

关于大角鹿类的进化

伊·维斯洛博柯娃

胡长康

(苏联科学院古生物研究所) (中国科学院古脊椎动物与古人类研究所)

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内 容 提 要

本文讨论了从中新世末期到晚更新世在欧亚大陆已绝灭的大角鹿类。原始大角鹿头骨某些特点与晚中新世的 *Cervavitus* 鹿相似。已知欧洲最古老的大角鹿化石是 *Neomegaloceros gracilis*, 亚洲是 *Praesinomegaceros asiaticus*。更新世时欧洲大角鹿类存在两个支系: 一支与 *Megaceros giganteus* 相连, 另一支与 *Praemegaceros verticornis* 相连。中国大角鹿类由晚上新世在苏联塔什干地区发现的塔什干大角鹿 *Sinomegaceros tadzhikistanis* 进化而来。

大角鹿类(鹿亚科 Cervinae, 大角鹿族 Megacerini) 是一类相当古老、已绝灭的鹿类。这一类鹿从中新世末期出现到目前为止已知有下列 8 个属: *Megaceros* Owen, 1844, *Sinomegaceros* Dietrich, 1933, *Praemegaceros* Portis, 1920, *Praedama* Portis, 1920, *Arvernoceros* Heintz, 1970, *Neomegaloceros* Korotkevitch, 1971, *Orchonoceros* Vislobokova, 1979 和 *Praesinomegaceros* Vislobokova 1983。

这一类鹿的进化历史, 在更新世阶段了解得较多, 几乎所有的学者都认为大角鹿在欧洲更新世时期存在两个分支: 一支与 *Megaceros giganteus* 相连 (Blumenbach, 1803), 另一支与 *Praemegaceros verticornis* (Dawkins, 1872) 相连; 尽管他们对这些鹿类的系统位置的看法不同 (Azzaroli, 1953; Ambrosetti, 1967; Radulesco, Samson, 1967; Gliozzi, Malatesta, 1982 等)。在亚洲更新世时期存在 *Sinomegaceros* (Young, 1932; Shikama, 1938; Shikama, Tsugawa, 1962 等)。

大角鹿类的早期历史知道得较少。它们的祖先似乎属于 Pliocervini 族(晚中新世—上新世), 包括一些鹿亚科中比较原始的代表。古老大角鹿头骨上一些形态特点类似于 *Cervavitus* Chomenko, 1913 (= *Cervocerus* Chomenko, 1913)——一类小型的原始鹿类, 具有扁平的角, 在晚中新世—早上新世广泛分布于东欧到中国的古北区温带地区。

在东欧最古老的大角鹿化石是 *Neomegaloceros gracilis* Korotkevitch 1971, 发现于苏联阿那吉尔到黑海北部的上中新世地层。亚洲最古老的大角鹿化石是蒙古 Hircis-Nur II 上中新世地层中的 *Praesinomegaceros asiaticus* Vislobokova, 1983。这种鹿的个体大小中等。雄性的具有扁平的角, 带有第一枝。第一枝在离角柄部有一相当距离处分叉。*Neomegaloceros gracilis* 的化石以一个近乎完整的左角和肢骨的破块为代表 (Korotkevitch, 1971)。根据 *N. gracilis* 的角的主枝的上部的形状和大小与 *Cervavitus variabilis* 的相似, 不同的是 *N. gracilis* 的角的第一枝的位置较高和有一很发育的后

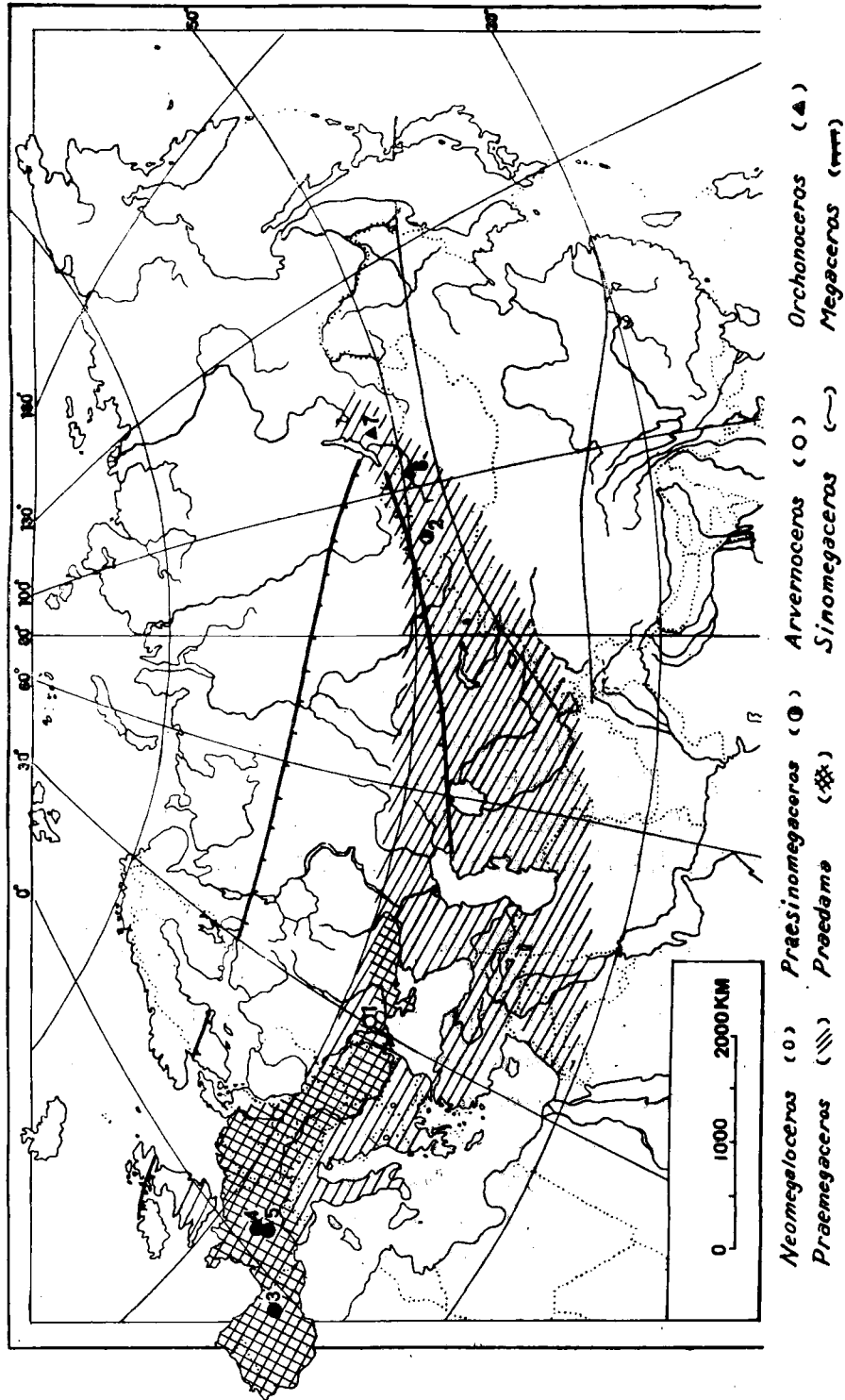


图1 几个大角鹿类地点及地区

Fig. 1 Some Megacerine localities and areas

- 1. Ananjev; 2. Hirgis-Nur; 3. Villaroya; 4. Etouaires; 5. Vialette; 6. Shamar; 7. Bergovaja

枝。这些差异使 *N. gracilis* 接近于 *Praemegaceros* 分支。*Praesinomegaceros asiaticus* 化石以一块角的基部,一块残破带有 D_1-M_2 的下颌骨,几块肢骨破块为代表,*P. asiaticus* 的角比 *N. gracilis* 的大些,它的第一枝的位置较低,呈水平的扁平型,在主枝和第一枝之间有一小的掌状突起,在上面增加了一分枝。下颌骨的肿厚程度中等。牙冠高度也适中。

大角鹿类的进化,总的说来是通过一系列的进步性的分化进行的,如身体体积的增大,社会化器官 (social organs) 的分化,头骨的变化致使感觉器官和营养孔特性的改进和能承受一个大而重的角的适应,下颌骨肿厚度的增强和骨架的粗壮。在晚更新世肿骨鹿类中显出身体和头骨的缩小和角的退化。在大角鹿类不同支系中各种特性的进化率是不同的。中更新世和晚更新世的大角鹿 (*Megaceros giganteus*) 的身材达到了最大的程度。它们的角的伸展长度可达 4 米,体重可达 43 公斤 (Geist, 1986)。它的角和有关身体的大小平均数显出它的角和身体正异速增长 (positive allometry, Gould, 1973)。根据 Gould (1973), 大角鹿 *M. giganteus* 的角,总的说来,与身体的大小相符合。Barnosky (1985) 的意见,在爱尔兰 Ballybetagh 泥炭层中的大角鹿化石具有比较小的角,这个现象和恶劣的环境相联系。

中国大角鹿属 (*Sinomegaceros*) 的一些种达到巨大型的时期似乎比大角鹿 (*M. giganteus*) 早一些。在苏联塔吉干 Lakhuti 村附近的 Kayrubak Suite 的沉积中发现了一种很大的中国大角鹿属类的化石。根据古地磁的资料该沉积的时代为 0.75—0.9 ma。这个雌性的头骨从头骨基点 $-P^2$ (Basion— P^2) 的长度大约为 29.85 厘米。

在进化过程中鹿的身体大小的增长主要和自然选择相联系,这种自然选择的倾向为整个居群的生存可能是最理想了。身体大小与环境非常符合,根据 Geist (1971), 在比较短的时期中侵占新的居住地和生存是大型身体为首迁居群 (pioneer population) 的特性。显示大角鹿扩散中的居群曲线在今后的研究中是可能的。目前的资料只能得到它们进化的一般趋势。

大角鹿类早上新世时期的进化仍旧是空白。当亚洲类型的后代到达西欧时似乎有一纬度迁栖时期,同时欧洲类型的有关种类迁栖到中亚地区。从晚上新世开始大角鹿在动物群的组成中起了显著的作用,从那个时候开始在大角鹿的进化中可以观察到三个支系:*Arvernoceros-Megaceros* 支系, *Sinomegaceros* 和 *Orchonoceros-Praemegaceros* 支系, *Arvernoceros-Megaceros* 和 *Sinomegaceros* 支系的根似乎又回到 *Praesinomegaceros*, *Orchonoceros-Praemegaceros* 支系,明显地,起源于 *Neomegaloceros*, 这些支系早期代表角的构造与晚中新世类型角的构造相似。*Arvernoceros ardei* Heintz, 1970 化石发现于法国和西班牙早维拉方的地点 (MN 16) (Heintz, 1970)。这是一种中等大小的鹿具有长长的头骨角后部和角柄从前额面稍稍倾斜,距离接近。这种鹿的特点具有简单的角,带第一支位在角节部上一段距离上。第一支是水平方向扁平,常常外加一小支。主枝微向后倾斜。掌状部小,离角节部较远。掌状部的平面近于垂直、牙冠高度中等,前臼齿列长、四肢纤细。

Arvernoceros-Megaceros 支系的发展趋势与大角鹿进化的总趋势相一致。这支系的代表角的变化与第一支的趋短、趋扁平 and 掌状部分适当发展相联系。下颌骨肿厚度的

增加;但它们的肿厚度未达到中国大角鹿属的肿厚度。

最原始的中国大角鹿属的代表,显然是发现于苏联塔什干的 Navrucha, Kuruksai Suite 的沉积中 (MN 17) 的 *Sinomegaceros tadjikistanis* Vislobokova. 这种鹿与 *Arvernoceros* 鹿相似,第一支带有附小支;主枝长,掌部狭;但是第一支的位置和方位与 *Arvernoceros* 属不同,是更新世中国大角鹿类前期特点。塔什干中国大角鹿,显然是已知中国大角鹿种类的祖先,如陕西兰田中更新世早期的公王岭大角鹿 (*S. konwanliensis* Chow, Hu et Lee, 1965) 周口店第一地点中更新世的肿骨鹿 (*S. pachyosteus* (Young 1932), 周口店第九,第十三地点中更新世的扁角肿骨鹿 (*S. flabellatus* Teilhard 1936, (Loc. 9, Young 1932; Teilhard de Chardin, 1936, Kahlke, Hu, 1957; Chow, Hu, Lee, 1965; Hu Qi, 1978)。

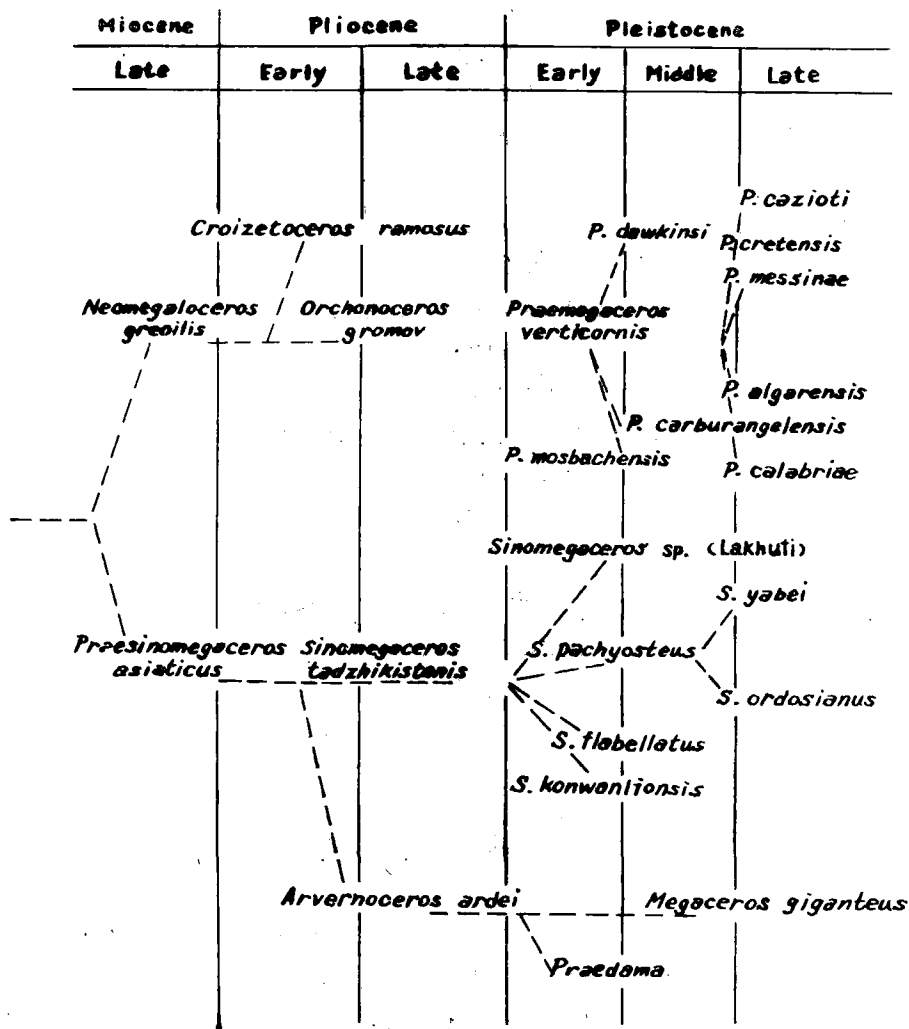


图2 大角鹿类进化略图

Fig. 2 The schema of evolution of megacerines

中国大角鹿属进化的结果是第一支强烈的扩展。向外扩展,与头骨矢状面呈一垂直的位置。中国大角鹿属的特点是角的主枝扁平,头骨和下颌骨强烈的肿厚。角的增大,相应地主枝向后向外的弯度增大和主枝上部向内转。中国大角鹿头骨构造某些原始特点(特别是短吻部,长头后角部)显示大角鹿的古老和代表一独立的支系。中国大角鹿属在晚更新世以中国北部(内蒙河套地区)的河套大角鹿 [*S. ordosianus*, (Young, 1932)] 及日本的 *S. yabei* (Shikama, 1938; Shikama, Tsugawa, 1962; Hasegawa, Ono, Otsuka, 1980) 为代表。晚更新世种的角的构造显示一些退化的特点,如角的大小和扁平程度都缩小了。中国大角鹿属的分布明显地限于亚洲内部。它们的分布界限似乎不超过北纬 50° ,在中亚和从日本至塔什干的东亚。北部界线与气候的条件和其他自然障碍的存在相适应。在晚更新世这地区移到亚洲的东南。

Orchonoceros—*Praemegaceros* 支系的进化是角的扁平程度和肿厚程度与其他支系比较起来都比较弱。*Orchonoceros gromovi* Vislobokova, 1979 具有赤鹿 (*Cervus elaphus* L.) 的大小。这个种的化石发现于蒙古 Shamar (MN 16) 和外贝加尔湖的 Beregovaja。*Orchonoceros* 在头骨和角的构造上与 *Praemegaceros* 相近,不同的是 *Orchonoceros* 有一长的脑腔和在主枝上缺乏 *Praemegaceros* 弯曲。第一支短,与主枝成锐角。

晚上新世副地中海的海侵,它的北岸可达北纬大约 57° ,这一重要事件影响了大角鹿类的分布。这个海侵似乎造成了这种北方类型如 *Arvernoceros* 和 *Sinomegaceroses* 扩散的障碍,也增加了欧洲和亚洲动物群的动物地理差异。

在早更新世时 *Orchonoceros* 被 *Praemegaceros* 替代。*Praemegaceros* 最老的化石与东欧 Taman 动物群组合相连系 (0.8-1 ma)。在塔什干的 Lakhuti 和在外贝加湖的 Zasuhino 发现的 *Praemegaceros* 化石是这个时期的。卡尔克 (Kahlke 1971) 发现的产有 *Praemegaceros* 化石地点 (Haprii, CisAzov) 的时代相当于中维拉方时期。

在中欧第一个 *Praemegaceros* 发现于 Cromerian, 当时 Cromerian 这地区在北欧亚温带区占有广阔的面积。在明德时期,它从大不列颠扩展到贝加尔湖。*Praemegaceros* 南边界线到达北纬 30° 。在中更新世 *Praemegaceros* 几乎到处被 *Megaceros* 排斥。在地中海隔离时期, *Praemegaceros* 的孤立子遗留下来。这一支系的后代,在晚更新世居住在科西嘉岛、撒丁岛、西西里岛和克里特岛。

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ON THE EVOLUTION OF MEGACERINES

Inesa Vislobokova

(Paleontological Institute of the USSR Academy of Sciences)

Hu Changkang

(Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica)

Key words Megacerines; evolution; Eurasia

The megacerine deer (the tribe Megacerini of the subfamily Cervinae) is a rather ancient extinct group, known from the end of the Miocene. The tribe comprises 8 genera: *Megaceros* Owen, 1844, *Sinomegaceros* Dietrich, 1933, *Praemegaceros* Portis, 1920, *Praedama* Portis, 1920, *Arvernoceros* Heintz, 1970, *Neomegaloceros* Korotkevitch, 1971, *Orchonoceros* Vislobokova, 1979 and *Praesinomegaceros* Vislobokova, 1983. The Pleistocene history of megacerines is much studied regarding the evolutionary stage of these deer. Almost all students recognize the existence of two branches of megacerines in the Pleistocene of Europe: one of these connected with *Megaceros giganteus* (Blumenbach, 1803) and the other with *Praemegaceros verticornis* (Dawkins, 1872), although the estimations of the systematic range of these cervids are different (Azzaroli,

1953; Ambrosetti, 1967; Radulesco, Samson, 1967; Gliozzi, Malatesta, 1982 and others). In the Pleistocene *Sinomegaceros* of Asia existed (Young, 1932; Shikama, 1938; Shikama, Tsugawa, 1962 and others).

The early history of megacerines is less clear. The ancestor of megacerines seems to have belonged to the tribe Pliocervini (Late Miocene—Pliocene), containing more primitive representatives of the subfamily. Some of morphological peculiarities of the skull of the ancient megacerines resemble these of *Cervavitus* Chomenko, 1913 (= *Cervocerus* Chomenko, 1913)—a small primitive deer with flattened antlers, widespread in late Miocene—early Pliocene in temperate zone of the Palearctic from East Europe to China. A number of these peculiarities, revealed by comparison of *Orchonoceros gromovi* Vislobokova, 1979 and *Cervavitus variabilis* skulls (Alexejev, 1913), are the following: an elongated post-antler part of the skull, a very weak deflection of the pedicles from the plane of the forehead, the form and the length of the basioccipitale, a declination of the basicranial line, a degree of the axial divergence of post-glenoid processes and tympanicum part in regard to the sagittal plane of the skull, the narrow rising part of orbitosphenoid, etc. (Vislobokova, 1981).

The most ancient remains of megacerines in East Europe belong to *Neomegaloceros gracilis* Korotkevitch, 1971 from the Upper Miocene of Ananjev to the north of the Black Sea, the USSR. The most ancient megacerine in Asia is *Praesinomegaceros asiaticus* Vislobokova, 1983 from the upper Miocene of Hirgis-Nur II, Mongolia (Fig. 1). They were medium-sized animals. The males had flattened antlers with the first tine, branching off at some distance above the burr. The remains of *Neomegaloceros gracilis* are represented by almost a complete left antler and fragments of limb bones (Korotkevitch, 1971). By dimension and form of the upper part of the beam an antler of *N. gracilis* resembles that in *Cervavitus variabilis*, differing from the latter by a higher position of the first tine and a developed posterior tine. These differences approximate *N. gracilis* to the *Praemegaceros* branch. *Praesinomegaceros asiaticus* is represented by a basal part of an antler, a fragment of a lower jaw with D_4-M_2 and fragments of limb bones. The antler of *P. asiaticus* is larger than that of *N. gracilis*. It displays a lower placed first tine, horizontally flattened. There is a small palmation between the beam and the base of the tine, bearing an additional tine on the upper edge. The hyperostosis of the lower jaw is moderate. The height of the crown is also moderate.

The evolution of megacerines, on the whole, went through a series of progressive specialization of social organs, directional changes of the skulls due to an improvement of sense organs and peculiarities of a nutrition, an accommodation for wearing large and heavy antlers, an intensification of hyperostosis of the lower jaw and a massiveness of the skeletons. A diminution of a body-size and skull feature and antler degeneration are marked among megacerines in late Pleistocene. The rate of evolution of separate characters in different branches of megacerines was not identically the same. *Megaceros giganteus* from middle and late Pleistocene was, apparently, maximum in size. The span of its antlers reached 4 m, and the weight was up to 43 kg (Geist, 1986). The comparative investigation of the dimension of an antler and a body-size showed the positive allometry of its antlers in relation to the body (Gould, 1973). According to Gould (1973), the antlers of *M. giganteus*, on the whole, corresponded to the size of the body. In Barnosky's (1985) opinion, the findings of remains of samples of *M. giganteus* with smaller antlers, in particular, in Ballybetagh Bog, Ireland, were connected with bed environments.

The species of the genus *Sinomegaceros* seem to have reached the stage of giantism much earlier than *M. giganteus*. The remains of a very large *Sinomegaceros* were discovered in the deposits of the Kayrubak Suite near Lakhuti Village, Tadjikistan, the USSR. The age of these deposits, according to the paleomagnetic data, was 0.75—0.9 ma. The Basion-P³ length of the female skull (no. 3858/676) is about 29.85 cm.

Increase of the deer body-size during the course of evolution was mainly connected with a trend of natural selection, providing such dimension of specimens which could be optimal for the existence of a whole population. The body-size was in close accordance with the environments. In According to Geist (1971), the large body-sizes are characteristic for pioneer population, invading new habitats and existing during a comparatively short period of time. It is possible, the future investigations allow to reveal population waves in megacerine dispersion. Available data permit to catch only the common trends of their evolution.

The early Pliocene evolution of megacerines is still a blank. It seems to have been a period of latitudinal migrations when the descendants of Asian forms had reached West Europe and the relatives of European forms had come to the districts of Central Asia. From the beginning of late Pliocene on megacerines played a marked role in composition of faunas. From that time three lineages were observed in their evolution: *Arvernoceros-Megaceros*, *Sinomegaceros* and *Orchonoceros-Praemegaceros* (Fig. 2). The roots of the *Arvernoceros-Megaceros* and *Sinomegaceros* lineage seem to go back to *Praesinomegaceros*, and the *Orchonoceros-Praemegaceros* lineage, apparently, originated *Neomegaloceros*. The early representatives of these lineages had the similar antler structure as those of the late Miocene megacerines.

The remains of *Arvernoceros ardei* Heintz, 1970 is known from the early Villafranchian localities of France and Spain (MN I6) (Heintz, 1970). It was the medium-sized deer with elongated antler part of the skull and closely spaced pedicles, slightly declined from the forehead plane. It is characterized by simple antlers with the first tine set at some distance above the burr. The first tine was horizontally flattened and bore often an additional small tine. The beam was slightly declined backwards. The palmation awes small, situated far from the burr. the plane of palmation is nearly vertical. The height of the crown were moderate. The premolar row was long. The limbs were slender.

The trends of development of the *Arvernoceros-Megaceros* lineage corresponded to the general tendency of the megacerine evolution. The changes of antlers in representatives of that lineage were connected with flattening and shortening of the first tine and with the considerable development of palmation. The hyperostosis of the lower increased, but it did not reach the sizes of that in *Sinomegaceros*.

The most primitive representative of the genus *Sinomegaceros* was, apparently, *S. tadzikistanis* Vislobokova (in press) from the deposits of Kuruksai Suite, Navrucho, Tadjikistan (MN 17). It was similar to *Arvernoceros* in a form of the first tine with the accessory small tine, a long beam, a narrow palmation. But a position and an orientation of the first tine were distinct from those of *Arvernoceros*, anticipating characters of the Pleistocene sinomegacerines. *S. tadzikistanis*, obviously, was a predecessor of all the known Chinese species: *S. konwanliensis* Chow, Hu et Lee, 1965 from the base of the Middle Pleistocene of Gongwangling, Lantian, Shaanxi, *S. pachyosteus* (Young, 1932) from the Middle Pleistocene of Zhoukoudian (Loc. I), *S. flabellatus* Teilhard, 1936 from the Middle Pleistocene of Zhoukoudian (Loc. 9 Young, 1932; Teilhard de Chardin, 1936; Kahlke, Hu, 1957; Chow, Hu, Lee, 1965; Hu, Qi, 1978).

The evolution of *Sinomegaceros* was resulted in strong expansion of the first tine, its twisting outside to assume a position perpendicular to the sagittal plane of the skull. It is characterized by considerable flattening of the beam and a strong pachynosis of the skull and the lower jaw. The increase in the size of the antlers was accompanied by the increase of the beam bend backwards and sideways and twisting the upper part of the beam inward. Some of the primitive features of the skull structure of sinomegaceroses (in particular, the short muzzle, the long postantler part of the skull, peculiarities of the palatine bones) show that megacerine to be ancient and to represent a distinct lineage. Sinomegaceroses were represented in late Pleistocene by the species *S. Ordosianus* (Young, 1932) in north China (Inner Mongolia, Ordos) and *S. yabei* Shikama, 1938 in Japan (Shikama, 1938; Shikama, Tsugawa, 1962; Hasegawa, Ono, Otsuka, 1980).

The structure of antlers of late Pleistocene species shows some regressive features such as a deminution of size and flattening of antlers. The distribution of *Sinomegaceros* was obviously limited within the territory of Asia. The north boundary of their distributional did not seems to go beyond 50° n.l. They were distributed in the districts of Central and East Asia from Tadjikistan to Japan. The north boundary well corresponded to climate conditions and the existence of other natural barriers. In late Pleistocene this area had removed to the south-east of Asia.

The evolution of the *Orchonoceros-Praemegaceros* lineage was accompanied by weaker flattening of antlers and weaker increasing of hyperostosis in comparison with other lineages. *Orchonoceros gromovi* Vislobokova, 1979 attained the size of *Cervus elaphus* L. Remains of that species were determined from the base of the Upper Pliocene in Shamar, Mongolia (MN16) and Beregovaja, the Trans-Baukal. *Orchonoceros* was close to *Praemegaceros* in the structure of the skull and antlers, but it differed in having a long braincase and absence of a "*Praemegaceros*"-bend of the beam, a short first tine, making an acute angle with the beam.

The important event, which influenced the distribution of megacerines, was the late Pliocene transgression of the Paratethys, the north coast of which had reached about 57° n.l. That transgression seems to have made the barrier on the route of dispersion of such boreal forms as *Arvernoceros* and *Sinomegaceros*. It promoted the increasing of zoogeography differences of European and Asian faunas.

Orchonoceros was replaced by *Praemegaceros* in early Pleistocene. Most ancient remains of the latter was, apparently, connected with the Taman faunistic complex of East Europe (0.8—1 ma). The remains of *Praemegaceros* found in Lakhuti, Tadjikistan, and in Zasuhiro, the Trans-Baikal, obviously, are of that time. Kahlke (1971) marked the presence of *Praemegaceros* in Hapri, the CisAzov, correlated with the Middle Villafranchian localities. In Central Europe the first *Praemegaceros* was indicated in Cromerian, when their area took an ample territory in temperate zoon of North Eurasia. It extended from Great Britain to the Baikal in Mindel time. The southern boundary of *Praemegaceros* distributional area fallen to 30° n.l. *Praemegaceros* was almost everywhere ousted by *Megaceros* in middle Pleistocene. Separate relicts of *Praemegaceros* remained during insulation in the Mediterranean.

The descendant of that lineage inhabited Corsica, Sardinia, Sicily and Crete in late Pleistocene.