New material of Cervidae (Artiodactyla, Mammalia) from Xinyaozi Ravine in Shanxi, North China (Postprint)

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Date: 2020-03-31T00:00:00+00:00

Abstract

Many cervid specimens were uncovered during the field exploration for Nihewan beds at the beginning of the 1980s from Taijiaping, Shuichongkou and Dazhuangke localities along Xinyaozi Ravine at Nangaoya Township of Tianzhen County, Shanxi Province in North China. Recent studies on the cervid material identified seven species of Cervidae in total: Muntiacus bohlini, Cervavitus cf. C. huadeensis, Axis shansius, Nipponicervus elegans, Elaphurus davidianus predavidianus, E. bifurcatus from the Early Pleistocene deposits at Taijiaping and Shuichongkou localities, and Cervus (Elaphus) elaphus from uncertain horizon at Dazhuangke. At least the previous six species of cervids were from Nihewan Formation (Nihewanian or equivalent to European middle and late Villafranchian), i.e. the Early Pleistocene, in Sangganhe Basin area.Cervavitus cf. C. huadeensis and A. shansius were survivors from the Late Neogene; M. bohlini,N. elegans, E. davidianus predavidianus and E. bifurcatus are new forms of the Early Pleistocene.If Dazhuangke horizon can be dated as those of Shuichongkou and Taijiaping localities, the appearance of elaphoid cervids could be traced back to the Early Pleistocene, and the evolution of elaphoid antler would start from absence to presence of bez tine. The presence of Elaphurus and Nipponicervus in mainland China and Japanese archipelago implies further that the sea level was dropped down that these cervids could migrate from the mainland to the islands. The abundance of folivorous cervid specimens in the Xinyaozi Ravine area indicates the existence of a certain scale of forested environment in Sangganhe Basin area during the Early Pleistocene.

Full Text

Preamble

New Material of Cervidae (Artiodactyla, Mammalia) from Xinyaozi Ravine in Shanxi, North China

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Abstract

Many cervid specimens were uncovered during field exploration for Nihewan beds in the early 1980s from Taijiaping, Shuichongkou, and Dazhuangke localities along Xinyaozi Ravine at Nangaoya Township of Tianzhen County, Shanxi Province in North China. Recent studies on the cervid material identified seven species in total: *Muntiacus bohlini*, *Cervavitus* cf. *C. huadeensis*, *Axis shansius*, *Nipponicervus elegans*, *Elaphurus davidianus predavidianus*, *E. bifurcatus* from the Early Pleistocene deposits at Taijiaping and Shuichongkou localities, and *Cervus (Elaphus) elaphus* from an uncertain horizon at Dazhuangke. At least the first six species originated from the Nihewan Formation (Nihewanian or equivalent to the European middle and late Villafranchian), i.e., the Early Pleistocene, in the Sangganhe Basin area.

Cervavitus cf. *C. huadeensis* and *A. shansius* were survivors from the Late Neogene; *M. bohlini*, *N. elegans*, *E. davidianus predavidianus*, and *E. bifurcatus* are new forms of the Early Pleistocene. If the Dazhuangke horizon can be dated to the same period as those of Shuichongkou and Taijiaping localities, the appearance of elaphoid cervids could be traced back to the Early Pleistocene, and the evolution of elaphoid antlers would have progressed from the absence to the presence of a bez tine. The presence of *Elaphurus* and *Nipponicervus* in mainland China and the Japanese archipelago further implies that sea levels dropped sufficiently for these cervids to migrate from the mainland to the islands. The abundance of folivorous cervid specimens in the Xinyaozi Ravine area indicates the existence of a forested environment of considerable scale in the Sangganhe Basin area during the Early Pleistocene.

Key words: Xinyaozi, Tianzhen County, Nihewan Formation; Sangganhe Basin, middle and late Villafranchian, Early Pleistocene; Cervidae

Citation: DONG Wei, BAI Wei-Peng, PAN Yue et al., in press. New material of Cervidae (Artiodactyla, Mammalia) from Xinyaozi Ravine in Shanxi, North China. *Vertebrata PalAsiatica.* DOI: 10.19615/j.cnki.1000-3118.200320

Funding: Supported by the Strategic Priority Research Program (Class B) of the Chinese Academy of Sciences (Grant No. XDB 26030304)

Received: 2019-12-12

1. Introduction

Field exploration for Nihewan beds conducted in the early 1980s by the team of Wei Qi (1997) resulted in the discovery of numerous cervid specimens from Taijiaping, Shuichongkou, and Dazhuangke localities along Xinyaozi Ravine at Nangaoya Township of Tianzhen County, Shanxi Province in North China. The mammalian fossils collected along the ravine were designated the Xinyaozi fauna (Wei, 1997; Tong et al., 2011) and yielded four cervid taxa: *Muntiacus bohlini*, *Elaphurus bifurcatus*, *Eucladoceros boulei*, and *Rusa elegans* (Wei, 1997).

Although these localities are in Shanxi Province, they are very close to the Xiashagou (=Hsia-sha-kou) localities (Teilhard de Chardin and Piveteau, 1930) in the Nihewan Basin of Hebei Province, which have yielded cervids such as *E. bifurcatus*, *Cervus (Rusa) elegans*, etc. The fossils unearthed from the Shuichongkou deposits include *Nyctereutes* sp., *Canis* sp., *Agriotherium* sp., *Ursus* sp., *Meles* sp., *Felis* sp., *Pachycrocuta* sp., *Postschizotherium intermedium*, *Plesiohipparion houfenense*, *Equus sanmeniensis*, *Axis* sp., etc. (Qiu et al., 2002), as well as *Spirocerus wongi* (Bai et al., 2019). This faunal composition indicates an earlier age than that of the classical Nihewan fauna, likely ranging between 1.8 Ma and 2.6 Ma (Qiu et al., 2002).

The fossils from Taijiaping deposits include *Canis chihliensis palmidens*, *Nyctereutes sinensis*, *Pachycrocuta licenti*, *Homotherium* sp., *Megantereon nihewanensis*, *Lynx* sp., *Felis* sp., *Proboscidipparion sinense*, *Equus sanmeniensis*, *Coelodonta yanshanensis*, *?Rhinoceros* sp., *Gazella* sp., *Elaphurus bifurcatus* (Qiu, 2002), as well as *E. davidianus predavidianus* (Dong et al., 2019). The geological age of this fauna can be considered roughly contemporary with the classical Nihewan fauna (Qiu, 2002), with an estimated age of ca. 2.2–1.7 Ma (Liu et al., 2012), equivalent to the upper part of MNQ17 to the lower part of MNQ18 (Woodburne, 2013). The deposits at Shuichongkou are therefore slightly earlier than those at Taijiaping.

However, many specimens collected during the 1980s explorations have not yet been systematically studied. We reinvestigated the localities along Xinyaozi Ravine in 2017, studied cervid specimens from Taijiaping locality, and identified two *Elaphurus* species (Dong et al., 2019). Here we systematically describe the remaining cervid specimens from Xinyaozi Ravine at Tianzhen and discuss their taxonomy and evolutionary history. Antler measurement methods follow Dong et al. (2019), and dental terminology follows Dong (2004). Unfortunately, complete skulls with both antlers and dentitions are absent from the collection. The taxonomic assignment of antlers, upper and lower dentitions was based on their relative dimensions and morphological comparison with available identified specimens. All described specimens are housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP).

2. Systematic Paleontology

Mammalia Linnaeus, 1758
Artiodactyla Owen, 1848
Ruminantia Scopoli, 1777
Pecora Flower, 1883
Cervoidea Simpson, 1931
Cervidae Gray, 1821
Muntiacinae Knottnerus-Meyer, 1907
Muntiacus Rafinesque, 1815
Muntiacus bohlini (Teilhard de Chardin, 1940) (Figs. 1-2; Tables 1-3)

Cervulus cf. *sinensis* Teilhard de Chardin and Piveteau, 1930, p.44-46
Cervulus bohlini sp. nov. Teilhard de Chardin, 1940, p.79-88
Muntiacus bohlini Hooijer, 1951, p.7
Muntiacus bohlini Wang and Wu, 1979, p.541
Muntiacus bohlini Wei, 1997, p.196

Material: A nearly complete left antler with burr and broken pedicle (IVPP V 26267.1) from Shuichongkou; a right maxillary fragment with M1-3 (V 26267.2), a left mandibular fragment with p2-m2 (V 26267.3), a right mandibular fragment with p3-m3 (V 26267.4), and a right mandibular fragment with dp4-m2 (V 26267.5) from Taijiaping.

Description: Specimen V 26267.1 (Fig. 1 [Figure 1: see original paper]) is a left mature but unshed antler from an adult individual (see Table 1 for measurements). Its pedicle is broken, but a small part remains just below the burr. The pedicle cross-sections are oval, and the pedicle surface is smooth. Although the burr is partially broken on the lateral side, it is moderately developed and composed of a series of bony nodes. The brow tine is broken; based on the scar, it was likely very small and positioned relatively high above the burr, as in muntjacs (Fig. 1D). The main beam is thick, initially developing backward and slightly laterally, then curving medially at two-thirds of its length. It is flattened near the base, with cross-sections that are roughly semicircular or somewhat triangular near the base and become oval distally. The antler ornamentation consists of well-developed longitudinal grooves and crests on the antler crown surface.

The preserved right maxillary fragment (V 26267.2) contains three molars (Fig. 2A [Figure 2: see original paper]). The M1, M2, and M3 each consist of four main cusps with similar length and width. Accessory elements such as the neocrista, entostyle, and spur are developed; the entocingulum is visible though undeveloped. Upper cheek tooth measurements are listed in Table 2 .

The p2 appears only on V 26267.3 and consists simply of a main cusp and some minor cusps (Fig. 2B). Its trigonid basin, entoflexid, and talonid basin are present and open lingually. The p3 appears on V 26267.4 and V 26267.5 and comprises two main cusps and some minor cusps (Fig. 2C-D). The paraflexid, trigonid basin, entoflexid, and talonid basin are all present and open lingually, and the hypoflexid is also present. The p4, also present on V 26267.4 and V 26267.5, is similar to p3 but evidently larger, with the metaconid extending mesiodistally (Fig. 2C-D). The dp4 (14.16×7.45×5.7 mm) appears on V 26267.5 and consists of three lobes with a buccal basal pillar between every two lobes (Fig. 2D).

The m1 and m2 appear on all three mandibular fragments and each consist of four selenodont main cusps. The Palaeomeryx fold is evidently absent, the precingulum is present but undeveloped, while the ectostylid is developed (Fig. 2B-D). The m3 appears only on V 26267.4 and consists of three lobes; the anterior two lobes resemble those of m1 and m2, but the third lobe comprises a developed hypoconulid and a small entoconulid (Fig. 2C). Lower cheek tooth measurements are listed in Table 3 .

Comparison and determination: The antler (V 26267.1) is small, with an obviously tiny missing brow tine and a small main beam that inclines medially at the distal part. It is therefore similar to specimens from Xiashagou previously identified as *M. cf. sinensis* (Teilhard de Chardin and Piveteau, 1930) and later revised as *M. bohlini* (Teilhard de Chardin, 1940). Its morphology falls well within the variation range of *M. bohlini* from Loc. 18 near Beijing (=Peking) (Teilhard de Chardin, 1940). It is also metrically similar to specimens from Xiashagou and Dong et al. - New material of Cervidae from Xinyaozi Ravine in Shanxi, North China and those from Loc. 18 (Table 1). The antler (V 26267.1) is also morphologically close to those of *M. lacustris* from Yushe Basin (Teilhard de Chardin and Trassaert, 1937) and from Juyuandong (Han, 1987). For example, the brow tine is tiny, the main beam is small and curves medially, and the dimensions are similar. However, its bifurcation position is evidently higher. It differs from *M. leilaoensis* (Dong et al., 2004) and *M. zhaotongensis* (Dong et al., 2014) in its smaller burr and simpler curvature of the main beam. It differs from *M. hengduanshanensis* from Yunnan (Zong et al., 1996) in its thinner and much longer main beam.

The upper dentition (V 26267.2) is generally close to that of *M. bohlini* (RV 4002) from Loc. 18 near Beijing (Teilhard de Chardin, 1940), e.g., in the presence of spur and entostyle, but its dimensions are slightly larger than those from Loc. 18. Compared with *M. lacustris* from Sanhe in Guangxi (Dong et al., 2011), V 26267.2 is evidently larger (Table 2), and accessory elements such as the neocrista and spur are obvious in V 26267.2 but weak in Sanhe specimens. V 26267.2 is metrically larger than extant *Muntiacus* sp. (OV 949) and the Late Miocene muntjaks from Zhaotong (Table 2). The lower dentitions, represented by two adult and one young mandibular fragments (V 26267.3-5), are close to those of *M. bohlini* from Xiashagou (Teilhard de Chardin and Piveteau, 1930) and Loc. 18 near Beijing (Teilhard de Chardin, 1940) both morphologically and metrically (Table 3). For example, in p3 and p4, the metaconid is rounded and not fused with the paraconid; the paraflexid, trigonid basin, entoflexid, talonid basin, and hypoflexid are all present and open in specimens from Taijiaping, Xiashagou, and Loc. 18. For molars, the precingulum is present but undeveloped while the ectostylid is developed in specimens from Taijiaping, Xiashagou, and Loc. 18. Compared with *M. lacustris* from Juyuandong and Sanhe in Guangxi and *Muntiacus* sp. from Longgudong in Hubei, the Taijiaping lower dentitions are obviously larger (Table 3).

Both described antler and dentitions generally accord with the diagnosis of *M. bohlini* and are evidently different from other muntjaks, and can be assigned to this taxon.

Muntiacus is placed in Muntiacinae under Cervidae based on morphology (e.g., Vislobokova, 1990; Wang, 2003; Azanza et al., 2013; Dong et al., 2018), while Gilbert et al. (2006) suggested reassigning the genus to Cervinae based on their analyses of two mitochondrial protein-coding genes and two nuclear introns. However, this reassignment is not yet widely accepted, and we follow the classical classification in the present work.

Pliocervinae Khomenko, 1913
Cervavitus Khomenko, 1913
Cervavitus cf. *C. huadeensis* Qiu, 1979 (Figs. 3–4; Tables 4–6)

Material: A right antler fragment with two broken tines (IVPP V 26268.1); a right maxillary fragment with DP4-M2 (V 26268.2) and a right maxillary fragment with DP2-4 (V 26268.3); a right mandibular fragment with dp2-m2 (V 26268.4), a right mandibular fragment with dp3-m3 (V 26268.5), and a right mandibular fragment with dp3-m1 (V 26268.6), all from Taijiaping.

Description: Specimen V 26268.1 is a right antler fragment with two broken tines (Fig. 3A [Figure 3: see original paper]-B). The pedicle emerges from the frontal just above the orbit and inclines backward (Fig. 3B). The pedicle is thinner than the antler base and of moderate length (Table 4). Pedicle cross-sections are oval, and the pedicle surface is smooth. The burr is not very developed based on the preserved part and consists of a series of bony nodes. The brow tine is set a short distance above the burr. The main beam is straight as a continuation from the antler base in medial view but curves smoothly upward from the antler base in lateral view. The antler surface is ornamented with longitudinal crests and furrows.

The DP2 appears as an elongated triangle, and the DP3 also appears triangular but wider in occlusal view. Both DP2 and DP3 consist of four selenodont main cusps. Their precingulum is very developed, the entocingulum is moderately developed, but the entostyle (lingual basal pillar) is absent. The DP4 is molarized and composed of four selenodont main cusps (Fig. 4A [Figure 4: see original paper]-B). Its precingulum and entocingulum are moderately developed, and the entostyle and spur are developed. The M1 and M2 each consist of four main cusps with similar length and width. The neocrista and entocingulum are visible but not developed, while the mesostyle is well developed, and the entostyle and spur are developed. Upper cheek tooth measurements are listed in Table 5 .

The dp2 (Fig. 4C) is dominated by a main selenodont cusp (protoconid). Its crown is little worn and very low compared with permanent teeth. The dp3 is dominated by two main cusps (protoconid and hypoconid). Its trigonid basin is widely open, but the talonid basin is very narrow. The dp4 is molarized and composed of three lobes with developed buccal basal pillars. The m1 and m2 consist of four selenodont main cusps with evident precingulid and developed ectostylid. The m3 is composed of three lobes; its anterior two lobes resemble those of m1 and m2, and the third lobe is small (Fig. 4D). Lower cheek tooth measurements are listed in Table 6 .

Comparison and determination: The described antler (IVPP V 26268.1) is evidently larger than that of *M. bohlini* from Shuichongkou but obviously smaller than antlers of other cervids from Xinyaozi Ravine. It is morphologically close to that (V 9378, Fig. 3C–D) of *Cervavitus shanxius* from Hounao in Yushe Basin (Dong and Hu, 1994) and that from Tuchengzi (Dong et al., 2018). For example, the pedicle is moderately long and inclines backward, the brow tine does not emerge from the burr but from the base a short distance above the burr, and the first bifurcation angle is moderate. However, the Hounao specimen is evidently thinner than the Taijiaping specimen (Fig. 3, Table 4). Compared with *C. huadeensis* from Tuchengzi (Qiu, 1979; Dong et al., 2018), the Taijiaping specimen is similar to Tuchengzi specimen V 5634.3 (Qiu, 1979), e.g., the pedicle is not long, the antler base or stem 1 is neither long, and the main beam is straight in medial view. However, the brow tine is set quite high above the burr in other specimens of *C. huadeensis* (Qiu, 1979), differing from that of Taijiaping. The Taijiaping antler differs from those of *C. fenqii* from Juyuandong (Han, 1987), Longgudong (Chen, 2004), and Renzidong (Dong et al., 2009) by its larger dimensions. It differs from those of *C. ultimus* (Lin et al., 1978) by its larger angle of the first bifurcation.

The described upper cheek teeth are characterized by the presence of neocrista, spur, and entostyle. The neocrista is present in *C. shanxius* from Hounao and Tuchengzi but is more developed than in Taijiaping specimens. The spur and entostyle are similarly developed in Taijiaping as well as in Hounao and Tuchengzi specimens. The upper dentition of *C. huadeensis* is not yet available from Tuchengzi specimens. Compared with *C. fenqii* from Juyuandong (Han, 1987), Longgudong (Chen, 2004), and Renzidong (Dong et al., 2009), Taijiaping specimens also have developed entostyle but have evident neocrista and developed spur, which are absent in Juyuandong and Longgudong specimens. Additionally, Taijiaping specimens are slightly larger (Table 5). The lower cheek teeth from Taijiaping are generally similar to those of *C. huadeensis* from Tuchengzi (Dong et al., 2018) both morphologically and metrically (Table 6). Taijiaping specimens are evidently larger than those of *C. fenqii* from Juyuandong, Longgudong, and Renzidong, as well as those of *C. shanxius* from Hounao and Tuchengzi (Table 6).

Comparison between Taijiaping specimens and those of *Cervavitus* from other localities indicates that Taijiaping specimens are closer to *C. huadeensis* from Tuchengzi than to *C. fenqii* and *C. shanxius*. However, some differences remain between Taijiaping specimens and *C. huadeensis*, e.g., antler ornamentation is more developed in Tuchengzi antlers than in Taijiaping specimens, and the ectostylid is less developed in Tuchengzi lower molars. Additionally, *C. huadeensis* was previously uncovered from Neogene rather than Pleistocene deposits, and the material from Taijiaping is limited to a broken antler and some fragmentary jaws. We provisionally assign them as a conformis species of *C. huadeensis*.

Cervinae Goldfuss, 1820
Axis Smith, 1827
Axis shansius Teilhard de Chardin & Trassaert, 1937 (Figs. 5-6; Tables 7-9)

Axis shansius Teilhard de Chardin and Trassaert, 1937, p.44-50
Axis cf. *shansius* Chi, 1975, p.173
Axis shansius Chia and Wang, 1978, p.21-23
Axis shansius Dong and Fang, 2004, p.299-302
Axis shansius Dong, 2006, p.335-338
Axis shansius Bai et al., 2017, p.821-823

Material: A large part of a left antler with partial frontal (IVPP V 26264.1); a left maxillary fragment with DP2-M1 (V 26264.2), a left maxillary fragment with a broken DP3 and complete DP4 and M1 (V 26264.3), a left maxillary fragment with DP3-4 (V 26264.4); a right mandibular fragment with p2-m3 (V 26264.5), a left mandibular fragment with a broken p2 and complete p3-m3 (V 26264.6), a left mandibular fragment with dp2-m1 (V 26264.7). All specimens are from Taijiaping.

Description: Specimen V 26264.1 is a large part of a left antler with partial frontal (Fig. 5 [Figure 5: see original paper]; see Table 7 for measurements). The pedicle is relatively short, with oval cross-sections. The burr is composed of a series of developed bony nodules. The antler base, or stem 1, is relatively short. The distance between the first bifurcation and the burr is similar to that between the frontal and burr. The brow tine is long and curved in the middle. The main beam is very long and lyrately curved. The first bifurcation angle is very large, but the second is relatively small. The second and third tines are broken near their base. The antler surface is ornamented with developed longitudinal crests and furrows.

The DP2 appears as an elongated triangle (Fig. 6A [Figure 6: see original paper]), and the DP3 (Fig. 6A, C) also appears triangular but wider in occlusal view. Both DP2 and DP3 consist of four selenodont main cusps. Their precingulum is very weak, the entocingulum is moderately developed, and the entostyle (lingual basal pillar) is present. The DP4 is molarized and composed of four selenodont main cusps (Fig. 6A-C). Its precingulum is absent, its entocingulum is moderately developed, while the entostyle and spur are developed. The M1 consists of four main cusps with similar length and width (Fig. 6A–B). The precingulum, neocrista, and entocingulum are visible but very weak, while the mesostyle, entostyle, and spur are developed. The M2 and M3 are not available but might be similar to M1. Upper cheek tooth measurements are listed in Table 8 .

The dp2 (Fig. 6F) is dominated by a main selenodont cusp (protoconid). The dp3 (Fig. 6F) is dominated by two main cusps (protoconid and hypoconid). Its trigonid basin is widely open, but the talonid basin is very narrow. The dp4 (Fig. 6F) is molarized and composed of three lobes with developed buccal basal pillars. The p2 (Fig. 6D) is dominated by a main selenodont cusp (protoconid); its trigonid and talonid basins are weak, but the entoflexid is very developed. The p3 (Fig. 6D–E) is also dominated by the protoconid. The trigonid basin is well developed and widely open. The entoflexid and talonid basin are very narrow. The p4 (Fig. 6D–E) is dominated by the protoconid and metaconid. The metaconid does not extend forward but backward. The trigonid basin is moderately developed and open. The entoflexid and talonid basin are narrow but still open. The m1 (Fig. 6D–F) and m2 (Fig. 6D–E) consist of four selenodont main cusps. The m3 (Fig. 6D–E) is composed of three lobes; its anterior two lobes resemble m1 and m2, and the third lobe is small. The Palaeomeryx fold and goat fold are absent in all molars, but the precingulid is present and weak on m1 and absent on m2 and m3. The ectostylid (buccal basal pillar) is developed on m1, evident on m2, and fully grown on m3. Lower cheek tooth measurements are listed in Table 9 .

Comparison and determination: The described antler has an unbranching brow tine and bifurcated posterior beam that distinguishes it from *Elaphurus*, although its size is similar to the latter. It differs from the stratigraphically associated *Cervavitus* cf. *C. huadeensis* by its long, lyrated main beam. It fits well with the diagnosis of *Axis shansius* (Teilhard de Chardin and Trassaert, 1937) in its lyrated main beam with three tines and widely opened first fork, as well as its very long first tine (brow tine). Compared with *A. shansius* from Yushe, the Taijiaping antler is very close to that of THP 12387 (=No. 12.387) (Teilhard de Chardin and Trassaert, 1937), although its main beam is less curved than that of the type. The dimensions of the Taijiaping antler fall well within the variation range of antlers of *A. shansius* from Yushe (Table 7). Both upper and lower dentitions of Taijiaping specimens are also metrically similar to those of *A. shansius* from Yushe (Tables 8–9). The Taijiaping antler is also close to that of *A. shansius* from Xihoudu (Chia and Wang, 1978), e.g., three-tined antler and lyrated main beam. However, the first bifurcation of Xihoudu specimens is closer to the burr, and the first bifurcation angle is larger. The Taijiaping antler is similar to that of *A. shansius* from Tuozidong (Dong and Fang, 2004) and Jinyuandong (Bai et al., 2017), e.g., in the curvature of the main beam and the form of the second bifurcation. Both upper and lower dentitions of Taijiaping specimens share the same morphological traits with those from Tuozidong and Dajushan (Dong, 2006), e.g., the presence of accessory elements such as precingulum, entostyle, and spur. Their dimensions are also close (Tables 8-9).

Compared with other *Axis* species, Taijiaping specimens are much larger than those of *A. speciosus* from Ertemte in Nei Mongol (Schlosser, 1924). For example, the main beam of the Taijiaping specimen is twice as long, the burr is twice as thick, and the dentitions are nearly one and a half times larger. The Taijiaping antler is moderately longer and thicker than that of *A. rugosus* from Tongshan at Yuanqu in Shanxi (Chow, 1954). Additionally, the brow tine is set very close to the burr (as in extant *A. axis*), and the furrow ornamentation is very developed in the Tongshan antler. The Taijiaping antler is moderately longer but slightly thinner than that of *A. lingjingensis* from the Lingjing Man site in Henan (Dong and Li, 2008; Bai et al., 2017), and its first bifurcation angle is larger than that in Lingjing specimens. Taijiaping specimens are therefore morphologically and metrically closest to *A. shansius* and clearly different from other *Axis* species.

Nipponicervus Kretzoi, 1941
Nipponicervus elegans (Teilhard de Chardin & Piveteau, 1930) (Figs. 7-8; Tables 10-12)

Cervus (Rusa) elegans Teilhard de Chardin and Piveteau, 1930, p.54-63
Rusa elegans Wei, 1997, p.196

Material: A broken skull with a pair of broken antlers (IVPP V 26265.1), a broken right antler with pedicle and partial frontal (V 26265.2), a broken left antler with pedicle and partial frontal (V 26265.3); specimens V 26265.1-3 are from Taijiaping. A left maxillary fragment with P2-M3 (V 26265.4), a right maxillary fragment with P2-M3 (V 26265.5), a left maxillary fragment with P3-M3 (V 26265.6), a right maxillary fragment with P2-4 (V 26265.7), a right mandibular fragment with p4-m3 (V 26265.8), a left mandibular fragment with p2-m3 (V 26265.9), a left mandibular fragment with p3-m2 (V 26265.10), and a right mandibular fragment with p4-m3 (V 26265.11) from Xinyaozi Ravine.

Description: Although the referred antlers are all broken, the length of the broken main beams indicates that the antlers bifurcate at least twice and have at least three tines. Specimen V 26265.1 is a broken skull with a pair of broken antlers (Fig. 7A [Figure 7: see original paper]-B). The frontals are flat and wide in anterior view. Two relatively short pedicles emerge from the lateral-posterior parts of the frontals above the orbits and extend backward and laterally. The distance between the bases of the two pedicles measures 37 mm, and the angle between the two pedicles is about 60°. Pedicle cross-sections are oval. The burrs are composed of a series of bony nodules and are moderately developed, although partially broken. The antler base or stem 1 of the pair is well preserved and moderately long. The first bifurcation angle is 50°-65°. The first tine (brow tine) is relatively long (Table 10) and curves slightly medially. Both left and right first tines are broken near their tips, and both left and right main beams are also broken. The antler surface is ornamented with longitudinal crests and furrows.

Specimen V 26265.2 is a broken right antler with pedicle and partial frontal (Fig. 7C–D). It is very similar to the right antler of specimen V 26265.1 described above, e.g., relatively short pedicle with oval cross-sections, burr formed with a ring of bony nodules, antler base and first tine moderately long (Table 10). However, its main beam continuously curves laterally and posteriorly instead of laterally and upward. It is also ornamented with longitudinal crests and furrows and has some bony nodules or pearling on the medial side.

Specimen V 26265.3 is a broken left antler with pedicle and partial frontal (Fig. 7E–F). It is also very similar to specimen V 26265.1 (see Table 10 for measurements). However, its ornamentation has many bony nodules on the medial side in addition to longitudinal crests and furrows.

The P2 is semi-molarized: the lingual main cusps (protocone and metaconule) are separated by the entoflexus, but the buccal main cusps (paracone and metacone) are fused end-to-end (Fig. 8A [Figure 8: see original paper]–B). The neocrista is developed, the entocingulum is very weak, but the precingulum, entostyle, and spur are absent. The P3 is similar to P2 but with larger dimensions (Fig. 8A–C).

The P4 is one-lobed and evidently different from P2 and P3: the anterior and posterior main cusps on both lingual and buccal sides are fused end-to-end; the precingulum, entocingulum, entostyle, and spur are all absent, but the neocrista is still present and developed (Fig. 8A–C). The M1 consists of four main cusps with similar length and width (Fig. 8A–C). The neocrista is absent, the precingulum and entocingulum are visible but not developed, while the mesostyle, entostyle, and spur are developed. The morphology of M2 is similar to that of M1, but its size is larger than that of M1, and its length is slightly larger than its width. There is a fold on the lingual side of the postprotocrista (posterior crest of protocone) equivalent to the Palaeomeryx fold of lower molars. It differs from the neocrista in its position on the lingual side, instead of the buccal side, of the postprotocrista. The morphology of M3 is also similar to that of M1, but its length is evidently larger than its width. Upper cheek tooth measurements are listed in Table 11 .

The p2 (Fig. 8E) is dominated by a main selenodont cusp (protoconid); the paraflexid is absent, its trigonid basin is developed and widely open, its entoflexid and talonid basins are very narrow, and its hypoflexid is very weak. The p3 (Fig. 8E–F) is also dominated by the protoconid; its paraflexid is present but very weak, its trigonid basin is well developed and widely open, its entoflexid and talonid basins are relatively narrow, and its hypoflexid is moderately developed. The p4 (Fig. 8D–E) is dominated by the protoconid and metaconid; its paraflexid is weak and open, its metaconid extends moderately forward and backward but leaves the trigonid basin and entoflexid open; the entoconid inclines backward and nearly closes the talonid basin. The m1 (Fig. 8D–F) and m2 (Fig. 8D–F) consist of four selenodont main cusps; the Palaeomeryx fold and goat fold are absent, but the precingulid is present and weak, and the ectostylid (buccal basal pillar) is developed; the dimensions of m2 are evidently larger than those of m1. The m3 (Fig. 8D–E) is composed of three lobes; its anterior two lobes resemble m1 and m2, and the third lobe is small. Lower cheek tooth measurements are listed in Table 12 .

Comparison and determination: The type and associated specimens of *Nipponicervus elegans*, previously named *Cervus (Rusa) elegans*, were collected from the Xiashagou area, i.e., the type locality, in the Nihewan Basin (Teilhard de Chardin and Piveteau, 1930). Compared with Xiashagou specimens, Xinyaozi specimens are very close to those from the type locality. For example, the pedicle is relatively short, the antler base is moderately long, the first bifurcation angle is moderate, the main beam is nearly straight, the brow tine is relatively long and curves slightly medially; the entoflexus is developed on P2 and P3, the entostyle is developed on upper molars; the trigonid basin is well open on p3 and p4, and the ectostylid is developed on lower molars. The dimensions of antlers and dentitions are also very close (Tables 10–12). Additionally, Xinyaozi specimens are geographically and stratigraphically close to Xiashagou specimens and can be regarded as the same species. Some antlers from Yushe Basin were assigned to *Cervus (Rusa)* cf. *elegans* (Teilhard de Chardin and Trassaert, 1937) and later revised as *N. elegans* (Qiu et al., 2004). Xinyaozi specimens are also similar to those from Yushe.

Compared with *N. longdanensis* from Longdan (Qiu et al., 2004), Xinyaozi antlers are similar in having a relatively long brow tine and nearly straight main beam but differ in having a longer antler base and smaller angle of the first bifurcation (Table 10). The Xinyaozi dentitions are also similar to those from Longdan (Tables 11–12).

Nipponicervus elegans from Xinyaozi and Xiashagou is comparable with *Cervus rhenanus* (Heintz, 1970; de Vos et al., 1995) in Europe. However, the latter’ s antlers are more slender, and its dentitions are smaller. *N. elegans* from Xinyaozi and Xiashagou is also comparable with *Arvernoceros ardei* from Étouaires in France (Heintz, 1970), especially in dentition dimensions (Tables 11–12). Nevertheless, the main beams are much longer and more curved, and the entocingulum of upper cheek teeth is very developed in French specimens.

Cervus (Elaphus) Smith, 1827
Cervus (E.) elaphus Linnaeus, 1758 (Fig. 9 [Figure 9: see original paper]; Table 13)

Material: An incomplete right antler with pedicle and partial frontal (IVPP V 26266) from Dazhuangkecun (Dazhuangke village), about 3 km southwest of Taijiaping.

Description: Specimen V 26266 is a right adult antler with pedicle and partial frontal (Fig. 9). The pedicle is relatively short and evidently thinner than the antler base; its cross-sections are oval. The burr is well developed and preserved, composed of a series of bony nodules. The antler base, Stem 1, is very short, with elongated oval cross-sections. The brow tine is broken, but its base is preserved; its preserved part indicates that it emerges from the antler base, or stem 1, anteriorly and upward. It is set very low, almost on the burr. The bez tine is absent, i.e., not developed at all. The trez tine is nearly complete, with only its tip missing; it is moderately long and curves slightly upward. Stem 2, the main beam between the first and second bifurcations, or between the bases of the brow and trez tines, is relatively long; its cross-sections are somewhat triangular near the first bifurcation and become elongated oval toward the second bifurcation. The part about 95 mm above the second bifurcation is missing. The ornamentation consists of moderate longitudinal furrows without crests.

Comparison and determination: The described antler is evidently different from other Xinyaozi specimens in its large size and large angle of the first bifurcation. It is very close to that of red deer, e.g., the brow tine set very low and almost on the burr, the angle between the brow tine and main beam is very large (Table 13), etc. However, it lacks a bez tine, as seen in some European red deer such as *Cervus elaphus aretinus* from Veneto to Calabria in Italy (Abbazzi, 1995). Compared with *C. canadensis mongoliae* from northern China (Zdansky, 1925), the Dazhuangke specimen lacks a bez tine and is slightly larger (Table 13); the remaining morphological characters are very similar. Compared with *C.* cf. *canadensis* from Yushu in northeastern China (Xue, 1959), besides the bez tine on antlers from Yushu, the Dazhuangke specimen appears more robust, but the burrs are more developed in Yushu specimens.

3. Discussion and Conclusion

Muntiacus bohlini was established by Teilhard de Chardin (1940) for specimens from Loc. 18, and he reassigned *M. cf. M. sinensis* from Xiashagou (Teilhard de Chardin and Piveteau, 1930) to this species. The present study on material from Xinyaozi reconfirms the presence of this taxon in the Nihewan Formation. Extant muntjaks range only in China, southern and southeastern Asia (Nowak and Paradiso, 1983). The earliest muntjak, *M. noringenensis*, was found at Tuosu Nor in the eastern Qaidam of the Qinghai-Tibetan Plateau from the lower part of the Upper Youshashan Formation (9-11 Ma), Late Miocene (Dong, 2007). This relatively large muntjak probably indicates that the genus originated in the Qinghai-Tibetan Plateau. The second earliest muntjak, *M. leilaoensis*, was discovered at the Leilao hominoid locality, Yuanmou in Yunnan Province (Dong et al., 2004) from the lower part of the Xiaohe Formation (8.2–7.2 Ma), Late Miocene (Qi et al., 2006). It is much smaller than *M. noringenensis* and very close to extant muntjaks. *M. zhaotongensis* was uncovered at the Shuitangba hominoid locality, Zhaotong in Yunnan Province (Dong et al., 2014) from the Shuitangba lignite beds (6.1-5.9 Ma), terminal Miocene (Ji et al., 2013). It is roughly contemporary with *M. lacustris* and *M. nanus* from Yushe Basin in Shanxi Province (Teilhard de Chardin and Trassaert, 1937). Early Pleistocene muntjaks are mainly survivors from the Neogene such as *M. nanus* and *M. lacustris*, and new members such as *M. bohlini* and *M. fenhoensis* (Chow, 1956) in northern China, as well as *M. hengduanshanensis* in southern China (Zong et al., 1996). The generic status of *M. ?huangi* from Yantouxi at Wushan (Dong and Chen, 2015) is uncertain; otherwise, it represents another Early Pleistocene muntjak. *M. lacustris* ranged across northern, central, and southern China, representing a widely distributed muntjak in the Early Pleistocene. In contrast, *M. bohlini* ranged mostly in Palearctic and transitional regions in China during the Early Pleistocene.

Cervavitus ranges mostly in the Neogene (Vislobokova, 1990), with two species –*Cervavitus fenqii* (Han, 1987) and *C. ultimus* (Lin et al., 1978)–surviving into the Early Pleistocene. The pliocervine from Xinyaozi is larger than other Pleistocene forms such as *C. fenqii* and *C. ultimus* but relatively close to the Late Miocene *C. huadeensis* (Tables 5-6). If the taxonomic status of *C. cf. C. huadeensis* from Xinyaozi specimens can be confirmed, its chronological range could extend from the Late Miocene to the Early Pleistocene, and its geographic distribution from Nei Mongol southward to Shanxi.

Axis originated in the Late Miocene and ranges to the present (Bai et al., 2017). *Axis shansius* first appeared in the Early Pliocene in Yushe Basin of North China (Teilhard de Chardin and Trassaert, 1937; Li et al., 1984; Tedford et al., 2013) and dispersed to Xihoudu (Chia and Wang, 1978) and Lantian (Chi, 1975) in North China, Tuozidong in East China (Dong and Fang, 2004), Yuanmou in South China (Lin et al., 1978), and Luotuoshan in Northeast China during the Early Pleistocene (Bai et al., 2017). It is therefore a common member of Pleistocene mammalian faunas in China.

Nipponicervus elegans was first uncovered in the Xiashagou locality in the Nihewan Basin and placed in the subgenus *Cervus (Rusa)* (Teilhard de Chardin and Piveteau, 1930). It was reported from Yushe (Teilhard de Chardin and Trassaert, 1937), Yangguo of Lantian (Chi, 1975), and Anping of Liaoyang (Zhang et al., 1980) and later reassigned to *Nipponicervus* (Qiu et al., 2004). Its chronological range is limited to the Early to Middle Pleistocene, and its geographic range to northern and northeastern China.

The taxonomic status of the red-deer-wapiti, or elaphoid group, is quite complicated. They have been regarded as a subgenus *Cervus* (e.g., Nowak and Paradiso, 1983) or *Elaphus* (e.g., Wang and Wu, 1979). The group includes many fossil and extant species or subspecies (e.g., Nowak and Paradiso, 1983; Sheng, 1992; Wang, 2003; Croitor and Obada, 2018; Croitor, in press). The first fossil red-deer-wapiti in China was described as *Cervus canadensis fossilis*, or *Cervus canadensis mongoliae* (Zdansky, 1925), later revised as *Cervus (Elaphus) canadensis* (Wang and Wu, 1979) and recently as *Cervus canadensis mongoliae* (Croitor, in press). The group in China was found mostly in northern regions such as Xujiayao (Hou et al., 2013), Salawusu (Qi, 1975; Hou et al., 2013), Shiyu (Jia et al., 1972), Upper Cave (Pei, 1940), Xiaogushan (Dong et al., 2010), Yanjiagang (Wei et al., 1986), etc. Morphology-based taxonomy regarded European and Asian red deer (*Cervus elaphus elaphus*) and North American wapiti (*Cervus elaphus canadensis*) as two subspecies (e.g., Nowak and Paradiso, 1983; Sheng, 1992; Wang, 2003), supported by the fully fertile hybrids that can be produced under captive conditions (Moore and Littlejohn, 1989; Perez-Espona et al., 2013). However, molecular evidence places them in two separate species (Kuwayama and Ozawa, 2000; Pitra et al., 2004), and combined evidence is very complicated (Groves and Grubb, 2011). The absence of a bez tine is mostly seen in European red deer (Abbazzi, 1995; Baker et al., 2014). The Dazhuangke specimen is therefore included in the European red deer group as *Cervus (Elaphus) elaphus*. However, the horizon of the Dazhuangke specimen is not yet certain. Because most elaphoid specimens were uncovered from Late Pleistocene deposits (Wang and Wu, 1979; Huang, 1991; Croitor, in press), some from the Middle Pleistocene (Abbazzi, 1995; Croitor, in press). Dazhuangke is about 2.8 km southwest of Taijiaping and 4.2 km southwest of Shuichongkou, although it is in Xinyaozi Ravine. No other identified specimens can help correlate the horizon. The described antler is the only identified specimen from Dazhuangke and appears unlike those from the Early Pleistocene deposits at Shuichongkou and Taijiaping localities. It is therefore probably not contemporary with the Early Pleistocene deposits at Shuichongkou and Taijiaping localities, but this remains uncertain.

In conclusion, a total of seven Cervidae species were identified from fossil specimens collected from Xinyaozi Ravine: *Muntiacus bohlini*, *Cervavitus* cf. *C. huadeensis*, *Axis shansius*, *Nipponicervus elegans*, *Elaphurus davidianus predavidianus*, *Elaphurus bifurcatus*, and *Cervus (Elaphus) elaphus*. The first six species, with different body sizes and antler patterns, are from Early Pleistocene deposits at Taijiaping and Shuichongkou localities (with a chronological range of 2.6–1.7 Ma), and the last one from an uncertain horizon at Dazhuangke.

At least six cervid species existed in and around the Sangganhe Basin during the Early Pleistocene. *C. cf. C. huadeensis* and *A. shansius* were survivors from the Late Neogene; *M. bohlini*, *N. elegans*, *E. davidianus predavidianus*, and *E. bifurcatus* are new forms of the Early Pleistocene. If the Dazhuangke horizon can be dated to the same period as those of Shuichongkou and Taijiaping, the appearance of elaphoid cervids could be traced back to the Early Pleistocene, and the evolution of elaphoid antlers would have progressed from the absence to the presence of a bez tine. Cronin et al. (1994) indicated that eight glacial events can be inferred between 2.7 and 2.3 Ma and that sea level dropped about 50–60 m in the Sea of Japan. The presence of Early Pleistocene *Elaphurus* and *Nipponicervus* in mainland China (Teilhard de Chardin and Piveteau, 1930; Chi, 1975; Chia and Wang, 1978; Qiu et al., 2004; Dong et al., 2019) and the Japanese archipelago (Otsuka, 1968, 1972; Otsuka and Hasegawa, 1976; Otsuka and Shikama, 1978) provides new evidence that sea levels dropped sufficiently for these cervids to migrate from the mainland to the islands. The abundance of folivorous cervid specimens in the Xinyaozi Ravine area implies the existence of a forested environment of considerable scale in the Sangganhe Basin area during the Early Pleistocene.

Acknowledgements: This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences, Grant No. XDB 26030304.

The authors acknowledge Professor Wei Qi for providing the material for this study and thank reviewers for comments and suggestions that improved the manuscript.

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Note: Figure translations are in progress. See original paper for figures.