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江苏溧阳上黄中始新世哺乳动物群的发现与意义[1)]

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摘要 扼要地介绍了发现于江苏溧阳上黄水母山裂隙堆积中的一个中始新世(距今约4500万年)哺乳动物群，共12目。其中中华曙猿(*Eosimias sinensis*)的发现表明高级灵长类起源于亚洲而不是非洲的可能性更大；其它的众多发现表明亚洲的东南部是早第三纪哺乳动物主要类群演化的重要舞台。

关键词 江苏 上黄，裂隙堆积，中始新世，哺乳动物群，中华曙猿

在江苏省溧阳市上黄镇(图1)水母山采石场裂隙堆积中发现了一个早第三纪哺乳动物群，称之为"上黄动物群"。该动物群分属12个目共60余种动物。动物群以小型动物

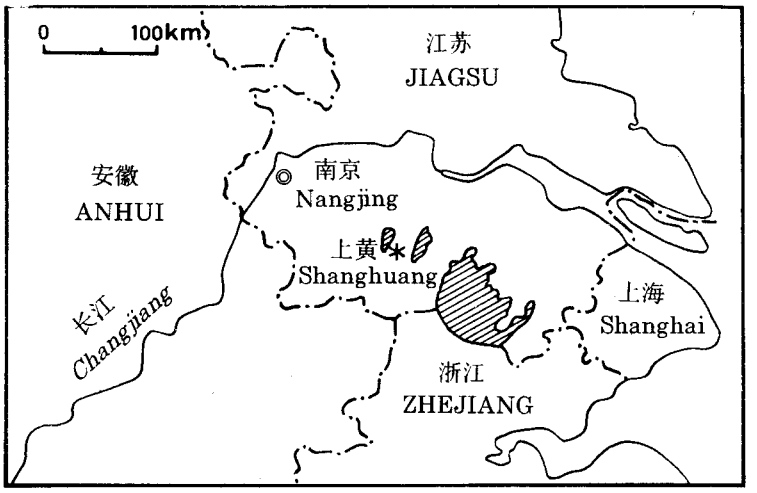

图1 上黄动物群地理位置示意图

Fig.1 The location of the Shanghuang Mammmlian Fauna

1) 上黄动物群的研究得到中国国家自然科学基金(项目号49372070)和美国国家自然科学基金的支持。
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为主，包括灵长类、有袋类、食虫类、啮齿类和翼手类等。其时代大约与内蒙古伊尔丁曼哈和沙拉木伦早期哺乳动物群的时代相当，为中始新世，距今约4500万年。

对上黄动物群的初步研究，使我们对众多哺乳动物的系统演化和历史生物地理有了新的见解。尤其是高级灵长类祖先类型的发现，证实了亚洲东部应是高级灵长类的起源地。

一、科考工作的回顾

1985年，中国科学院古脊椎动物与古人类研究所的古人类学家林一璞先生向本文作者之一(齐陶)提供了在上黄镇水母山采石场的裂隙堆积物中发现化石哺乳动物的信息，并展示了与内蒙古古鼷鹿(*Archaeomeryx*)牙齿相类似的零碎牙齿。齐陶据此判断这些牙齿所代表的动物的时代应为早第三纪并且意识到这一信息的潜在意义，从而制定了在上黄地区开展野外工作的计划。1986年古脊椎所宗冠福和王元青曾去上黄地区进行调查，证实了裂隙堆积中早第三纪哺乳动物的存在，并且采集到卢氏细齿兽(*Miacis lushiensis*)和洛河卢氏兔(*Lushilagus lohoensis*)等化石(齐陶等，1991)。

上黄动物群的主要工作和众多发现是在1987年后的近10年中取得并完成的。1992年初，美国的M. R. 道森和K. C. 毕尔德到上黄地区观察地质情况，并达成古脊椎动物与古人类研究所与卡内基自然历史博物馆合作研究的协议。随后，灵长类化石的初步研究报告在1992年5月于杜克大学(Duke University)的"猿猴亚目起源(Origin of Anthropoidea)"的专业会议上进行了宣读。自1993年起中美双方联合进行了野外工作．1994年美国自然历史博物馆的拉斯·麦可菲博士一度也加入了研究行列。

几乎所有的化石都是用筛洗方法获得的。目前，共发现5处含化石的裂隙堆积物(即A、B、C、D、E点裂隙)，区分出时代略有不同的5个动物群。其中D点时代较早，C点较年轻。这些裂隙堆积物的围岩全部是下三叠统上青龙组石灰岩。所有裂隙均位于采石场石灰岩掌子面的底部，从掌子面的顶部至底部大约50米至70米。

二、上黄动物群概况

1. 灵长目(Primates)

上黄发现的灵长目动物分属低级灵长类(原猿类)(Prosimii)和高级灵长类(猿猴类)(Anthropoidea)。低级灵长类有兔猴科(Adapidae)、始镜猴科(Omomyidae)以及眼镜猴科(Tarsiidae)。高级灵长类则是一个新科——曙猿科(Eosimiidae)。

A. 兔猴类:

兔猴科是一类与狐猴类相近的动物，与现生的捻鼻猴(Strepsirhines)关系密切。上黄的两种兔猴科动物都发现在D点裂隙中。一种与欧洲狐猴(*Europolemur*)很接近，但是仅发现了两颗上臼齿(M1(V11019)和M2(V11020))。另外一种则是兔猴亚族(Adapina)的一新属种——穴居似兔猴(*Adapoides troglodytes*)。欧洲兔猴(德国中始新世)和上黄兔猴类动物共同的特点是上臼齿都没有次尖，这是一种原始特征；但上黄兔猴类个体更

小，我们暂称之为"近似欧洲狐猴(*Europolemur*-like adapiform)"。穴居似兔猴是一种小型的兔猴类，正型标本为一段下颌骨，具两颗下臼齿(m2－3)(V11023)。除体形小之外，这两颗牙齿无下后附尖，这也是原始特征；但是它还具有一个深的下跟座凹缺以及一条粗壮的连接下原尖和下后尖的齿脊等衍生特征。

上黄的两种兔猴类动物的发现解决了有关兔猴科动物的两个长期存在的问题。其一，我们推断发现于美国德克萨斯州西部的杜显尼安(Duchenean)期(晚始新世)的有争议的兔猴类动物—— *Mahgarita sevensi* (斯氏马嘎利塔猴)是从亚洲迁徙到美洲的。以前，亚洲没有发现 *Mahgarita* 近亲的化石，而上黄"近似欧洲狐猴"正代表了马嘎利塔猴的亚洲中始新世的祖先类型，从而证实了这一令人迷惘的动物起源于亚洲的假设。第二个问题是，上黄兔猴类的发现对兔猴亚族的系统发育和生物地理分布亦具启发。兔猴亚族包括好几个属动物(*Adapis*, *Leptadapis*, *Cryptadapis* 以及 *Adapoides* 等)，以前的化石记录仅限于欧洲，而且突然出现在 Rodiacian (晚始新世)的初期，其系统演化和地理起源一直不清楚。上黄兔猴类的发现表明兔猴亚族是从亚洲而不是非洲迁入欧洲的。

上黄的兔猴类与中新世印度、巴基斯坦和云南的 Sivaladapinae 亚科的动物没有什么相似之处。

B. 眼镜猴类:

上黄的眼镜猴类动物包括两个科：始镜猴科和眼镜猴科。

归入始镜猴科的动物是大眼镜猴属中的一个新种—— 长江大眼镜猴(*Macrotarsius macrorhysis*)。仅发现两颗牙，即：p4 (正型标本，V11025)以及一颗 m1 (V11024)。p4 个体小，具一明显的臼齿化下三角座；m1 除外齿带不完整外与北美 Uintan 早期(中始新世)的 *M. jepsoni* 没有什么差别。

上黄眼镜猴类的另一种—— 始新眼镜猴(*Tarsius eocaenus*)，正型标本是一右第一下臼齿(m1)(V11030)，产自 C 点裂隙。另外还有一左 m1 (V11026) 和一右 m3 (V11027)，均产自 A点裂隙；此外尚有一右 m3 (V11031) 和一p3 (V11029)，均产自 C 点裂隙。这种始新眼镜猴的牙齿与现生的眼镜猴无大区别，但个体却非常小。上黄眼镜猴的发现第一次表明始眼镜猴类和眼镜猴类实际上同是中国东南部中始新世时的动物。大眼镜猴在亚洲的发现，证实了过去对始镜猴类中始新世时在北美和亚洲之间扩散的推断。更具戏剧性的是，始新眼镜猴时代之久远几乎将过去发现的中新世眼镜猴化石记录的时间向前推进了三倍长。

C. 原始高级灵长类:

至少有 4 个种。现有证据还不能确定它们是组成了一个单系类群(monophyletic)还是并系类群(paraphyletic)。

这里优先记述的是猿猴亚目(Anthropoidea)中的一个新科，曙猿科(Eosimiidae)。科型属是曙猿(*Eosimias*)，属型种为中华曙猿(*E. sinensis*, Beard *et al.*, 1994)。

中华曙猿的正型标本是一右下颌骨，具 p4－m1 以及 c1，p2－3，以及 m3 的齿槽(V10591)。产自 B 点裂隙。

中华曙猿不同于其它高级灵长类的特征是：a. 保留了一个未愈合的下颌联合部以及 m1－2 上突出的下前尖；b. p4 下后尖位置相当靠后，而齿尖低于下原尖，同时也没

有齿脊将这两个齿尖连接起来；c. m1－2上具后部突起的下次小尖和 d. m1－2无双齿尖的下内尖以及下次小尖。

除了个体小(根据现生灵长类 m1 对动物个体大小的恢复方法推断，上黄的灵长类体重大约在 47— 137 克之间)、下颌联合部未愈合以及 m1－2 上具突起的下前尖这些原始的特征以外，中华曙猿与原始高级灵长类比较还表现出以下近裔共性：齿式 2－1－3－3；p2 单根；p3－4 前后短，位置斜，以及适度的向唇侧凸涨的"exodaenodont"齿形；m1－2具加大的下原尖，它与下后尖相距较远，前下后脊出现，以及下内尖位置靠前。

近来，古生物学上的发现表明早期高级灵长类的牙齿仍保留有许多原始特征，使得对早期高级灵长类的系统发育的构想更复杂化。但无论如何，中华曙猿在猿猴亚目中占有一个非常原始的位置，肯定发生在 Parapithecidae，Oligopithecinae，Platyrrhini 和 Catarrhini 之前。

中华曙猿的这种系统演化位置引发了灵长类系统演化关系的新见解。有一种看法认为早期的高级灵长类起源于始新世的兔猴类，中华曙猿的年代和解剖学特征对此提出了质疑。

中华曙猿的发现也涉及到高级灵长类起源的生物地理中心问题。非洲始新世高级灵长类的发现强调了它们的古老性，导致有人推测高级灵长类可能出现于非洲大陆；而上黄的中华曙猿的原始特征和久远年代至少也可说亚洲的东南部也是一个早期高级灵长类演化的重要舞台。在亚洲和非洲这两个大陆没有进一步的古生物证据之前，高级灵长类起源于亚洲而不是非洲的可能性是不能被否认的。

总之，上黄灵长类令人吃惊的分化状况，反映出亚洲早期灵长类在演化中所扮演的复杂角色。上黄两种兔猴类展示出与欧洲种类的清楚的亲缘关系，当然这种类似欧洲种类的兔猴与北美的也有关系。象长白亚洲始镜猴(*Asiomomys changbaicus*)一样，上黄的大眼镜猴也与北美的始镜猴类有着密切的关系。而包括始新眼镜猴在内的眼镜猴则是亚洲地方特有的动物。尽管上黄灵长类的辐射与较晚的亚洲灵长类有关，但同样也显示出与非洲有古老的生物地理联系(？古新世)。

2. 有袋目(Marsupialia)

自 B 点和 C 点裂隙中，发现了 10 多颗上下牙齿。这种与亚洲负鼠(*Asiodidelphis*)相似的有袋类(*Asiodidelphis*-like)动物在我国是首次发现。亚洲负鼠是曾发现于哈萨克斯坦渐新世的阿克塞依尔组(Aksyir Formation)的一种有袋类动物(Gabunia *et al.*, 1990)。

3. 啮齿目(Rodentia)

至少有 5 个科发现于上黄的裂隙堆积之中，其中以仓鼠科的化石最为丰富。现生的仓鼠类广泛地分布在世界各地。上黄 D 点裂隙的始祖仓鼠(*Pappocricetodon antiquus*)是目前已知的最古老、最原始的仓鼠，由此可以推测仓鼠科动物起源于亚洲(Wang and Dawson, 1994)。它较山西垣曲盆地的任村祖仓鼠(*P. rencunensis*，童永生，1992)稍原始。除 D 点的祖仓鼠外，还在 A、B、C 和 E 点裂隙中也发现有仓鼠类动物，包括 *P. rencunensis*，*P. schaubi* 以及 *Eucricetodon*。

除仓鼠类外，上黄还发现有以下几科化石：壮鼠科(Ischyromyidae)、豫鼠科(Yuomyidae)、梳趾鼠科(Ctenodactylidae)以及一个新科(未命名)。上黄的壮鼠科化石包括一个新属以及其它几个种。

4. 翼手目(Chiroptera)

至少有两个小翼手亚目动物发现于上黄哺乳动物群中，这些化石尚待详细研究。

5. 裂齿目(Tillodontia)

上黄的裂隙中发现了两种裂齿类动物。较大的一种(B点和C点)与山东中始新世早期官庄组的 *Kuanchuanius*（周明镇，1963）相似。而采自D点裂隙堆积中的单个牙齿则属于一种小型的裂齿类动物，其牙齿构造与广东南雄古新世罗佛寨组（上湖段）中发现的低冠罗佛寨兽(*Lofochaius brachyodus*)(周明镇等，1977)有相似之处。

6. 踝节目(Codylarthra)

仅发现豕齿兽科(Hyopsodontidae)的一颗上第一臼齿(M1)。这种动物在北美十分普遍，而在亚洲则十分稀少。早始新世的 *Hyopsodus* 标本发现于新疆的吐鲁番盆地(翟人杰，1978)以及蒙古的那兰布拉克。上黄化石是亚洲第一个中始新世豕齿科动物。

7. 食肉目(Carnivora)

共发现两个科。细齿兽科(Miacidae)包含了卢氏细齿兽(*Miacis lushiensis* 齐陶等，1991)、*M. gracilis* 以及 *Vulpavus* sp.。D点裂隙中发现的诸多单个牙齿属于犬科的最早成员—— *Procynoditis*。此属在北美出现在犹因坦期(Uintan)。

8. 肉齿目(Creodonta)

所有上黄的肉齿类动物都属于鬣齿兽科(Hyaenodontidae)。湖犬兽属(*Limnocyon*)发现于D点裂隙中。过去此属动物仅发现于北美的中始新世地层。发现于D点裂隙的翼齿兽(*Pterodon*)和鬣齿兽(*Hyaenodon*)则在亚洲和北美均有发现。此外，在B点裂隙中尚发现一种小型的鬣齿类动物。

9. 食虫目(Insectivora)

上黄的每一个裂隙堆积都含有食虫类化石，至少有6个种。其中 *Ardynictis* 的发现颇令人感兴趣，因为该属过去仅在蒙古和内蒙古的早渐新世地层中有所发现。其它食虫类大部属于猬科(Erinaceidae)动物。

10. 兔形目(Lagomorpha)

兔形目化石数量很大，在上黄的各个裂隙中都有发现，但种类单调，其中有一种比已报道的卢氏兔(齐陶等，1991)更为原始。

11. 偶蹄目(Artiodactyla)

至少有4个科的偶蹄类动物发现在上黄的裂隙中，它们是最为丰富的大型哺乳动物。有两种偶蹄类动物在各个裂隙中都特别丰富，而且显然是新的属。它们与沙拉木伦组的古鹿鹿(*Archaeomeryx*)比较接近，但更为原始。有些偶蹄类则属于Homacodontidae。另外，在D点裂隙中发现一种可能归入始巨猪属(*Eoentelodon*)的非常原始的石炭兽类动物以及一种小型的原始石炭兽类动物。上黄的巨猪类和石炭兽类动物都是这些科中的早期记录，进一步研究这些化石有助于巨猪类和石炭兽类起源的研究。

12. 奇蹄类(Perissodactyla)

多种奇蹄类动物在上黄出现：

爪兽科(Chalicotheriidae)：*Eomorpus* sp.；

雷兽科(Brontotheriidae)：*Microtitan mongoliensis*；小型雷兽，属种未定；

貘巨科(Megafamily Tapirida)：*Heptodon* sp.；

貘超科(Tapiroidea)：*Helaletes mongoliensis*；*H.* sp.；

红山貘科(Rhodopagidae)：*Rhodopagus* sp.；

蹄齿犀科(Hyracodontidae)：*Forstercooperia* sp.；

两栖犀科(Amynodontidae)：*Caenolophus* sp.；

犀超科(Rhinocerotoidea)：*Hyrachyus* sp.；

古兽科(Palaeotheriidae)：一尚未记述的新属种。

上述大部分奇蹄类均出现在内蒙古中始新世伊尔丁曼哈动物群内。它们在上黄的出现最起码更进一步证实了上黄裂隙堆积的时代与伊尔丁曼哈哺乳动物群的时代是一致的。

这里我们要对两种奇蹄类动物作一介绍：

第一个是目前世界上最小的雷兽——上黄“迷你雷兽”。它的牙齿比贵州盘县石脑发现的盘县侏儒雷兽(*Pygmaetitan panxianensis*，苗德岁，1982)的牙齿更小更具原始特征。

上黄原始古兽类的发现证实了 Franzen (1989) 有关欧洲的古马类——古兽科(Palaeotheriidae)生物地理起源及扩散路线的假想。Franzen (1989, P.104) 推测，“由于它们在中、晚始新世交接的时期突然出现在欧洲，这样就出现了一个问题：无论是从系统演化还是从古地理方面考虑，古兽类最早是从什么地方来的。一种可能是从亚洲迁徙来的，但没有来自那个大陆的有关系的种类被发现。整个古新世和始新世亚洲和欧洲是被土尔盖海(Turgai Sea)隔开的。”然而，上黄中始新世裂隙堆积中的原始古兽类的发现使得上述问题有了一种答案，即：中始新世时，亚洲与欧洲之间的土尔盖海并不是哺乳动物扩散的一个不可逾越的障碍。

三、结　　语

1. 中华曙猿的发现表明出现在亚洲和非洲的早期高级灵长类动物起源于亚洲的可能性更大。

2. 中国至少在中始新世时曾经有有袋类动物生活。

3. 众多的早期原始的哺乳动物在上黄的出现表明亚洲的东南部是早第三纪哺乳动物主要类群演化的重要舞台。

4. 一些上黄哺乳动物可用来在亚洲和北美之间作生物地层学上的对比，也可以在亚洲和欧洲之间作比较。

5. 上黄动物群中也有一些亚洲的地方性动物。

6. 裂隙堆积物是亚洲中始新世化石哺乳类材料独特而又重要的来源。上黄动物群与相同时代的中亚动物群的主要差异无疑揭示了不同的古环境和埋藏学方面的情况。

7. 沿太平洋西岸的一系列化石哺乳动物群的发现，如：山东早始新世五图动物群、吉林中始新世桦甸动物群以及泰国南部褐煤矿中灵长类和偶蹄类等的发现都展现出亚洲大陆的同时代动物群令人感兴趣的差异，表明亚洲动物群的不同的地方风貌早在早第三纪时就已经有所发展，从而显示出太平洋西岸地区对研究古动物及古环境的突出的重要性。

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The Shanghuang Mammalian Fauna, Middle Eocene of Jiangsu: History of Discovery and Significance

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Summary

A Paleogene mammalian fauna, here named the Shanghuang fauna, was discovered near the village of Shanghuang, close to Liyang City, Jiangsu Province, China (Fig.1). At present, roughly sixty species of fossil mammals have been recognized in the Shanghuang fauna. Many of these mammal taxa are new to science, and others represent new occurrences for the Eocene of China. Particularly well represented in the Shanghuang fauna are micromammals (including marsupials, insectivores, rodents, lagomorphs, primates, and bats) that have seldom if ever been found in other Eocene Asian localities. Biostratigraphic correlations suggest that the Shanghuang fauna represents the Irdinmanhan and early Sharamurunian Land Mammal Ages and is likely to be about 45 million years old. Ongoing study of the Shanghuang mammal fauna promises to shed new insight into the phylogeny and historical biogeography of numerous higher-level mammalian taxa. Here, we provide a history of field activities at Shanghuang and an overview of mammalian diversity at Shanghuang.

In 1985 Mr. Lin Yipu, a paleoanthropologist at the IVPP, informed one of us (Qi Tao) about the occurrence of fossil mammals in fissure-fillings near Shanghuang. The presence of several isolated teeth of primitive artiodactyls similar to *Archaeomeryx* in these initial collections showed that the Shanghuang fauna was Paleogene in age. Realizing the potential significance of this, Qi Tao made plans for further field work at Shanghuang. In 1986 Zong Guanfu and Wang Yuanqing investigated the occurrence at Shanghuang. This field trip further confirmed that Paleogene Mammals were present in fissure-fillings, by obtaining specimens of *Miacis* and *Lushilagus* from the fissures (Qi *et al.*, 1991). Over the course of almost a decade, the true diversity of Paleogene mammals at Shanghuang has been demonstrated by field efforts every year since 1987 by Qi Tao. In January, 1992 Qi Tao invited Mary Dawson and K.

Christopher Beard to come to China and visit the locality at Shanghuang. This trip formed the basis for collaboration between IVPP and Carnegie Museum of Natural History on the fossil mammals from the Shanghuang fissure-fillings. Initial reports on the fossil primates from Shanghuang were presented at a special symposium on "Anthropoid Origins" held at Duke University in May, 1992. Joint field work by IVPP and Carnegie Museum of Natural History paleontologists has taken place at Shanghuang every year since 1993. In 1994 Dr. Ross MacPhee of the American Museum of Natural History also joined the research team.

Most of fossils were obtained by washing.

All the fossils were collected from fissure fillings which were surrounded by the limestone of Triassic Shangqinglong Formation. A total of five fissure filiings were found in Shuimushan limestone quarry of Shanhuang (i.e. fissures A, B, C, D and E). All the fissures are located at the bottom of the limestone face about 50 to 70m from the top of the face to the bottom. The limestone face is constantly extending now.

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1. Primates

The Shanghuang fissures have yielded abundant fossil primates, including representatives of Adapidae, Omomyidae, the newly named basal simian family Eosimiidae, and the earliest known Tarsiidae. Although several species of eosimiids are known from Shanghuang, only *Eosimias sinensis* has been described to date (Beard *et al.*, 1994). The most notable characteristic of the Shanghuang primate fauna is its surprising diversity of higher-level primate clades. In middle Eocene localities of Europe and North America, only adapids and omomyids have been recovered. The Shanghuang primate fauna demonstrates that a much greater taxonomic diversity of primates inhabited coastal regions of southeastern China during the middle Eocene. This differential pattern of primate diversity on Holarctic continents suggests that southeastern Asia was a very important theater of early primate evolution, and may have been the site of origin for such taxa as Tarsiidae and Anthropoidea.

There are at least two species of adapids in the Shanghuang fauna, both of which exhibit clear affinities with European taxa. Isolated molars from fissure D are very similar to those of *Europolemur*, but more nearly complete fossils of this species will be necessary to assign these specimens to *Europolemur* with confidence. *Adapoides troglodytes* from Shanghuang fissure B is a small, basal member of the otherwise European clade Adapina (which also includes *Adapis*, *Leptadapis*, and *Cryptadapis*).

Biogeographically, the Shanghuang adapids demonstrate that primates were able to disperse across the Turgai Straits near the middle-late Eocene boundary.

Macrotarsius macrorhysis from fissure D is the only omomyid primate represented in the Shanghuang fauna to date. *Macrotarsius* is otherwise known only from North America, where it occurs in localities of Uintan and possibly younger age.

Tarsius eocaenus is represented by isolated teeth from fissures A and C. This tiny tarsiid is smaller than any of the living species of *Tarsius*. It is also the oldest fossil tarsiid currently known.

Eosimiidae are the most common primates in each of the Shanghuang fissures. These primates possess a combination of primitive and derived dental traits that suggest they are basal members of the anthropoid radiation. In addition to *Eosimias sinensis* and its close relatives, several other distinctive clades of basal anthropoids are represented in the Shanghuang fissures. These include close relatives of *Hoanghonius stehlini* and a distinctive new genus and species without lower molar paraconids, among other taxa. Postcranial and cranial elements apparently pertaining to eosimiids are also known from the Shanghuang fissures. Among these, a small primate petrosal bone from Shanghuang fissure D has been described by MacPhee *et al.* (1995).

2. Marsupialia

More than ten cheek teeth were recognized from the matrix of fissures B and C. The *Asiadidelphis*-like opossum (Didelphidae) is the first discovery of a fossil marsupial in China. *Asiadidelphis* was found from the early Oligocene Aksyir Formation in Kazakhstan (Gabunia *et al.*, 1990).

3. Rodentia

A total of at least five families of rodents have been recovered from the Shanghuang fissures. (1) Cricetidae: Cricetids widely distributed in the world. *Pappocricetodon antiquus* from fissure D is the oldest and most primitive known cricetid, and it suggests that the origin of the Cricetidae occurred in Asia (Wang and Dawson, 1994). *Pappocricetodon antiquus* is slightly more primitive than *Pappocricetodon rencunensis* from the Yuanqu Basin, Shanxi Province (Tong, 1992). In addition to *P. antiquus*, slightly more derived taxa of cricetids occur in fissures A, B. C and E at Shanghuang. These species include *P. rencunensis*, *P. schaubi.* and *Eucricetodon.*

Besides cricetids there are still several families (or superfamilies) of rodents found in Shanghuang: Ischyromyidae, Yuomyidae, Ctenodactylidae and a new family. The Ischyromyidae from Shanghuang, including a new genus and several other taxa, are being described by Wang and Dawson.

4. Chiroptera

At least two species of microchiropteran bats are represented in the Shanghuang

mammalian fauna, but these have yet to be studied in detail.

5. Tillodontia

Two species of tillodonts are present in the Shanghuang fissures. The larger of these, represented by isolated teeth from fissures B and C, resembles *Kuanchuanius* (Chow, 1963) from the early middle Eocene Guanzhuang Formation, Shangdong Province. The smaller species, represented by isolated teeth from fissure D, bears some resemblances with *Lofochaius brachyodus* (Zhou *et al.*, 1977) from the Paleocene Lofochai Formation (Shanghu Member), Guangdong Province.

6. Condylarthra

Only one M1 from fissure D represents the Hyopsodontidae, which were very common during the Eocene in North America, but were very rare in Asia. Early Eocene specimens of *Hyopsodus* have been reported from the Turfan Basin, Xinjiang (Zhai, 1978) and Naran Bulak, Mongolia (Dashzeveg, 1977). The Shanghuang record is the first middle Eocene hyopsodontid from Asia.

7. Carnivora

Two families have been recovered from the Shanghuang fissures. Miacids are represented by *Miacis lushiensis* (Qi *et al.*, 1991), *Miacis gracilis* and *Vulpavus* sp. Isolated teeth from fissure D belong to the primitive canid genus *Procynodictis*. To our knowledge, the earliest member of the Canidae appeared in the Uintan of North America.

8. Creodonta

All of the Shanghuang specimens belong to the Hyaenodontidae. Specimens of *Limnocyon* have been recovered from fissure D. This genus was previously known only from the middle Eocene of North America. *Pterodon* and *Hyaenodon* have also been recovered from fissure D, but these genera were previously known from both Asia and North America. An additional small hyaenodontid is known from fissure B.

9. Insectivora

Fossil insectivores have been found in every fissure at Shanghuang. At least 6 species are represented. The discovery of *Ardynictis* in fissure D is interesting, because it was found in early Oligocene beds in Mongolia and Nei Mongol (Inner Mongolia) in the past. Numerous other insectivores are represented in the Shanghuang fissures, including erinaceids.

10. Lagomorpha

A lagomorph more primitive than *Lushilagus* is abundantly represented in the Shanghuang fissure-fillings.

11. Artiodactyla

At least four families of artiodactyls have been recovered from the Shanghuang fissures, where they are the most abundant large mammals. Two artiodactyls (both

apparently new at the genus level) are especially abundant in all of the Shanghuang fissures: one is close to (but more primitive than) *Archaeomeryx*; the other may represent the family Homacodontidae. A very primitive entelodont, perhaps referable to *Eoentelodon*, and a small, primitive anthracothere are represented by isolated teeth from fissure D. The Shanghuang entelodont and anthracothere are both early records for these families, and further study of these fossils may shed light on the origin of Entelodontidae and Anthracotheriidae.

12. Perissodactyla

There are many kinds of perissodactyls collected from Shanghuang fissures:

Chalicotheriidae: *Eomorpus* sp.;

Brontotheriidae: *Microtitan mongoliensis*; *Nanotitan shanghuangensis* gen. et sp. nov.;

Tapirida (Megafamily): *Heptodon* sp.;

Tapiroidea: *Helaletes mongliensis*; *Helaletes* sp.;

Rhodopagidae: *Rhodopagus* sp.;

Hyracodontidae: *Forstercooperia* sp.;

Amynodontidae: *Caenolophus* sp.;

Rhinocerotoidea: *Hyrachyus* sp.;

Palaeotheriidae: an undescribed new genus and species.

Most of these taxa first appear in Asia in the middle Eocene Irdin Manha fauna of Nei Mongol, and their presence in the Shanghuang fissures further corroborates the view that the Shanghuang fissures are at least partly correlative with the Irdinmanhan Land Mammal Age.

Two of the Shanghuang perissodactyls deserve further comments here.

The first of these is the smallest brontothere yet discovered, *Nanotitan shanghuangensis* (Qi and Beard, in press). Its cheek teeth are much smaller than those of early Oligocene *Pygmaetitan panxianensis* (Miao, 1982) from near Shinao Vallage, Panxian County, Guizhou Province. Indeed, some of the teeth originally referred to this genus as milk teeth resemble those of *Nanotitan* in size, but some differences in dental morphology remain.

The discovery of a primitive palaeothere at Shanghuang confirms one of Franzen's (1989) hypotheses regarding the biogeographic origin and subsequent dispersal routes of the Palaeotheriidae. Franzen (1989, p.104) suggested that "Since they appear suddenly in Europe at the turnover from middle to late Eocene, the question arises of where the paleotheres originally came from, palaeogeographically as well as phylogenetically. One possibility is that they immigrated from Asia, but no related taxon has ever been discovered from that continent. During the whole Paleocene and Eocene, Asia was isolated from Europe by the Turgai Sea." However, the discovery

of a primitive palaeothere in middle Eocene fissure-fillings at Shanghuang invalidates the problems cited by Franzen for an Asian origin for palaeotheres. Other aspects of the Shanghuang mammal fauna, particularly the adapid primates, also show biogeographic affinities with western European middle-late Eocene faunas, suggesting that the Turgai Straits were not an impenetrable barrier to mammalian dispersal between Asia and Europe in the middle Eocene. We also suggest that *Qianohippus magicus*, which occurs in the same fauna as *Pygmaetitan* (Miao, 1982), is also a palaeothere, not a hyracotheriine equid as he suggested.

Conclusions

1. The discovery of *Eosimias sinensis* demonstrates that early simians were present in both Asia and Africa, so that the possibility that simians originated in Asia rather than Africa cannot be rejected.
2. Fossil marsupials have been discovered in China for the first time.
3. Early, basal representatives of such distinctive mammalian clades as Cricetidae, Entelodontidae, and Palaeotheriidae are represented in the Shanghuang fissures, demonstrating that southeast Asia was an important theater of diversification of major groups of Paleogene mammals.
4. Some of the fossil mammals from Shanghuang can be used to make biostratigraphic correlations between Asia and North America (e.g., *Macrotarsius* and Hyopsodontidae) and between Asia and Europe (e.g., *Adapoides* and Palaeotheriidae).
5. Other members of the Shanghuang mammalian fauna are endemic to Asia (e.g., Tarsiidae, certain rodents, and Didymoconidae).
6. The Shanghuang fissure-fillings are a distinctive and important source of data regarding the true diversity of fossil mammals in the middle Eocene of Asia. Major differences between the mammalian fauna from Shanghuang and faunas of similar age in central Asia are undoubtedly attributable to different paleoenvironmental and taphonomic conditions.
7. Other distinctive mammal faunas from near the Pacific Coast of China, such as the early Eocene Wutu fauna from Shandong Province and the middle Eocene Huadian fauna from Jilin Province, also show interesting differences from faunas of similar age in the interior of the Asian continent, suggesting that significant faunal provincialism within Asia had developed by Paleogene time.