, 一种可能是趋同现象, 但目前也不能完全排除另一种可能性, 即其间有较接近的亲缘关系。有利于前一种可能性是黄河猴类和渐新猿类在齿式、上臼齿和下颌骨之间存在非常显著的差异, 同时, 近来在非洲早第三纪地层中发现不少灵长类化石, 或许渐新猿起源与同一大陆的灵长类有关。对第二种可能性有利的证据除下臼齿相似性外, 还在于始新世后期非洲和亚洲哺乳动物已有交流的证据。如北非早渐新世 Fayum 动物群中的鬣齿兽类(hyaenodontids)和石炭兽类(anthrocotheriids)可能与亚洲始新世种类有关(Simons, 1968; Rasmussen et al., 1992), 甚至, 有人将垣曲盆地白水发现的石炭兽化石归入到北非属(*Bothriogenyx*) (徐余瑄, 1962; 王择义和胡长康, 1963; Russell and Zhai, 1987; 童永生, 1989; Wang, 1992)。又如, 在亚洲和非洲早第三纪地层中都发现眼镜猴形灵长动物(Tarsiiformes), 在 Fayum 早渐新世地层中发现非洲眼镜猴 *Afrotarsius* (Simons and Bown, 1985), 在中国的中始新世地层中发现两种眼镜猴: 始新眼镜猴 *Tarsius eocaenus* (Beard et al., 1994) 和塔氏黄河眼镜猴 *Xanthorhysis tabrumi* (Beard, 1998)。目前这些眼镜猴形灵长类之间的系统关系还不清楚, 归入眼镜猴形次目也缺少具有齿梳(tooth comb)的下颌骨实证, 因为至今尚未在下第三系发现带齿梳的灵长类化石。但两大洲类似眼镜猴的下颌骨的发现或许有利于始新世中、晚期亚洲和非洲的哺乳动物有过交往的假设。这些间接的证据也有利于黄河猴类与非洲的渐新猿类有关的设想。当然, 在已知的非洲早第三纪灵长类中, 似乎在下臼齿形态上还没有比黄河猴类更接近渐新猿类的类群, 这一点也有利于后一种设想。虽然

1) 据 Kappelman 等(1992)古地磁测定, L-41 地点化石层沉积时期相当于 15 反向极性时, 年龄为 35.56Ma~35.94Ma。

2) *Proteopithecus sylviae* 新近发现的下颌骨表明它具有 3 个前臼齿, 与副猿科(Parapithecidae)的前臼齿一致。

3) *Plesiopithecus teras* 可能是一种裸鼻猴类(Strepsirrhini), 具有某些懒猴类的特征(Simons and Rasmussen, 1994; Rasmussen and Nekaris, 1998; Simons, 1998)。

4) *Arsinoea kallimos* 可能是一种副猿类, Kay 和 Williams(1994)将 *Arsinoea* 和 *Serapia* 归入他们新建的 Qatraninae 亚科。

如此, 目前对这两种可能性还不能做任何的肯定回答, 有待于进一步的发现来证实。

黄河猴类是一支相当特化的兔猴形灵长类, 主要表现在上臼齿上有发育的次尖和围尖, 前脊直接与前尖内侧相连, 前小尖前棱退化。上臼齿与其他灵长类如此不同, 以至有人认为是偶蹄类的上臼齿(Dashzeveg and McKenna, 1977)。黄河猴类的下颊齿也相当特别, 也使人怀疑它是一种偶蹄类(Delson, 1977)。确实, 亚洲始新世的黄河猴类与其他大陆同期的灵长类有明显的差别。虽然有人认为黄河猴与欧洲和北美的始新世早期的 *Pericodon* 或 *Protoadapis* 有关(Gingerich, 1976, 1977), 但也很难令人信服。*Protoadapis* 的上臼齿与黄河猴一样具有发育的次尖和围尖, 而其他方面两者相差甚远, 与之相关的下臼齿在形态上也很难将两者联系起来。看来黄河猴的祖先只能在亚洲大陆找寻。

在垣曲盆地, 至少有3个始新世化石地点发现黄河猴类, 两个在河南渑池的上河村附近, 在河堤组任村段下化石层发现周氏任村猴(*Rencunius zhoui*), 在上化石层有吴氏任村猴(*R. wui*) (童永生, 1997), 斯氏黄河猴则是出自寨里村东土桥沟的河堤组寨里段。从层位较低的任村猴到层位较高的黄河猴显示出性状的连续性, 黄河猴基本上继承了任村猴牙齿构造格局, 某些方面进一步加强, 又出现了一些新的性状。在黄河猴中新的性状有初始的中附尖和后附尖, 次尖有伸向三角凹的弱棱; 得到进一步增强的性状有上臼齿围尖进一步发育, 齿脊发育, 三角凹、下三角凹和下跟凹加深, p4 跟座增大, m1 三角座显得前后收缩, 下前尖比较退化, m2 下前尖消失(*R. zhoui* 具有小的下前尖), m1~2 下次小尖更加舌位, 相对增大, 与下内尖之间齿谷变窄, m3 下次小尖增大, 向后突出。也就是说, 原始的黄河猴类上臼齿的围尖不会很大, 次尖可能也不会很发育, 下臼齿下次小尖不大, m1~2 下次小尖不大向舌侧位移, 即不与下内尖孪生。如果是这样, 黄河猴的祖先类型与已知的假熊猴科中的 *Cercamoniinae* 亚科成员有些相似。在亚洲现在尚未发现确定的 *cercamoniines* 的化石, 但亚洲始新世灵长类已相当分化, 某些种类在形态上与其他大陆同期的种属相近, 而另一些差异明显, 很可能是亚洲地区的特有种类。*Asiomomys* 和 *Adapoides* 可认为属于前一种情况, 吉林桦甸的长白亚洲始镜猴(*Asiomomys changbaicus*)与北美尤因塔早期的 *Stockia powayensis* 的下颊齿很相似(王伴月和李春田, 1990; Beard and Wang, 1991)。Godinot (1998) 将江苏溧阳发现的穴居似兔猴(*Adapoides troglodytes*)(Beard et al., 1994)、欧洲的 *Caenopithecus* 和北美的 *Mahgarita* 归入兔猴科的 *Caenopithecinae* 亚科, 甚至怀疑非洲的 *Aframomius* 也可归入同一亚科。而 *Lushius* 和黄河猴类可能是亚洲特有的种类, 缅甸始新世的 *Pondaungia* 和 *Amphipithecus* 以及印巴次大陆的 *Kohatius* 和 *Panobius* 可能也是这样的情况。亚洲始新世早期的灵长类化石发现不多, 只在蒙古布姆巴段(Bumban Member)中发现始镜猴类 *Altanius*, 它与欧洲和北美同时期的灵长类有明显不同之处, 可能也是亚洲特有的种类。虽然在上古新统中也有灵长类报道, 不论石猴(*Petrolemur*)还是娇齿兽(*Decoredon*)都还有一些需要探讨的问题。不过, 在始新世中期之前亚洲灵长类已经分化, 可能影响到世界其他大陆的灵长类发展。

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**DISCOVERY OF A NEARLY COMPLETE LOWER JAW OF
HOANGHONIUS STEHLINI ZDANSKY, 1930
(MAMMALIA, PRIMATES)**

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Key words Yuanqu, Shanxi, Eocene, *Hoanghonius*, lower jaw

Summary

Hoanghonius found in the "River section" of Yuanqu Basin, Shanxi Province is the earliest discovered Eocene Primates of China. The materials are a fragmentary lower jaw with only two lower molars on it and an isolated upper molar. For above specimens Zdansky (1930) named as *Hoanghonius stehlini* and pointed out that the lower cheek teeth of this animal resembled those of notharctids while the upper molar was similar to omomyids, so the systematic position of *Hoanghonius* was Primates *incertae sedis*. Later on *Hoanghonius* was placed in Omomyidae (Hill, 1955; Woo and Chow, 1957; Romer, 1966). But in the past twenty years it was normally placed to Adapidae (Szalay, 1974; Gingerich, 1976; 1977; Rasmussen and Simons, 1988). Someone, however, thought it to be related to living cheirogleids of Madagascar (Schwartz, 1986). Owing to some similarities in lower cheek teeth between *Hoanghonius* and earlier anthropoids—*Oligopithecus*, some people believed that *Hoanghonius* might have something to do with origin of anthropoids.

Why the systematic position of *Hoanghonius* is so different? The main reason is no complete materials have been found. In the past five years we worked in Yuanqu Basin and found precious *Eosiamis* as well as many other mammalian fossils, including incomplete lower jaws and isolated teeth of *Hoanghonius*. Fortunately we discovered a rather complete lower jaw of *Hoanghonius* in the recent field work, which is the best specimen ever found since it has been created. This specimen not only provides many new morphological information but also is useful for determining *Hoanghonius'* systematic position and its relationships with early anthropoids.

Primates Linnaeus, 1758

Adapiformes Hoffstetter, 1977(Szalay et Delson, 1979)

Sivaladapidae Thomas et Verma, 1979

Hoanghoniinae Gingerich, Holroyd, et Ciochon, 1994

***Hoanghonius stehlini* Zdansky, 1930**

(fig.1; pl.I)

Newly discovered specimen A rather complete left lower jaw with c~m3 (IVPP V10220).

Locality and horizon Tuqiaogou, Zhaili Village, Gucheng Town, Yuanqu County, Shanxi Province; Zhaili Member, Hedi Formation, late Middle Eocene.

Description The horizontal ramus is more elongate, being 7.2mm high at m1. The symphysis of mandible terminates below rear root of p2. There are two foramen, bigger one in front, situating below the front roots of p2 and p4, respectively. c is cone-like, somewhat backward at the tip, external wall relatively convex while the internal one rather flat. The front crest bends towards the internal base while the rear one is rather straight. There are three lower premolars, all double-rooted. p2 is constrictive transversely, the main cusp high. The front crest extending from the main cusp is short and steep while the rear one is long and gentle slope. There is a small cusp in the heel. Internal cingulum is weak but distinct. There is short diastema between p2 and p3, as well as p2 and c. p3 is similar to p2, but bigger, the front crest being almost as long as the rear one, heel bigger with distinct cusp. p4 trigonid consists of large protoconid and rudimentary metaconid. The paralophid extends forwards and downwards, connecting the front part of internal cingulum, and forming basin-like trigonid. The metaconid is very small, situating at the posterointernal of protoconid. The talonid surrounded by posterior cingulum is bigger than that in p3. The hypoconid is small and localized in the middle of posterior margin. On the posterointernal corner there is a cusp, probably entoconid, which is very small but distinct.

The lower molar tooth-row is somewhat longer than the premolar one. The molar is long (comparable with *Oligopithecus*) and brachydont. The trigonid is narrower but little higher than the talonid. m1's trigonid is less compressible anteroposteriorly than that in m2 and m3. The paraconid of m1 is small but distinct, situating at the anteroexternal of big metaconid. The talonid is long. The cristid obliqua connects posterior wall of the protoconid. The posterior arm of hypoconid extends towards posterointernal corner and links with the hypoconulid. The hypoconulid is somewhat bigger than the entoconid, which also situates at the posterointernal corner of the tooth, with narrow but distinct valley in between, the situation resembles that of *Sinoadapis*. The labial cingulum is strong at the trigonid but weak at talonid. The posterior cingulum extends from the posterior part of hypoconulid to the base of hypoconid. m2 is similar to m1 in talonid, but trigonid being distinctly compressible anteroposteriorly. The paraconid is reduced. The paralophid extends anterointernally first then posterointernally. So the shape of trigonid is rectangular. There is a valley between the metaconid and paralophid, so the trigonid opens lingually. The labial cingulum is not as developed as in m1. The trigonid of m3 is similar to that of m2,

but the paralophid shorter. m₃ has long talonid and big hypoconulid. The entoconid is small, cone-like, connecting with the hypoconulid by a weak crest.

Comparison and discussion New specimen came from Tuqiaogou, east of Zhaili Village, the same locality with the type of *Hoanghonius stehlini*. This specimen should belong to *H. stehlini* according both to size (see table 1) and to tooth morphology. The hypoconulid of m₃ on new jaw is not as developed as that in type, which can be explained as individual variation.

Gingerich *et al.* (1994) created Hoanghoniinae under the Adapidae, including *Hoanghonius* and *Rencunius*. They pointed out that this subfamily differs from other adapiform primates in having developed hypocone and pericone on lingual cingulum of upper molars, and rather developed hypoconulid and entoconid on posterointernal corner of lower molars. New material adds something on above characteristics: p₁ absent (differs from other adapids and some notharctids), P₄ and p₄ unmolariform, m₁ paraconid distinct but in m_{2~3} reduced. The trigonid of lower cheek teeth compresses anteroposteriorly, being rectangular in shape (differs from northarctids).

Recently Ducrocq *et al.* (1995) described a primates—*Waileka orientale*, from the Eocene of Krabi Basin, Thailand, and thought it to be related with *Oligopithecus*. In fact, the similarities between the two forms recognized by above authors can be seen in Hoanghoniinae and Sivaladapinae, as already pointed out by Godinot (1998), and Qi and Beard (1998). Judging from the shallow trigonid and talonid of m_{2~3}, *Waileka* is more similar to *Hoanghonius*. So it seems to be placed to Hoanghoniinae. Very recently Qi and Beard (1998) described a new primates—*Cuangxilemur tongi* from the Eocene of Bose Basin, Guangxi Province, which is also pertained to Hoanghoniinae. Thus, Hoanghoniinae contains four genera—*Hoanghonius*, *Rencunius*, *Waileka* and *Guangxilemur*, and distributed widely in Asia.

Sivaladapis, and *Indoloris* from the Miocene of South Asia were placed to Lorisidae in the past and now they were thought to be members of Adapidae. Thomas and Verma (1979) created a new subfamily—Sivaladapinae for the two genera. In the recent years it was promoted to Sivaladapidae by many workers (Groves, 1989; Tattersall *et al.*, 1988; Tong, 1997; Godinot, 1998; Qi and Beard, 1998), containing two subfamilies—Sivaladapinae and Hoanghoniinae (Tong, 1997; Godinot, 1998; Qi and Beard, 1998), the latter may be ancestral type of the former. Some evolutionary tendencies seen from *Rencunius* to *Hoanghonius* also exist in genera from Hoanghoniinae to Sivaladapinae. For instance, more and more developed styles on upper molars, deepening trigonid and talonid basins, enlarging hypoconulid and deepening valley between hypoconulid and entoconid of lower molars. Besides, Hoanghoniinae differs from Sivaladapinae in having hypocone and pericone, and distinct styles on upper molars, mandibular symphysis unfused, double-rooted p₂,

unmolariform p4, shallow valley between hypoconulid and entoconid on lower molars (compared to *Sinoadapis*), and relatively long trigonid of m1.

Yet, the diagnosis of Sivaladapidae has not been given, although Thomas and Verma diagnosed Sivaladapinae as follows when they created the subfamily: "Strepsirhini asiatiques de petite, formule dentaire 2133 / 2133, P4 / 4 très molarisées, I et C ne constituant pas de peigne dentaire; absence d' hypocône, développement très marqué de l'hypoconulide sur les molaires, tubercles pointus et généralement élevés". Up to the present no skull and postcranial skeleton has been found in this family, and only *Sivaladapis* and *Sinoadapis* possess more complete lower jaw. Now the discovery of more complete lower jaw of *Hoanghonius* provides more information about family Sivaladapidae: cheek teeth brachyodont, incisor spatulate, canine large, P1 and p1 absent, p2 single-rooted in Miocene forms but double-rooted in Eocene ones, P4 and p4 unmolariform in Hoangoniinae but molariform in Sivaladapinae. Trigonid in m1 relatively long with distinct paraconid, while in m2~3 it compressible anteroposteriorly and paraconid reduced. The hypoconulid situated lingually. The mandible elongate and symphysis fused in Miocene members but unfused in Eocene ones.

The similarity of lower cheek teeth between *Hoanghonius* and early anthropoids of Egypt has been noticed for more than twenty years. Gingerich (1977) figured some similar characteristics of lower molars between *Hoanghonius* and *Oligopithecus* though he did not discussed it in detail. Szalay and Delson (1979) also pointed out the similarity of lower molars between *Hoanghonius* and Egyptian forms as well as south Asian Miocene adapids. Rasmussen and Simons (1988) further recognized seven similar features of lower molars between *Hoanghonius* and *Oligopithecus* when they listed the difference between *Oligopithecus* and other primates. They are: having hypoconulid in m1~2, hypoconulid and entoconid being twin, trigonid compressible anteroposteriorly in m2~3, in m2 paraconid absent, anterior arm of metaconid distinct, no metastylid and enamel smooth. For these Gingerich *et al.* (1994) concluded: "*Hoanghonius* is inextricably bound up in nexus of genera and morphological characteristics connecting the origin of Anthropoidea backward in geological time to Eocene ancestors".

In the recent years Eocene and Oligocene mammalian faunas, including about a dozen Early Tertiary anthropoid localities, have been widely investigated in Africa and adjacent areas. Among them Fayum area is the most important and typical one, where Late Eocene anthropoids, such as *Catopithecus browni*, *Proteopithecus sylviae* and *Serapia eocaena* have been found apart from other mammalian fossils. Simons (1989) created a new subfamily Oligopithecinae for *Oligopithecus* and *Catopithecus*. Like *Oligopithecus*, however, *Catopithecus* resembles *Hoanghonius* in lower cheek teeth

morphology, whereas differs distinctly in upper molars. But the discovery of new lower jaw further indicates the difference in lower jaw and lower dentation between *Hoanghonius* and early African anthropoids. *Hoanghonius* has p2, small talonid of p3, small talonid with distinct cusp of p4, enlarged hypoconulid of m3, unfused symphysis, shallow horizontal ramus, etc. Of course, the similarities in anteroposteriorly compressed trigonid and twinned hypoconulid and entoconid between early African anthropoids and *Hoanghonius* as well as other sivaladapids are still distinct and should be paid attention.

There are two possibilities in explaining the similarities of the lower molars between *Hoanghonius* and Oligopithecinae—convergence or closer relationship. The facts supporting the first one are: the difference in dental formula, lower jaw and upper molars morphology. Besides, in recent years many primates fossils have been found in the Early Tertiary strata of Africa, which indicates Oligopithecinae may originate from the primates of the same land. Apart from the similarity of lower molars between the two forms, evidence of mammalian exchange between Africa and Asia in Late Eocene also supports close relationships between *Hoanghonius* and Oligopithecinae. For instance, hyaenodonts and anthracotheriids from Fayum fauna may relate with the taxa of Asia (Simons, 1968; Rasmussen *et al.*, 1992). Moreover, some scientists placed the anthracotheriid from Yuanqu Basin where *Hoanghonius* has been found to North African genus *Bothriogenyx* (Russell and Zhai, 1987; Wang, 1992). *Afrotarsius* has been found in the Early Oligocene of Fayum (Simons and Bown, 1985). Recently *Tarsius eocanus* and *Xanthorhysis tabrumi* have been reported from the Eocene of Shanghuang and Yuanqu basins, respectively (Beard *et al.*, 1994; Beard, 1998). Tarsiiformes found both in Africa and Asia demonstrate that in the Eocene mammals had exchanged between the two continents. All the above evidence indicates *Hoanghonius* may be related to Oligopithecinae. The final conclusion, however, can not be made at present.

In Yuanqu Basin there are at least three localities of Hoangoniinae. In the Rencun Member of Hedi Formation at Shanghe Village, Mianchi County, Henan Province yielded *Rencunius*, while in the upper layer, Zhaili Member at Tuqiaogou, Zhaili Village, Yuanqu County, Shanxi Province, *Hoanghonius* has been found. Some evolutionary tendency can be seen from *Rencunius* to *Hoanghonius*. Such as more and more developed crests and pericone of upper molars, deepened trigon, trigonid and talonid basins, enlarged talonid of p2, reduced paraconid and anteroposteriorly compressed trigonid of m1, no paraconid of m2, enlarged and lingually situated hypoconulid of m1~2, enlarged and posteriorly project hypoconulid of m3. These suggest that primitive Hoangoniinae possess small pericone, undeveloped hypocone, small hypoconulid, not lingually situated hypoconulid in m1~2. Above features

somewhat resemble those of Cercamoniinae though this subfamily fossils have not been found in Asia yet. In Asia Eocene primates had already diversified, some are close to other continents' taxa in tooth morphology while the others are endemic. *Asiomomys* and *Adapoides* may belong to the first condition, and *Lushius*, *Hoanghonius*, *Pondangia* and *Amphipithecus* may be endemic.

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图版 I 说明(Explanations of plate I)

斯氏黄河猴(*Hoanghonius stehlini* Zdansky, 1930), 左下颌骨具 c~m3 (left lower jaw with c~m3)(IVPP V10220),
 × 3

1. 冠面视(立体)(stereopairs, occlusal view)
2. 内侧视(立体)(stereopairs, internal view)
3. 外侧视(external view)

