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中国新生代哺乳动物区系演变[1)]

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摘要 自始新世以后中国南、北方动物群分异越来越明显，可能与青藏高原的逐渐隆起密切相关。中国新生代哺乳动物与欧洲和北美大陆都有过交往，早期与北美大陆交流较多，晚期则与欧洲关系更为密切。

关键词 中国，新生代，哺乳动物，区系和交流

童永生等(1995)在"中国新生代哺乳动物分期"一文中，根据哺乳动物群性质和演替将中国新生代划分成十八个哺乳动物期。六千五百万年以来，由于板块运动所造成的陆海分布、地形以及气候的变化，制约了哺乳动物的起源、演化和迁移，使得哺乳动物区系也不断发生变化。在划分中国新生代哺乳动物期的基础上，进一步探讨从古新世到更新世不同时期的哺乳动物区系演变及其与其他大陆间哺乳动物间交流就很有必要。

本文分别由郑绍华(第四纪)、邱铸鼎(晚第三纪)和童永生(早第三纪)执笔。

一、生态环境与区域分异

我国幅员辽阔，自然环境复杂，为哺乳动物的生存提供了不同类型的生态环境。现代中国存在两个大的的动物区系。这两个区系大体以秦岭—淮河一线为界，界线以北为古北界，以南为东洋界。目前所发现的新生代哺乳动物虽然还不足以描绘出每一时期的动物区系的全貌，却可以初步证明我国现代两个动物区系的形成经历了漫长且复杂的过程(图1)。

古新世时古地中海把我国西南部与印度板块隔开，我国绝大部分地区位于现代的北纬5—40°的范围内(王蓉、沈后，1992)，年平均气温比现代高，广大的中部地区属于亚热带半干旱环境。我国已知的古新世哺乳动物地点大多集中在中部地区，只有少数地点见于北部的温暖带，如内蒙古脑木根和新疆台子村(叶得泉等，1993)。在动物群组成上中部地区较为一致，但北部地点却发现了中部地区所缺少的纹齿兽类(taeniolabidids)。尽管这些地点的层位可能较高，但作为一个时期而言，我国古新世时在动物群组成上已显现出某些地区差别。推测古新世中部的东部沿海地区比较潮湿，可能存在一个与中部内陆地区不同的动物群类型。目前东部沿海地区还未发现化石，然而可从孢粉资料，含有机质的暗色地层的存在，也可从早始新世五图动物群得到印证(童永生、王景文，

1) 本文属中国科学院支持的"八五"院重点科研项目。
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1994)。

由于印度板块与欧亚板块的碰撞，始新世时古地中海逐渐在喜玛拉雅山地区退出。早始新世早期东部沿海与中部地区的动物群在组成上有较大的差别。五图动物群可作为东部沿海地区的早始新世哺乳动物群的代表。在这个动物群中啮齿类的组合以副鼠类为主，而中部地区却由原始梳趾鼠类组成，至今尚未发现副鼠类化石。五图动物群还有多瘤齿兽类、食果猴类(carpolestids)、以及与现生鼩鼱、毛猬有关的食虫类，而未发现其他地点常见的宽臼兽类(eurymylids)，它反映的是一个相对暖湿的自然环境。这说明了我国早始新世早期的气候基本上继承了古新世气候带的格局。在早始新世晚期我国气候比较"均一"，中部干旱—半干旱区似乎消失，*Rhombomylus*－*Heptodon* 组合广泛分布。

中始新世我国各哺乳动物群在科一级的组成上差别不大，但至沙拉木仑期，云南的路美邑上部动物群和广西洞均动物群含有较多的戴氏猴类(deperetellids)(三属五种)、巨犀类(indricotheriines)(二属四种)和其他真犀类(rhinoceratids)(二属五种)，而华北同期动物群中这些成分相对较少。

中晚始新世的那读期，南方动物群中偶蹄类的多样性与北方动物群的相对单一形成鲜明对照。在广西的那读动物群中猪类和西猯类(tayassuids)开始分化，已记述的石炭兽类达五属("*Anthracokeryx*"、*Anthracothema*、*Huananothema*、*Heothema* 和 *Bothriodon*)，反刍类两属("*Indomeryx*"和 *Notomeryx*)。而华北的寨里动物群中猪超科尚未发现，也未见到南方类型的反刍类化石，石炭兽类只有"*Anthracokeryx*"和 *Brachyodus*? 两属。

总的来说，始新世时我国南、北方哺乳动物群在组成上相对比较均一，但在始新世后半期南北哺乳动物群有些差异，反映南北方气候分异已显得较为明显。

比较肯定的渐新世化石地点仅分布在北方。乌兰戈楚期动物群中常见相当特化的雷兽类和两栖犀类，或许表明当时有比较湿润的环境。而以啮齿类和鼠兔类化石为主的乌

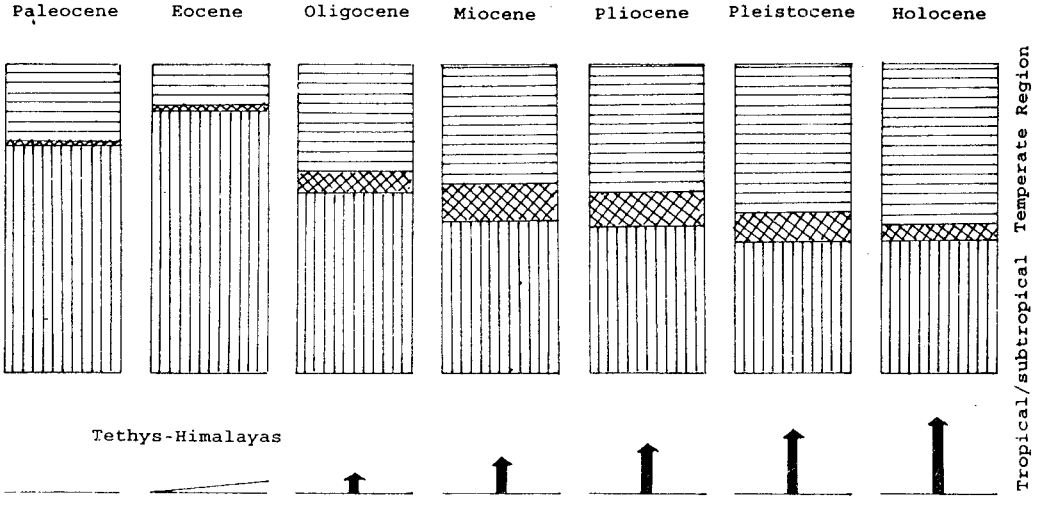

图 1 中国南北方哺乳动物群的分异历史

Fig.1 Sketch showing differentiation of mammalian faunas in China

兰塔塔尔期和塔朋布拉格期动物群却指示干旱—半干旱的自然环境。这说明在渐新世后期，我国北方已出现了与现代古北界相似的自然环境。推测这时青藏高原也已抬升到了一定的高度，并开始影响我国的气候格局。

中新世时，我国哺乳动物在组成上不仅存在南方和北方的明显差异，而且东部和西部也有很大的不同。中新世早期的青海谢家动物群含林跳鼠类、塔塔鼠类和旱松鼠类等耐旱型动物，而同一时代东部的江苏下草湾动物群则含毛猬类、河狸类和竹鼠类等喜湿或湿热型动物。内蒙古中中新世通古尔动物群含有我国现代北方属于古北界特有的六个科中的五个科，即河狸科、林跳鼠科、鼠兔科、跳鼠科和睡鼠科(通古尔动物群未见现代的鼢鼠科，只有其祖先类型)，而无一系现代生存于华南热带—亚热带、属于东洋界的科。与此不同的是，同一时代云南的开远动物群含有猿类、猴类和河猪类，都属于现代东洋界的成员，却无一现代古北界特有的科。这种差异在晚中新世时更为清楚，如内蒙古二登图动物群含有现代全北区特有或主要分布在古北区的河狸科、睡鼠科、林跳鼠科、跳鼠科、鼢鼠科、鼠兔科和刺猬亚科，却无一分布于现代东洋界的科或亚科；而云南禄丰石灰坝动物群含有现代东洋界特有或主要分布在旧大陆热带—亚热带的树鼩科、毛猬亚科、狐蝠科、蹄蝠科、猪尾鼠科、竹鼠科、豪猪科、大熊猫科、长臂猿科、麝鹿科和灵猫科等，属于现代全北区或古北区特有的只有河狸科和仓鼠科。前者指示一个温带干旱、半干旱，以草原、森林草原为主的自然环境，与现代古北界相似；后者反映的是热带—亚热带、以湿热森林为主的自然环境，与现代东洋界相似。

上新世时，我国南方和北方动物群的组成与所指示的生态环境已初具现代面貌，但曾经于晚中新世仍分布在云南地区的仓鼠类，特别是非常繁盛的科氏仓鼠属(*Kowalskia*)再也没出现在上新世的元谋动物群。这种情况很可能表明这时哺乳动物区系的分化比起晚中新世时更为清楚了。

更新世时，华北和华南哺乳动物在科一级的分布上与现代的情况基本一致，说明了现代的古北区和东洋区这时在我国已客观存在。但在更新世早期，南、北方哺乳动物分布上的分异并没有现代那样清楚，仍保留较明显的上新世痕迹，属于现代古北区的一些种类仍出在长江以南，如仓鼠类和鼢类；而现代东洋界的一些属却散布于华北的南部，如竹鼠、豪猪和灵猫等。早更新世中期后，两个区系之间的哺乳动物随着全球气候的变化而频繁地在小范围内扩散和交流，而且以北迁为主。一些属，如*Hystrix*、*Stegodon*、*Ailuropoda*、*Tapirus*等深入华北，也许说明这一时期的某些时段气候相对较为温湿。更新世以来两个区系间的哺乳动物分布上的变化还表明在过去的几十万年里，气候发生过多次冷暖交替变化。

从以上看来，我国南北方哺乳动物群分异的历史，至少可以追溯到印度板块与欧亚板块相碰撞的始新世。我国自然环境的变化，以及动物分布上的差异，显然与两板块碰撞后青藏高原的逐渐抬升密切相关。

二、与欧、美大陆动物群的关系

我国古新世哺乳动物具有浓厚的地方色彩，出现了特有的狍兽目(Anagalida)和一些特有的科，如Bemalambdidae、Harpyodidae、Archaeolambdidae、Pastoralodontidae、

Didymoconidae 和Phenacolophidae 等，它们占整个动物群绝大部分。同时与北美有较密切的联系，有 42% 的科与北美古新世动物群共有，如中兽科、豕齿兽科(Hyopsodontidae)、凿食兽科(Esthonychidae)、古灵猫科和北柱兽科等。从它们的时代分布来看，豕齿兽类和古灵猫类可能从北美向亚洲扩散(也有人认为这两类动物从亚洲向北美迁移)，而中兽类、凿食兽类和北柱兽类则可以肯定地说是从亚洲向北美迁移。另外，从早始新世五图动物群判断，在华南古新统中尚未发现的新斜沟齿兽类多瘤齿兽(neoplagiaucid multituberculats)、食果猴类更猴(carpolestid plesiadapoids)等在古新世的亚洲大陆可能业已存在。相反在这期间，不仅没有与欧洲相同的属，而且相同的科也只有一、二个，仅占所发现材料的 1.5%。显然，古新世时我国哺乳动物与欧洲的关系远没有与北美那样密切(图 2)。

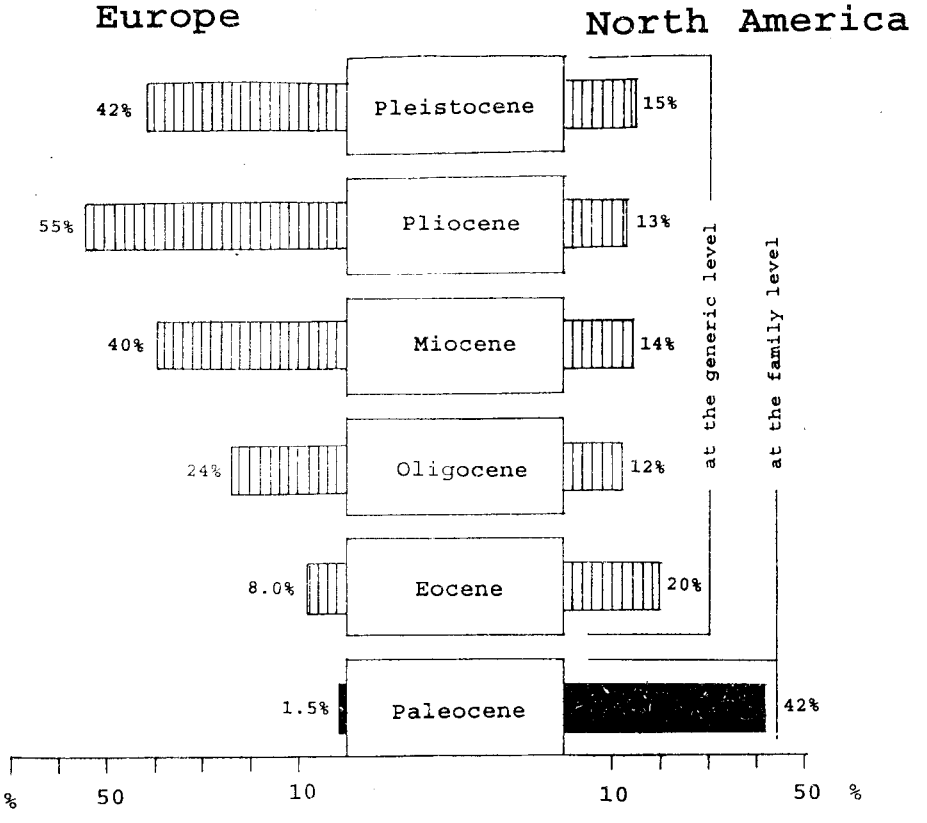

图 2 中国与欧洲和北美新生代各时期相同属(科)哺乳动物的比例

Fig.2 Sketch showing biogeographic relationships of mammals

早始新世早期出现一些与北美、欧洲同属哺乳动物，如细齿兽(*Miacis*)、冠齿兽(*Coryphodon*)、双尖中兽(*Dissacus*)、软食中兽(*Hapalodectes*)、豕齿兽(*Hyopsodus*)、始祖猴(*Homogalax*)、犀猴(*Heptodon*)、？原厚脊兽(？*Propachynolophus*)和悬副鼠(*Acritoparamys*)等，蒙古国的早始新世地层中还发现了始马(*Hyracotherium*)。其中，冠齿兽、豕齿兽、双尖中兽、始马和细齿兽等是三个北方大陆共同的属，原厚脊兽与欧洲

大陆共有，其余则与北美共有。这些事实似乎说明连接亚洲和北美大陆的白令陆桥不仅存在，而且适于哺乳动物交往。当然，白令陆桥也不是对所有哺乳动物都畅通无阻，古新世时在亚洲很繁盛的狮兽类，阶齿兽类、双锥齿兽类、伪脊齿兽类等尚未在北美发现。同样，北美也有一些特有科、目未能通过白令陆桥来到亚洲，如纽齿目(Taeniodontia)和古新世特有的全齿兽类(pantodonts)(如Pantolambdidae，Barylambdidae 等)。早始新世前后这一通道虽然比较畅通，但对某些动物的迁移仍很困难，如亚洲早始新世前后出现的原始梳趾鼠类和 Eurymyidae 等。欧洲类型的 ?*Propachynolophus* 在中国的出现，说明亚、欧两大陆之间这时也有过哺乳动物的交流。

大概由于早始新世后期气温逐渐下降，哺乳动物越来越不像始新世初那样容易通过纬度较高的白令陆桥，亚洲和北美哺乳动物交流相对减少，土尔盖海峡(Turgai Straits)也阻碍了欧亚两大陆哺乳类的交流。结果，中始新世时在亚洲繁衍出一些新的类型，如树鼩类(tupaiids)、原始高等灵长类——始猿类(eosimiids)、眼镜猴类(tarsiids)、仓鼠类、林跳鼠类和原始兔形类。同时，某些特有的科相当繁盛，如脊齿猴类(lophialetids)、戴氏猴类(deperetellids)、似鼠类(Tamquammyidae)、豫鼠类(yuomyids)和石炭兽类(anthracotheres)。然而，亚洲和北美、欧洲的哺乳动物交流仍未停止，只是规模不如早始新世初期。中始新世时亚洲哺乳动物与北美间的来往还是比欧洲多。我国哺乳动物与北美大陆共有的属有大眼镜猴(*Macrotarsius*)、沙犬(*Thinocyon*)、尤因他兽(*Unitatherium*)、中兽(*Mesonyx*)、沼雷兽(*Telmatherium*)、始爪兽(*Eomoropus*)、沼猴(*Helaletes*)、猴犀(*Hyrachyus*)等；但此时尚未发现与欧洲同期共有的属，不过江苏上黄发现的穴居似兔猴(*Adapoides troglodytes*)在形态上与欧洲中始新世的 *Europolemur* 相类似(Beard *et al.*，1994)。

始新世晚期亚洲与北美大陆哺乳动物间的交流似乎仍比亚洲与欧洲间频繁，中始新世出现的原始仓鼠、猯类(entelodonts)、石炭兽类、西猯类(tayassuids)等在卡特隆期进入北美。这时我国与欧洲也出现了一些共同的属，如 *Hyaenodon*、*Pterodon*、*Prohyracodon* 等。

亚洲始新世哺乳动物群与北美同属者占所发现的 20%；与欧洲同属的只有 8%。

始新世末渐新世初一些源于亚洲的哺乳动物先后迁入欧洲，如仓鼠类、林跳鼠类、兔形类、裂脚食肉类、进步的奇蹄类和偶蹄类(如雷兽、犀类、猯类、石炭兽类、猪类、西猯类等)。这些动物的进入，使欧洲渐新世与始新世哺乳动物群面貌有了明显的差异，出现所谓大间隔("Grande Coupure")。渐新世欧亚共同的属有真仓鼠(*Eucricetodon*)、始鼠(*Eomys*)、伪兽鼠(*Pseudotheridomys*)、链兔(*Desmatolagus*)、无角犀(*Aceratherium*)、猯(*Entelodon*)、脊齿鼷鹿(*Lophiomeryx*)、还有食肉类的半犬(*Amphicyon*)、指犬(*Cynodictis*)和 *Palaeogale*、*Nimravus* 等，占我国渐新世已知属的 24%。这个时期与北美相同的属不很多，除了肉食动物 *Hyaenodon*、*Palaeogale* 和 *Nimravus* 外，仅知 *Entelodon*、*Elomeryx*、*Leptomeryx*? 等，约占 12%。始新世末或渐新世初似乎是欧洲、亚洲以及北美大陆间新生代哺乳动物交流中的一个转折点，在这之前亚洲与北美大陆的交流是主要的，而自渐新世起亚洲与欧洲，甚至与北非的交往渐渐地占主导地位。也就是说，现代古北区在渐新世似已初见轮廓。

随着渐新世的结束和土尔盖海峡的消失，欧、亚大陆之间的哺乳动物逐渐出现更加频繁的迁移和扩散。虽然在中新世初期(谢家期)我国哺乳动物群与欧洲同一时代动物群相同的属还不多(也因为发现得不多)，但到了山旺期欧亚两大陆突然增加许多相同的属，如 *Microdyromys*，*Megacricetodon*，*Democricetodon*，*Amphicyon*，*Sansanosmilus*，*Gomphotherium*，*Anchitherium* 和 *Lagomeryx* 等。在各个地方动物群中相同的属一般占三分之一以上，如在下草湾动物群已知的 34 属中，与欧洲相同的属近占半数；通古尔动物群的 51 属中，与欧洲共有的达 26 属。

中新世至上新世已连成一体的欧亚大陆尽管存在局部生态小区上的差异，各自形成一些土著的动物类型，但欧亚大陆基本上属于一个草原—森林草原的自然环境，在这一广阔的区域中，生活着广义的三趾马动物群，相同的属就更多了，如内蒙古二登图动物群的 52 属中有 34 属可以在欧洲同时代的动物群中找到。

晚第三纪时，亚洲与北美哺乳动物的交流也远没有与欧洲的那样广泛，也许是连接两大陆的白令陆桥时通时断，使迁移和扩散受到限制。中新世的通古尔期与北美同期相同的属相对较多，如 *Leptodontomys*，*Anchitheriomys*，*Amphicyon*，*Serridentinus*，*Anchitherium* 等，在通古尔动物群中约占总数的 23%；但在整个晚第三纪，相同属的比例约为 13%—14%，与渐新世的比例接近。

在第四纪我国与欧洲不仅仍有许多相同的属，如 *Erinaceus*，*Sorex*，*Talpa*，*Allocricetus*，*Mimomys*，*Apodemus*，*Ursus*，*Mustela*，*Hyaene*，*Felis* 和 *Tapirus* 等(约占 42% 左右，其中萨拉乌苏期达 56%)，而且有不少相同的种，如 *Crocidura russula*，*Castor fiber*，*Trogontherium cuvieri*，*Apodemus sylvaticus*，*Micromys minutus*，*Pitymys hintoni*，*Ursus etruscus*，*Meles meles*，*Sus scrofa* 和 *Palaeoloxodon namedicus* 等。这一期间与北美相同的属有 *Sorex*，*Mimomys*，*Microtus*，*Canis*，*Ursus*，*Mustela*，*Equus*，*Tapirus* 和 *Cervus* 等，所占比例虽比晚第三纪略有增加，但并不明显。

从上可见，我国新生代哺乳动物群与欧洲和北美有着密切的关系，属于世界性的哺乳动物属可以追溯到古新世。我国大部分与北美相同的属又都出现于欧洲大陆，这无疑说明自古新世以来哺乳动物通过白令陆桥在相当于现代全北区内的迁移和扩散即已存在。在这些相同的属中，大哺乳动物所占的比例较大。另外，与欧洲和北美相同的科和属所占比例的变化同土尔盖海峡和白令海峡的存在与否及全球气候的变化有关。自渐新世以来我国的哺乳动物与欧洲相同的属比北美的多，显然是由于白令陆桥所起的“过滤”作用。

中国新生代哺乳动物群不仅与欧洲和北美，而且与南亚和北非都有密切的关系。与南亚的交流也至少可以追溯到早始新世晚期印度板块和欧亚板块连接的时候。随着特提斯海(Tethys)向西退缩，东亚(亚洲本土)与南亚次大陆的哺乳动物的交往变得更加明显。近二十年的研究表明，巴基斯坦与印度始新世早—中期哺乳动物大部分种类肯定是从亚洲本土进入，后在当地演化而成的(Sahni，1989)。我国南方晚第三纪和第四纪哺乳动物在组成和生态上与南亚的相似就更明显了。石炭兽类也见于北非的始新世晚期和渐新世早期地层中。更为值得注意的是渐新世时亚洲与北非哺乳动物之间的交流，北非早渐新世也有 *Hyaenodon* 和类似 *Pterodon* 的 *Apterodon* 属。中中新世我国与北非相同的

属至少有 *Atlantoxerus*, *Microdyromys* *Protalactaga* 和 *Democricetodon* 四属。东亚与北非哺乳动物的交流和扩散路线除通过中东外，西欧与北非的陆桥也不可排除。

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参　考　文　献

王蓉，沈后，1992. 孢粉资料定量研究古气候的尝试. 石油学报，**13**(2)：184—190.

叶得泉，钟筱春，姚益民等，1993. 中国油气区第三系：总论. 北京：石油工业出版社.

童永生，王景文，1994. 山东昌乐早始新世五图组多瘤齿兽类(哺乳纲). 古脊椎动物学报，**32**(4)：275—284.

童永生，郑绍华，邱铸鼎，1995. 中国新生代哺乳动物期. 古脊椎动物学报，**33**(4)：290—314.

Beard K C, Qi T, Dawson N R *et al.*, 1994. A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature*, **368**: 604—609.

Sahni A, 1989. Eocene rodents of South Asia: origins, disperals, and Paleoecology. In: Black C C., Dawson M R eds. Papers on fossil rodents. in honor of A E Wood. *Nat. Hist. Mus. Los Angeles County. Sci. Ser.* **33**: 147—156.

EVOLUTION OF CENOZOIC MAMMALIAN FAUNAL REGIONS OF CHINA

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Summary

Since the Cenozoic, changes of mammals in taxonomic composition and distribution have taken place in China, mainly due to collision of plates, changes of topography and climate. The paper discusses some problems of ecology and biogeography involving the Chinese Cenozoic mammals, after the recognition of the 18 mammal ages based on nature and magnitude of the faunal changes (Tong *et al.*, 1995).

Biogeographic provinces and ecology

China is vast in territory and the climate between the northern and southern parts differs. The present mammalian distribution indicates distinct provinciality and latitudinal ecological variation in taxonomic composition, which demonstrate two

zoogeographical provinces. Roughly, a line from the Qin Ling Mt. to the Huaihe River separates the northern Palearctic realm from the southern Oriental realm.

Although the updated collections are not large enough to delimit zoogeographical regions throughout the Cenozoic, the record demonstrates a long and complicated course of zoogeographical differentiation leading to formation of the present faunal provinces (Fig.1).

Paleocene

During the Paleocene the Tethys Sea separated the southwestern part of China from the Indian Plate. Most of the Chinese territory spanned latitudes 5°—40°, with a subtropic semiarid-arid environment (Wang & Shen, 1992). Most remains were collected from the central part of China, but late Paleocene mammals also occur in Nei Mongol and Xinjiang. Faunal composition of central China corresponds basically to that of North China; minor differences are the taeniolabidids in the northern faunas of the later Paleocene. This may imply an existence of provincial ecological variation during the late Paleocene.

Eocene

During the Eocene the Tethys disappeared due mainly to the collision of the Indian plate and the Eurasian plate. Faunal composition differs between the eastern coast and central part of China in the early Eocene. For example, the rodent assemblage in the Wutu Fauna in the east is dominated by paramyids, while central China faunas are composed mainly of primitive cocomyid, tamquammyid and yuomyid ctenodactyloids. In addition, the Wutu Fauna, including carpolestid plesiadapoids, neoplagiaulacid multituberculates and soricid / echinosoricid-like insectivores, seems to reflect a warm and moist environment, while central faunae and florae appear to inherit a relatively drier Paleocene climate.

All the middle Eocene faunas found in this country are quite similar in composition; minor differences are the relative abundance of Deperetellidae, Indricotheriinae and other rhinocerotids of the Sharamurunian upper Lumeiyi Fauna in Yunnan, indicating probably a warmer and moister environment for the southern fauna.

In the later Eocene the high diversity of Artiodactyla in South China contrasts to North China. The Nadu Fauna of Guangxi includes 5 genera of anthracotheriids, two each of ruminants, suids and tayassuids, while in the Zhaili Fauna of Shanxi no suid or ruminant, and only two anthracotheriids have been found. This might suggest an initial differentiation in faunal elements in China.

Generally speaking, mammals from southern China in the Eocene are identical at the family level with those of northern China. The Eocene faunas indicate a transitional environment from dry to moist during most of this period, except the

early Eocene fauna of the eastern coast and the late Eocene fauna in the south, which reflect a rather warmer and moister environment.

Oligocene

Definite Oligocene faunas are known only from North China. The Ulangochuian faunas, containing specialized brontotheriids and amynodontids, might indicate a relatively moist environment, but other middle and late Oligocene faunas, consisting mainly of *Tataromys*-like ctenodactyloids, cylindrodontids, zapodids and ochotonids, reflect a temperate semiarid or dry climate. It is likely that a faunal province preceding the present day Palearctic Region was initiated in North China during the Oligocene.

The Qinghai－Xizang Plateau obviously rose to an altitude that began to effect paleobiogeography at this time.

Miocene

With the uplift of the Qinghai－Xizang Plateau, differentiation in distribution of mammals between North and South China became more distinct in the Miocene.

The middle Miocene Tunggur Fauna in the North includes 5 of 6 families of land mammals living today in the Chinese Holarctic Region, but not a single family which is limited to the present-day Oriental Region. These families are Castoridae, Zapodidae, Ochotonidae, Dipodidae and Gliridae. The Kaiyuan Fauna of the same age in the South, however, contains apes, *Tapirus*, and *Propotamochoerus*, which represent the Oriental Region today, and lacks any family particular to the Palearctic Region. This indicates that the Tunggur Fauna in North China is more Holarctic in character, while the southern Kaiyuan Fauna is more Oriental during the middle Miocene.

The latitudinal ecological variation in faunal elements was more obvious during the late Miocene. The Ertemte Fauna of Nei Mongol contains families peculiar to, or mainly distributed over the Holarctic and Palearctic Regions, such as Erinaceidae, Castoridae, Zapodidae, Gliridae, Dipodidae, Cricetidae, Siphneidae and Ochotonidae. No family of mammals only known in the Oriental Region occurred in the Ertemte Fauna. The Lufeng Fauna of Yunnan presents families peculiar to, or mainly concentrated in the Oriental Region and the tropical or subtropical areas, such as Pteropidae, Hipposideridae, Tupaiidae, Echinosoricidae, Platacanthomyidae, Rhizomyidae, Hystricidae, Hylobatidae, Viverridae, Tragulidae. It is clear that the Ertemte Fauna reflects a temperate zone, like the drier steppic environments of the Holarctic Region, while the Lufeng Fauna reflects a tropical or subtropical mesic forest environment like that of the present day Oriental Province. The Lufeng Fauna contains Cricetidae and Castoridae which flourish in the Palearctic Region today. This may imply that the zoogeographical differentiation was not as distinct in late Miocene time as it is

today.

Pliocene

Such a differentiation in Pliocene time was similar to that of the late Miocene, but possibly became more distinct during the Pliocene. Cricetids no longer occurred in the Yunnan area, and rhizomyids withdrew from Shanxi of North China during this time.

Pleistocene

Generally, distribution of mammals at the family level during the Pleistocene was consistent with that of the present day.

This indicates that two distinct zoogeographic divisions, the Palearctic realm and the Oriental realm, existed in China at this time. Nevertheless, the two provinces were not as distinct at the beginning of the Pleistocene as they are today and there continued certain Yushean vestiges. In the early Nihewanian some taxa distributed in the Palearctic Region today, such as cricetids and arvicolids, occurred south of the Yangtze River, and some present-day Oriental Region taxa, rhizomyids, hystricids and viverrids for instance, spread into North China.

Since the middle Nihewanian, dispersal or immigration events frequently took place between the two provinces, due probably to global climatic shifts. A relatively warm and moist climate in the middle and late Nihewanian was suggested by the chiefly northward immigration of mammals from the south. Some taxa, such as *Hystrix*, *Stegodon*, *Ailuropoda* and *Tapirus* spread far up into North China at this time. Records of mammalian fossils also indicate alternate changes of warm and cool climates during the Zhoukoudian age.

In a word, the history of differentiation of mammals in China can be traced back to the collision of the Indian plate and Eurasian plate in Eocene. The change of environment and differentiation of mammals between North and South China seems to be related to the forming and uplifting of the Qinghai－Xizang Plateau.

Biogeographic relationships

Most of the Chinese early and middle Paleocene mammals are confined to East Asia. These endemic taxa are Anagalida, Bemalambdidae, Harpyodidae, Archaeolambdidae, Pastoralodontidae, Didymoconidae, Phenacolophidae, etc. About 42% of the total families are shared with North American faunas. They are Mesonychidae, Hyopsodontidae, Esthonychidae, Viverravidae, Arctostylopidae and others. This seems to imply an existence of close phylogenetic relationship between the mammals of Asia and North America, but only at the taxonomic level of the family. The records appear to show that hyopsodontids and viverravids might have immigrated from North America to Asia, and mesonychids, esthonychids and

arctostylopids spread in the opposite direction. During the Paleocene, only one or two families are shared with Europe.

Some cosmopolitan genera are found in the early Eocene faunas of China. Among them, *Miacis*, *Coryphodon*, *Dissacus*, *Hyopsodus* and *Hyracotherium* are commonly known in Europe and North America, *Hapalodectes*, *Homogalax*, *Heptodon* and *Acritoparamys* can be seen in North America, and ? *Propachynolophus* is found in Europe. It appears that dispersal of mammals between Asia and North America, via Bering land bridge, had taken place to some extent during the early Eocene.

At the end of early Eocene, a clear decrease of temperature is indicated. Dispersal of mammals between Asia and North America was distinctly reduced, and some new families restricted to Asia, such as Tupaiidae, Tarsidae, Eosimidae, Cricetidae, Lophialetidae and Deperetellidae, developed in the middle Eocene. Limited interchange of mammals between Asia and North America continued, and indicated by a number of congeneric forms, such as *Macrotarsius*, *Thinocyon*, *Unitatherium*, *Mesonyx*, *Telmatherium*, *Eomoropus*, *Helaletes* and *Hyrachyus*, but no congenus has been found yet from the middle Eocene of Europe.

In the late Eocene there were a few cosmopolitan genera. *Hyaenodon* and *Pterodon* were found either in Europe or in North America. A considerable dispersal still took place between Asia and North America at this period, but the variety of immigrants entering Europe was less than that entering North America.

On the whole, among the known Chinese Eocene mammals, about 20% are congeneric with North American representatives and 8% with Europe.

At the end of the Eocene and beginning of the Oligocene, some Asian original taxa, such as ciricetids, zapodids, lagomorphs, fissiped canivores, advanced perissodactyls and some artiodactyls (entelodontids, anthracotheres, suids and tayassuids) migrated to Europe. This invasion influenced European faunas greatly and numerous genera (*Eucricetodon*, *Eomys*, *Pseudotheridomys*, *Desmatolagus*, *Amphicyon*, *Cynodictis*, *Palaeogale*, *Nimravus*, *Aceratherium*, *Entelodon*, *Lophiomeryx*, etc.) occurred in the Eurasian Oligocene faunas. The congenera with Europe in Chinese Oligocene faunas amount to 24%. As contrasted to Europe, fewer common genera with North American faunas are known at this time (12%). It is likely that Oligocene time was a turning point in the history of mammalian dispersal events. Before this, during Paleocene and Eocene epochs, immigrations chiefly happened between Asia and North America, but less importantly between Asia and Europe. It is highly suggestive that formation of the Palearctic realm began in Oligocene time.

With the end of the Oligocene epoch and disappearance of the "Turgai Straits", immigration of mammals between Asia and Europe increased progressively. Congeneras with European faunas jumped in Shanwangian age. Usually, more than one third of

the genera found in Shanwangian faunas are shared with Europe. Such taxa are *Microdyromys*, *Megacricetodon*, *Democricetodon*, *Amphicyon*, *Sansanosmilus*, *Gomphotherium*, *Anchitherium*, *Lagomeryx* and others. Immigration and dispersal of mammals between Asia and Europe further developed during the middle Miocene. In the Tunggur Fauna, about half of the genera have systematic relationships with Europe.

In the late Miocene and Pliocene, more genera, especially those from North China, had a Palearctic distribution. In the Ertemte Fauna, for example, 34 of 52 genera can be found in Europe. Assemblages from China and Europe of this age may differ in ecotype, but they belong to the same *Hipparion* fauna (sl) of a great, dry steppes as suggested by Kurten in 1951.

During Neogene time, mammals congeneric with North America are much fewer than those with Europe (Fig.2). This may indicate that the path connecting the two continents was sometimes interrupted and dispersal of mammals between Asia and North America was restricted during this period. Common genera with North America did increase in quantity (23%) in the Tunggur Fauna. These genera include *Leptodontomys*, *Anchitheriomys*, *Amphicyon*, *Serridentinus* and *Anchitherium* and others. As a whole, however, the proportion of congenera with North America in the Neogene is almost the same as in the Oligocene.

In the Pleistocene faunas, about 42% of the total genera such as *Erinaceus*, *Sorex*, *Talpa*, *Allocricetus*, *Mimomys*, *Apodemus*, *Ursus*, *Mustela*, *Hyaena*, *Felis* and *Tapirus* are congeneric with contemporary European faunas. In the Salawusuan faunas, congeners amount to 56% of the total. Pleistocene assemblages share not only genera, but also some forms at the species level, such as *Trogontherium cuvieri*, *Pitymys hintoni*, *Ursus etruscus*, *Paleoloxodon namedicus* in Nihewanian faunas, and *Crocidura russula*, *Castor fiber*, *Apodemus sylvaticus*, *Micromys minus*, *Mustela eversmani*, *Meles meles*, *Canis lupus*, *Sus scrofa*, *Cervus elaphus* in Zhoukoudian faunas. Congenera with North America, for example *Sorex*, *Mimomys*, *Microtus*, *Canis*, *Ursus*, *Mustela*, *Equus*, *Tapirus*, and *Cervus* are also found in the Pleistocene faunas.

From the above, Chinese mammals have close biogeographic relationships with both Europe and North America. Cosmopolitan genera can be found back to the late Eocene and most taxa showing affinity with North America are also found in Europe. This implies that an interchange of mammals, via the Bering land bridge, had taken place in Holarctic Region since the Eocene. Among these genera large mammals dominate small mammals. This might be explained by large mammals having a great ability for far-ranging migration than small mammals. Since the Oligocene, the greater similarity of the Palearctic Chinese mammals to those of Europe than North America may reflect filtering action of the Bering land bridge.

Close biogeographic relationships of Chinese mammals with South Asia and North Africa are also notable, and these can be traced back to Eocene time. Study in the last 20 years shows that quite a few Eocene mammals from the Indian subcontinent migrated from eastern and central Asia (Sahni, 1989). It is obvious that Neogene mammalian faunas of South China were related to those of the subcontinent in composition and ecology. Statistics show that about 20% of the genera from the early Nihewanian faunas are share with Pinjor faunas. These congenera are *Hystrix*, *Lutra*, *Canis*, *Virerra*, *Megantereon*, *Rhinoceros*, *Stegodon* and others. The Chinese Eocene anthracotheriids have long been known for their affinities to those of North Africa. Other taxa shared by the two continents can be seen in successive faunas; e.g. *Hyaenodon* in the Oligocene and *Atlantoxerus*, *Microdyromys*, *Protalactaga* and *Democricetodon* in the Miocene.

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