



Systematic Paleontology (Vertebrate Paleontology)

New material of Muntiacinae (Artiodactyla, Mammalia) from the Late Miocene of the northeastern Qinghai-Tibetan Plateau, China

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Abstract

Recent expeditions in the northeastern Qinghai-Tibetan Plateau have produced additional mammalian fossils from the Lower Baodean (equivalent to Vallesian, Late Miocene), and, significantly, a new large and the earliest muntjac, *Muntiacus noringenensis* sp. nov. It is phylogenetically closer to the Late Pliocene *M. fenghoensis* and extant *M. vuqangensis* than the other fossil and extant muntjacs are. The existence of this muntjac and other folivores in the Late Miocene Qaidam Basin suggests a forested period in the basin and the evolution from a forested and humid environment to a desert one today. Such a dramatic evolution in environments is an evidence of the effect of the uplift of the Qinghai-Tibetan Plateau and of its influence on continental climates. **To cite this article:** *W. Dong, C. R. Palevol 6 (2007).*

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Résumé

Le nouveau matériel de Muntiacinae (Artiodactyla, Mammalia) du Miocène supérieur du Nord-Est du plateau Qinghai-Tibet, Chine. Les récentes expéditions dans le Nord-Est du plateau Qinghai-Tibet ont livré de nouveaux mammifères du Baodéen inférieur (équivalent du Vallésien, Miocène supérieur) et, en particulier, un nouveau muntjak de grande taille, le plus ancien connu, attribué à une espèce nouvelle, *Muntiacus noringenensis* sp. nov. Il est phylogénétiquement plus proche de *M. fenghoensis* du Pliocène supérieur et de la forme actuelle *M. vuqangensis* que ne le sont les autres muntjaks, tant fossiles qu'actuels. La présence de ce muntjak, associée à celle d'autres espèces folivores, suggère un paysage forestier dans ces régions au Miocène supérieur. L'évolution d'un environnement forestier humide vers le désert semi-aride qui existe aujourd'hui est une conséquence de l'élévation progressive du plateau Qinghai-Tibet et de son influence sur les climats continentaux. **Pour citer cet article :** *W. Dong, C. R. Palevol 6 (2007).*

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Keywords: *Muntiacus*; Cervidae; Artiodactyla; Qaidam Basin; Qinghai-Tibetan Plateau; Late Miocene

Mots clés : *Muntiacus* ; Cervidae ; Artiodactyla ; Bassin du Qaidam ; Plateau Qinghai-Tibet ; Miocène supérieur

Version française abrégée

Découverte au cours des expéditions sino-suédoises en 1927–1933, la localité de Tuosu Nor, dans l'Est du bassin de Qaidam, a été le premier site à vertébrés

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fossiles du plateau Qinghai-Tibet. Les gisements du Miocène supérieur de Tuosu Nor avaient livré des bois de cervidés primitifs. Cependant, la taxonomie de ces matériaux était difficile à préciser, du fait de leur état fragmentaire ; Bohlin a reconnu cinq taxons de cervidés [3]. Les fouilles récentes dans le bassin [27] ont livré des éléments additionnels de cervidés et, surtout, un nouveau muntjak.

Mammalia Linnaeus, 1758
 Artiodactyla Owen, 1848
 Cervoida Gray, 1821
 Cervidae Gray, 1821
 Muntiacinae Pocock, 1923
Muntiacus Rafinesque, 1815
Muntiacus noringenensis sp. nov.

Holotype : IVPP V13086, un bois droit de chute, presque complet (Fig. 2a et b).

Localité : localité de l'IVPP CD9805 (Fig. 1).

Horizon : niveaux sableux moyen et inférieur du gisement, partie inférieure de la formation supérieure de Youshashan, Baodéen inférieur (équivalent du Vallésien), Miocène supérieur.

Étymologie : la nouvelle espèce tire son nom d'une petite rivière (Noringen Gol) connectant le lac du Qurliq au lac du Tuosu.

Diagnose : muntjak de grande taille, proche de celles de *Muntiacus fenghoensis* et de *M. vuquangensis*. Son merrain est plus long que chez *M. fenghoensis*, mais l'andouiller basilaire et la base du bois sont plus petits. La base de son merrain est beaucoup plus comprimée que chez *M. vuquangensis*. La base comprimée et la courbure de son merrain sont proches de celles de *M. lacustris*, mais sa taille est double de celle de *M. lacustris*. Il se distingue des autres espèces du genre par sa taille, à l'évidence plus grande. Son andouiller basilaire est beaucoup plus petit que son merrain, mais il est plus grand que celui des espèces actuelles, comme *M. muntjak*, *M. reevesi*, *M. feai*, etc., ainsi que des formes fossiles, comme *M. leilaensis*.

Description : l'holotype IVPP V13086 (Fig. 2a et b) est un bois de chute. Le bois a été soumis à une certaine usure due au transport ou à l'action du vent de sable lors de son exposition à l'air libre, ce qui a réduit son ornementation et la meule. Le merrain et l'andouiller basilaire bifurquent très près de la meule. La partie proximale du merrain est aplatie et courbe. Le diamètre du merrain au-dessus de la meule est de 40,3 mm au maximum et de 17,8 mm au minimum. La partie distale du merrain est cassée à 187 mm au-dessus de la meule. L'andouiller

basilaire est beaucoup plus petit que le merrain. Son diamètre au milieu de l'andouiller basilaire mesure 16,7 mm au maximum et 12,2 mm au minimum. La partie distale, 54 mm au-dessus de la meule, est cassée. L'ornementation du bois est assez usée, mais montre encore des sillons longitudinaux sur la surface du bois.

Comparaison et discussion

Les merrain et andouiller du spécimen décrit ci-dessus sont très simples ; la bifurcation est très proche de la meule. Ces sont là des caractères distinctifs des Muntiacinae. Ils diffèrent de *Dicrocerus* du Miocène moyen [26] par la présence évidente de la meule, par la partie proximale du merrain aplatie et par la plus grande taille du bois. Ils diffèrent d'*Euprox* du Miocène moyen et supérieur [7,10,22] par une bifurcation située plus près de la meule et la partie proximale du merrain aplatie. Ils diffèrent d'*Eostyloceros* du Miocène supérieur [31] par leur moins grande taille et par une partie proximale du merrain aplatie. La bifurcation du bois très près de la meule, le merrain courbe et la partie proximale du merrain aplatie, etc., tous ces caractères du spécimen décrit dessus sont typiques de *Muntiacus* ; nous attribuons donc notre individu à ce genre.

D'après la morphologie du spécimen IVPP V13086, celui-ci était un muntjak de grande taille. Le seul muntjak de taille voisine découvert en Chine est *M. fenghoensis* (Fig. 2c), du Pliocène supérieur de Shanxi [6]. Le spécimen du Qaidam et celui de *M. fenghoensis* ont un merrain et un andouiller basilaire aplatis, mais la meule et l'ornementation des sillons du premier sont moins développées que dans le cas du second ; le merrain du spécimen du Qaidam est plus long que celui de *M. fenghoensis*, mais l'andouiller basilaire du premier est plus court que celui du second et la base du bois du premier est plus petite que celle du second. Ces différences substantielles distinguent clairement le spécimen du Qaidam de *M. fenghoensis*. Le seul muntjak actuel de taille voisine est la forme indochinoise *M. vuquangensis*. Mais, chez le spécimen du Qaidam, la base du merrain est beaucoup plus comprimée que chez *M. vuquangensis*, et l'angle entre le merrain et l'andouiller basilaire beaucoup plus grand. Comparées avec les autres espèces fossiles du genre, les dimensions du bois et de l'andouiller basilaire du spécimen du Qaidam sont à l'évidence plus grandes. On peut conclure que le spécimen du Qaidam représente une nouvelle espèce de *Muntiacus*.

D'après une analyse cladistique (Tableau 1, Fig. 3), la nouvelle espèce est phylogénétiquement plus proche de *M. fenghoensis* et de *M. vuquangensis* que des autres

Muntiacus (*s. s.*), d'*Eostyloceros blainvillei*, de *Paracervulus australis* et d'*Euprox robustus*. *M. vuqangensis* était attribué à *Megamuntiacus*, mais Schaller et Vrba ont montré que les données morphologiques et génomiques ADN suggèrent qu'il appartenait, avec d'autres muntjaks, au genre *Muntiacus*, au lieu de constituer un genre propre [20]. Si l'on accepte d'attribuer *M. vuqangensis* au genre *Muntiacus*, on peut sans doute placer la nouvelle espèce à l'intérieur de ce genre ; mais si l'on fait de *M. vuqangensis* un genre propre, on doit probablement inscrire la nouvelle espèce dans le genre *Megamuntiacus*, si on se réfère au cladogramme de la Fig. 3. Il est plus prudent, à l'heure actuelle, de transiger, pour attribuer le muntjak géant au genre *Muntiacus* (*s.l.*), par opposition à *Muntiacus* (*s.s.*), excluant le muntjak géant, et d'attendre de disposer de davantage de preuves pour résoudre le problème.

L'existence de ce muntjak, accompagnée par celle d'autres folivores du Miocène supérieur du bassin du Qaidam, suggère la présence d'un milieu forestier dans ce bassin. Le passage d'un environnement forestier et humide au climat désertique et aride d'aujourd'hui découle des effets de l'élévation du plateau Qinghai-Tibet et de son influence sur les climats continentaux.

1. Introduction

After serving as the project representative on behalf of the Rockefeller Foundation in the Peking Man Site at the Zhoukoudian (Choukoutian) in 1927 and 1928 [14], the Swedish paleontologist Birger Bohlin shifted his interests to northwestern China, and carried out a series of Sino-Swedish Expeditions from 1927 to 1933, which resulted in the discovery of the Tuosu Nor locality (Fig. 1) in the eastern Qaidam

Basin, the first Cenozoic vertebrate fossil locality in the Qinghai-Tibetan Plateau [3]. The uplifted Himalayas and Kunlun Mountains south of the Qaidam Basin form two immense barriers for the humid Indian Monsoon and make this basin of about 200 000 km², with an average altitude of 2800 m, an arid area. The harsh natural environment makes most of the basin little peopled and poorly explored. The mammal-bearing beds of the Late Miocene on the western shore of the Tuosu Nor have produced a tantalizing array of antlers of primitive deer (members of the family Cervidae) – up to five taxa were recognized, although Bohlin [3] refrained from naming most of them because of the fragmentary nature of the antlers. In recent years, renewed exploration carried out in the Qaidam Basin by Xiaoming Wang et al. [27] have produced additional materials of cervids, and significantly, a muntjac is among the new discoveries. The associated mammals include *Ictitherium*, *Adcrocuta eximia*, *Chalicotherium brevirostris*, *Hipparion teilhardi*, Sivatherinae indet., *Euprox* sp., *Olonbulukia tsaidamensis*, *Qurliknorina* sp., *Tossunoria*, *Tsaidamotherium*, *Protoryx* sp., *Tetralophodon*, and *Struthio*. The fauna is restricted to the lower part of the Upper Youshashan Formation and is biochronologically dated from the Lower Baodean (Late Miocene), or equivalent to the European Vallesian (MN9–10); the horizon is correlated to magnetic polarity C5–C4A (11–9 Ma) [27].

2. Systematic Description

Mammalia Linnaeus, 1758
 Artiodactyla Owen, 1848
 Cervoidea Gray, 1821
 Cervidae Gray, 1821

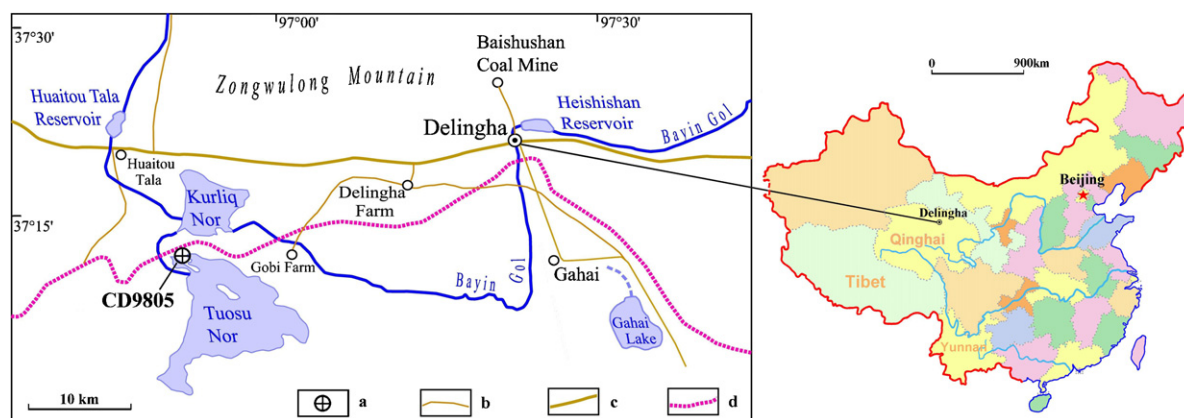


Fig. 1. Geographic location of fossil locality IVPP CD9805. (a) Fossil locality; (b) dirt road; (c) paved road; (d) railroad.

Fig. 1. Localisation géographique de la localité fossile IVPP CD9805. (a) Localité fossile ; (b) piste de terre ; (c) chaussée ; (d) chemin de fer.

Muntiacinae Pocock, 1923

Muntiacus Rafinesque, 1815

Muntiacus noringenensis sp. nov.

Holotype: IVPP V13086, a nearly complete shed right antler, housed in the IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing).

Type locality: IVPP locality CD9805, northwestern shore of the Tuosu Lake (Tossun Nor), near the mouth of the Noringen Gol River, eastern Qaidam (=Tsaidam, Caidam, or Chaidamu) Basin, Haixi Mongolian and Tibetan Autonomous Region, Qinghai Province, China (Fig. 1).

Type stratum: middle and lower green sandstone, the lower part of the Upper Youshashan Formation, Lower Baodean (equivalent to Vallesian), Late Miocene.

Etymology: the species is named after the small Noringen Gol (River) that connects the Kelike (Qurliq) Lake and Tuosu Lake.

Diagnosis: a large muntjac, close in size to that of *Muntiacus fenghoensis* and *M. vuquangensis*. But its main beam is longer, its brow tine is shorter and its antler base is smaller than those of *M. fenghoensis*; and its main beam base is much more flattened than that of *M. vuquangensis*. The great basal flattening and curvatures of the beam are similar to those of *M. lacustris*, but its size doubles that of *M. lacustris*. It differs from the other fossil and extant species of the genus by its larger size. Its brow tine is much smaller than the main beam, but it is larger than that of extant muntjacs such as *M. muntjak*, *M. reevesi*, *M. feai*, etc., as well as of fossil *M. leilaoensis*.

Description: the type specimen IVPP V13086 (Fig. 2a et b) is a shed antler. The specimen was water worn during fluvial transport prior to deposition and aeolian sand blasting after exposure, which may have reduced the ornamentation of the burr and the longitudinal ridges. The antler crown is composed of a main beam and a brow tine. They arise almost together from the burr. The main beam projects somewhat laterally from the burr and forms an angle of about 40° with the plane of the burr, and then gradually curves inward. The main beam is much flattened proximally, but less so distally. The flattened plane of the main beam forms an angle of about 60° with the plane of the main beam and the brow tine. The maximum diameter of the main beam above the burr is 40.3 mm and the minimum diameter at the same location is 17.8 mm; the maximum diameter of the main beam at the distal part of the beam is 20.7 mm and its minimum diameter is 17.0 mm. The distal part of the main beam is broken about 187 mm from the burr. The full length of the original beam is estimated to be about 210 mm, similar to that of extant *M. vuquangensis* from Laos [20]. The brow tine is placed on the burr and projected inward at the base, as in most extant muntjacs. However, it seems to continue growing less upward than in the antler of *M. fenghoensis* (Fig. 2). Compared with the main beam, it is much shorter and smaller. Its cross sections are somewhat triangular and they are gradually flattened towards the distal end. The maximum diameter of the brow tine at its middle is 16.7 mm and the minimum diameter is 12.2 mm. The distal end of the tine, 54 mm from the burr, is worn. The estimated full length of the brow tine is about 60 mm. The angle between the

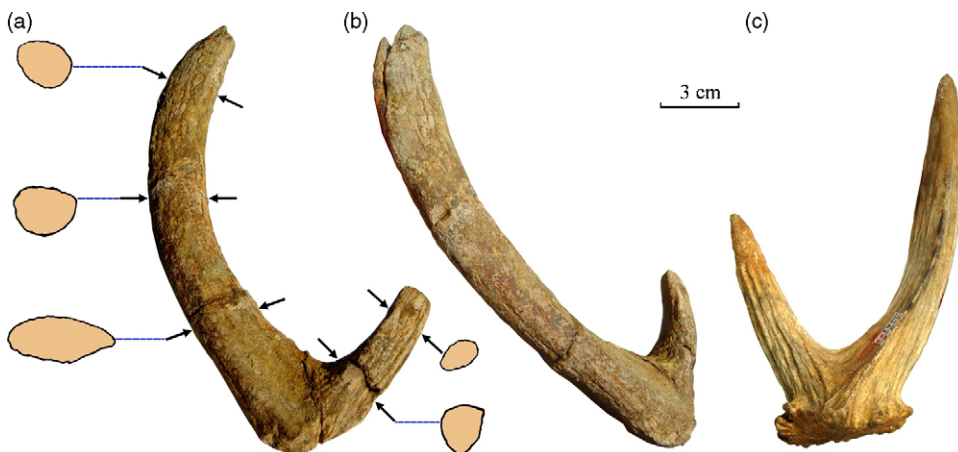


Fig. 2. Comparison between *Muntiacus noringenensis* sp. nov. and *M. fenghoensis*. Anterior view (a) and lateral view (b) of IVPP V13086, holotype (*M. noringenensis* sp. nov.); anterior view (c) of IVPP V815, holotype (*M. fenghoensis*).

Fig. 2. Comparaison entre *Muntiacus noringenensis* sp. nov. et *M. fenghoensis*. Vue antérieure (a) et vue latérale (b) de IVPP V13086, holotype (*M. noringenensis* sp. nov.); vue antérieure (c) d'IVPP V815, holotype (*M. fenghoensis*).

main beam and brow tine measures about 80° . The ornamentation of the antler is abraded, but retains its original surface texture of parallel longitudinal ridges and grooves.

Comparison and discussion: the above-described antler is very simple. It has only two tines, and its main beam and brow tine arise simultaneously from the burr and are separated from each other just a little distance from the burr. These characteristics are consistent with the morphology of the traditionally defined subfamily Muntiacinae [26], which includes common Eurasiatic genera, such as *Dicrocerus*, *Euprox*, *Eostyloceros*, *Muntiacus*, etc. Of these four genera, *Dicrocerus* seems to be the most primitive in its general lack of a true burr [4,5]. Indeed, Azanza [2] proposed a phylogeny of Miocene cervids, in which she placed *Euprox* plus tribe Muntiancini in the subfamily Muntiacinae. In this cladistic framework, the Muntiacinae was considered a sister-group to the advanced deer (Cervinae) because of their common possession of such derived characters as a burr, a posteriorly reclined pedicle, and a posterior location of the pedicle. Furthermore, the Muntiacinae was defined by a single autapomorphy of ‘strongly inclined pedicles’ [2].

Although it is not possible to check the condition of its pedicle, the new Qaidam material seems readily to fall in Azanza’s concept of the Muntiacinae. Among Chinese European Miocene muntiacines, there are several reported occurrences of *Euprox*, such as the Middle Miocene *Euprox* sp. (previously named as *Dicrocerus* sp.) from Tunggur [7,8], *Euprox* cf. *furcatus* (previously called *Dicrocerus* cf. *D. furcatus*) from Shanxi Province of northern China [31], *Euprox robustus* from the Yuanmou Basin of southern China [10], and *Euprox furcatus* from the European Late Miocene [4,12,22,25]. They all possess two-tined, simple antlers, as well as a burr. The same occurs in the Late Miocene *Eostyloceros blainvillei* (type species of the genus) from northern China [24,31]. *Muntiacus* also has these derived characters, but differs from *Euprox* by its larger angle of bifurcation and shorter distance from the bifurcation to the burr. Furthermore, *Muntiacus* tends to have an arched main beam with an elongated oval cross section, in contrast to a less curved beam that has a nearly rounded cross section in *Euprox*. The Qaidam specimen resembles *Eostyloceros* by its arched main beam, but differs from *Eostyloceros* by the flattened main beam and smaller antler size. Therefore, in overall morphology, the Qaidam specimen seems best placed in *Muntiacus* with its curved main beam, flattened cross section, and large bifurcation angle, which arises immediately above the burr.

Based on the size of the described specimen, IVPP V13086 represents a large muntjac among known species of the genus. The only similar sized fossil muntjac discovered so far in China is *M. fenghoensis* (Fig. 2c) from the Late Pliocene of Shanxi Province [6]. The Qaidam specimen and *M. fenghoensis* have a curved and somewhat flattened main beam and brow tine, although the latter’s main beam features a sharper medial ridge along the flattened edge. But the burr and the ornamentation of the grooves and ridges of the former are less developed than those of *M. fenghoensis*. Particularly, the main beam of the Qaidam specimen is longer and more curved, its base is much more flattened than those of *M. fenghoensis*, but its brow tine is shorter and closer to the burr than that of *M. fenghoensis*. The antler base of the Qaidam specimen is smaller than that of *M. fenghoensis*. The longer length and similar thickness of the main beam of the Qaidam specimen demonstrates that it is an adult antler instead of a juvenile state of *M. fenghoensis*. The shape of the Qaidam specimen is regular, no pathological trace can be observed, and it can be considered as a normal adult antler. These substantial differences clearly distinguish the Qaidam specimen from *M. fenghoensis*. On the other hand, the great basal flattening and curvatures of the beam are similar to those of *M. lacustris* from Shansi [24], but its size doubles that of *M. lacustris*.

The only similar sized extant muntjac known so far is the giant muntjac (*M. vuquangensis* = *Megamuntiacus vuquangensis*) from Indochina [20]. Compared with this giant muntjac, the Qaidam specimen has the similar dimensions of the main beam and brow tine, the position of bifurcation is nearly on the burr as in giant muntjac, but the Qaidam specimen has larger bifurcation angle, its main beam base is much more flattened, its main beam curves gradually inward instead of curving weakly from its base and then strongly at about two-thirds from the burr, as in giant muntjac.

Compared with *M. leilaoensis* [11], the oldest muntjac known before from the Late Miocene of the Yuanmou Basin in southern China, they share the same characters, such as simple antler, only one bifurcation, brow tine very close to the burr, curved main beam, flattened main beam base, etc., but the dimensions of the Qaidam specimen are twice over those of *M. leilaoensis*, its main beam base being much more flattened and its brow tine longer. Compared with other fossil species of the genus, such as *M. nanus* [24], *M. bohlini* [23], the overall dimensions and the brow tine of the Qaidam specimen are evidently larger and the burr is less developed. It can be concluded that the Qaidam specimen represents a new species of the *Muntiacus*.

Table 1
Data matrix of the characters
Tableau 1
Matrice des caractères

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
Hypothetic ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Procervulus ginsburgi</i> [1]	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	?	?	?	?	?	0
<i>Heteroprox larteti</i> [25]	1	0	?	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	?	?	0
<i>Dicrocerus elegans</i> [26]	0	1	0	0	1	1	1	0	1	0	1	2	0	1	1	1	0	?	?	?	?	?	?	1
<i>Muntiacus nanus</i> [24]	?	?	?	?	?	2	0	1	1	0	0	0	0	2	1	0	?	?	?	?	?	?	?	0
<i>Muntiacus bohlini</i> [23]	0	1	2	2	0	2	0	1	1	1	0	0	0	2	1	0	1	?	?	?	1	?	?	0
<i>Muntiacus lacustris</i> [24]	?	?	?	?	?	2	0	1	2	1	0	0	0	2	1	0	?	?	?	?	?	?	?	0
<i>Muntiacus leilaoensis</i> [11]	0	1	2	2	0	2	0	1	1	2	0	0	1	2	1	0	?	?	?	?	?	?	?	0
<i>Muntiacus reevesi</i> [16]	0	1	2	2	0	2	0	1	1	1	0	0	0	2	1	0	1	0	1	2	0	1	0	0
<i>Muntiacus muntjak</i> [16]	0	1	2	2	0	2	0	1	1	2	0	0	0	2	1	0	1	1	1	0	2	1	0	0
<i>Muntiacus feae</i> [16]	0	1	2	2	0	2	0	1	1	1	0	0	0	2	1	0	1	1	0	2	1	1	0	0
<i>Muntiacus noringenensis</i> sp. nov.	?	?	?	?	?	2	0	1	2	1	1	1	1	2	1	1	?	?	?	?	?	?	?	1
<i>Muntiacus fenghoensis</i> [6]	?	?	?	?	?	2	0	1	1	2	1	1	0	2	1	1	?	?	?	?	?	?	?	1
<i>Muntiacus vuquangensis</i> [20]	0	1	2	2	0	2	0	1	1	2	1	1	0	2	1	1	?	1	?	2	2	1	1	1
<i>Eostyloceros blainvillei</i> [24]	0	1	1	1	0	2	0	1	0	1	2	2	0	2	1	2	?	?	?	?	?	?	?	2
<i>Euprox robustus</i> [10]	0	1	1	1	0	2	0	1	0	0	1	1	0	2	1	2	1	?	?	?	?	?	?	2
<i>Paracervulus australis</i> [26]	0	1	1	1	0	2	0	1	0	0	2	1	0	2	1	2	1	?	?	?	?	?	?	2

N.B. '?' in the matrix means missing character due to incomplete material.

N.B. « ? » dans la matrice représente le caractère perdu pour cause de matériel incomplet.

3. Phylogenetic relations

3.1. Materials and methods

In order to find the phylogenetic position of the Qaidam muntjac, nine species of *Muntiacus*, in which five fossil species and four extant ones, three other species of Muntiacinae (sensu Azanza), a species of Dicrocerinae (sensu Azanza), and two species of Procervulinae (sensu Azanza) were selected, together with the Qaidam muntjac, for cladistic analysis (Table 1). A hypothetic ancestor is also included, whose characters are all set as plesiomorph (coded as '0'). Sixteen characters of frontal appendages, one dental character, three cranial characters, one postcranial character, one soft tissue character (frontal gland, unique character of extant *Muntiacus* [16]) and body size character were selected for constructing the data matrix. These characters were chosen as criteria for taxonomic identification and classification by some authors, as indicated in Table 1. NEXUS Data Editor (Version 0.4.8 by Roderic D.M. Page) was employed for editing data matrix. The matrix was then processed with PAUP* (Version 4.0b10 for 32-bit Microsoft Windows by David L. Swofford). The options used in process are as follows: heuristic search settings: optimality criterion = parsimony; character weight was set as EQUAL; starting tree(s) obtained via stepwise addition; addition sequence: simple (reference taxon = hypothetic ancestor); number of trees held at

each step during stepwise addition = 1; branch-swapping algorithm: tree-bisection-reconnection (TBR); steepest descent option not in effect; branches collapsed (creating polytomies) if maximum branch length is zero; 'MulTrees' option in effect; topological constraints not enforced; the option to search for consensus tree from all best trees was set as STRICT; the consensus tree was rooted by using default outgroup. The best trees and strict consensus tree were saved and then organized with TreeViewX (Version 0.5.0 by Roderic D.M. Page).

3.2. Characters used for constructing data matrix

- 1- Parallel pedicles: (0) no; (1) yes.
- 2- Position of pedicle: (0) above orbit; (1) behind orbit.
- 3- Pedicle crest on frontal: (0) weak; (1) medium; (2) strong.
- 4- Backward pedicle inclination: (0) weak; (1) medium; (2) strong.
- 5- Compressed pedicle: (0) no; (1) yes.
- 6- Burr development (ordered): (0) weak; (1) medium; (2) strong.
- 7- Antler basal segment: (0) present; (1) absent.
- 8- Centripetal mineralization of antler: (0) absent; (1) present.
- 9- Cross section of main beam base: (0) nearly round; (1) oval; (2) elongated.
- 10- The growth style of the main beam (ordered): (0) nearly straight; (1) simply curved; (2) multi-curved.

- 11- Main beam size: (0) small; (1) medium; (2) large.
- 12- Brow tine size: (0) small; (1) medium; (2) large.
- 13- Angle between main beam and brow tine: (0) small; (1) large.
- 14- Antler shedding: (0) uncertain; (1) irregular; (2) regular.
- 15- Antler ornamentation: (0) absent; (1) present.
- 16- Antler size: (0) small; (1) medium; (2) large.
- 17- *Palaeomeryx* fold on lower molars (ordered): (0) present; (1) absent.
- 18- Relation between nasal and maxilla: (0) separate; (1) connected.
- 19- Anterior margin of lachrymal: (0) with projection; (1) without projection.
- 20- Lachrymal pit: (0) small; (1) medium; (2) large.
- 21- Metatarsal length: (0) short; (1) medium; (2) long.
- 22- Frontal gland: (0) absent; (1) present.
- 23- Body size (ordered): (0) small; (1) medium; (2) large.

Because the evolution of the burr is very clear from without or weak burr, as in *Procervulus*, to primitive burr, as in *Dicrocerus*, and then to developed burr, as in Muntiacinae and Cervinae, the primitive antlers without burr are found only in the Middle Miocene or earlier, the antlers with primitive burr are found only from the Middle Miocene or slightly later, the antlers with developed burr are found only in the Late Miocene or later, the polarity of character 6 is clear and thus ordered in the matrix. The grow style of the main beam is also from nearly straight to simple curved and then to double or multi-curved, character 10 is thus ordered in the matrix. The *Palaeomeryx* fold is found only in fossil cervids from the Miocene or earlier, the polarity of character 17 is thus clear and ordered. Character 23 is ordered according to D ep eret’s law of augmentation [17]. The polarity of the remaining 19 characters is not certain, and these characters are not ordered in the matrix.

4. Results and discussion

Heuristic search results show that out of 23 total characters, four characters are of the ‘ordered’ type (Wagner), 19 characters are of the ‘unordered’ type, all characters have equal weight, three characters are parsimony-uninformative, number of parsimony-informative characters=20, score of best tree(s) found=48. A strict consensus tree from the 48 best trees is obtained, as in Fig. 3. Its tree length=51; consistency index (CI)=0.6863; homoplasy index (HI)=0.3137; CI excluding uninformative characters=0.6667; HI excluding uninformative characters=0.3333; retention index

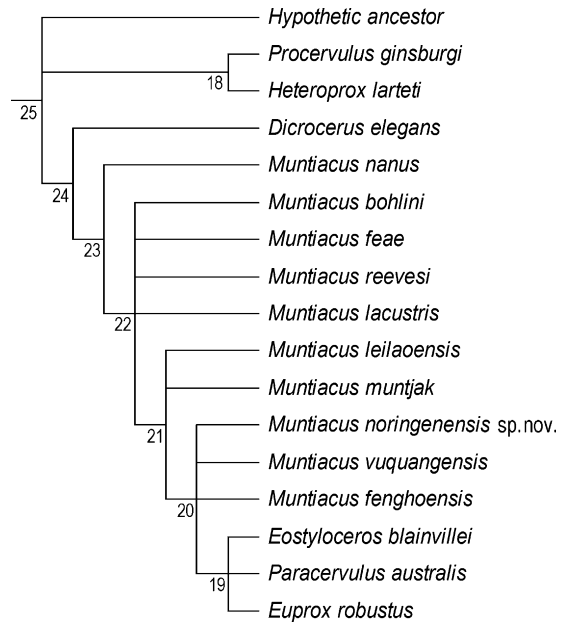


Fig. 3. Strict consensus tree. Apomorphies support the monophyletic branches: node 24: 2 (1), 6 (1), 9 (1), 14 (1), 15 (1), 18 (1), 19 (1), 20 (2), 22 (1); node 23: 3 (2), 4 (2), 6 (2), 8 (1), 14 (2), 17 (1); node 22: 10 (1); node 21: 10 (2), 21 (2); node 20: 11 (1), 12 (1), 16 (1) 1, 23 (1); node 19: 3 (1, reversed), 4 (1, reversed), 9 (0, reversed), 10 (0, reversed), 11 (2), 16 (2), 23 (2); node 18: 1 (1), 12 (1).

Fig. 3. Arbre de consensus strict. Les apomorphies supportent les branches monophyl tiques : n ud 24 : 2 (1), 6 (1), 9 (1), 14 (1), 15 (1), 18 (1), 19 (1), 20 (2), 22 (1); n ud 23 : 3 (2), 4 (2), 6 (2), 8 (1), 14 (2), 17 (1); n ud 22 : 10 (1); n ud 21 : 10 (2), 21 (2); n ud 20 : 11 (1), 12 (1), 16 (1) 1, 23 (1); n ud 19 : 3 (1, invers ), 4 (1, invers ), 9 (0, invers ), 10 (0, invers ), 11 (2), 16 (2), 23 (2); n ud 18 : 1 (1), 12 (1).

(RI)=0.7746; rescaled consistency index (RC)=0.5316. Characters 1 to 8, 14, 15, 17, 21, and 22 are not homoplastic (CI=1), and the others are more or less homoplastic, with CI from 0.333 to 0.667.

As shown in Fig. 3, the new species falls in node 20, and is phylogenetically next to *M. fenghoensis* and *M. vuquangensis*, as well as to node 19. *M. vuquangensis* was included into *Megamuntiacus*, but Schaller and Vrba showed that morphological and genomic DNA data suggested it being with other muntjacs in the genus *Muntiacus* and not in a genus of its own [20]. Node 19 is composed of *Eostyloceros blainvillei*, *Paracervulus australis*, and *Euprox robustus*, another group of large muntiacine, different from *M. noringensis* sp. nov., *M. fenghoensis*, and *M. vuquangensis*. The fossil and extant *Muntiacus* (s. s.) species fall in nodes 21, 22, and 23. That is to say, the Qaidam species falls between the groups of *Muntiacus* (s. s.) and the group composed of *Eostyloceros blainvillei*, *Paracervulus australis* and *Euprox robustus*, and in the group with *M. fenghoensis*

and *M. vuqangensis*. If we accept that *M. vuqangensis* belongs to genus *Muntiacus*, there is no doubt that we can also include the new species into this genus; but if we accept that *M. vuqangensis* belongs to a genus of its own, then we should probably include the new species into *Megamuntiacus*, based on the cladogramme in Fig. 3. It is more prudent for the time being to compromise by including the giant muntjacs into *Muntiacus* (s. l.), in contrast to *Muntiacus* (s. s.), excluding giant muntjacs, and to wait for more evidence to be found to settle the issue.

Based on the cladogramme in Fig. 3, node 23 is supported by characters 2 (presence of pedicle crest on frontal), 4 (backward pedicle inclination), 6 (well developed burr), 8 (presence of centripetal mineralization of antler), 14 (regular antler shedding), and 17 (absence of *Palaeomeryx* fold on lower molars). The node falls well in Azanza's concept of the Muntiacinae [2]. *Procervulus* and *Heteroprox* appear as a monophyly in node 18, which is supported by characters 1 (parallel pedicles) and 12 (brow tine medium sized). They were grouped as Procervulinae by Azanza [2], and the present cladistic analysis reconfirmed this classification.

Four fossil and three extant *Muntiacus* (s. s.) species appear in nodes 21, 22 and 23, they are next to each other and not interrupted by another genus, although they appear as polyphyly in the cladogramme in Fig. 3. It is remarkable that there is no character reversion from node 24 to node 20, and the fossil and extant *Muntiacus* (s. l.) species fall in this section. But four character reversions occur from node 20 to node 19, the latter being composed of three species of other genera. That is to say, if node 19 evolved independently without such reversions, the fossil and extant *Muntiacus* (s. l.) species will form a monophyly, and their status as one genus is thus acceptable.

5. Implications of the Qaidam fauna

Modern muntjacs represent the most primitive group of true deer that have deciduous antlers, and as browsers in dense vegetations, are restricted to the forests of southern Asia [21,28]. The fossil history of the muntiacines is represented by some scattered records in the Pliocene through the Pleistocene of northern China [6,9,24]. The first Late Miocene muntjac was reported recently from southwestern China [11]. The new muntjac described herein is the second Late Miocene muntjac. As mentioned in the introduction, the horizon yielding the new muntjac was dated back to 11–9 Ma, and that yielding *M. leilaoensis* was dated back to 9–7 Ma [11]; the new muntjac from Qaidam becomes the earliest muntjac

found so far in China. It not only suggests a greater diversity of muntjacs, but also provides new evidence for a much milder climate on the high plateau than occurs at present. The existence of this muntjac and other folivores in the Late Miocene Qaidam Basin suggests a forested landscape, in contrast to a desert one such as the arid climate that prevails today. Such a dramatic contrast in environments is one more piece of evidence of the effect of the uplift of the Qinghai-Tibetan Plateau and of its influence on continental climates [15,18,19].

The relationship of the Qaidam fauna with the Late Miocene hominoid fauna from the Siwaliks and that from Yunnan before the strong Plio-Pleistocene uplift of the Qinghai-Tibetan Plateau by the third Himalayan Movement has not yet been studied. But the presence of the Middle Miocene *Pliopithecus* in Tongxin [13] and in the Junggar Basins [29], that of *Dryopithecus* in Wudu of northwestern China [30], as well as that of a forested environment in the Late Miocene of the Qaidam Basin, indicate that the basin was a suitable region for Miocene hominoids. The understudied Qaidam Basin is therefore a promising place for paleontological research, as well as for paleoenvironmental research.

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