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内蒙古四子王旗大庙中新世的真角鹿一新种[1)]

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摘要：描述了内蒙古四子王旗大庙中中新世化石地点（DM01）产出的真角鹿一新种：高枝真角鹿 *Euprox altus* sp. nov.。新种具真正的角节，角节之上一定高度的两个分枝，长的角柄；牙齿低冠，上臼齿的前附尖和中附尖发育，新棱和齿带存在；p4 的下后尖发育，下次凹存在；下臼齿具古鹿褶。这些特征可作为其归入真角鹿属 *Euprox* 的依据。*Euprox altus* 最主要的特征是其分叉起始位置比属内其他种的高。分叉起始位置的标志是角基的突然变宽，它不同于分叉的位置，可作为一个新的鉴定特征。角冠表面纵向分布不均的沟棱、更低冠的牙齿、P4 原尖后棱上的脊、p4 不明显的下前凹和不是很发育的下三角凹、下臼齿上发育较弱的古鹿褶等特征都是新种区别于属内其他种的重要特征。*Euprox altus* 所指示的可能是温暖湿润的生活环境，与大庙现在干旱、恶劣的景象截然不同。

关键词：内蒙古四子王旗大庙，中新世，鹿科，真角鹿
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A NEW SPECIES OF *EUPROX* (CERVIDAE, MAMMALIA) FROM THE MIDDLE MIOCENE OF DAMIAO, NEI MONGOL, CHINA

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Abstract A new species of cervid, *Euprox altus*, from the Middle Miocene fossil locality of Damiao, Siziwangqi, Nei Mongol, is described and studied in detail. It is assigned to *Euprox* based on its true burrs, bifurcation above the burr, long pedicles, brachyodont cheek teeth, developed parastyle and mesostyle, neocrista and cingulum on each upper molar, developed metaconid and hypoflexid on p4 and *Palaeomeryx* folds on lower molars. The diagnostic character of *E. altus* is that the bifurcation begins at a higher position than in other species. The beginning of the bifurcation is indicated by an abrupt widening of the antler base. This position can be used as a new distinguishing feature, distinct from the overall position of bifurcation. The uneven longitudinal grooves, more brachyodont teeth, fold on the P4 postprotocrista, almost invisible paraflexid and small trigonid basin on p4, and weak *Palaeomeryx* fold on the lower molars further differentiate the new species from other *Euprox* species. The presence of *E. altus* may indicate a warm and humid environment during the latest Middle Miocene in the Damiao area, in sharp contrast to the current dry and harsh environment.

Key words Damiao, Nei Mongol, Middle Miocene, Cervidae, *Euprox*

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1 Introduction

Euprox was named by Stehlin in 1928 when he studied fossil cervids from Steinheim in Germany. This genus, in which translation of the pedicle base and elongation of the frontal bone are incipient, appears to be the sister group of Muntiacini based on the shared presence of strongly inclined pedicles which seem to be a diagnostic synapomorphy of the subfamily Muntiacinae (Azanza, 1993; McKenna and Bell, 1997). *Euprox* emerged in the early Astaracian in MN6 (about 16 Ma), and its last known representative was the Vallesian *Euprox dicrancerus* (Gentry, 1994). The fork of the antler in *Euprox* arose somewhat above the prominent burr (Colbert, 1940), but the exact distance between the burr and the fork has been a point of uncertainty. Before that it is important to find out the starting position of the bifurcation, distinct from the overall position of bifurcation. The point where the antler base begins to widen coincides with the beginning of the bifurcation of the antler. The point of widening can be used as a new distinguishing feature in *Euprox*.

The American Museum of Natural History's Central Asiatic Expeditions of the early 20th century, led by R. C. Andrews, discovered rich fossil mammals in Nei Mongol, including the Tunggur fauna, representative fauna of the Chinese Middle Miocene Tunggurian age. According to Colbert (1940), they found some *Euprox* antler material. During the field seasons from 2006 to 2009, we found a total of 34 mammalian fossil localities near Damiao village. Richest among these was a Middle Miocene locality, DM01 (Fig. 1), produced many antlers and teeth. These antlers differ from those of other known *Euprox* species, representing a new form of *Euprox*. This paper will describe the new species and discuss the starting position of the bifurcation in *Euprox* antlers. At last, we will briefly discuss the environment in which the new species lived.

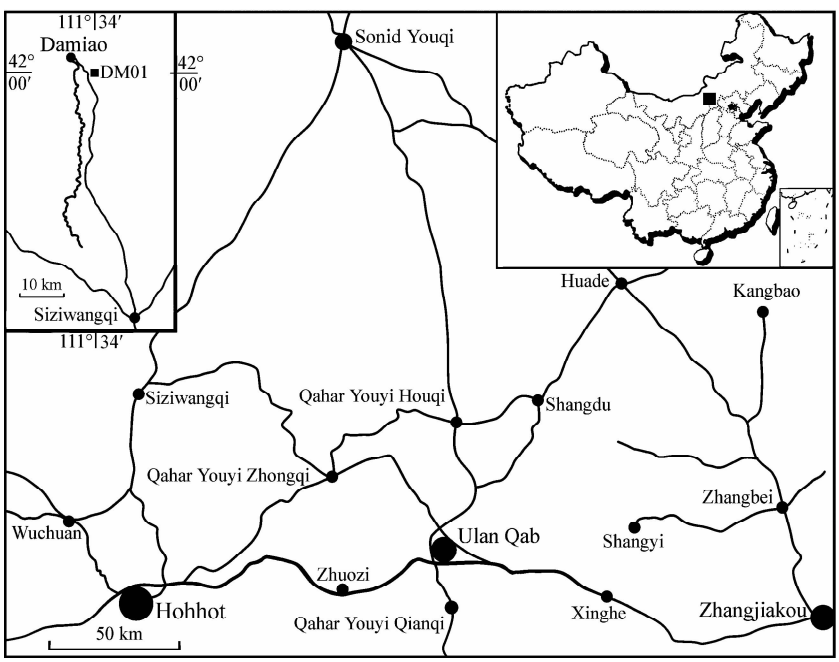

Fig. 1 The traffic location of DM01

DM01(N 42°00′31.4″, E 111°34′50″) is near Damiao village, about 65 km northwest of Wulanhua town, Siziwangqi, Nei Mongol. The outcrop is in a small gulley near the Shara Murun River. The fossil-bearing layer is about 3 m in thickness. It is a gravel lens in horizontally bedded brown silty clays. The lens is mainly composed of carbonate nodules but containing small amounts of quartz and feldspar. The color of the fossil-bearing layer is black to dark gray. In 1975, this deposition was named the Damiao Formation (Zheng et al., 1999). The mammalian fossils from DM01 resemble the Tunggur fauna. However, the presence of the pliopithecid and other small mammals suggests that the geological age of DM01 can provisionally be considered latest Middle Miocene, whereas the Tunggur fauna may be slightly older (Zhang and Harrison, 2008).

We follow Dong (2004, 2008) with respect to the terminology of dentition and antler. The specimens described in this paper are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing.

2 Systematic paleontology

Mammalia Linnaeus, 1758
Artiodactyla Owen, 1848
Cervidae Gray, 1821
Muntiacinae Pocock, 1923
***Euprox* Stehlin, 1928**
***Euprox altus* sp. nov.**
(***Figs.*** 2-3; ***Table*** 1-2)

Holotype A nearly complete shed right antler from the DM01 locality (IVPP V 17738.5).

Included material 26 antlers or anther fragments(V 17738.1-4, V 17738.6-27), 9 teeth (2 left P4, 1 left M1, 2 left M2, 1 right M1, 1 right p4, 1 left m1, 1 right m2)(V 17738.28-36).

Type locality and stratum DM01, Siziwangqi, Nei Mongol, Damiao Formation.

Etymology Altus, Latin, high. The antlers of the new species begin to bifurcate at a high position than in other species of *Euprox*.

Diagnosis A small *Euprox* species, having two-tined antlers with prominent burrs. The fork of the antler starts high above the true burr. The antler surface is ornamented unevenly with longitudinal grooves. The cheek teeth are brachyodont. The fold on the postprotocrista of P4 is developed. The precingulum, entocingulum and postcingulum are present and linked together on the upper molars. The *Palaeomeryx* fold is present but weak on the lower molars.

Measurements See Tables 1-2.

Description Antler The type specimen (V 17738.5)(Fig. 2E) is a two-tined right antler with a prominent burr, lacking the tips of the tines. The antler base grew about 17.4 mm above the burr before it began widening. The line "ab" in the figure shows the point of widening. Finally, the main beam and the brow tine diverge from each other at a point 44.2 mm above the burr, forming an angle of 80 degrees. The cross section of the tine is round. The burr is composed of a series of developed bony nodes and resembles a cluster of pearl ring. Its shedding scar is very distinct and round, forming a small bump. The cross section of the antler base is oval. The antler bears longitudinally aligned grooves on both the anterior and posterior sides. In addition to the type specimen, 26 other antler specimens are available. A right antler with a broken brow tine, main tine and pedicle (V 17738.1)(Fig. 2A) belongs to a young individual. Though its burr was worn during the process of transportation and preservation, the exist-

Table 1 Antler measurements of *Euprox altus* sp. nov. from DM01 (mm)

Specimen number	Distance between burr and bifurcation	Height of starting position of bifurcation	Antero-posterior diameter of burr
V 17738.1	31.0	8.3	>24.8
V 17738.2	32.1	8.3	>29.4
V 17738.3	>48.5	17.6	>24.7
V 17738.4	42.7	16.2	>24.8
V 17738.5	44.2	17.4	31.4
V 17738.6	>>26.5	>26.5	>30.2
V 17738.7	59.9	26.3	35.7
V 17738.9	>35.4	21.6	>22.3
V 17738.10	>>52.4	>>52.4	>30.8
V 17738.11	>72.9	45.7	>24.3
V 17738.12	>>49.0	>>49.0	30.0
V 17738.13	>>59.5	34.6	—
V 17738.14	71.7	37.8	>>24.0

Table 2 Dental measurements of *Euprox altus* sp. nov. from DM01 (mm)

Tooth	Length	Width	Height
P4 (left)	9.3	13.1	7.0
	—	10.2	8.9
M1 (left)	13.7	16.5	7.0
M2 (left)	13.6	15.4	5.6
	13.7	16.7	7.9
M1 (right)	14.5	17.4	7.1
p4 (right)	11.7	7.7	5.4
m1 (left)	12.1	10.6	4.8
m2 (right)	14.5	12.0	8.0

ence of a burr can still be deduced from the round pedicle. On the surface, a few shallow grooves longitudinally align. V 17738.2(Fig.2B) is an injured two-tined antler. A small new tine was growing from the broken brow tine. However, the small new tine only grew a small amount before the whole antler crown was shed. The antler base is flat in lateral view. Two shed antlers, V 17738.3 and V 17738.4(Fig.2C, D), have lost their tines but each preserves the antler base and an evident burr. In both specimens, the point of widening is high above the burr. The middle part of the scar on V 17738.3 forms a bump like that on the type specimen V 17738.5, but the bump is absent in V 17738.4. There are some longitudinally aligned grooves on their surface. V 17738.6(Fig.2F) is an antler retaining a small part of the antler base and an evident burr. The preserved antler base is of constant diameter, including the preserved part that is entirely below the level of the bifurcation. The cross section of the antler base is oval. Several grooves align longitudinally on its surface. Another specimen (V 17738.7)(Fig.2G) is a right adult shed antler with two broken tines and a prominent burr. The bifurcation is located 59.9 mm above the burr, and the point of widening is 26.3 mm above the burr. The antler base is slightly curved outward. Unlike the type specimen, the middle of the round scar on this antler dose not form a bump. Grooves developed mainly on the anterior and posterior sides, as in the type specimen.

V 17738.9(Fig.2I) is a small sized antler belonging to a young deer. Its surface is rough and the scar forms a bump. V 17738.10(Fig.2J) is an antler with a distinct burr and long antler base. The antler base is directed posteriorly and the anterior part of the burr is better developed than the posterior part. The shedding scar is oval. The preserved long antler base shows no sign of the beginning of the bifurcation. Grooves are visible. V 17738.11(Fig.2K) has a prominent burr and very long antler base. The preserved part of the antler base is about 71.0 mm long. In this specimen the point of widening is very high. Although the antler base begins

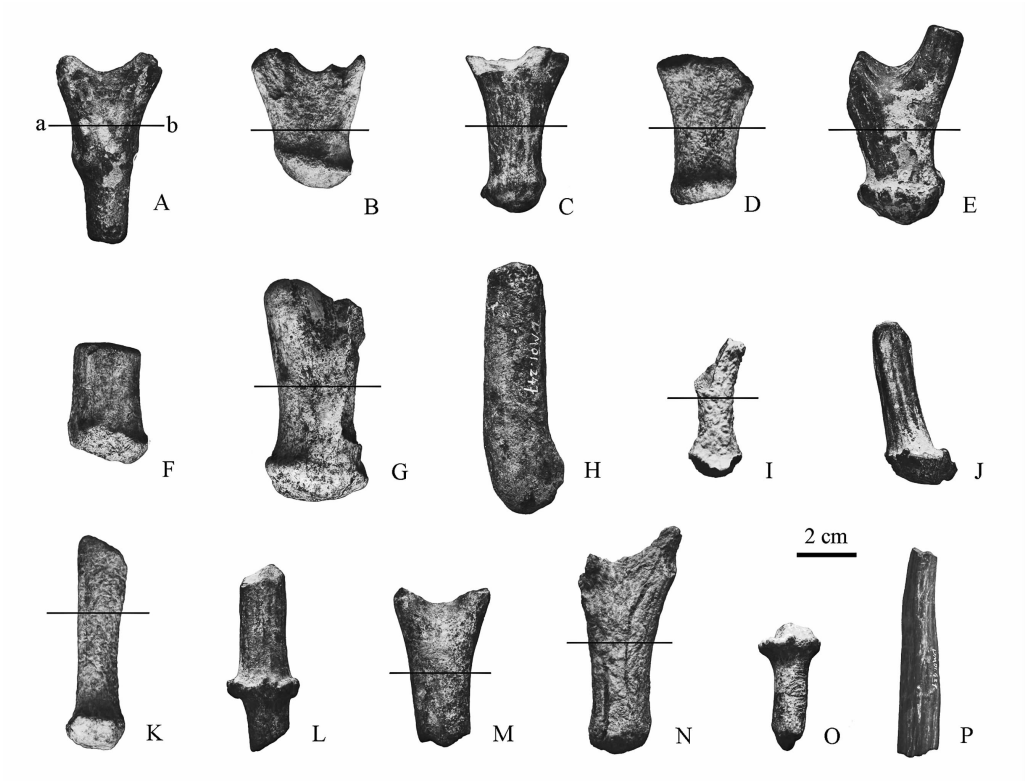

Fig. 2　Antlers of *Euprox altus* sp. nov. from DM01, Nei Mongol
A. V 17738.1; B. V 17738.2; C. V 17738.3; D. V 17738.4; E. V 17738.5 (Holotype); F. V 17738.6; G. V 17738. 7; H. V 17738.8; I. V 17738.9; J. V 17738.10; K. V 17738.11; L. V 17738.12; M. V 17738.13; N. V 17738.14; O. V 17738. 15; P. V 17738.16; line ab: the point of widening

to widen, the actual bifurcation is not visible. The scar is round and slightly depressed. V 17738.12 (Fig. 2L) is an antler with part of the antler base, a prominent burr and part of the pedicle. Its burr is a typical cluster of pearl-shaped nodes. There are many grooves on the surface of the antler base, but the surface of the pedicle is less grooved. As in V 17738.10, the preserved long antler base shows no sign of the beginning of the bifurcation. V 17738.13 (Fig. 2M) is an antler with a broken bifurcation and an incomplete, crooked antler base. The point of widening is very high. V 17738.14 (Fig. 2N) is an antler with a complete antler base, two broken tines and a worn burr. The burr is badly worn but the oval-shaped scar is still visible. Very deep grooves are present on the surface of the antler base and the point of widening is very high.

V 17738.8 (Fig. 2H) is a part of pedicle. The total preserved length is about 91.6 mm. Although the attachment to the antler crown is missing, it is clear from what is preserved that the pedicle is long. The cross section of the proximal end is slightly oval, whereas that of the distal end is round as in V 17738.1 and also V 17738.15. V 17738.15 (Fig. 2O) is a partial pedicle with a prominent burr. It belongs to a young deer, judging by its small size. V 17738.16 (Fig. 2P) is the middle part of a tine with deep grooves. Its distal end is slightly curved. Other specimens are not well preserved to give detailed morphologic characters. Antlers of *Euprox altus* show three kinds of scar: 1) a round scar with a bump (V 17738.3, V 17738.5 and V 17738.9); 2) a round and slightly concave scar (V 17738.4, V 17738.6, V 17738.7 and

V 17738.11); 3) an oval and slightly convex scar (V 17738.2, V 17738.10 and V 17738.14). The grooved surface ornament occurs mainly on the anterior and posterior sides of the antler base in the new *Euprox*.

Table 1 shows the antler measurements of *Euprox altus* sp. nov. The distance between the bifurcation and the burr varies greatly, from 31.0 to >72.9 mm. The burrs are rather consistent in size, the diameter from >22.3 to 35.7 mm. Czyżewska (1968) described *Euprox furcatus* from Poland. She mentioned that the bifurcation of the antler could be either high or low in *E. furcatus*, and this is also true of *E. altus* from Damiao. Although the distance between the bifurcation and the burr varies greatly, it is probably intraspecific. This is one reason we refer all these specimens to a single species. Another reason is the high starting position of the bifurcation, as opposed to the position of the bifurcation itself. The specimens from DM01 show that the growth of the antler base took place in two phases. The first is the growth of the antler base prior to bifurcation. The diameter of the antler base is minimizing after it grows from the burr, or keeps the same diameter before the antler base begins to widen. The second phase is the bifurcation. The starting point of the bifurcation is marked by widening of the antler base and the starting position is well below the forking.

Dentition Nine teeth from DM01 are referred to *Euprox altus* sp. nov. (Fig. 3; Table 2).

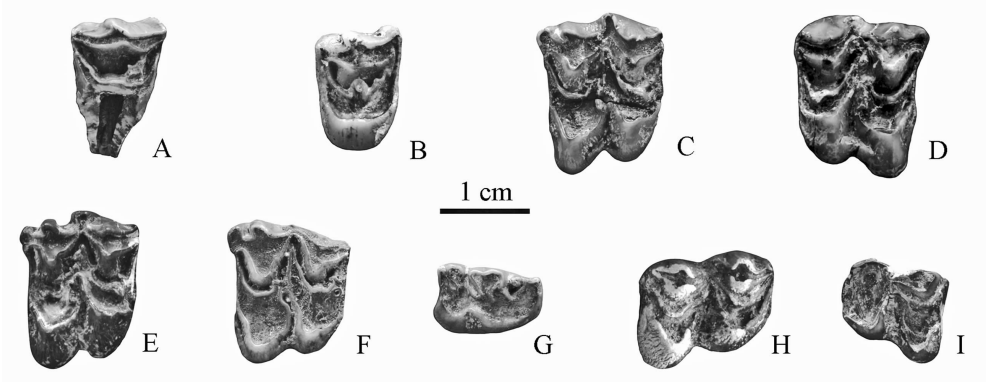

Fig. 3 Cheek teeth of *Euprox altus* sp. nov. in occlusal view
A. l P4 (V 17738.28); B. l P4 (V 17738.29); C. l M1 (V 17738.30); D. r M1 (V 17738.31); E. l M2 (V 17738.32); F. l M2 (V 17738.33); G. r p4 (V 17738.34); H. r m2 (V 17738.35); I. l m1 (V 17738.36)

Two left P4 were recovered from DM01. The width of the better-preserved one (V 17738.29) is greater than its length. This P4 is composed of two main selenodont cusps, a paracone and a protocone. The protocone is lower than the paracone. A fold on the postprotocrista indicates incipient molarization of the tooth (Dong, 2004). The parastyle, metastyle and rib of the paracone are developed. The precingulum and postcingulum are developed on the lingual wall. The entocingulum is very weak but bears some wrinkles on its surface. Another P4 is incomplete, but the fold on the postprotocrista is evident. Although the lingual wall has been destroyed, the precingulum and postcingulum are still visible.

A single left M1 and a single right M1 (V 17738.30-31) are present. The width is slightly greater than the length. Each tooth is composed of four selenodont main cusps. The lingual main cusps are lower than the buccal ones. The protocone is larger than the metaconule. The postprotocrista bears the neocrista and the spur on the postmetaconule crista is absent. On the buccal wall, the parastyle, rib and mesostyle are prominent. The metastyle is very weak. On the lingual wall, the precingulum, entocingulum and postcingulum are well-developed.

There are two left M2 (V 17738.32-33). The tooth is similar to M1, but the two M2

bears the spur on the postmetaconule crista. V 17738.33 is heavily worn. The parastyle of M2 is more prominent than that of M1.

The outline of p4 (V 17738.34) in occlusal view is nearly rectangular. The protoconid and hypoconid are developed. A hypoflexid exists between the protoconid and hypoconid on the buccal wall. The paraflexid is almost invisible because of the fusion of the paraconid and parastylid. The paraconid extends towards the premetacristid without reaching it, leaving an open trigonid basin. The metaconid is large with a concave lingual side, and is located slightly distal to the protoconid. The entoconid is more robust than the entostylid and the talonid basin between them is very narrow.

The m1 (V 17738.36) is well worn and the trigonid is narrower than the talonid. The hypoconid is buccally well set off, forming a wide talonid basin. There is a remnant of the ectostylid on the labial wall.

The m2 (V 17738.35) is composed of four main selenodont cusps. The buccal main cusps are more robust but lower than those of the lingual ones. *Palaeomeryx* fold is present but weak on the postprotocrista. The ectostylid is not developed. The precingulid, postcingulid, parastylid and metastylid are weak.

3 Comparison and discussion

3.1 Comparisons among Miocene cervids with two-tined antlers

Previously discovered Miocene two-tined cervids have been assigned to *Procervulus* Gaudry, 1878, *Acteocemas* Ginsburg, 1985, *Heteroprox* Stehlin, 1928, *Dicrocerus* Lartet, 1837, *Euprox* Stehlin, 1928, *Muntiacus* Rafineque, 1815, *Paracervulus* Teilhard de Chardin & Trassaert, 1937, *Eostyloceros* Zdansky, 1925, *Amphiprox* Haupt, 1935, and *Lucentia* Azanza & Montoya, 1995(Fig. 4; Table 3).

The earliest cervid with two-pronged antlers is *Procervulus* Gaudry, 1878 from the Early Miocene in Spain (DeMiguel et al., 2008). *Procervulus* has a distal fork on a long, straight pedicle. An antler with this kind of distal fork, lacking an obvious burr or coronet, is called a protoantler (Gentry, 1994; Gentry et al., 1999). *Euprox* antlers have a typical burr, making them easily distinguishable from the protoantlers of *Procervulus*.

As summarized by Gentry (1994), the earliest antlered deer are *Heteroprox* and *Dicrocerus*, both of which appear in the Late Orleanian in MN5 (Pitra et al., 2004). *Heteroprox* is a probable descendant of *Procervulus*, based on similarity in size and the presence of a protoantler. *Heteroprox* is characterized by its rugose surfaces of the tines extending downwards to a level slightly below the fork (Gentry, 1994; Gentry et al., 1999). The grooves on the antlers of *Euprox* are less pronounced than those on the antlers of *Heteroprox*, and *Euprox* has the true burr. Not all specimens of *Heteroprox* have exactly two tines (Ginsburg and Crouzel, 1976).

Dicrocerus was the largest known cervid of this age. Its protoantlers each bears a burr-like structure. Straight prongs originate from the wide basal plate and diverge anteroposteriorly. *Dicrocerus* is considered to have originated from *Acteocemas* Ginsburg, 1985. In the latter taxon the antler consists of a short, ornamented, two-pronged fork mounted on a short pedicle, equipped with a delicate burr-like structure around the base (Gentry et al., 1999; Thenius, 1948; Wang et al., 2009). *Euprox*, another Middle Miocene deer, has a complete burr rather than a burr-like structure of the type present in *Dicrocerus* and *Acteocemas*. Moreover, *Euprox* lacks the wide basal plate of *Dicrocerus* and the tines of *Euprox* curve inwards slightly, rather than being straight as in *Dicrocerus*. Another distinguishing feature is that the position of the fork is higher in *Euprox* than in *Dicrocerus*.

During the Late Miocene, the dichotomous antler with more or less equal prongs gradually gave way to an asymmetric antler with a main branch and a smaller anterior branch, and the

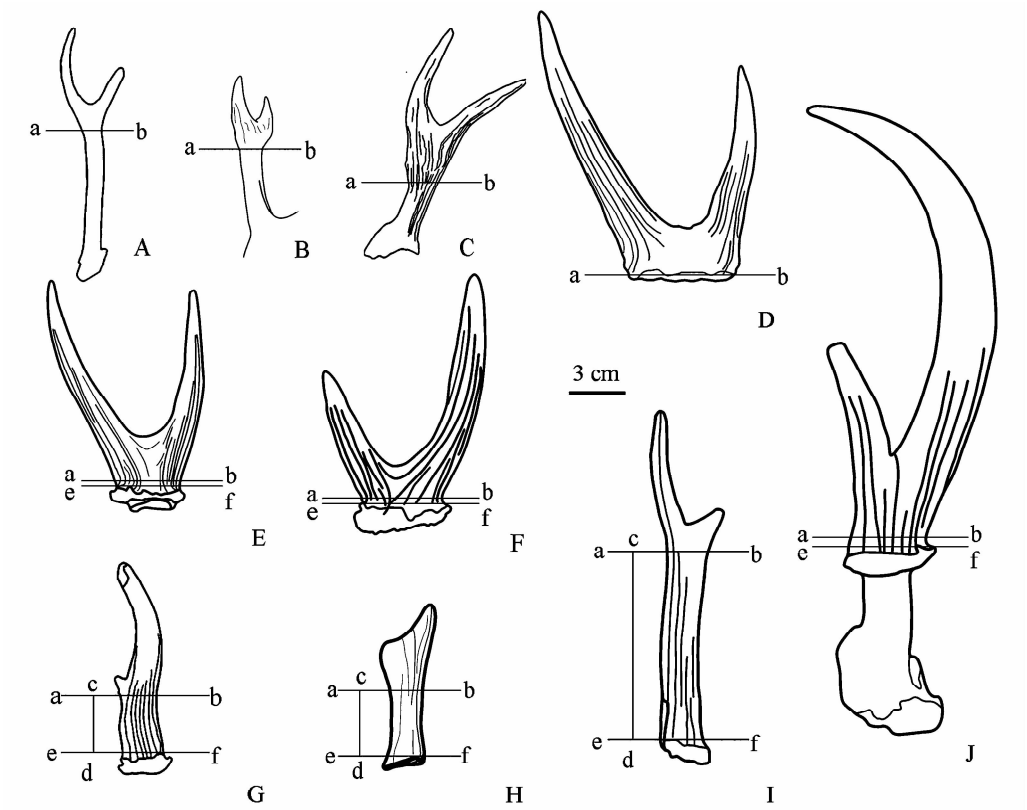

Fig. 4 Antlers of Miocene two-tined cervids

A. *Procervulus dichotomus* (Ginsburg and Bulot, 1987); B. *Acteocemas infans* (Stehlin, 1939); C. *Heteroprox lartelti* (Stehlin, 1928); D. *Dicrocerus elegans* (Thenius, 1948); E. *Euprox furcatus* (Thenius, 1948); F. *Muntiacus noringenensis* (Dong, 2007); G. *Paracervulus brevis* (Teilhard de Chardin and Trassaert, 1937); H. *Amphiprox anocerus* (Thenius, 1948); I. *Lucentia iberica* (Azanza and Montoya, 1995); J. *Eostyloceros blainvillei* (Zdansky, 1925)

Line ab: the point of widening; Line cd: the height of the starting position of the bifurcation above the burr; Line ef: the highest extent of the burr

Table 3 Comparison of antler morphology among Miocene cervids with two-tined antler crowns

Genus	Burr	Ornament	Basal plate	Fork position	Antler base
Procervulus	absent	absent	absent	distal fork	absent
Acteocemas	burr-like	grooves	present	low	short
Heteroprox	burr-like	rugose surface	absent	normal	straight
Dicrocerus	burr-like	grooves	obvious	low	short
Euprox	true burr	grooves	absent	variable	straight
Muntiacus	true burr	grooves	absent	low	short
Paracervulus	true burr	grooves	absent	very high	straight
Eostyloceros	true burr	grooves	absent	low	short
Amphiprox	true burr	grooves	absent	very high	straight
Lucentia	true burr	grooves	absent	very high	sharply curved

number of distal tines subsequently increased. The antler base also evolved, with the pedicle shortening (Gentry et al., 1999). *Muntiacus* Rafineque, 1815, *Paracervulus* Teilhard de Chardin & Trassaert, 1937, *Eostyloceros* Zdansky, 1925 and *Amphiprox* Haupt, 1935 all appeared during this time. The earliest *Muntiacus* known at present is *Muntiacus noringenensis* from the Late Miocene of the northeastern Qinghai-Tibetan Plateau, China (Dong, 2007). This taxon has an obvious burr, but differs from *Euprox* in having a low, much smaller brow tine and a more curved main tine tip. In addition to the differences of antlers, molars of *Muntiacus* are devoid of the *Palaeomeryx* fold and cingulum (Czyżewska, 1968) but the teeth from DM01 assigned to *Euprox altus* sp. nov. have *Palaeomeryx* fold and cingulum. *Paracervulus* was discribed by Teilhard de Chardin and Trassaert in 1937 based on specimens from the Yushe Basin. It is characterized by a higher position of divergence between the brow tine and the main tine. The brow tine is very small, and even disappears in *Paracervulus simplex* (Dong et al., 1994). *Eostyloceros* has a short and straight brow tine compared with the longer and curved main tine. These are different from *Euprox* (Zadansky, 1925).

Amphiprox Haupt, 1935 was restricted to Europe. In comparison to *Euprox*, it has a longer shaft between the burr and the bifurcation, a very small brow tine and a different pedicle position (Gentry et al., 1999; Thenius, 1948). *Lucentia* Azanza & Montoya, 1995, which was recovered from the lower Turolian (MN 11) of Spain, is not a representative of Muntiacinae and is probably the sister taxon of the clade Cervinae-Odocoileinae. Its very long beam is longitudinally compressed and sharply bent inward. Small tine points diverge at an acute angle from the anterior margin of the beam. The pedicles are not prolonged as ridges on the sides of the skull roof (Azanza and Montoya, 1995; Bernor et al., 2002; Hillenbrand et al., 2009). These characters are absent in *Euprox*.

The line "ab" in each panel of Fig. 4 shows the point of widening, the line "cd" shows the height of the starting position of the bifurcation above the burr and the line "ef" shows the highest extent of the burr. The height of the point of widening varies among genera. In *Dicrocerus elegans* (Thenius, 1948), *Euprox furcatus* (Thenius, 1948), *Muntiacus noringenensis* (Dong, 2007) and *Eostyloceros blainvillei* (Zdansky, 1925), the point of widening starts in a relatively low position. In *Paracervulus brevis* (Teilhard de Chardin and Trassaert, 1937), *Amphiprox anocerus* (Thenius, 1948) and *Lucentia iberica* (Azanza and Montoya, 1995), the point of widening is higher.

3.2 Comparisons among antlers within *Euprox*

Euprox is a group of widely distributed cervids recorded from Middle to Upper Miocene fossil localities. *Euprox furcatus*, the type species, is well documented at many Middle Miocene fossil localities (Morales and Soria, 1981; Thenius, 1948; Gentry et al., 1999). The Damiao species is very similar to *E. furcatus* in having an evident burr located some distance below the bifurcation. Compared to *E. furcatus*, the distance separating the burr from the bifurcation is longer in *E. altus* and the antler is more slender (Fig. 5).

In *E. furcatus* the bifurcation starts close to the burr. An even lower position is observed in *Dicrocerus elegans*, in which the bifurcation starts directly from the wide basal plate. Two specimens of *E. altus*, V 17738.5 and V 17738.7 (Fig. 5E, F), show a higher point of widening. *Euprox robustus* from the Yuanmou Basin of Yunnan Province (Dong et al., 2003) is much larger than *E. altus* sp. nov. In addition to being robust, antlers of *E. robustus* display a much lower point of widening (Fig. 5C). *Euprox dicranocerus* is a characteristic species of the early Vallesian ruminant assemblages of Central Europe (Vislobokova, 2005, 2006; Gentry, 1993). *E. dicranocerus* (Thenius, 1948) is considerably different from *E. altus* sp. nov. in having well developed grooves and crests on the surface of the antler base, the grooves even connecting with the burr. The point of widening in *E. dicranocerus* is higher than in *E. furcatus* and *E. ro-*

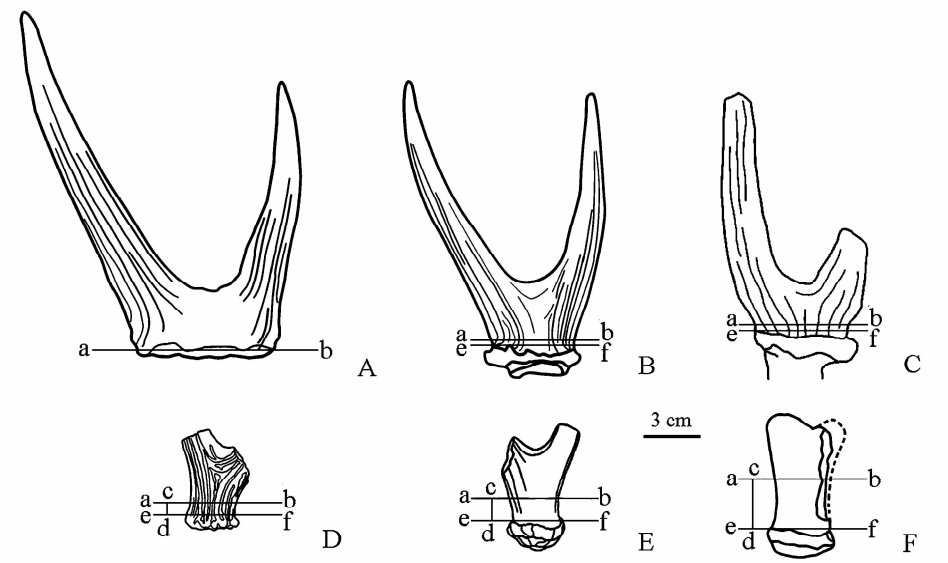

Fig. 5 Comparison of the antlers in *Euprox*
A. *Dicrocerus elegans* (Thenius, 1948), for comparison; B. *Euprox furcatus* (Thenius, 1948); C. *Euprox robustus* (Dong et al., 2003); D. *Euprox dicranocerus* (Thenius, 1948); E-F. *Euprox altus* sp. nov., E. V 17738.5, F. V 17738.7; explanations for lines ab, cd and ef see Fig. 4

bustus, but lower than in *E. altus*.

Dicroceros [sic; recte *Dicrocerus*] *minimus* Toula, 1884 was named on the basis of some cervoid teeth from Goriach, Austria, and was later reassigned to *Euprox* Stehlin, 1928 (Gentry, 1993). Thenius (1948) mentioned an antler of *E. minimus* belonging to a pricket, and suggested that this species produced antlers only in the form of prickets just as modern mazama (Czyżewska and Stefaniak, 1994).

Vislobokova (1983) demonstrated the presence of an expanded basal plate and burr-like structure in *Euprox margaritae*. We believe that this species may possibly belong to *Dicrocerus*.

Euprox cf. *E. furcatus*, from Upper Miocene of Shanxi Province (Zdansky, 1925), has a straight main tine and an obliquely directed brow tine. In *E. altus*, the main tine is not so straight and the two tines both diverge at the same angle. *Euprox* sp. from Tsaidam Basin, Qinghai Province (Bohlin, 1937) is much larger than *E. altus* from Damiao. Colbert (1936) described some material from Tunggur as *Dicrocerus* sp. Subsequently, in 1940, he changed his mind and considered these specimens to be comparable to the European *E. furcatus*. They all show a true burr and a bifurcation above the burr, indicating that they should be assigned to *Euprox*. However, *Euprox* from DM01 has a more evident burr and very long antler base, in contrast to the Tunggur specimens.

3.3 Comparisons regarding the teeth of *Euprox altus* sp. nov.

The cheek teeth found at DM01 are low crowned. The parastyle and mesostyle are deve loped; and a neocrista and cingulum are present on each upper molar. On p4, the metaconid is developed and a hypoflexid is present. On the lower molars, *Palaeomeryx* fold is present. These are characters of *Euprox* Stehlin, 1928. However, the p4 differs from those of *E. robustus* and *E. furcatus* in having an almost invisible paraflexid and a small trigonid basin. The weak *Palaeomeryx* fold on the lower molars distinguishes them from those of *E. robustus*, but is a point of resemblance to *E. furcatus*. The existence of a fold on the postprotocrista of P4 in *E. altus* contrasts

with the larger basin in *E. furcatus* (Czyżewska and Stefaniak, 1994). The right M1 (V 17738.31) and the right m2 (V 17738.35) are unique among the nine available teeth in having similar abrasion with the ones from Przeworno and Yuanmou. Comparing the hypsodont indices (Table 4), the two teeth of *E. altus* are both lower than teeth of *E. furcatus* and *E. robustus*.

Table 4　Hypsodont indices (height/length ×100) of *Euprox* species

Locality	DM01	Przeworno	Yuanmou
Species	*E. altus* sp. nov.	*E. furcatus* (Czyżewska and Stefaniak., 1994)	*E. robustus* (Dong et al., 2003)
M1	48.79 ~ 51.06	78.30	48.22 ~ 67.65
m2	55.35	66.1 ~ 74.33	56.86 ~ 62.84

4　Interpretation of the paleoenvironment of *Euprox altus* sp. nov. from Damiao

Euprox is well represented by fossil material from Steinheim in Germany. Reconstruction of the paleoenvironment and paleoclimate of the Middle Miocene lake in the Steinheim Basin, based on C, O and Sr isotopes analyses of fossil remains, indicated warm-temperate climatic conditions, possibly combined with high humidity (Tütken et al., 2006).

Dong et al. (2003) suggested that *Euprox robustus* possibly fed on sap-rich and tender leaves of dicotyledonous plants, based on its brachyodont cheek teeth and long cingula. Such vegetation could only thrive in a humid and temperate climate. Table 4 shows that hypsodont indice of *Euprox altus* is lower than those of the other two *Euprox* species. These evidences may confirm that the habitat of *E. altus* was also warm and humid, in sharp contrast to the current dry and harsh environment.

Zhang and Harrison (2008) discussed the pliopithecid found from DM01. They speculated the absence of primates in northern China during the Late Miocene might be related to the onset of the East Asian Monsoon, which produced a dry and strongly seasonal climate. The finding of *Euprox altus* suggests that during the latest Middle Miocene the monsoon had not yet formed or had not influenced the Damiao area at least.

5　Conclusion

The new species of cervid, *Euprox altus* sp. nov., from the DM01, is assigned to *Euprox* Stehlin, 1928. *E. altus* shows its evident true burr, high starting position of the bifurcation above the burr, long pedicle, brachyodont cheek teeth, developed parastyle and mesostyle, the presence of neocrista and cingulum on the upper molars, developed metaconid and hypoflexid on the p4, the presence of *Palaeomeryx* fold on the lower molars. Tooth morphology and comparison with other species suggest that during the latest Middle Miocene the Damiao area was a warm and humid environment.

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References

Azanza B, 1993. Sur la nature des appendices frontaux des cervidés (Artiodactyla, Mammalia) du Miocène inférieur et moyen, Remarques sur leur systématique et leur phylogénie. C R Acad Sci, Sér II, **316**: 1163 – 1169

Azanza B, Montoya P, 1995. A new deer from the lower Turolian of Spain. Paleont J, **69**(6): 1163 – 1175

Bernor R L, Kordos L, Rook L, 2002. Recent advances on multidisciplinary research at Rudabánya, Late Miocene (MN9), Hungary: a compendium. Palaeontogr Ital, **89**: 3 – 36

Bohlin B, 1937. Eine tertiäre Säugetier-Faune aus Tsaidam. Palaeont Sin, Ser C, **14**(1): 1 – 71

Colbert E H, 1936. Tertiary deer discovered by the American Museum Asiatic Expeditions. Am Mus Novit, (854): 1 – 21

Colbert E H, 1940. Some cervid teeth from the Tung Gur Formation of Mongolia, and additional notes on the genera *Stephanocemas* and *Lagomeryx*. Am Mus Novit, (1062): 1 – 6

Czyżewska T, 1968. Deers from Węzé and their relationship with the Pliocene and recent Eurasiatic Cervidae. Acta Palaeont Pol, **8**(4): 537 – 593

Czyżewska T, Stefaniak K, 1994. *Euprox furcatus* (Hensel, 1859) (Cervidae, Mammalia) from Przeworno (Middle Miocene, Lower Silesia, Poland). Acta Zool Cracov, **37**(1): 55 – 74

DeMiguel D, Fortelius M, Azanza B et al. 2008. Ancestral feeding state of ruminants reconsidered: earliest grazin adaptation claims a mixed condition for Cervidae. Evol Biol, **8**(13): 1 – 13

Dong W(董为), 2004. The morphological characteristics and evolution of teeth of fossil cervid. Acta Anthropol Sin(人类学学报), **23**(Suppl): 286 – 295(in Chinese)

Dong W(董为), 2007. New material of Muntiacinae (Artiodactyla, Mammalia) from the Late Miocene of northeastern Qinghai-Tibetan Plateau, China. C R Palevol, **6**(5): 335 – 343

Dong W(董为), 2008. A review of the morphological evolution of antler. In: Dong W ed. Proceedings of the Eleventh Annual Meeting of the Chinese Society of Vertebrate Paleontology. Beijing: China Ocean Press. 127 – 144(in Chinese)

Dong W(董为), Hu C K(胡长康), 1994. The Late Miocene Cervidae from Hounao, Yushe, Shanxi. Vert PalAsiat(古脊椎动物学报), **32**(3): 209 – 227(in Chinese)

Dong W, Liu J H, Pan Y R, 2003. A new *Euprox* from the Late Miocene of Yuanmou, Yunnan Province, China, with interpretation of its paleoenvironment. Chin Sci Bull, **48**(5): 485 – 491

Gentry A W, 1993. *Lagomeryx* Roger, 1904(Mammalia, Artiodactyla): proposed designation of *L. ruetimeyeri* Thenius, 1948 as the type species. Bull Zool Nomencl, **50**(2): 133 – 136

Gentry A W, 1994. The Miocene differentiation of Old World Pecora (Mammalia). Hist Biol, **7**: 115 – 158

Gentry A W, Rössner G E, Heizmann E, 1999. Suborder Ruminantia. In: Rössner G E, Heissig K eds. The Miocene Land Mammals of Europe. Munich: Verlag Dr Friedrich Pfeil. 225 – 258

Ginsburg L, Bulot C, 1987. Les Artiodactyles seleodontes du Miocène de Bézian à la Romieu (Gers). Bull Mus Natl Hist Nat, Paris, Sér 9, Sect C, **1**: 63 – 95

Ginsburg L, Crouzel F, 1976. Contribution à la connaissance d'*Heteroprox larteti* (Filhol) Cervidé de Miocène européen. Bull Mus Natl Hist Nat, Paris, Sér 3, **399**: 345 – 357

Hillenbrand V, Göhlich U B, Rössner G E, 2009. The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria) 7. Ruminantia. Ann Naturhist Mus Wien, **111A**: 519 – 556

McKenna M C, Bell S K, 1997. Classification of Mammals Above the Species Level. New York: Columbia University Press. 1 – 425

Morales J, Soria D, 1981. Los Artiodactilos de los Valles de Fuentidueña (Segovia). Estud Geol, **37**: 477 – 501

Pitra C, Fickel J, Meijaard E et al., 2004. Evolution and phylogeny of old world deer. Mol Phyl Evol, **33**: 880 – 895

Stehlin H G, 1928. Bemerkungen über die Hirsche von Steinheim am Aalbuch. Eclogae Geol Helv, **21**: 245 – 256

Stehlin H G, 1939. *Dicroceros elegans* und sein Geweihwechsel. Schweiz Palaeontol Ges, **32**: 162 – 179

Teilhard de Chardin P, Trassaert M, 1937. Pliocene Camelidae, Giraffidae and Cervidae of S. E. Shansi. Palaeont Sin, Ner Ser C, **102**: 1 – 56

Thenius E, 1948. Zur Kenntnis der fossilen Hirsche des Wiener Beckens, unter besondrer Berücksichtigung ihrer stratigraphischen Bedeutung. Ann Naturhist Mus Wein, **56**: 262 – 307

Tütken T, Vennemann T W, Janz H et al., 2006. Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim Basin, SW Germany: a reconstruction from C, O and Sr isotopes of fossil remains. Palaeogeogr, Palaeoclimatol, Palaeoecol, **241**: 457 – 491

Vislobokova I A, 1983. The Fossil Deer of Mongolia. Moscow: Sciences Press. 1 – 80

Vislobokova I A, 2005. The importance of Late Miocene faunal exchanges between eastern Mediterranean areas and Central Europe. Ann Paléont, **91**: 241 – 255

Vislobokova I A, 2006. Associations of ruminants in Miocene ecosystems of eastern Alpine Region. Paleont J, **40**(4): 438 – 447

Wang X M, Xie G P, Dong W, 2009. A new species of crown-antlered deer *Stephanocemas* (Artiodactyla, Cervidae) from the Middle Miocene of Qaidam Basin, northern Tibetan Plateau, China, and a preliminary evaluation of its phylogeny. Zool J Linn Soc, **156**: 680 – 695

Zdansky O, 1925. Fossile Hirsche Chinas. Palaeont Sin, Ser C, **2**(3): 1 – 94

Zhang Z Q, Harrison T, 2008. A new Middle Miocene pliopithecid from Inner Mongolia, China. J Hum Evol, **54**: 444 – 447

Zheng J J(郑家坚), He X X(何希贤), Liu S W(陈淑文) et al., 1999. Chinese Formation Code: the Tertiary. Bejing: Geological Publishing House. 1 – 163(in Chinese)