

# 关于柄杯鹿亚科 (*Lagomerycinae*) 的 系统位置

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**关键词** 柄杯鹿亚科 古鹿 系统位置

## 内 容 提 要

柄杯鹿亚科的系统位置争论已久。争论的焦点是它们属于鹿科中的亚科还是麒麟鹿超科。经过对头骨和头后骨骼形态特点的研究和用扫描电镜检查角的结构显出柄杯鹿具有原始的角,而这种原始的角与后期鹿类的角柄同源。因此认为柄杯鹿科是鹿类中独立的一分支。

1941 年 Pilgrim 建立了柄杯鹿科 *Lagomerycidae*, 这一科包含三个属 *Lagomeryx* Roger, 1904, *Procervulus* Gaudry, 1878, *Climacoceras* MacInnes, 1936。古生物学者对这些动物的系统位置已争论了很长时期: 1) 认为它们属于鹿科 *Cervidae* 中的一亚科(德日进, 1939; Crusafont Pairo, 1952; Viret, 1961; Vislobokova, 1983); 2) 认为是麒麟鹿超科 *Giraffoidea* 中的一科 (Pilgrim, 1941; Simpson, 1945; Young, 1964); 3) 麒麟鹿超科中古鹿科的同物异名 (Stirton, 1944; Withworth, 1958; Hamilton, 1973); 4) 认为属于麂类 (*Muntiacini*) (周本雄等, 1978)。

1904 年 Roger 记述 *Lagomeryx* 属的鹿是古鹿属 (*Palaeomeryx* Meyer, 1834) 的一小种, 带不脱落的角。模式种是奥地利 Goriach 中中新世的梅氏古鹿 (*Palaeomeryx meyeri* Hofmann, 1893)。有些学者怀疑 *Lagomeryx* 属的有效性, 认为它是 *Palaeomeryx* 属的同物异名 (Withworth, 1958; Hamilton, 1973)。*Procervulus* 属是 Gaudry (1878) 以法国 Pont-Levoy 地点的模式种 *Cervus aurelianensis* Gervais, 1859 为基础定的。有些学者认为 *Procervulus* 接近于鹿类 (Zittel, 1925; Ginsburg, Crouzel, 1976)。

MacInnes 把肯尼亚中中新世的 *Climacoceras* 属归于鹿科。1936 年 MacInnes 鉴定在 Maboko 发现的模式种 *Climacoceras africanus* 为一化石鹿。Hamilton (1978) 把 *Climacoceras* 属放在麒麟鹿超科中的 *Climacocervidae*。另一种从 Fort Ternan 发现的 *C. gentryi* Hamilton, 1978, 被记述了具有一双叶的下犬齿 (Hamilton, 1978)。

Ginsburg, Heintz (1966) 和邱占祥等 (1985) 的研究都详细说明了古鹿科 (*Palaeomerycidae*) 的分类位置。Ginsburg 和 Heintz (1966) 指出, *Palaeomeryx* 有确切的麒麟鹿型的皮骨角。山东临朐山旺中新世湖相沉积中完整的古鹿骨架 *Palaeomeryx tricornis* 的发现告诉我们, *Palaeomeryx* 比鹿类更具有麒麟鹿类的进化性质。*Palaeomeryx* 类只有一些近祖性状的特征 (Plesiomorphic characters) 与鹿类相似 (邱等, 1985)。有些进步特征, 例如一个封闭的蹠骨沟, 在这两类中可以通过平行进化获得的。古生物证据说明这一特征——鹿类的特点, 在反刍类不同类群中独立地进化, 特别是在 *Protoceratidea*, *Leptomerycidae* 和 *Moschidae* 中。邱占祥等的研究使人相信 *Palaeomerycidae* 是古老麒麟鹿类的一分支。

柄杯鹿亚科的角的构造与 *Palaeomeryx* 鹿的皮骨角的构造基本不同之处在于: 首先, 在柄杯鹿科中缺少额骨和皮骨角的分界线; 这一点在 *Palaeomeryx* 和麒麟鹿类中非常清楚。第二, 柄杯鹿亚科和 *Palaeomerycidae* 的角的构造是很不相同的。用 SEM (扫描电镜照相) 观察角的显微结构表明它与鹿的角柄 (Pedicel) 和不脱落角接近 (图版 I)。

杨钟健得到柄杯鹿类准确的系统位置的新资料是发现了山旺的一完整柄杯鹿 (*Lagomeryx colberti* Young, 1937) 骨架以后。*L. colberti* 的头骨比较接近于鹿科中最原始的亚科 *Dremotheriinae* 的代表, 这一类化石是中渐新世时期的。Ginsburg 和 Heintz (1966) 认为 *dremotheriids* 是鹿科和麒麟鹿科的祖先。Vislobokova (1983) 认为 *dremotheriids* 只是鹿科的祖先。柄杯鹿具有下列相似于 *dremotheriid* 的特点: 1) 具有矢状脊; 2) 强壮的枕脊; 3) 低而长的脑颅; 4) 形态特别的颞道 (meatus temporalis); 5) 头骨的面部短; 6) 眼眶前缘的位置在  $M^2$  的水平面上; 7) 有一眶前窝; 8) 有一筛裂缝; 9) 有一圆锥形的斜腹肌窝; 10) 前颌骨短; 11) 有一眼眶内面下壁倾斜; 12) 下第一前臼齿有时出现 (如山旺博物馆标本号 700023, 雌性, 和 1939 年德日进描述的标本图 5); 13) 雄性标本中具有剑状的上犬齿; 14) 前臼齿臼齿化程度很弱, 但是已经鹿型; 15) 臼齿低冠型; 16) 在下臼齿中出现古鹿褶 (*Palaeomeryx fold*); 17) 封闭型蹠骨沟; 18) 退化的但是完整的侧掌骨。有些特征 (1—5, 10, 15) 都是原始性的, 可能从遥远的祖先类型中进化而来。其他特征似乎从 *dremotheriins* 鹿类进化而来。

柄杯鹿 (*Lagomeryx*) 具有一些在其他鹿类中 (麂亚科 *Muntiacinae*, 鹿亚科 *Cervinae*, 驼鹿亚科 *Alcinae*, *Odocoileinae*) 所具有的衍生特征。它们是: 1) 在泪骨上有两个泪孔 (上面一个泪孔在眼眶脊上, 下面泪孔在眼眶内, 标本编号 700025)。*Dremotherium* 在眼眶内有一泪孔。依照 Leinders 和 Heints (1980), 鹿类的泪管在眼眶脊上开两个泪孔是从中新世开始的。*Heteroprox* Stehlin, 1928 已经有这样的泪孔位置了; 2) 作为头盖骨附件的角的出现。进步的特征是鼻骨后缘的位置在眼眶前 (这是麂类和鹿类的特点); 此外和 *Dremotheriins* 鹿相比较, 外听道较长 (在獐 *Hydropotes* 和麂 *Muntiacini* 中外听道的长度中等)。

颞道的构造 (700026 号头骨) 比麂亚科的原始。根据这一点不能同意周本雄等 (1978) 把柄杯鹿放在麂类内。麂亚科和鹿亚科具有连接岩骨和乳后突的骨桥, 后者在近中侧封闭耳道。

如上所述, 我们可以相信柄杯鹿科十分可能是鹿类中独立的一分支。正如 1939 年德

日进建议的。这些鹿类具有原始的角,这种原始的角与后期鹿类的角柄同源。

所有其他鹿类的亚科,它们的进化方向趋向于角的复杂化和牙齿更适合于粗糙的混合草类。依据 *Lagomeryx colberti* 骨骼的特征可以设想这类鹿适应于跳跃式奔跑。它们生活于近水的灌木丛和具有低矮灌木的林中。第三趾骨的形态表示它们适应于相当湿的土地。

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## ON THE SYSTEMATIC POSITION OF THE LAGOMERYCINAE

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### Summary

The family Lagomerycidae, established by Pilgrim in 1941, includes three genera: *Lago-*

*meryx* Roger, 1904, *Procervulus* Gaudry, 1878 and *Climacoceras* MacInnes, 1936. The affinity and systematic position of the family has been disputable for a long time. They were considered as: 1) a subfamily of the family Cervidae (Teilhard de Chardin, 1939; Crusafont Pairo, 1952; Viret, 1961; Vislobokova, 1983); 2) a family of the superfamily Giraffoidea (Pilgrim, 1941; Simpson, 1945; Young, 1964); 3) a synonym of the Palaeomerycidae of the superfamily Giraffoidea (Stirton, 1944; Withworth, 1958; Hamilton, 1973); 4) the Muntiacini (Chow, Shih, 1978).

The genus *Lagomeryx* was defined by Roger (1904) based on a species of *Palaeomeryx* Meyer, 1834 with non-deciduous antlers. The type species is *Palaeomeryx meyeri* Hofmann, 1893 from the Middle Miocene of Goriach, Austria. Some investigators casted doubts on the validity of the genus *Lagomeryx*, considering it to be a synonym of the genus *Palaeomeryx* (Withworth, 1958; Hamilton, 1973).

The genus *Procervulus* was established by Gaudry (1878), based on the type species *Cervus aurelianensis* Gervais, 1859 from Pont-Levoy, France. Some students thought that *Procervulus* was close to cervids (Zittel, 1925; Ginsburg, Crouzel, 1976).

The genus *Climacoceras* from the Middle Miocene of Kenya was grouped by MacInnes with the Cervidae. MacInnes identified the type species *Climacoceras africanus* MacInnes, 1936 from Maboko as a true deer. Hamilton (1978) placed *Climacoceras* in the giraffoid family Climacocervidae. The other species *C. gentryi* Hamilton from Fort Ternan was described to possess a bilobed lower canine (Hamilton, 1978).

The definition of the Palaeomerycidae was based on the investigation of Ginsburg, Heintz (1966) and Qiu, Yan, Jia, Sun, 1985). Ginsburg and Heintz (1966) showed, that the genus *Palaeomeryx* has ossicones of definitely giraffid type. The discovery of the complete skeleton of *Palaeomeryx tricornis* from the lake deposits of the Middle Miocene in Shanwang, Linqu, Shandong, shows that *Palaeomeryx* had more derived characters with giraffids than with cervids. They have only some plesiomorphic characters similar to those of the last one (Qiu, Yan, Jia, Sun, 1985). Some progressive features, such as a closed metatarsal groove, could be derived through parallel evolution in these two groups. The palaeontological evidences show that this feature, characteristic of cervids, derived independently in different groups of the Ruminantia and, in particular, in the Protoceratidae, Leptomerycidae and Moschidae. The studies of the Chinese paleontologists gave convincing evidence to indicate that the Palaeomerycidae is a separate branch of ancient giraffoids.

The structure of the antler of the Lagomerycinae differs essentially from the structure of the ossicones of *Palaeomeryx*: firstly, the boundary demarcating the frontal bone and ossicone is absent in the Lagomerycidae, but very distinct in *Palaeomeryx* and giraffids, and, secondly, the structures of the antlers of the Lagomerycinae and Palaeomerycidae are quite different. The examination of the antler structure with the SEM shows that it is close to the structure of the pedicle and non-deciduous antler (pl. I) of the deer.

The new data for more precisely defining of the position of lagomericines were from complete skeletons of *Lagomeryx colberti* (Young, 1937) found in Shanwang. The skull of *L. colberti* is closely comparable to that of representatives of the Dremotheriinae, the most primitive subfamily of the Cervidae, known from the Middle Oligocene. Ginsburg and Heintz (1966) considered dremotheriids ancestral to the Cervidae and Giraffidae. It was considered to be ancestral only to the Cervids (Vislobokova, 1983). *Lagomeryx* possesses the following features resembling those of dremotheriids in having: 1) a sagittal crest; 2) a powerful occipital crest;

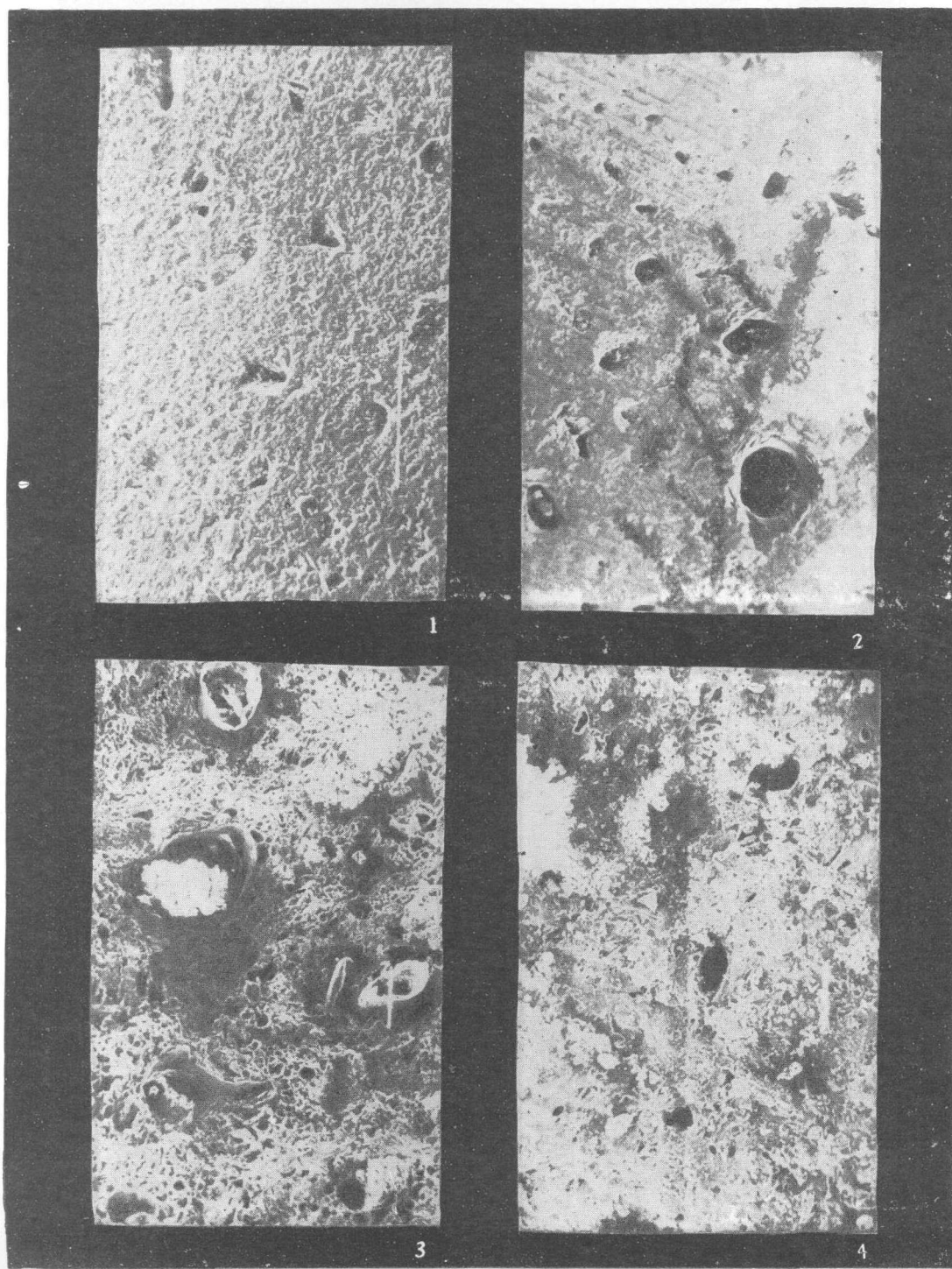
3) a long low braincase; 4) morphological peculiarities of meatus temporalis (postglenoid process does not connect the petrosal bone with isthmus); 5) a short facial part of the skull; 6) different position of the anterior edge of the orbit on the level of  $M^2$ ; 7) a praeorbital fossa; 8) a fissura ethmoidalis; 9) a cone-shaped pit for musculus obliquus ventralis; 10) a short prae-maxillary bones; 11) an inclination of the lower wall of the orbit insides; 12) an inconstant presence of the first lower  $P_1$  (it is developed, for example, in specimen no. 700023, belonging to a female, and in specimen, described by Teilhard de Chardin (1939, fig. 5); 13) saber-like upper canines in male; 14) simple, faintly molarized premolars, but already of cervid type; 15) brachyodont molars; 16) the presence of *Palaeomeryx* fold in the lower molars; 17) a closed metatarsal gully; 18) reduced, but complete lateral metacarpals. Some of these features (1—5, 10, 15) are primitive, possibly, derived from distant ancestors, the others seem to be derived from dremotheriines.

*Lagomeryx* also exhibits advanced derived features which are present among other cervids (Muntiacinae, Cervinae, Alcinae, Odocoileinae). They are: 1) two lacrimal orifices in the lacrimal bone (the upper one on the orbital rim, and the lower one inside the orbit, specimen no. 700025). *Dremotherium* has one orifice inside the orbit. According to Leinders and Heints (1980), the lacrimal duct of cervids open into two orifices on the rim of the orbit since the Middle Miocene and *Heteroprox* Stehlin, 1928 has already had such position of lacrimal orifices; 2) the presence of antlers as cranial appendages. Advanced feature seems to be a position of the posterior border of nasal bones in front of the orbits (it is characteristic for the Muntiacini and Cervini); and besides, some elongation of the external auditory meatus as compared with that in dremotheriines (the external auditory meatus is of moderate length in *Hydropotes* and Muntiacini).

The structure of meatus temporalis (skull no. 700026) is more primitive, than in that of the Muntiacinae. It does not agree with the viewpoints of Chow and Shih (1978), including lagomericines in the Muntiacini. The Muntiacinae, as well as the Cervinae, possessed the bone isthmus which connected the postglenoid process with the petrosal bone and medially limited the foramen of meatus temporalis.

Thus, it is reasonable to believe that the Lagomerycidae was quite probably a unique branch of cervids, as Teilhard de Chardin (1939) suggested. These cervids had primitive antlers analogous to pedicles of the later deer.

As all other subfamilies of cervids, they showed evolutionary trends towards the complication of antlers and dental system adapted to a nutrition of more coarse forage with an admixture of grass. Skeleton characters of the *Lagomeryx colberti* also suggest that they were adaptive to jumping. They appear to have lived in overgrowth of the bushes and the woodland with low thickets near the water. The morphology of ph III (long, narrow, with a narrow heel) shows they are adapted to fairly damp ground.



**The structure of antlers**

1. *Lagomeryx* sp. (Olhon, the Baikal);
2. *Procerovulus gracilis* (Mongolia);
3. *Euprox margaritae* (Mongolia);
4. *Euprox margaritae*, the pedicle (Mongolia)