New material of the Late Miocene Moschus (Artiodactyla, Mammalia) from Huade, Nei Mongol, North China (Postprint)

Authors: DONG Wei, LIU Wen-Hui, ZHANG Li-Min, Bai Wei-Peng, CAI Bao-Quan

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Abstract

Moschus grandaevus was firstly uncovered from the Late Miocene deposits at Ertemte, Olan Chorea, Harr Obo and Hua Ba in or around Huade County in the middle part of Nei Mongol and was described by Schlosser in 1924. The excavations by Sino-Soviet Joint Paleontological Team in 1959 and recent excavations since 2013 at Tuchengzi (Tuchetse), another locality at Huade, accumulated many specimens of the musk deer. The morphology and metric studies show that the musk deer specimens from Tuchengzi are the same as those described by Schlosser and can be included into the same species. M. grandaevus ranges from Siberia of Russia to North China, and likely to southern China, in the Late Miocene and Pliocene. The appearance of such folivorous musk deer in the Late Miocene deposits at Tuchengzi indicates that there were forests there during that period. The cladistic analyses show that the fossil species of Moschus are closely related to each other and can be grouped together as Moschini or Moschinae. Micromeryx is closer to Moschus and Cervidae, but the relationship between Micromeryx and Moschus is more complicated than previously considered; nonetheless Hispanomeryx is closer to Bovidae.

Schlosser (1924) described Moschus grandaevus from specimens initially discovered at Ertemte, Olan Chorea, Harr Obo, and Hua Ba in or around Huade County in Nei Mongol. In 1959, the Sino-Soviet Joint Paleontological Team collected many fossil musk deer specimens from Tuchengzi, another locality in Huade. Since 2013, field excavations conducted by the authors at Tuchengzi have accumulated more fossil specimens of the musk deer. The Tuchengzi specimens are very close to the musk deer from Ertemte and other localities in both morphology and metrics, and can be assigned to the same species. Based on available data, M. grandaevus ranges from Siberia in Russia to North China, likely extending to southern China, with a geological age range of Late Miocene

to Pliocene. The occurrence of such folivorous musk deer in the Late Miocene strata at Tuchengzi indicates that forest environments existed in the Tuchengzi area during that period. Cladistic analyses reveal that the fossil species of Moschus are phylogenetically very closely related and can be grouped together as Moschini or Moschinae; Micromeryx is closer to Moschus and Cervidae, but the relationship between Micromeryx and Moschus is more complex than previously considered, while Hispanomeryx is closer to Bovidae.

Full Text

Preamble

New Material of the Late Miocene Moschus (Artiodactyla, Mammalia) from Huade, Nei Mongol, North China

DONG Wei[1],[2], LIU Wen-Hui[1],[3], ZHANG Li-Min[1], BAI Wei-Peng[1],[3], CAI Bao-Quan
(1 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, dongwei@ivpp.ac.cn)
(2 Center for Excellence in Life and Paleoenvironment, Beijing 100049)
(3 University of Chinese Academy of Sciences, Beijing 100049)
(4 Department of History, Xiamen University, Xiamen 361005)

Abstract

Moschus grandaevus was first uncovered from the Late Miocene deposits at Ertemte, Olan Chorea, Harr Obo and Hua Ba in or around Huade County in the middle part of Nei Mongol and was described by Schlosser in 1924. The excavations by the Sino-Soviet Joint Paleontological Team in 1959 and recent excavations since 2013 at Tuchengzi (Tuchetse), another locality at Huade, have accumulated many specimens of the musk deer. Morphological and metric studies show that the musk deer specimens from Tuchengzi are the same as those described by Schlosser and can be included in the same species. *M. grandaevus* ranges from Siberia of Russia to North China, and likely to southern China, in the Late Miocene and Pliocene. The appearance of such folivorous musk deer in the Late Miocene deposits at Tuchengzi indicates that there were forests there during that period. Cladistic analyses show that the fossil species of *Moschus* are closely related to each other and can be grouped together as Moschini or Moschinae. *Micromeryx* is closer to *Moschus* and Cervidae, but the relationship between *Micromeryx* and *Moschus* is more complicated than previously considered; nonetheless *Hispanomeryx* is closer to Bovidae.

Key words Tuchengzi, Huade, Nei Mongol; Late Miocene; Moschidae, *Moschus*

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1 Introduction

Musk deer are well known for their musk gland, which is highly valued in Chinese medicine. Extant musk deer belong to only one genus, *Moschus*. However, the taxonomic composition and phylogenetic relationships of fossil musk deer remain quite controversial (Viret, 1961; Morales et al., 1981; Moyà-Solà, 1986; Janis and Scott, 1987, 1988; Scott and Janis, 1993; McKenna and Bell, 1997; Gentry et al., 1999; Vislobokava and Lavrov, 2009; Sánchez et al., 2010, 2015; Wang et al., 2015; Aiglstorfer et al., 2017). A small and early true musk deer, *Moschus grandaevus*, was reported by Schlosser in 1924, represented by some fragmentary dentitions and a few limb bones from Ertemte, Olan Chorea, Harr Obo and Hua Ba in Huade County, a northeastern county of Ulanqab Municipality in central Nei Mongol, North China.

The area was first explored by Swedish geologist and paleontologist Johan Gunna Andersson and his Chinese collaborators in 1919 and 1920 (Andersson, 1923), then by Schlosser (1924), and later by a Sino-Soviet Joint Expedition Team in 1959 (Zhai, 1963; Qiu, 1979). The 1959 excavation collected many specimens of *M. grandaevus* from a locality at Tuchengzi (Tuchetse). The Tuchengzi locality (Google map address: https://goo.gl/maps/q4JfefaNs2H2; Baidu map address: http://j.map.baidu.com/k9M5N) with Late Miocene deposits is about 16.3 km directly south of the Ertemte locality. The musk deer specimens collected in 1959 were identified but only briefly described (Qiu, 1979). Recent excavations since 2013 at Tuchengzi (Dong et al., 2014, 2016, 2018) have enriched the collection of musk deer. Here we systematically describe the new material of musk deer collected from Tuchengzi in recent excavations, together with previously undescribed limb bones collected in 1959, and discuss the phylogenetic and taxonomic relationships of fossil musk deer with other related taxa.

Dental terminology follows Dong (2004), with upper teeth abbreviated in uppercase and lower teeth in lowercase. Measurement methods follow Heintz (1970). All specimens described are housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

2 Systematic Paleontology

Mammalia Linnaeus, 1758
(Clade: Cetartiodactyla Montgelard et al., 1997)
Artiodactyla Owen, 1848
Ruminantia Scopoli, 1777
Pecora Flower, 1883
Cervoidea Simpson, 1931
Moschidae Gray, 1821
Moschinae Zittel, 1893
Moschus Linnaeus, 1758
Moschus grandaevus Schlosser, 1924

2014 *Moschus grandaevus*, Dong, p. 24-25

Material

Two left maxillary fragments with DP4-M3 (IVPP V 23514.1) and M1-3 (V 23514.2); two right maxillary fragments with M2-3 (V 23514.3) and M2-3 (V 23514.4); eight right mandibular fragments with p3-m3 (V 23515.1), with p3-m3 (V 23515.3), with broken p4 and complete m1-3 (V 23515.4), with complete m1-2 and broken m3 (V 23515.5), with dp4-m1 (V 23515.7), with m2-3 (V 23515.9), with dp4 (V 23515.10) and with p2-m2 (V 23515.11); three left mandibular fragments with p3-m3 (V 23515.2), with dp4-m2 (V 23515.6) and with m2-3 (V 23515.8). A proximal fragment of right metacarpus (V 23516.3); two distal fragments of metacarpus (V 23516.1-2); two left astragalus (V 23516.4-5); two proximal middle phalanges (V 23516.6-7); three intermediate middle phalanges (V 23516.8-10); a distal middle phalange (V 23516.11).

Description

The maxillary dentition available only ranges from DP4 to M3 (see Table 1 for measurements). The DP4 (5.78 mm × 5.92 mm) is composed of four simple main cusps in two distinct lobes (Fig. 1A [Figure 1: see original paper]), with the buccal main cusps higher than the lingual ones. The entostyle is present and moderate, but other accessory elements such as precingulum, entocingulum, postcingulum, spur, neocrista, etc. are absent. The maxillary molars are morphologically similar to each other and relatively simple; accessory elements such as precingulum, postcingulum, neocrista, entostyle (basal pillar), etc. are absent. However, the molars are characterized by the presence of a metaconule spur, which is not evident on M1, slightly evident on M2, and very clear on M3. The expression of the spur is probably related to the degree of wear; it is very evident on unworn or slightly worn molars (Fig. 1A, D), but might disappear on heavily worn crowns, especially on M1. The entocingulum is also present on the molars but poorly developed.

The mandibular dentition available ranges from the second premolar to the last molar, as well as a last deciduous tooth (Fig. 2 [Figure 2: see original paper]). Measurements of lower teeth are listed in Table 2 and comparisons in Table 3 .

The p2 is composed of two main cusps. The paraflexid and talonid basin are not evident; the trigonid basin and entoflexid are present and open lingually, while the hypoflexid is absent. The p3 is composed of two main cusps and some minor cusps (Fig. 2A-C). The paraflexid, trigonid basin, entoflexid, and talonid basin are all present and open lingually, and the hypoflexid is also present but poorly developed. The p4 is characterized by molarization. The premetacristid extends forward and reaches the parastylid, so that the paraflexid and trigonid basin are completely closed. The paraconid is reduced and enclosed by the extended premetacristid, making the anterior lobe of p4 analogous to that of the lower molars (Fig. 2A-C). The entoflexid and hypoflexid are well developed and open. The entoconid extends lingually and backwards so that it reaches the entostylid to close the talonid basin. The posterior lobe of p4 is also similar to that of lower molars, but its size is much smaller than the anterior one.

The m1 is composed of four selenodont main cusps; the Palaeomeryx fold is evidently absent. The precingulid is present, but at the superior part of the crown. The postcingulid and ectocingulid are both absent. The ectostylid is present and developed, but quite isolated (Fig. 2A, C–E). The m2 morphology (Fig. 2A–E) resembles that of m1. The m3 is composed of three lobes; the anterior two lobes resemble those of m1 and m2, but the third lobe is composed of a developed hypoconulid and a small entoconulid (Fig. 2A–D).

The dp4 is completely molarized (Fig. 2E). It is composed of three lobes, with the width of the lobes increasing from the first to the last.

The enamel on both upper and lower dentitions is generally smooth.

Eleven pieces of limb bones of a very small-sized artiodactyl (V 23516.1–11) are recognized as belonging to *M. grandaevus* (Fig. 3 [Figure 3: see original paper]). They are dimensionally very small (see Table 4 for measurements) among all artiodactyl materials from the Tuchengzi locality and proportionally match well with the teeth described above.

The metacarpus is represented by three fragments: a proximal one (V 23516.3) and two distal ones (V 23516.1–2). The proximal view is nearly triangular (Fig. 3Aa), with the medial side the shortest and the posterior or palm side curving inwards. The distal part of the metacarpus shows a nutrient foramen (medullary foramina) on both the anterior side (Fig. 3Bb) and posterior side (Fig. 3Bc). The metacarpal gully is not evident on either the anterior (dorsal) or posterior (palm) sides; the fusion of metacarpus III and IV is quite complete.

The astragalus or talus is represented by two complete specimens (V 23516.4–5), both left ones (Fig. 3C–D). The proximal trochlea (trochlea tali) is well developed. The crest for articulation with the fibula and calcaneus is more developed, wider, and higher than that for articulation with the tibia. The distal part of the talus, or head of the talus (caput tali), forms a second trochlea as in all artiodactyls, although less developed than the proximal trochlea.

The proximal middle phalange (Fig. 3E) is represented by two specimens (V 23516.6–7), the intermediate middle phalange (Fig. 3F) by three specimens (V 23516.8–10), and the distal middle phalange by only one specimen (V 23516.11). It is not evident whether they are from the third or fourth digit, or from the anterior or posterior limbs. They are very typical of artiodactyls, and the only peculiar trait is that the distal middle phalange is significantly narrow (Fig. 3G).

Many limb bones of *M. grandaevus* from the same locality under one same number IVPP V 5631.3 were collected by the Sino-Soviet Joint Expedition in 1959 and mentioned by Qiu (1979), but not yet described. Some representatives of these old specimens (Fig. 4 [Figure 4: see original paper]), i.e., the parts not present in the new materials depicted above, are described below and measurements are given in Table 5 .

Two incomplete scapula specimens are available (Fig. 4A–B). Their dorsal margin is broken and missing. The lateral view of the scapula is rather narrow. The scapula spine (spina scapulae) is developed but its outer margin is also incompletely preserved. The infraspinous fossa (fossa infraspinata) is much larger than the supraspinous fossa (fossa supraspinata), which appears very limited. The acromion is not evident, but the tuberculum supraglenoidale is well developed. In medial view, the subscapula fossa (fossa subscapularis) is generally flat and slightly concave.

The available humerus consists of two distal fragments. In anterior view (Fig. 4Cb), the humerus condyle is composed of the humerus trochlea on the medial side and the humerus capitulum with a sagittal crest on the lateral side. The radius fossa is developed above the humerus condyle. In posterior view (Fig. 4Cc), both medial and lateral epicondyles are well developed, with a developed olecranon fossa in between. In distal view (Fig. 4Cf), the medial and lateral epicondyles are divided by a trochlea gully, and both epicondyles are nearly equal in size.

The available radius is a distal end of a left one (Fig. 4D). The transversal crest is evident on the posterior side. A moderate trochlea is developed on the distal end for articulation with the carpus.

The available femur is a proximal end of a right one (Fig. 4E). The femur head (caput ossis femoris) is eminent and protrudes medially. The major trochanter is also eminent and protrudes posteriorly. They are aligned at the same level and separated from each other by the femur neck and trochanter fossa. The minor trochanter is well developed.

The available tibia consists of three distal fragments. The anterior side is concave longitudinally (Fig. 4Fb), and the posterior side convex (Fig. 4Fc). The medial malleolus is well developed (Fig. 4Fd) and the lateral one is moderate (Fig. 4Fe). The distal surface for articulation with the talus is composed of two fossae or gullies, with the medial one longer than the lateral one (Fig. 4Ff).

The available calcaneus consists of two complete left specimens (Fig. 4G–H). The calcaneal tuber is half semicircular in both medial and lateral views. The calcaneal body is plank-like. The sustentaculum tali is well developed. The processus coracoideus is eminent. The base of the calcaneus, or distal end, is also developed into a coracoid processus.

No complete metatarsus is available. The identifiable metatarsus consists of three proximal fragments; the distal fragments are not distinct from those of the metacarpus. The proximal view of the metatarsus is polygonal, with the anterior-posterior diameter close to that of the medial-lateral one (Fig. 4Ia). The metatarsal gully is evident on the anterior side and eminent on the posterior side (Fig. 4Ib, c). The medial and lateral sides are nearly flat (Fig. 4Id, e).

Comparison

The Tuchengzi specimens are nearly identical to those of *Moschus grandaevus* from Ertemte and Olan Chorea established by Schlosser (1924) both metrically (Tables 1, 3-5) and morphologically, and they can be grouped into the same taxon. Vislobokova and Lavrov (2009) discussed some specimens of *M. grandaevus* from Yushe in northern China. These specimens are metrically very close to those from Tuchengzi (Tables 1, 3) and can also be included in the same species. Vislobokova and Lavrov (2009) also described other specimens of *M. grandaevus* from Olkhon Island in Baikal and Taralyk-Cher in Tuva, Russia. The dimensions of Olkhon specimens are generally very close to, except for a few parts slightly larger than, those of Tuchengzi specimens (Tables 3-5). The cingula are absent on upper molars, the Palaeomeryx fold is absent but the ectostylid is present on lower molars, and the anterior lobe of p4 is well molarized, in both Tuchengzi and Olkhon specimens. Differences appear in the limb bones: the proximal crest of the talus for articulation with the fibula and calcaneus is more developed and the shaft of the metapodials is more slender in Olkhon specimens.

There are only two fossil species of *Moschus*: *M. grandaevus* and *M. primaevus*. Compared with *M. primaevus* from the Early Pliocene deposits in the Huiteng River (Chitong-gol) area established by Teilhard de Chardin (1926), the dentitions of both forms share the following traits: brachyodonty, similar measurements (Tables 1, 3-5), presence of the spur on the metaconule of upper molars, and molarization of the anterior lobe of p4. However, the most significant morphological difference is that the Palaeomeryx fold is evidently present in Huiteng River specimens and absent in those from Ertemte and Tuchengzi.

There are six extant species of *Moschus* in China: *M. moschiferus*, *M. anhuiensis*, *M. berezovskii*, *M. fuscus*, *M. chrysogaster* and *M. leucogaster* (Wang, 2003). However, only *M. moschiferus*, with three subspecies, is present in the geological record: *M. moschiferus moschiferus*, *M. moschiferus pekinensis* and *M. moschiferus plicodon*. Compared with *M. moschiferus pekinensis* from the Middle Pleistocene Localities 1 and 3 of Zhoukoudian described by Young (1932) and Pei (1936), Tuchengzi specimens are characterized by lower tooth crowns and smaller dimensions (Tables 1, 3-5). The metaconule spur on upper cheek teeth and ectostylid on lower molars are present in both Zhoukoudian and Tuchengzi specimens, but more developed in Zhoukoudian specimens. The metaconule spur is absent in extant *M. moschiferus* (Young, 1932).

Moschus moschiferus plicodon from the Middle Pleistocene deposits of Yanjinggou (Yenchingkou) established by Colbert and Hooijer (1953) differs from Tuchengzi specimens by having higher tooth crowns, presence of precingulid on lower molars, and larger dimensions (Tables 1, 3). Nevertheless, both forms have a molarized anterior lobe of p4, presence of ectostylid, and absence of Palaeomeryx fold on lower molars.

Compared with *Moschus moschiferus moschiferus* from the Late Pleistocene deposits in Xianren Cave at Ji’ an in Jilin Province (Dong and Jiang, 1993), Tuchengzi specimens share the same characters such as a molarized anterior lobe of p4, presence of ectostylid, and absence of Palaeomeryx fold on lower molars. However, the crown height and other dimensions of Ji' an specimens are evidently larger than those of Tuchengzi specimens (Tables 1, 3).

Compared with extant musk deer such as that mentioned by Teilhard de Chardin (1926), that from Asia housed at the Laboratoire d'Anatomie Comparée de Paris, as well as *Moschus chrysogaster sifanicus* of Sichuan (Colbert and Hooijer, 1953), Tuchengzi specimens are metrically smaller (Tables 1, 3).

Three maxillary fragments and more than three dozen mandibular fragments of *Moschus* sp. were mentioned by Han (1985) in her preliminary report on the artiodactyls from the type locality of *Lufengpithecus* at Shihuiba, Lufeng, Yunnan Province in southern China. The specimens were not described but were briefly indicated as generally close to *M. grandaevus* of Ertemte and different from *M. primaevus* by the absence of Palaeomeryx fold. The specimens are unfortunately unavailable for comparison. However, another *Moschus* sp. from Yuanmou *Lufengpithecus* localities near Lufeng with a similar horizon is probably the same species as that from Shihuiba (Pan et al., 2006). Compared with Tuchengzi specimens, Yuanmou specimens are metrically larger and morphologically simpler. The metaconule spur and ectostylid are present in Tuchengzi specimens but absent in Yuanmou specimens. However, the Palaeomeryx fold is absent in both forms.

3.1 Geographic and Geological Ranges of Fossil Musk Deer

Moschus grandaevus (Schlosser, 1924) is the first fossil musk deer reported in China; the specimens were from Ertemte, Olan Chorea, Harr Obo and Hua Ba in or around Huade County in the middle part of Nei Mongol. The species was discovered again during the 1959 Sino-Soviet expedition but at the Tuchengzi locality (Qiu, 1979), also from the Late Miocene in Huade County. It was later uncovered from the Pliocene deposits in the Yushe Basin in Shanxi Province (Tedford et al., 1991; Vislobokova and Lavrov, 2009). As mentioned above, *Moschus* sp. from the Late Miocene deposits of Lufeng and Yuanmou in Yunnan Province in southern China shows some similarities to *M. grandaevus* of Huade and might be the same species or a closely related species.

The second fossil musk deer, *M. primaevus* (Teilhard de Chardin, 1926), was from the Huiteng River area southwest of Xilinhot in eastern Nei Mongol (Li et al., 2003). The species has not yet been found elsewhere. The presence of Palaeomeryx fold on the lower molars of this species distinguishes it from other musk deer, and it was considered as *Lagomeryx primaevus* (Vislobokova, 1990; Vislobokova and Lavrov, 2009).

In the Middle Pleistocene, two fossil subspecies of *M. moschiferus* were reported. *Moschus moschiferus pekinensis* was found from the Middle Pleistocene Locality 1 and Locality 3 of Zhoukoudian in Beijing (Young, 1932; Pei, 1936), then from the Early Pleistocene Locality 18 of Zhoukoudian (Teilhard de Chardin, 1940), and later from the Late Pleistocene Xiaogushan Paleolithic site in Liaoning Province of northeastern China (Zhang et al., 1985). *Moschus moschiferus* *plicodon* was found from the Middle Pleistocene of Yanjinggou (Yenchingkou) (Colbert and Hooijer, 1953), and later from the Early Pleistocene Longgupo site (Huang et al., 1991); both sites are in Chongqing Municipality of central China. *Moschus moschiferus*, or *M. moschiferus moschiferus* from Ji' an in Jilin Province in northeastern China (Dong and Jiang, 1993) is a fossil representative of extant *M. m. moschiferus*, indicating that the subspecies appeared as early as the Late Pleistocene in northeastern China.

Micromeryx is another fossil genus of Moschidae reported in China (Lee and Wu, 1978; Qiu et al., 1981; Wang et al., 2015). Two species, *Micromeryx* cf. *M. flourensianus* from the Middle Miocene Nanyu Quarry, Gansu Province and *Micromeryx* sp. (IVPP V 18969) from the Middle Miocene Lengshuigou in Shaanxi Province, were recently confirmed and described (Wang et al., 2015). If the fragmentary specimens of putative *Micromeryx* sp. from locality DM 16 of Damiao (as early as MN1 or MN2) in Nei Mongol reported by Zhang et al. (2011) can be confirmed for their taxonomic status, it would be the earliest Moschidae from China. Two other *Micromeryx* species, *Micromeryx* sp. (IVPP V 3208 and V 3208.1) from the Middle Miocene Lengshuigou in Shaanxi Province (Lee and Wu, 1978) and *Micromeryx* sp. (IVPP V 6023 and V 6023.1-2) from Lierbao Quarry, Qinghai Province, the Middle Miocene Xianshuihe Formation (Qiu et al., 1981), were revised as *Hispanomeryx* sp. 1 and *Hispanomeryx* sp. 2 respectively and described recently (Wang et al., 2015).

3.2 Paleo-ecological Consideration

The brachyodont dentitions of *Moschus grandaevus* imply that it was a browser. Its proportionally long limbs indicate that the musk deer was a good jumper. Extant musk deer are partially arboreal (Sheng et al., 1992), which extends their browsing range and helps them escape from large-sized predators. The narrow and sharp hooves (Fig. 3) and lightly built body size of *M. grandaevus* suggest it could also have been partially arboreal. Its habitat might have been a mixture of shrubs and large trees. It could hide in the shrubs, jump onto the branches of shrubs, and jump further onto the branches of large trees for a wider range of leaves or to get rid of predators.

3.3 Phylogenetic Relationship of Musk Deer

Hispanomeryx is a controversial genus of Moschidae. Its taxonomic and systematic status has been referred either to Moschidae (e.g., Morales et al., 1981; McKenna and Bell, 1997; Vislobokava and Lavrov, 2009) or to Bovoidea (e.g., Moyà-Solà, 1986; Gentry et al., 1999). Likewise, Moschidae was considered either closely related to Cervidae (e.g., Janis and Scott, 1987, 1988; Scott and Janis, 1993; Su et al., 1999; Hernández Fernández and Vrba, 2005; Aiglstorfer et al., 2017) or closely related to Bovidae (e.g., Sánchez et al., 2010, 2015; DeMiguel et al., 2014). Here we test the phylogenetic relationship of fossil musk deer with cervids, bovids, and other related taxa (see Table 6 for data matrix) by cladistic analyses with PAUP4.0a (Build 159) programmed by Swofford (2002).

Eighteen fossil taxa with as many available characters as possible, including a hypothetical ancestor, all species of *Moschus*, two *Micromeryx*, three *Hispanomeryx*, two cervids and two bovids, a palaeomerycid, and a tragulid, were selected for cladistic analyses with data sources as follows: *Dorcabune* cf. *D. progressus* (Pan et al., 2006); *Palaeomeryx tricornis* (Qiu et al., 1985); *Moschus grandaevus*; *M. primaevus* (Teilhard de Chardin, 1926); *Moschus* sp. (from Yuanmou, Yunnan; Pan et al., 2006); *M. moschiferus pekinensis* (Young, 1932); *M. m. plicodon* (Colbert and Hooijer, 1953); *M. m. moschiferus* (Dong and Jiang, 1993); *Micromeryx* cf. *M. flourensianus* (Wang et al., 2015); *Micromeryx azanzae* (Sánchez and Morales, 2008); *Hispanomeryx* sp. 1 (from Lengshuigou, Shaanxi; Wang et al., 2015); *H. andrewsi* (Sánchez et al., 2011); *H. daamsi* (Sánchez et al., 2010); *Hydropotes inermis* (Young, 1932); *Cervavitus shanxius* (Dong and Hu, 1994; Dong et al., 2018); *Gazella sinensis* (Dong et al., 2013) and *Leptobos (Smertiobos) crassus* (Dong, 2008). The characters chosen and their states are as follows:

4. Number of main cusps on P2: 0. four; 1. three; 2. two.

5. Lingual cusp fold(s) on P2: 0. absent; 1. weak (present but not developed, just one fold); 2. strong (developed and with two or more folds).

6. Number of main cusps on P3: 0. four; 1. three; 2. two.

7. Lingual cusp fold(s) on P3: 0. absent; 1. weak (present but not developed, just one fold); 2. strong (developed and with two or more folds).

8. Number of main cusps on P4: 0. four; 1. three; 2. two.

9. Lingual cusp fold(s) on P4: 0. absent; 1. weak (present but not developed, just one fold); 2. strong (developed and with two or more folds).

10. Pattern of lingual main cusps on upper molars and buccal main cusps on lower ones: 0. nearly conical; 1. selenodont; 2. nearly triangular.

11. Pattern of buccal main cusps on upper molars and lingual main cusps on lower ones: 0. somewhat conical; 1. selenodont; 2. nearly cylindrical; 3. nearly semi-circular.

12. Entocingulum on upper molars: 0. absent; 1. weak; 2. developed.

13. Entostyle (basal pillar) on upper molars: 0. absent; 1. moderate; 2. developed; 3. very developed.

14. Size of paraconid on p4: 0. moderately developed; 1. present but reduced.

15. Opening of trigonid basin (lingual valley between paraconid and metaconid) on p4: 0. widely open; 1. half open; 2. closed by anterior extension of premetacristid.

16. Paraflexid state on p4: 0. present and open; 1. present but closed by anterior extension of premetacristid; 2. disappeared.

17. Opening of talonid basin (lingual valley between entoconid and entostylid) on p4: 0. widely open; 1. half open; 2. closed.

18. Palaeomeryx fold: 0. developed; 1. present but weak; 2. absent.

19. Crown ratio of the lower molars: 0. relatively shorter and broader; 1. relatively narrower and elongated.

20. Precingulid on lower molars: 0. absent; 1. moderate; 2. hypertrophied.

21. Orientation of the prehypocristid on lower molars: 0. straight and pointing to the center of the teeth; 1. lingually-turned and fused with the pre-entocristid.

22. Ectocingulid on lower molars: 0. absent; 1. present but weak; 2. developed.

23. Ectostylid (basal pillar) on lower molars: 0. absent; 1. present but weak; 2. developed; 3. hypertrophied.

24. Hypotalonid basin of the m3: 0. distally open; 1. distally closed.

25. Entoconulid vs. hypoconulid on m3: 0. the lengths of entoconulid and hypoconulid nearly the same; 1. hypoconulid evidently longer than entoconulid.

26. Morphology of the articular facet for the semilunate in the radius: 0. without lateral notch; 1. with lateral notch.

27. Morphology of the tuber calcanei: 0. short and broad; 1. transversally compressed and dorsoplantarly elongated.

28. General morphology of the astragalus: 0. slender and elongated; 1. short and wide.

29. Morphology of the lateral condyle in the distal trochlea of the astragalus: 0. very inclined and sporting a triangular and well-marked proximal notch; 1. vertical or slightly inclined, without proximal notch.

30. Metatarsal gully: 0. little developed; 1. moderately developed; 2. very developed.

All characters in Table 6 are unordered and equally weighted. The heuristic search found 101 most parsimonious trees, of which 18 optimal trees were retained. The strict and semistrict consensus trees based on all optimal trees are the same. The Adams consensus tree (Fig. 5 [Figure 5: see original paper]) is nearly the same as the strict and semistrict consensus trees, with the only difference that *Dorcabune* cf. *D. progressus* and *Palaeomeryx tricornis* derive together from the first node in strict and semistrict consensus trees rather than from the second node as in the Adams consensus tree. As the cladogram illustrates, three Neogene musk deer species, *Moschus grandaevus*, *M. primaevus* and *Moschus* sp. (from Yunnan), form a monophyly; and three Quaternary musk deer subspecies, *M. moschiferus pekinensis*, *M. m. plicodon* and *M. m. moschiferus*, form another monophyly. They are sister groups and form a further monophyly which can be grouped as Moschini or even as a subfamily Moschinae because *Micromeryx* does not form a monophyly with *Moschus* and could not be placed in Moschinae. *Micromeryx* is closer to *Moschus* and cervids (*Cervavitus shanxius* and *Hydropotes inermis*) than to *Hispanomeryx*. The latter is closer to *Gazella sinensis* than to cervids and musk deer.

This result in Fig. 5 is based on available material, mostly dentitions and a few post-cranial skeletons, and all characters are unordered and equally weighted. The result may vary if some characters are ordered and weighted, or with the accumulation of new and more complete specimens.

4 Conclusions

The musk deer specimens from Tuchengzi are the same as those of *Moschus grandaevus* from Ertemte, Olan Chorea, Harr Obo and Hua Ba in or around Huade County in the middle part of Nei Mongol, and can be included in the same species. It ranges from Siberia of Russia to North China, and likely to southern China, in the Late Miocene and Pliocene. The appearance of folivorous and partially arboreal musk deer in the Late Miocene deposits at Tuchengzi indicates that there were forests there during that period. The fossil species of *Moschus* are closely related to each other and can be grouped together as Moschini or Moschinae. *Micromeryx* is closer to *Moschus* and Cervidae than to *Hispanomeryx*, but the relationship between *Micromeryx* and *Moschus* is more complicated than previously considered; nonetheless *Hispanomeryx* is closer to Bovidae. The systematic status of *Micromeryx* and *Hispanomeryx* remains to be further investigated with more complete materials.

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