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Early Pleistocene forerunners of *Mammuthus-Coelodonta* Faunal Complex in Nihewan Basin, North China

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ABSTRACT

The typical *Mammuthus-Coelodonta* Faunal Complex dominated the mid- and high latitudes of continental Eurasia during the Mid-Late Pleistocene; the dominant taxa include woolly mammoth (*Mammuthus primigenius*), woolly rhino (*Coelodonta antiquitatis*), steppe bison (*Bison priscus*) and diverse horses (*Equus* spp.), etc. Recent excavations at the Early Pleistocene site Shanshenmiaozui in Nihewan Basin of North China resulted in the discoveries of rich mammalian fossils which include steppe mammoth (*Mammuthus trogontherii*), Nihowan woolly rhino (*Coelodonta nihowanensis*), archaic Chinese bison (*Bison* (*Eobison*) *palaeosinensis*) and rich collections of early horse fossil. In Nihewan Basin, a couple of sites (Xiashagou, Shanshenmiaozui and Yeniupo) yielded the *Mammuthus-Coelodonta-Bison* assemblage, which can be regarded as the closest ancestors of the *Mammuthus - Coelodonta* Faunal Complex or the forerunners of the later *Mammuthus - Coelodonta* Faunal Complex. Nihewan Basin bears the richest and most complete fossils of Early Pleistocene *Coelodonta* and *Bison* to date, and the juvenile specimens of *M. trogontherii* also represent the richest collection for its kind and its geologic age.

1. Introduction

Pei (1957) first proposed the expression "*primigenius-antiquitatis* fauna" for Asian cold adapted mammal assemblages of Late Pleistocene age, which was modified as "*Mammuthus-Coelodonta* fauna" by Chow (1959) and "*Mammuthus-Coelodonta* Faunal Complex" by Kahlke (1999, 2014), while the latter covers not only Asian but also European faunas. The *Mammuthus-Coelodonta* Faunal Complex is one of the most widespread faunas that once roamed continental Eurasia during the later part of the Pleistocene Epoch. The dominant animals of the Faunal Complex include *Mammuthus*, *Coelodonta*, *Bison*, *Equus*, *Crocuta*, *Ursus*, *Canis*, *Panthera*, *Megaloceros*, *Gazella*, *Saiga*, *Rangifer*, *Alces*, *Spirocerus* and ovibovines, etc. (Kahlke, 1999, 2014). While the iconic giants of the fauna, including *Mammuthus*, *Coelodonta* and *Bison*, appeared earlier than 1.5 Ma in North China, and the three even coexisted in several sites in the Nihewan Basin; furthermore, most of the faunal members mentioned above made their appearance in Nihewan Basin during the Early Pleistocene, except *Rangifer* and *Alces*. Therefore, the Nihewan fauna represents the forerunner of the later *Mammuthus-Coelodonta* Faunal Complex, and the Nihewan Basin formed part of the area of origin of the *Mammuthus-Coelodonta* Faunal Complex. This paper is going to give a brief introduction of the most important Nihewan fossil materials which are closely related to the initial members of the *Mammuthus - Coelodonta* Faunal Complex.

2. Site information

Nihewan Basin is located in Yangyuan County of Hebei Province in North China (Fig. 1), which is regarded as the type locality for the Early Pleistocene terrestrial strata and mammalian fauna in North China (Qiu, 2006). The scientific significance of Nihewan Basin was recognized in the 1920s (Barbour, 1924, 1925; Barbour et al., 1927; Teilhard de Chardin and Piveteau, 1930), and since then, more localities and more fossil materials were recovered. Up to now, more than 150 prehistoric fossil sites have been recovered and dozens of them have been excavated in the past decades, which cover different stages from Late Pliocene to

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Holocene; while the majority of the sites were discovered in the lower Pleistocene fluvio-lacustrine deposits which contain rich fossils including not only mammals, but also mollusks and ostracods as well as sporopollens, and even Paleolithic tools.

The assemblage of early mammoth, woolly rhino and bison had been identified in the classic Nihewan fauna unearthed from the Xiashagou area as early as the 1920s (Barbour et al., 1927; Teilhard de Chardin and Piveteau, 1930). During the last decade, quite well-preserved fossils of *Mammuthus trogontherii*, *Coelodonta nihowanensis* and *Bison palaeosinensis* have been recovered from the recently discovered localities of Shanshenmiaozui (Tong, 2012; Tong and Chen, 2016; Chen and Tong, 2017; Tong and Wang, 2014; Tong et al., 2017) and Yeniupo (Li et al., 2021) (Table 1; Fig. 1).

Abbreviations of site and organization names: **BJZ**, Bajiazui; **DNG**, Danangou site of Nihewan**; GH**, Gonghe in Qinghai Province; **IMM,** Inner Mongolia Museum; **IVPP V**, prefix in the catalog numbers for fossils in the Institute of Vertebrate Paleontology and Paleoanthropology; **JYC**, Jinyuan Cave; **LD**, Longdan site in Gansu Province; **MJG**,

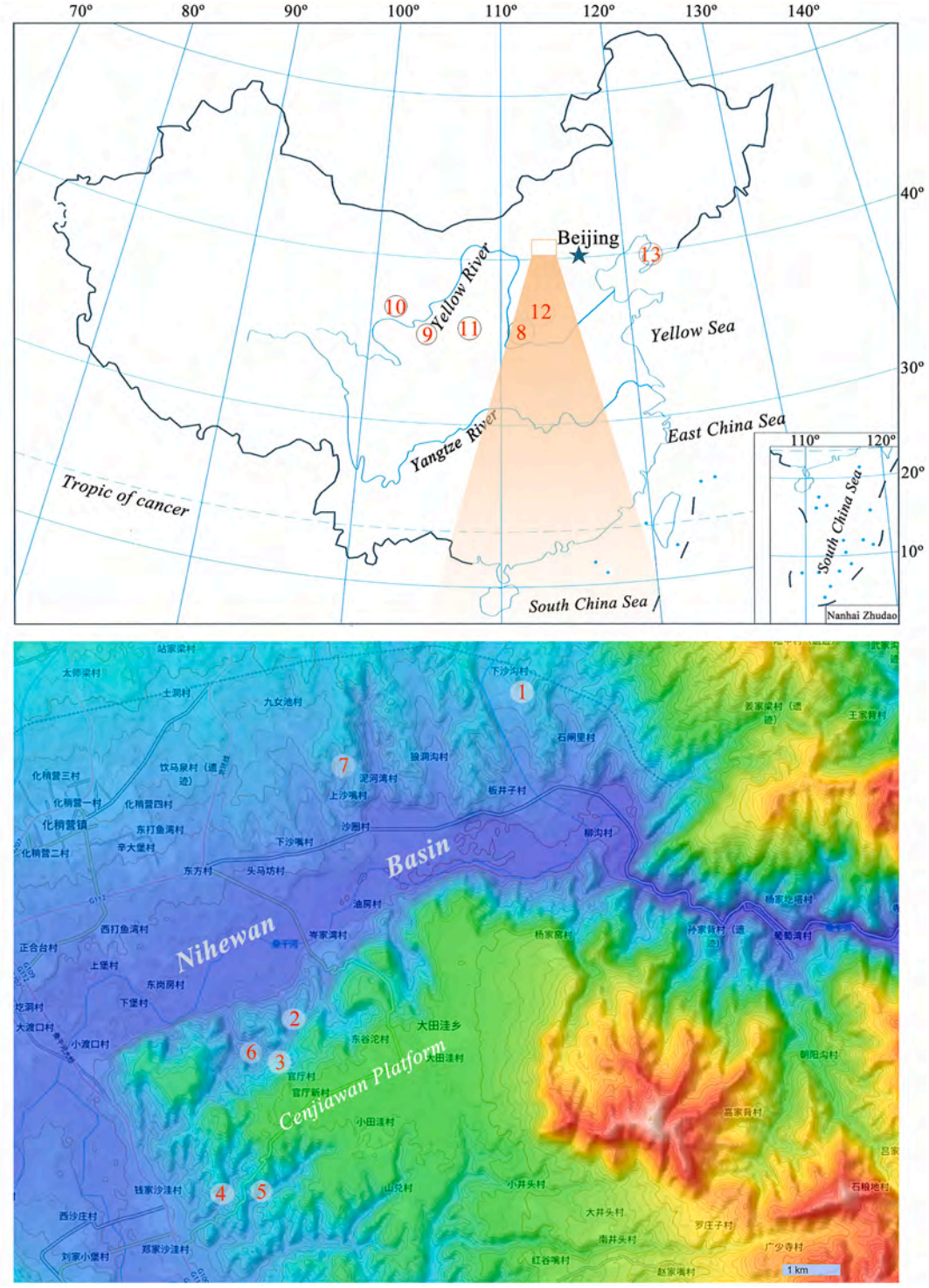

Fig. 1. Localities bearing *Mammthus-Coelodonta-Bison* assemblages of Early Pleistocene age in Nihewan Basin and adjacent areas. ①Xiashagou; ②Majuangou; ③Shanshenmiaozui; ④Yeniupo; ⑤Xiangtoushan; ⑥Xiaochangliang; ⑦Shangshazui; ⑧Xihoudu; ⑨Longdan; ⑩Gonghe; ⑪Bajiazui; ⑫Yushe; ⑬Jinyuan Cave.

Table 1
Localities bearing the early *Mammuthus-Coelodonta-Bison* assemblage in Nihewan Basin, compared with other related sites of Eurasia.

Sites	Geologic age	*Mammuthus*	*Coelodonta*	*Bison*	Sources
XSG of Nihewan, Hebei, China	Early Pleistocene, (2.2–1.7 Ma) Liu et al. (2012)	***Elephas* cf. *trogontherii*** (Barbour et al. (1927), *Elephas namadicus* (T & P): several tooth remains, including one complete dp3, fragment of mandible, distal part of radio-ulna, one carpal bone and one navicular bone.	***Rhinoceros* cf. *tichorhinus***: juvenile maxilla with DP1-4, deciduous lower teeth, fragments of mandibles with lower teeth, quite a number of postcranial bones.	***B. palaeosinensis***: three incomplete skulls with horn-cores, many jaw bones and postcranial bones	Barbour et al. (1927), Teilhard de Chardin and Piveteau (1930)
SSMZ of Nihewan, Hebei, China	Early Pleistocene, (>1.2 Ma) (Liu et al., 2016)	***M. trogontherii***: juvenile crania and mandibles with deciduous teeth, scapula, partial ulna and radius, tibia, carpal and tarsal bones	***C. nihowanensis***: juvenile crania and mandibles with deciduous teeth, adult limb bones	***B. palaeosinensis***: partial maxilla, complete adult mandible with teeth, juvenile mandible with teeth, postcranial bones	Tong and Wang (2014), Tong and Chen (2016), Tong et al. (2017)
YNP of Nihewan, Hebei, China	Early Pleistocene, (ca. 1.7 Ma)	**?*M. trogontherii***: nearly complete adult mandible with teeth (unpublished)	***C. nihowanensis* (*C. antiquitatis*)**: complete adult skull (no catalog number)	***B. palaeosinensis***: nearly complete skull and rich postcranial bones (no catalog number)	Li et al. (2021)
JYC, Liaoning, China	Jinyuan lower fauna (2.60–1.7 Ma)	***Mammuthus* cf. *meridionalis*:** (unpublished)	***C. nihowanensis*:** nearly complete skull with dentition (DLJ1711001)	***B. palaeosinensis***: partial skull with horn-cores (DLJ1711018)	Jin et al. (2021)
XHD, Shanxi, China	Early Pleistocene, (ca. 1.8 Ma (Jia and Wei, 1982) or ca. 2.43 Ma (Shen et al., 2020)	***M. trogontherii*** (Wei et al., 2006) = *Archidiskodon planifrons* and *Palaeoloxodn* cf. *namadicus* (Chia and Wang, 1978): isolated teeth and one semi-mandible	***C. antiquitatis shansius***: one complete adult skull (IVPP V 2850), one partial skull, 3 M3s and one m3	***B. palaeosinensis***: one horn-core (IVPP V 2861)	Chia and Wang (1978)
LD, Gansu, China	Early Pleistocene, (2.5–2.2 Ma)	***Mammuthus meridionalis***: molars (Jin et al., 2021) (unpublished)	***C. nihowanensis***: skull and mandible (HMV0980), humerus, radius, ulna, carpals, metacarpals,	***Bison* sp.**: A complete skull with long and curved horn-cores (Shi, 2023) (unpublished)	Deng (2002), Qiu et al. (2004), Deng (2008)
BJZ, Gansu, China	Early Pleistocene, 2.55–1.8 Ma	No record	***C. nihowanensis***: partial maxilla with DP1-DP3; partial mandibles with dp1-dp3; 3 isolated deciduous teeth	***Bison* sp.**: one M2, partial mandibles with lower p4-m3	Wang (2006)
72104 of GH, Qinghai, China	Early- Middle Pleistocene	**? *Mammuthus* sp.** (=*Palaeoloxodon* sp.by Zheng et al., 1985): 2 pieces of tooth plates, one carpal bone	***C. antiquitatis***: 2 partial juvenile skulls, 2 juvenile mandibles; one old adult skull (V 5567) from Loc. 72106	***B.* (*Superbison*) *crassicornis***: one old adult skull (V5569), one juvenile skull with mandible (V5570)	Zheng et al. (1985)
Dmanisi, Georgia	Early Pleistocene, (*c.* 1.8 Ma)	***M. meridionalis*:** lower left m3 (D′2295) (Ros-Montoya, 2010)	No record	***B.* (*Eobison*) *georgicus***: partial skull with partial horn-core (Burchak-Abramovich et al., 1994; Bukhsianidze, 2005)	Bartolini-Lucenti et al. (2022)
Untermassfeld, Germany	Early Pleistocene (1.07–1.06 Ma)	***M. trogontherii trogontherii***: (Dubrovo, 2001); ***M. meridionalis*:** juvenile cranium and deciduous teeth (van Essen, 2022)	No record	***B. menneri***: cranial and postcranial bones (Sher, 1997; Bukhsianidze, 2020)	Kahlke (2000, 2022)

Majuangou site of Nihewan; **MNHN**, Muséum National d'Histoire Naturelle; **NIH**, prefix in the catalog numbers for fossils in MNHN; **NNNRM**, Nihewan National Nature Reserve Management; **SSMZ**, Shanshenmiaozui site of Nihewan; **SSZ**, Shangshazui site of Nihewan; **TNHM**, Tianjin Natural History Museum; **TNP**: prefix in the catalog numbers for fossils in Tianjin Natural History Museum; **XCL**, Xiaochangliang site of Nihewan; **XHD**, Xihoudu Site in Shanxi Province; **XSG**, Xiashagou site of Nihewan; **XTS**, Xiangtoushan site of Nihewan; **YNP**: Yeniupo site of Nihewan.

Abbreviations of anatomy: **L**: length; **W**: width; **MNQ**: Mammifères néogènes et quaternaires (= Mammals Neogene-Quaternary).

3. Early mammoth fossil records in Nihewan

Nihewan Basin is very rich in fossil records of Quaternary proboscideans (Tong, 2010b; Li et al., 2016; Zhao et al., 2016); up to now, the proboscidean taxa ever reported include *Anancus* sp. (including *Pentalophodon* sp.) (Zong and Wei, 1993), *Zygolophodon* sp. (Tang, 1980), *Palaeoloxodon namadicus* (Wei, 1976), *P. naumanni* (Tong, 2010b), *Elephas maximus* (Jia and Wei, 1980; Turvey et al., 2013; revised as *P. naumanni* by Tong et al., 2024), *Mammuthus meridionalis* (Wei et al., 2006; Zhao et al., 2016), *M. trogontherii* (Wei et al., 2003, 2006; Tong, 2010b, 2012; Tong and Chen, 2016; Chen and Tong, 2017).

During the past decade, the important proboscidean fossils unearthed in Nihewan Basin include the earliest fossil record of *M. trogontherii* from MJG site which was dated back to 1.66 Ma (Wei et al., 2003, 2006), rich collections of *M. trogontherii* from SSMZ, including a juvenile skull and mandibles, postcranial bones of both juvenile and adult individuals (Tong, 2012; Tong and Chen, 2016; Chen and Tong, 2017); a nearly complete skull of *M. meridionalis* from XTS (Zhao et al., 2016), the study on the new specimen is not finished yet; an adult mandible of *Mammuthus* sp. from YNP (personal communication with Prof. Wei), the material is also not studied yet. The numerical age for the fossil records of *M. meridionalis* in Nihewan is 2.6–1.8 Ma (Wei et al., 2005).

It's worth mentioning that most of the Early Pleistocene elephantid fossils were misidentified as *Palaeoloxodon* and/or *Archidiskodon* in the past, and the situation changed since 2000 (Wei et al., 2003, 2006).

The tooth fragment from Gonghe was identified as *Palaeoloxodon* sp. by Zheng et al. (1985), but according to photo 5 of Plate V, both the tooth plate and the enamel layer are too thin to be a *Palaeoloxodon*, meanwhile it most probably belongs to a mammoth. The geologic age is Early Pleistocene, but the tooth fragment is from the upper stratigraphic level.

The early mammoth fossils were recovered in a couple of sites in Northern China, such as Yushe, Xihoudu, and Linyi in Shanxi Province;

Dali in Shaanxi Province; Pingliang and Heshui in Gansu Province; Mengyin and Penglai in Shandong Province (Wei et al., 2006); Gonghe in Qinghai Province. Moreover, the recent discoveries of early mammoth show that Nihewan Basin is very likely to be an evolutionary center for the early mammoth, where the best preserved and most complete fossil materials have been unearthed in the past decade; furthermore, the fossils are rich in number and diverse in taxonomy as well as continuous in temporal distribution (Fig. 2). In Nihewan Basin, the steppe mammoth even survived into the Late Pleistocene (Tong, 2010a).

Although the early mammoth and doubtful bison were recognized in the fauna from Dmanisi site in Georgia at the gate of Europe, they are *M. meridionalis* (Konidaris et al., 2020) and *Bison* (*Eobison*) *georgicus* (Sorbelli et al., 2021), which are not the direct ancestor of the later *Mammuthus-Coelodonta* Faunal Complex. The Asian *M. trogontherii*, the direct ancestor of *M. primigenius*, arrived in Europe at about the Early/Middle Pleistocene boundary (Konidaris et al., 2020).

The evolutionary pattern of the Eurasian *Mammuthus* is usually presented as a succession of chronologically overlapping species, including (from earliest to latest) *M. meridionalis* (southern mammoths) → *M. trogontherii* (steppe mammoths) → *M. primigenius* (woolly mammoths) (Lister et al., 2005; Wei et al., 2010; Chang et al., 2017), while all of the *Mammuthus* species were poorly defined because of either poor materials or regional variations. Moreover, the species of *Mammuthus* not only extensively overlapped in temporal ranges, but also have mosaic morphological characters.

A simplified key to the *Mammuthus* species according to Maglio (1973) and Wei et al. (2005) is as follows.

1. The number of complete tooth plate is 8–10 on M3, and 10 on m3 ————————————*M. rumanus*
2. The number of complete tooth plate is usually 12–15 on both M3 and m3—— *M. meridionalis*
3. The number of complete tooth plate is 17–22 on both M3 and m3———————————— *M. trogontherii*
4. The number of complete tooth plate is 20–27 on M3 and 20–25 on m3———————— *M. primigenius*

Although it's not easy to distinctly define each of the *Mammuthus* species, the general pattern of their evolution can be summarized as follows: body size increasing but finally decreasing, elevated but anteroposteriorly compressed skull, tusk getting more curved and twisted, cheek teeth with more but mesiodistally compressed plates (lamellae), increasing lamellar frequency and hypsodonty index, decreasing enamel thickness etc. (mainly according to Maglio, 1973; Larramendi, 2015; Lister, 2022).

M. rumanus arrived in Eurasia between 3.5 and 3.0 Ma, and reached East Asia and Europe immediately. *M. meridionalis* derived from *M. rumanus* between 2.6 and 2.5 Ma, and evolved into *M. trogontherii* at about 1.8–1.7 Ma in East Asia (Wei et al., 2010; Markova et al., 2013; Lister and Sher, 2015). The earliest fossils referable to *M. trogontherii* and *M. primigenius* have since been recorded in eastern Asia (Lister, 2022), and the *M. primigenius* originated from *M. trogontherii* at 0.8–0.7 Ma (Lister et al., 2005; Wei et al., 2010) or 0.6–0.5 Ma (Van der Valk et al., 2021) in east Siberia and spread to other parts of Eurasia and North America. The recent study shows that there were two dispersal movements of mammoth to North America: *M. trogontherii* at ca.1.5 Ma and *M. primigenius* at the beginning of Late Pleistocene (Lister and Sher,

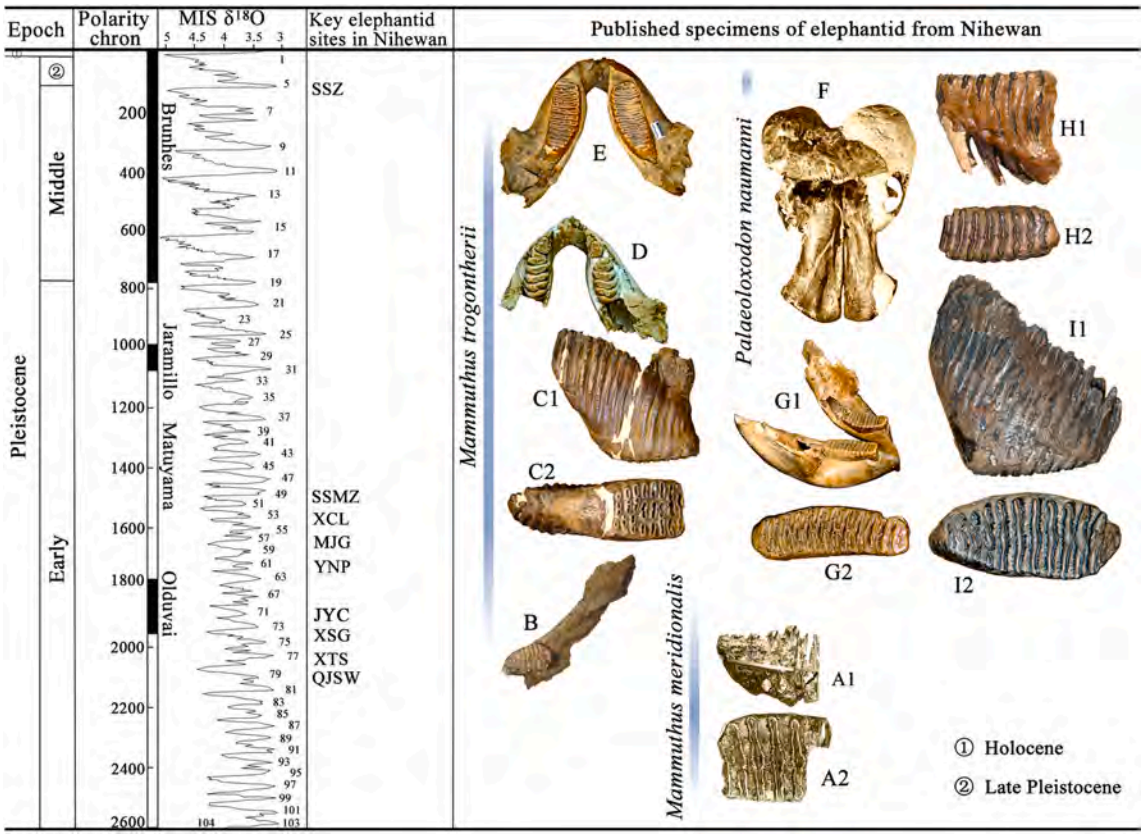

Fig. 2. Fossil records of Quaternary elephantids in Nihewan Basin (modified from Tong, 2010b). A1-A2, partial left m2 or m3 of *M. meridionalis* from QJSW (Wei et al., 2006: Pl 6, Figs. 1 and 2); B-E, *M. trogontherii*; B, partial right mandible with dp4 from XSG, NIH 158; C1–C2, left M3 from MJG, IVPP V 13610; D, juvenile mandible with dp2-3 from SSMZ, IVPP V18010.1; E, mandible from DNG, IVPP V 15715; F-G, *P. naumanni*; F, skull from SSZ, IVPP V 4443, anterior view (Wei, 1976: Pl I); G1-G2, mandible from Nihewan, uncataloged specimen in NNNRM; H–I, *P. naumanni* from Dingjiabu; H1–H2, right dp4, IVPP RV80010; I1–I2, right M3, IVPP RV 80005. A1, buccal view; C1, H1 and I1, lingual views; A2, B, C2, D, E, G2, H2 and I2, occlusal views. Not to scale.

2015). Actually, the issues on the early mammoth of America are still debatable (Lucas et al., 2017).

The early mammoth also has rich and diversified records in Europe since 3.5 Ma BP onward (Lister and Van Essen, 2003; Konidaris et al., 2020), while the *M. trogontherii* arrived in Europe at as late as 0.8–0.78 Ma (Lister, 1996; Lister et al., 2012; Muttoni et al., 2015) or no more than 1 Ma (Chang et al., 2017); in Europe, the transition from the steppe mammoth (*M. trogontherii*) to the true woolly mammoth (*M. primigenius*) occurred at late Middle Pleistocene (ca. 0.425–0.125 Ma), and the latter was an immigrant from Asia (Lister, 2022), which is quite later than in the northeastern Asia (Lister, 1996; Lister et al., 2005; Lister and Sher, 2001, 2015; Wei et al., 2010). Regarding the mammoth fossils from Untermassfeld, their taxonomic determinations are still controversial, Dubrovo (2001) once referred them to *M. trogontherii*, while the recent determination is *M. meridionalis* (Van Essen, 2022).

4. Early woolly rhino of Nihewan

The *Coelodonta* lineage is a very special and distinct group in the family Rhinocerotidae, which can be diagnosed as follows: (1) tandem-horned dolichocephalic skull (Fig. 3-A1); (2) completely (partially in the early forms) ossified nasal septum in adult individuals (Fig. 3-A3); (3) occipital crest elevated and occiput backwardly inclined (Fig. 3-A3); (4) very high and robust vomer ridge (Fig. 3-A2); (5) backward extension of nasal notch and facial elongation (Fig. 3-A3); (6) loss of the incisors (Fig. 3-A2); (7) moderately high tooth crowns with rough enamel and coronal cement (Fig. 3-D); (8) upper cheek teeth (except M3) with three fossettes at the early stage of wear: crista joints crochet to form the medifossette; protocone meets hypocone to form a closed median valley which is confluent with the prefossette; the posterior cingulum unites with the hypostyle to form the hinder wall of the postfossette (Fig. 3-C); (9) the reappearance of metastyle (Heissig, 1989) in the upper M3 results in a non-triangular crown outline (Fig. 3-B) (mainly in the advanced forms); (10) lower cheek teeth with buccal ribs (paraconid and protoconid ribs) (Fig. 3-E-G); (11) buccal walls of cheek teeth are wavy (developed paracone rib) (Fig. 3-D); (12) quite straight occlusion rims (less wavy) (Fig. 3-D); (13) the two cross-crests (or transverse ridge) in upper teeth are very oblique relative to the ectoloph and the protocone is posteriorly positioned (Fig. 3-B) (mainly in the advanced forms); (14) upper cheek teeth with developed crista (Fig. 3-B, C) (mainly in the advanced forms) (expanded from Guérin, 1980, 2010; Groves, 1983; Prothero et al., 1989; Kahlke, 1999; Qiu et al., 2004; Deng et al., 2011; Tong and Wang, 2014; Handa et al., 2021; Uzunidis et al., 2022). The species and subspecies ever named under the genus *Coelodonta* are summarized in Table 2.

In China, quite a number of complete skulls and mandibles of early woolly rhinos have been unearthed in the past decades, such as the skull and mandible of the earliest woolly rhino—*Coelodonta thibetana* from Tibet (or Xizang) (Deng et al., 2011); the skulls and mandibles of *C. nihowanensis* from Longdan in Gansu Province (Qiu et al., 2004); a complete skull of *C. nihowanensis* from YNP in Nihewan (Li et al., 2021); complete skull and mandible of juvenile *C. nihowanensis* from SSMZ in Nihewan (Tong and Wang, 2014) (Fig. 4); a nearly complete skull of *C. nihowanensis* from JYC in Liaoning Province (Jin et al., 2021). These fossil materials are very helpful in understanding the origin and evolutionary history of the *Coelodonta* lineage. The up-to-date data shows that China is the most probable origin and evolutionary center for early woolly rhinos, and the fossil records of *Coelodonta* occurred throughout the whole period of the Pleistocene Epoch in northern China (Fig. 5).

The early woolly rhinos are characterized by the following traits: Less high-crowned molars; thinner tooth enamel; smaller body size; slender extremities (Beliajeva, 1966; Kahlke, 1967, 1969; Chow, 1978; Guérin, 2010). The "Evolutionary trends in the *Coelodonta* lineage include elongation and narrowing of the skull, which became more inclined and low-slung, a posterior shift of the orbits, changes in the position of the cheek tooth rows and the thickening of enamel and secondary cementum. All the changes can be seen as adaptations for efficient grazing" (Kahlke and Lacombat, 2008; Deng et al., 2011; Stuart and Lister, 2012). Furthermore, other key characteristics of the *Coelodonta* lineage also have distinct evolutionary tendencies, which will be

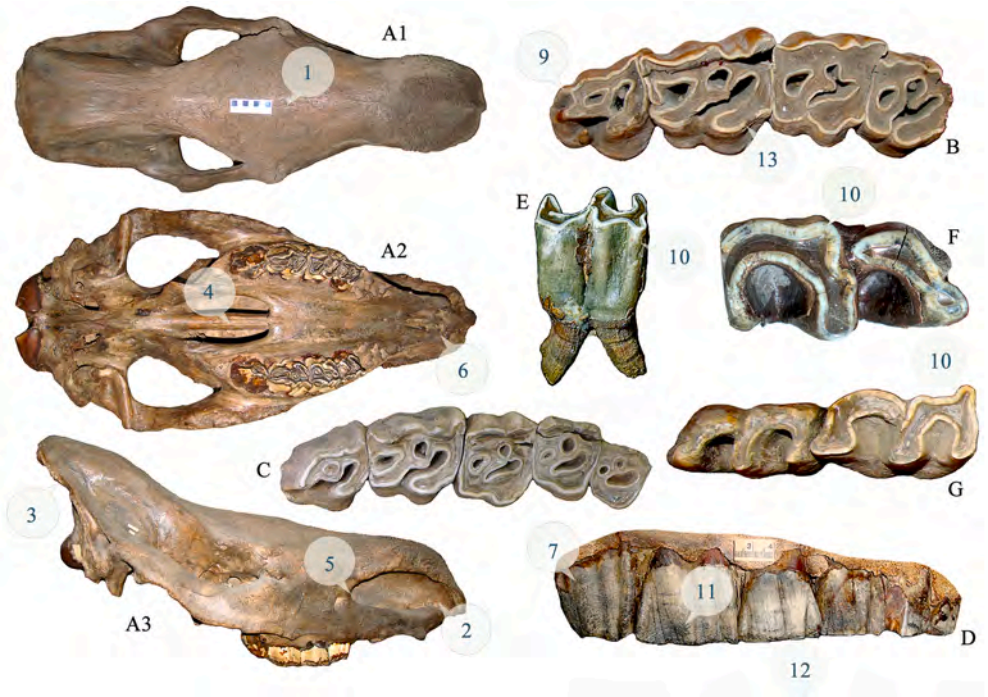

Fig. 3. Diagnostic characteristics of *Coelodonta* lineage. A1-A3, skull, V2130, Inner Mongolia, Late Pleistocene; B, right upper P4-M3, V6769, Hutouliang of Nihewan, late Early Pleistocene; C, right upper P3-M3, TNP 07611, Salawusu, Late Pleistocene; D, right upper P2-M3, No. 82.6, Maqu, Pleistocene; E, right lower m1 or m2, web photo; F, right lower m3, V2136, Yushu, Late Pleistocene; G, left lower m2-3, V6769-3, Hutouliang of Nihewan, late Early Pleistocene; the circled numbers respectively correspond with the diagnostic characteristics described in the text.

Table 2
Checklist of species and subspecies of the genus *Coelodonta* Bronn, 1831.

Species or/and subspecies names	Author	Type locality	Other localities	Geologic age
Coelodonta antiquitatis	Blumenbach, 1799	Häufig in Western Siberia; aber auch in Deutschland[a,b]	Northern Eurasia	Late Pleistocene
Coelodonta tologoijensis	Beliajeva (=Belayeva), 1966	Tologoj Mountain on the Selenga of Transbaikalia, China	Nalaikha, Mongolia (Eisenmann and Kuznetsova, 2004); Zasukhino 2, Russia (Alexeeva and Erbajeva, 2005); Ust-Obor, Russia (Alexeeva and Erbajeva, 2005); Zasukhino 3, Russia (Alexeeva and Erbajeva, 2005); Bad Frankenhausen, Germany (Kahlke and Lacombat, 2008)	Early-Middle Pleistocene (Epivillafranchian)
Coelodonta nihowanensis	Kahlke (1967)	Nihewan	Linyi and Gonghe (Chow, 1978); Longdan (Qiu et al., 2004); SSMZ (Tong and Wang, 2014);	Early Pleistocene (Late Villafranchian)
Coelodonta antiquitatis jacuticus	Rusanov, 1968	Yakutian region, Russia		Late Pleistocene
Coelodonta antiquitatis humilis	Rusanov, 1968	Yakutian region, Russia		Late Pleistocene
Coelodonta antiquitatis chilinensis	Jiang (1977)	Jilin, China	Northeast China	Late Pleistocene
Coelodonta antiquitatis shansius	Chia and Wang (1978)	Xihoudu, Shanxi, China		Early Pleistocene (1.8 Ma)
Coelodonta antiquitatis yenshanensis	Chow (1978)	Zhoukoudian Loc. 1, China	Zhoukoudian Loc. 9, 13, China (Chow, 1979)	Middle Pleistocene
Coelodonta antiquitatis praecursor	Guérin (1980)	La Fage, France	Romain-la-Roche (Guérin, 2010); Les Rameaux (Uzunidis et al., 2022)	Late Middle Pleistocene
Coelodonta thibetana	Deng et al. (2011)	Zanda, Tibet, China		Late Pliocene (3.7 Ma)

[a] https://species.wikimedia.org/wiki/Coelodonta_antiquitatis.
[b] Gehler, A., Mol, D., Reich, M., Van der Plicht, H., 2007. The type material of *Coelodonta antiquitatis* (Blumenbach) (Mammalia: Perissodactyla: Rhinocerotidae). Presentation at [4]th International Mammoth Conference 18–22 June 2007, Yakutsk.

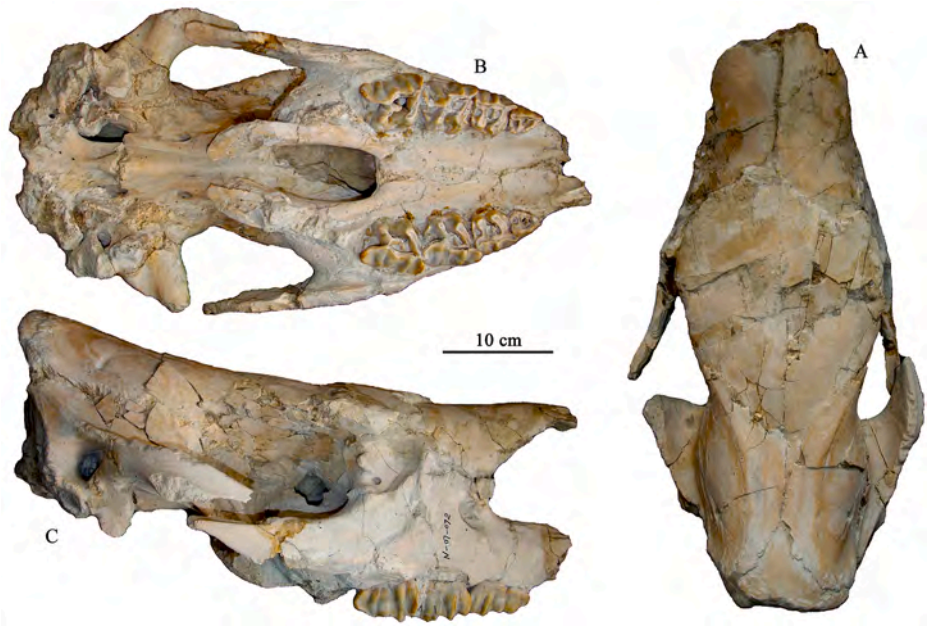

Fig. 4. Juvenile skull of *Coelodonta nihowanensis* from SSMZ (IVPP V 17616.1) at Nihewan. A, dorsal view; B, ventral view; C, lateral view.

summarized as follows (Fig. 5): 1) the ossification of the nasal septum was getting more complete with time: in the earliest forms, such as *C. thibetana* and early *C. nihowanensis* from Longdan, the nasal septum was only partially and incompletely ossified; 2) in *C. thibetana* and *C. nihowanensis*, the metastyle of M3 was completely absent and the outline is triangular as in other true rhinoceros (except the specimen of Jinyuan Cave bears faint but distinct metastyle); while the metastyle of M3 reappeared (Heissig, 1989; Prothero, 1998) in the later forms quite often, which made the occlusal outline of the tooth not a typical triangle but somewhat quadrangular; 3) the nasal tip more downwardly bent in the later forms: in the early forms of Early Pleistocene, the nasal tip is above the level of the premaxilla which left a higher opening of the nostril; 4) the tooth crown became higher and more hollowed: in the early forms as in *C. thibetana* and early *C. nihowanensis* from Longdan, the tooth crown is less hypsodont and the medial valley got closed at quite late stage of wear. It is worth mentioning that some of these

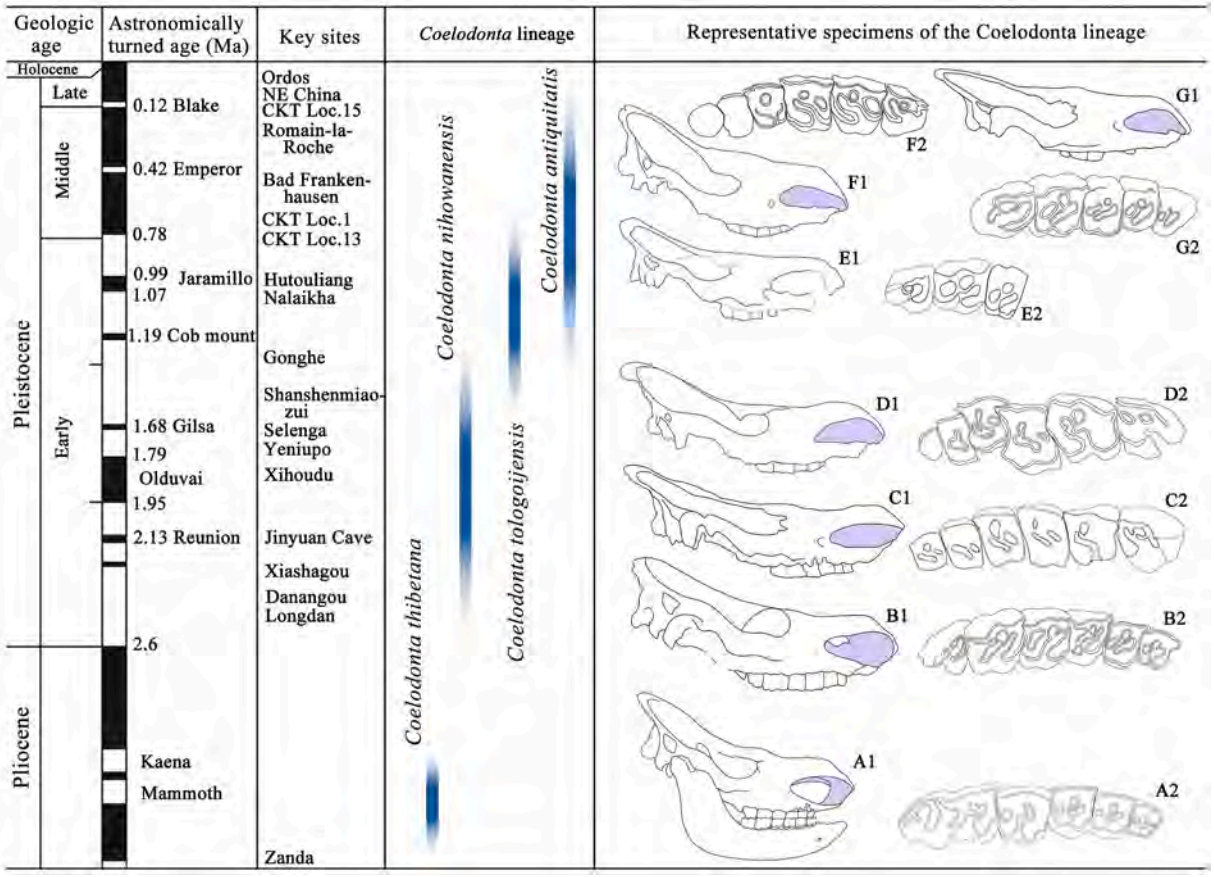

Fig. 5. Sketches of the skulls and upper tooth rows of the keystone species and/or subspecies of the *Coelodonta* lineage. A1-A2, *C. thibetana*, IVPP V15908, Zanda of China, 3.7 Ma (Deng et al., 2011); B1–B2, *C. nihowanensis*, HMV0980, Longdan of China, ca. 2.2 Ma (Qiu et al., 2004); C1–C2, *C. antiquitatis shansius*, IVPP V 2850, Xihoudu, China, 1.8 Ma (Chia and Wang, 1978); D1-D2, *C. nihowanensis*, no catalog number, Yeniupo of China, ca. 1.7 Ma (Li et al., 2021); E1-E2, *C. tologoijensis*, IQW 1974/14 011(Frkhn. 13 965), Bad Frankenhausen, Germany, 0.46 Ma (Kahlke and Lacombat, 2008); F1–F2, *C. antiquitatis praecursor*, n° RHI 1, Romain-la-Roche, France, ca. 0.13 Ma (Guérin, 2010); G1-G2, *C. antiquitatis*, MNHN SJA 65 and TNP 07611, Sjara-osso-gol, China, Late Pleistocene (Boule et al., 1928). The shadowed parts in the skulls represent the ossified nasal septum.

characters could appear in a mosaic pattern, rather than always tightly corresponded.

Among the early woolly rhino fossils as known currently, the JYC skull is very advanced in its fully ossified nasal septum, developed vomer ridge, and the typical *Coelodonta*-type of upper M3 which has a prominent metastyle.

Concerning the complete skull from YNP of Nihewan, it was initially referred to the species *C. antiquitatis* (Li et al., 2021), but it differs from the Late Pleistocene *C. antiquitatis* in its larger ratio of zygomatic width/skull length, less downwardly bent nasal tip, triangular M3, less oblique cross-crests in upper molars, larger W/L ratio of upper molars, and less wavy buccal walls of the cheek teeth, all of which indicate it's a somewhat primitive form in the *Coelodonta* lineage; on the other hand, it also shows such derived characteristics as the fully ossified nasal septum, the elevated occipital crest and the strong backwardly inclined occiput. It is worth mentioning that the YNP skull represents the best preserved and most complete adult skull of the early *Coelodonta* ever reported. Although the YNP specimens were reassigned to the species *C. nihowanensis* in this paper mainly because of its geologic age and some primitive characters, actually it morphologically resembles *C. antiquitatis* more closely than the *C. nihowanensis* from Longdan, which can be attributed to the higher biostratigraphic horizon of the YNP site.

Among the *Mammuthus-Coelodonta-Bison* assemblage, *Coelodonta* was the latest to arrive in western Eurasia; while the *Stephanorhinus* clade exclusively dominated the rhino fauna in western Eurasia during the Early to early Middle Pleistocene (Loose, 1975; Guérin, 1980; Fortelius et al., 1993; Van der Made, 2010; Pandolfi et al., 2021), and some species of *Stephanorhinus* are very similar to *Coelodonta* both in skull morphology and ecology, such as *Stephanorhinus hemitoechus* (Fortelius et al., 1993; Van der Made and Grübe, 2010; Pandolfi and Maiorino, 2016; Iurino et al., 2020); furthermore, the smaller species *S. etruscus* and the longer-headed species *S. hundsheimensis* were browsers or mixed feeders in open environments (Fortelius et al., 1993), which could be regarded as the very probable competitors for the woolly rhinos. It's worth pointing out that *Coelodonta* never reached the western hemisphere.

With regards to the complete dentitions and mandible of *C. antiquitatis* from Hutouliang (Pei, 2001) in Nihewan, its chronology is still under debate, but the teeth are obviously more advanced than the YNP specimens.

The fossil records of early woolly rhinos are quite poor outside China. The pre-Late Pleistocene woolly rhino records outside China have been reviewed by Uzunidis et al. (2022), namely Transbaikal area of Russia (Beliajeva, 1966; Kahlke,1999; Erbajeva and Alexeeva, 2000; Alexeeva and Erbajeva, 2005); Nalaika of Mongolia (Eisenmann and Kuznetsova, 2004); Bad Frankenhausen (Kahlke and Lacombat, 2008) and Neumark-Nord (Van der Made, 2010) of Germany; La Fage (Guérin, 1973), Romain-la-Roche (Guérin, 2010) and Les Rameaux (Uzunidis et al., 2022) of France.

The first record of the woolly rhinoceros *Coelodonta* in Europe is from Bad Frankenhausen and Bornhausen (Koenigswald and Heinrich, 1999; Kahlke and Lacombat, 2008) as well as the Tunel Wielki Cave in Poland, the latter was dated back to 600–400 kyr or MIS 14–11 (Stefaniak et al.,

2023). The earliest westward dispersal of *C. tologoijensis* to Central Europe took place in early Middle Pleistocene, corresponding to MIS16, or 0.65 Ma BP numerically (Van der Made et al., 2017), which gave rise to the origin of the true woolly rhino in Europe (Kahlke and Lacombat, 2008). Guérin (1980) named the subspecies *Coelodonta antiquitatis praecursor* based on fossils from La Fage (ca 0.25 Ma) of France. Kahlke and Lacombat (2008) proposed that the La Fage specimen is similar to the species *C. tologoijensis* from Bad Frankenhausen in spite of the much younger age of the former. It seems that the European woolly rhinos differ from the Chinese ones in their even more inclined occipital plane, which may be resulted from the abrupt lift of the skull posterior to the frontal bone; on the other hand, in the Chinese forms, the supraoccipital crests stretch far backward like a roof overhang. The inclination of the occipital plane can be demonstrated by the angle between the occipital plane and the occlusal plane (Fig. 6), which is more practical and easier to be measured than the angle "Y" used by previous authors (Borsuk-Bialynicka, 1973; Loose, 1975).

Regarding the origin of the true woolly rhino *C. antiquitatis*, it's still controversial because of the absence of complete skull fossils for the *Coelodonta* in the time span between 1.2 and 0.5 Ma (Tong and Moigne, 2000); furthermore, the crucial characteristics of *Coelodonta* made their appearance in a mosaic pattern. The skull of *C. nihowanensis* from YNP resembles the Late Pleistocene *C. antiquitatis* in most of its cranial characteristics. It's quite common that *C. nihowanensis* coexisted with *Elasmotherium*, the largest true rhino or the biggest rhino of the late Cenozoic (Mallet et al., 2022), in the sites of Early Pleistocene age in North China (Tong et al., 2018).

5. Occurrence of early bison in Nihewan

In spite of bison fossils were frequently recovered in North America and northern Eurasia, the earliest fossil records of the bison lineage unexceptionally occur in South and East Asia. The Siwalik region was regarded as the origin place for the bison lineage (Pilgrim, 1939, 1947; McDonald, 1981; Sher, 1997; Vislobokova, 2008; Khan et al., 2010, 2011), and the Nihewan Basin in North China was the type locality for *Bison palaeosinensis* which gave rise to the true bisons (Flerov, 1979; Sher, 1997; Croitor, 2016), which means the specimens of early bison from Nihewan resemble the true bison more than any Early Pleistocene bison does.

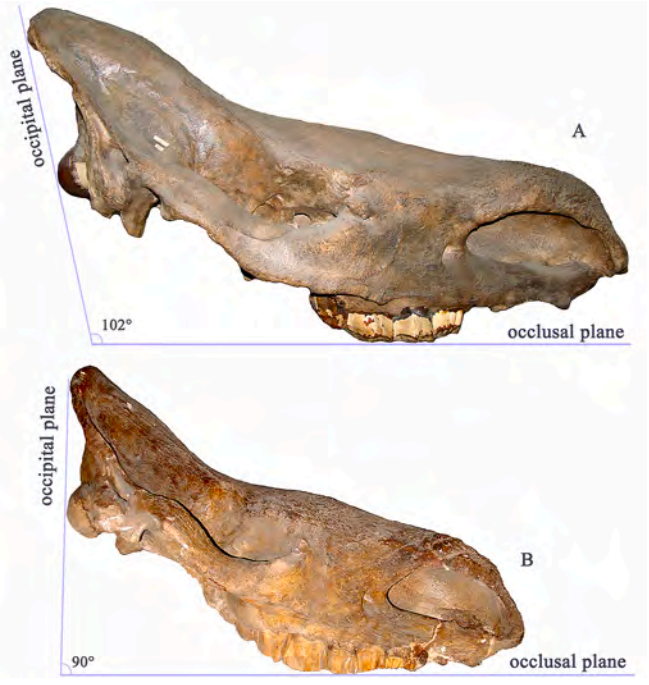

Fig. 6. The occipital-occlusal plane angle of *C. antiquitatis*. A, skull from Inner Mongolia of China, IVPP V2130; B, skull from Gnadenfeld of Europe, unlabelled specimen in the IVPP collection.

In Nihewan Basin, the most complete and most abundant fossils of the early bison were recovered, which include nearly complete skulls (Fig. 7), mandibles and postcranial bones; the best fossil materials were unearthed from the following sites (Table 1): XSG (Teilhard de Chardin and Piveteau, 1930), YNP (Li et al., 2021) and SSMZ (Tong et al., 2017). Large quantities of *B. palaeosinensis* unearthed recently at YNP site remain unstudied and unpublished.

The species *B. palaeosinensis* is primitive in the following aspects: The skull is generally smaller; the largest occipital width are 210–235.9 mm (Teilhard de Chardin and Piveteau, 1930; Li et al., 2021); the P2–M3 length is 140 mm (Li et al., 2021), which is quite short; distance between the temporal grooves is 90–94 mm (Teilhard de Chardin and Piveteau, 1930) or 122.1 mm (Li et al., 2021) measured at the occipital plane, which are much smaller than those of the *Bison priscus* of Late Pleistocene (Prat et al., 2003; Tong et al., 2013). In morphology, it differs from the later true bisons in its temporal fossae which extend high up along the lateral sides; the divergence angle of the horns is less than 150 mm; the pedicle of the horn-core is longer than in the later forms of bison; in the male, the horn-cores are posterolaterally extended and moderately depressed on the proximal one-third of their length before curving sharply upward, with moderately recurved tips which appear to have a posterior twist; Limb bones are quite slender and shorter (after Teilhard de Chardin and Piveteau, 1930; Skinner and Kaisen, 1947; Tong et al., 2017). Furthermore, the supraorbital foramens in the YNP specimen are very large, but the major palatine foramens are not so developed; it seems that the orbits are less tubular, and the facial tuberosity is less pronounced than in the later forms of bison; the orientation of the long axis of the orbit is also different from the later bisons. Actually, the early bisons from Nihewan are far from clear, especially the determinations of the syntype specimens of *B. palaeosinensis* (cranium A and B described by Teilhard de Chardin and Piveteau, 1930) are still controversial: according to Skinner and Kaisen (1947), the lectotype (cranium A) should be a male *B. palaeosinensis*, while the paratype (cranium B) should be a female *B. palaeosinensis*; on the other hand, McDonald (1981) referred cranium A to the species *B. priscus* and cranium B to the species *B. sivalensis* respectively; furthermore, other alternative scenario of classification is also possible (personal communication with Van der Made).

Leptobos is unexpectedly absent in the Nihewan fauna, while it did appear in several contemporaneous sites in northern China and even coexisted with the early bison at such sites as Xihoudu, Bajiazui, Jinyuan Cave (Jin et al., 2021) and Gonghe. *Leptobos* can distinguish itself from *Bison* in its following characteristics: longer post-cornual portion of the cranial roof, less divergence of the two horns (diverge at an angle between 65° and 80°, with a few reaching 105°), females are hornless, the hinder ends of the temporal fossae approach each other, and slender limbs (Tong et al., 2017). *Leptobos* has close relationship with *Bison*, at least they two are in the same evolutionary lineage (Pilgrim, 1947; Duvernois, 1990) or phyletic group (Geraads, 1992), which means the distinctions between them are actually not easy; we still need more fossil materials to be recovered.

Besides Nihewan, Yushe (Teilhard de Chardin and Trassaert, 1938) and some other localities (Chia and Wang, 1978) in Shanxi Province also yielded early bison fossils, all of them are exclusively Early Pleistocene sites; the age of the *Bison* bearing stratum in Yushe Basin is 2.5–1.9 Ma (Tedford et al., 1991). Furthermore, some sites in northwest China also bear bison fossils, such as BJZ in Gansu (Wang, 2006) and GH in Qinghai. Partial skull with complete horn-cores of *B. palaeosinensis* from Jinyuan Cave in Liaoning Province dated back to 2.6–1.7 Ma (Jin et al., 2021). The stratum bearing the bison fossil in Gonghe Basin was initially referred to Middle Pleistocene by Zheng et al. (1985), but it's still controversial.

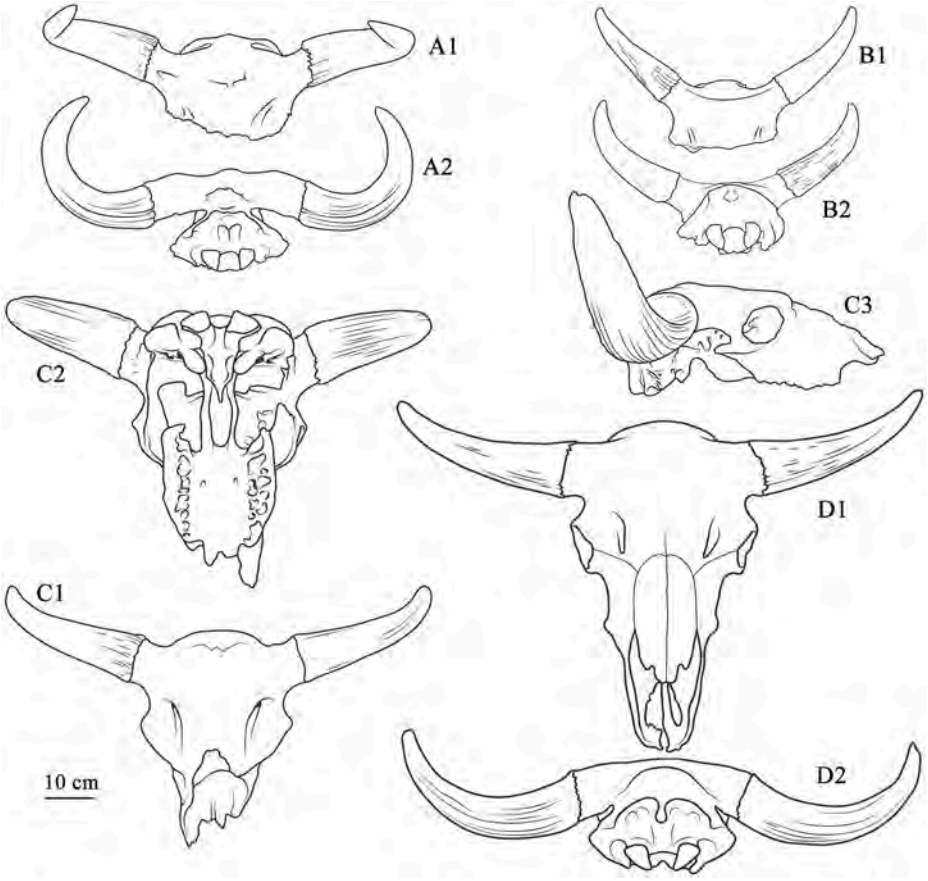

Fig. 7. Sketches of the skulls of *Bison palaeosinensis* (A1-C2) recovered in Nihewan, compared with the Late Pleistocene *Bison priscus* (D1-D2). A1-A2, skull A from XSG (Teilhard de Chardin and Piveteau, 1930: Pl XV: 1-1a); B1–B2, skull B from XSG (Teilhard de Chardin and Piveteau, 1930: Pl XV: 2); C1–C3, partial skull from YNP (Li et al., 2021: Figs. 6–8); D1-D2, V 18783 from NE China, late Pleistocene (Tong et al., 2013: Fig. 1). A1, B1, C1 and D1, dorsal views; A2, B2 and D2, occipital views; C2, palatal view; C3, lateral view.

The history of the *Bison* lineage in China doesn't seem to be continuous, because the Middle Pleistocene fossil records are very poor and even doubtful. It's very probable that the Late Pleistocene *Bison* in Northeast China migrated from Siberia (Tong et al., 2013).

Although the earliest occurrences of *Bison* in East and West Europe are at 1.77 Ma (Dmanisi) and 1.5 Ma (Venta Micena) respectively (Martínez-Navarro et al., 2011), the earliest "true" bison appeared in Europe about 1.2 Ma; and most of the bison fossils dated around 1.2–0.5 Ma are referred to the species *Bison schoetensacki* (Sorbelli et al., 2021). Europe is another important evolutionary center for early bisons, because the Early Pleistocene bison is more morphologically diversified there than in Asia.

The key sites for early bisons in Europe and western Eurasia can be summarized as follows: (1) Dmanisi, Georgia (1.77 Ma) –*B.* (*Eobison*) *georgicus* (Burchak-Abramovich et al., 1994); (2) Mygdonia Basin, Greece (1.7–1.2 Ma) –*Bison* cf. *degiulii* (Kostopoulos et al., 2018; Sorbelli et al., 2021); (3) Pirro Nord, Italy (ca. 1.6–1.2 Ma) –*B.* (*Eobison*) *degiulii* Masini (1989) (Sorbelli et al., 2021); (4) Pietrafitta, Italy (ca. 1.5 Ma) –*B.* (*Eobison*) *degiulii* (Sorbelli et al., 2023); (5) Venta Micena, Spain (1.37–1.1 Ma: Ortiz et al., 2000; Duval et al., 2011) –*Bison* sp. (Moyà-Solà, 1987; Martínez-Navarro et al., 2011; Sorbelli et al., 2021); (6) Untermassfeld, Germany (1.2–0.9 Ma) –*B. menneri* Sher (1997); Kahlke (2022); (7) Vallonnet, France (ca. 1.2–1.1 Ma) –*B.* (*Bison*) *schoetensacki* Freudenberg (1910) (de Lumley et al., 1988; Moullé et al., 2006); (8) Mosbach, Germany (0.6 Ma) –*B.* (*Bison*) *priscus* (Bojanus, 1825; Sher, 1997) (Fig. 8: C).

Croitor (2016) proposed two Early Pleistocene lineages of bison as follows: the boreal lineage—*B.* (*Eobison*) *palaeosinensis* – *B. menneri* – *Bison* sp. from China and the Tiraspolian gravel; the southern lineage—*B.* (*Eobison*) *sivalensis* – *B.* (*Eobison*) *georgicus* – *B.* (*Eobison*) *tamanensis* – *B.* (*Eobison*) *degiulii* from Indian Subcontinent and Mediterranean Area.

Based on fossil records, the evolutionary sequence of the *Bison* lineage in Europe was outlined by Sorbelli et al. (2021) as follows: *Bison* (*Eobison*) spp. (1.77–1.2 Ma)–*B.* (*Bison*) *menneri* (1.2–0.9 Ma)–*B.* (*Bison*) *schoetensacki* (1.2–0.4 Ma)–*B.* (*Bison*) *priscus* (0.6–0.012 Ma)–*B. bonasus* (ca. 0.01 Ma). Furthermore, the updated data shows that "*Bison* (*Eobison*) only has three valid species, namely *B.* (*E.*) *palaeosinensis*, *B.* (*E.*) *georgicus*, and *B.* (*E.*) *degiulii* (Sorbelli et al., 2023).

Bukhsianidze (2020) proposed that *B. menneri* Sher (1997) has more affinity with the yak, and assigned the species to *Poephagus* like *B.* (*Poephagus*) *menneri* Sher (1997); and she also thought the Untermassfeld fossils represent the earliest and most western occurrence of fossil yak. The authors of this paper also think that *B. menneri* from Untermassfeld is quite different from the true bisons in its skull shape and the longer postcranial bones, and they are also far from the yak in their extremely long postcranial bones; *B. menneri* Sher (1997) should be an extinct side branch of the early bovini.

Although bison was among the most important mammals and the only survived Pleistocene large mammal in North America, it appeared there quite late relative to Eurasia; just by 195–135 kyr ago, the bison dispersed to America from Asia via the Bering Land Bridge (Froese et al., 2017), rather than at 1.2 Ma (Harington, 1984) as previously proposed. Although the history of bison was short in America, it did experience an explosive evolution and left rich collections of fossils there (Skinner and Kaisen,1947; Guthrie, 1970; McDonald, 1981).

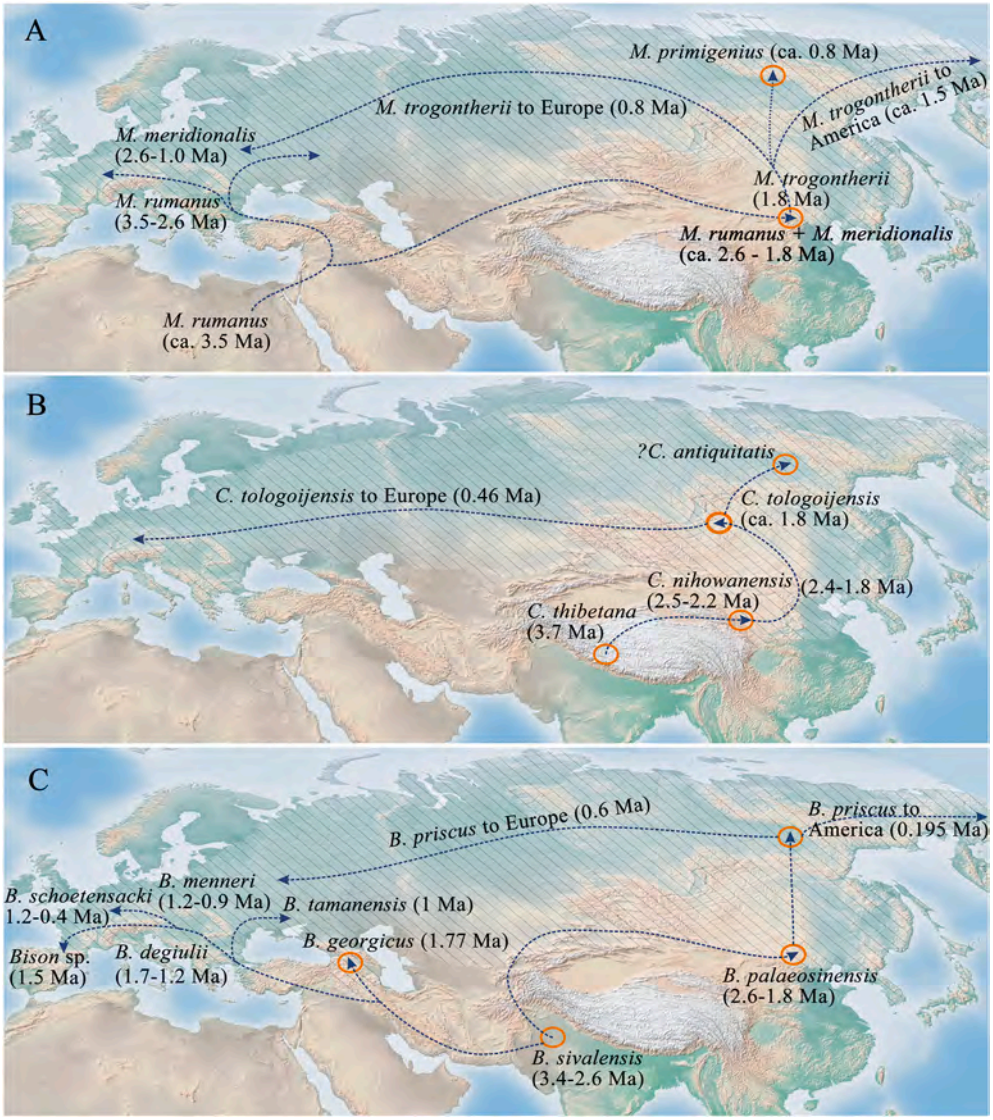

Fig. 8. Key sites of early *Mammuthus* (A), *Coelodonta* (B) and *Bison* (C). The hatched area represent the maximum Eurasian distributions of Late Pleistocene *M. primigenius* (A), *C. antiquitatis* (B) and *B. priscus* (C) respectively. Data is adopted from Chow (1978), Tong and Moigne (2000), Markova et al. (2013), Kahlke (2014) and Puzachenko et al. (2017).

The recent genomic and paleogenomic studies show that the bison (*Bison*) and cattle (*Bos*) lineages started to diverge at ca. 1.7 Ma (Grange et al., 2018), which is not supported by the fossil records.

6. Discussions

The cold-adapted land mammals of the modern world mainly occur in the polar regions and the high mountains, which can be categorized as the polar type and the alpine type respectively. The polar type can be well represented by the Arctic mammalian fauna, while the alpine type on the Tibetan Plateau is very typical for its kind.

Concerning the links between the Arctic and the Tibetan Plateau mammalian faunas, it's still controversial.

The terrestrial Arctic mammals of today include the polar bear (*Ursus maritimus*), polar wolf (*Canis lupus*), Arctic fox (*Vulpes lagopus*), ermine (*Mustela ermina*), muskox (*Ovibos moschatus*), reindeer/caribou (*Rangifer tarandus*), Arctic hare (*Lepus arcticus*) and lemming (*Dicrostonyx* sp./ *Lemmus* sp.) (Blix, 2016), most of them should have Subarctic to Arctic origin, such as muskox, reindeer, and Arctic fox (Kahlke, 2014), while some one proposed that the Arctic fox and sheep should be out of Tibet (Wang et al., 2014).

The Tibetan Plateau is the largest alpine biome on the earth today. On the Tibetan Plateau, totally around 24 species of ungulates can survive at the elevation of 4000 m, and most of them even can reach higher altitude (Jiang et al., 2018), which means they only live in habitats of alpine meadow or tundra above the forest zone (Chang and Chiang, 1973). Moreover, no mammal was recorded above the elevation of 6000 m (Hu et al., 2018). The elevation ranges for the iconic species of the Tibetan Plateau are as follows: the highest record for Pallas's cats (*Otocolobus manul*) is 5050 m (Fox and Dorji, 2007; Jutzeler et al., 2010); 2700–5300 m for the kiang or Tibetan wild ass (*Equus kiang*) (St-Louis and Côté, 2009); 3000–5500 m for the wild yak (*Bos grunniens*) (Leslie and Schaller, 2009); 3250–5500 m for the chiru or Tibetan antelope (*Pantholops hodgsonii*) (Leslie and Schaller, 2008); 3000–5750 m (Leslie, 2010) or 5000–5750 m (Jiang et al., 2018) for the Tibetan gazelle (*Procapra picticaudata*); 2400–6000 m for the blue sheep (*Pseudois nayaur*) (Jiang et al., 2018); 4000–5000 m (Ohtaishi and Gao, 1990) or 3500–5200 m (Jiang et al., 2018) for the white-lipped deer or Thorold's deer (*Cervus albirostris* Przewalski, 1883); 3500–5000 m for the Tibetan red deer (*Cervus wallichii*) (Jiang et al., 2018). Most of the species mentioned above are endemic to Tibetan Plateau and have local origins (Zhang and Zheng, 1985; Wang et al., 2015); while the origin of the wild

yak is still open to question, the fossil species *Bos* (*Poephagus*) *baikalensis* from the Transbaikal region is inferred as the ancestor of the modern yak (Kahlke, 1999). Although one of the iconic Tibetan mammals, the endemic Tibetan antelope, can be traced back to the Late Miocene (Wang et al., 2015), most of them don't have a deep history on the plateau. In the Early Pleistocene, the average elevation of the Tibetan Plateau was only ca. 2000 m, and until the Middle Pleistocene, such genera as *Equus*, *Bos*, *Ovis*, *Moschus*, and *Cervus* etc. made their first appearances on the Plateau (Feng et al., 1986).

At the generic level, *Pantholops* is the only extant taxon endemic to the Tibetan Plateau, which means the modern mammalian fauna of the Tibetan Plateau doesn't have a long history (Feng et al., 1986); on the other hand, it also means that the Tibetan Plateau also has extensive exchanges with the adjacent areas in mammalian fauna.

Except for the endemic taxa of today, the Himalayan fauna also contributed a lot to the Eurasian Pleistocene fauna. The convincing "out of Tibet" hypothesis postulates that cold-tolerant species in Pliocene high Tibet were pre-adapted to conditions for the subsequent Pleistocene global ice age and the Tibetan Plateau could be regarded as a cradle for ice age megafauna (Deng et al., 2011, 2023). The best examples for the "out of Tibet" scenario include the Tibetan woolly rhinoceros (*Coelodonta thibetana*), Tibetan bharal (*Pseudois*), Asian hunting dog (*Sinicuon*), and ancestral snow leopard (*Panthera blytheae*) (Wang et al., 2015); the woolly rhino (*Coelodonta*) once roamed the whole area of the middle to high latitude of the continental Eurasia during Mid-Late Pleistocene, and the Tibetan bharal or blue sheep became widespread in northern China and the Tibetan Plateau since Middle or Late Pleistocene onward. Furthermore, the extant Arctic fox, *Vulpes lagopus* probably can be traced back to the Pliocene Tibetan fox, *Vulpes qiuzhudingi* (Wang et al., 2014); the newly discovered fossils of a primitive species (*Protovis himalayensis*) of sheep and the existing molecular phylogeny suggest that the Tibetan Plateau represents the ancestral home range(s) for all extant species of *Ovis* (Wang et al., 2016).

It seems that the *Mammuthus-Coelodonta* Faunal Complex is a composition of both the Arctic originated and the Tibetan Plateau originated faunas. Phylogenetic ancestors of a significant number of iconic species of Eurasian mammoth faunas, such as saiga (*Saiga borealis*), bisons (*Bison* spp.), woolly rhinoceroses (*Coelodonta tologoijensis*, *C. antiquitatis*) and steppe mammoth (*Mammuthus trogontherii*) descended from species of Central Asian origin. While such species as *Ovibos moschatus*, *Rangifer tarandus*, *Mammuthus primigenius* and *Alopex lagopus* (=*Vulpes lagopus*) are of Subarctic to Arctic origins (Kahlke, 2014).

The dominate taxa in the Nihewan fauna include *Canis* spp., *Equus* spp., *Coelodonta nihowanensis*, *Gazella sinensis*, *Mammuthus trogontherii*, *Bison palaeosinensis*, diverse cervids and early *Acinonyx* etc. (Tong et al., 2024), and all of them have tight evolutionary relationships with the later *Mammuthus-Coelodonta* fauna. In the *Mammuthus-Coelodonta* Faunal Complex, *Canis lupus*, *M. primigenius*, *C. antiquitatis* and *B. priscus* are the most widespread taxa (Kahlke, 1999) (Fig. 8), and all of them have very closely related ancestor taxa in the Nihewan Basin. The local big wolf *Canis chihliensis* resembles the grey wolf *C. lupus* both in size and form (Tong et al., 2012); it's the *M. trogontherii* gave rise to the true woolly mammoth (*M. primigenius*); the recently discovered complete skull of *C. nihowanensis* from Nihewan resembles the true woolly rhino (*C. antiquitatis*) in many aspects; the fossils of *B. palaeosinensis* from Nihewan represents the earliest and most bison-like taxon and has the richest fossil collection among the early bisons. Furthermore, the Nihewan fauna shows a typical Palearctic character, which is exclusively composed of the boreal animals, except one tooth of porcupine (*Hystrix*) and few fossils of early muntjac (*Muntiacus*).

Although Europe also had rich fossil records of early mammoth and diverse fossil bisons, the woolly rhino reached there quite late, which very probably was resulted from the competition from the morphologically and ecologically convergent rhino species of *Stephanorhinus* which used to be the most common rhino taxa in Europe during Early-Middle Pleistocene. Previous author thought *Coelodonta* represents the ultimate evolution of the Dicerorhininae lineage and *C. antiquitatis* was of Asian origin, and the true woolly rhino or the nominate subspecies appeared in Europe at a quite late time, which was MNQ zones 25 and 26, corresponding to Late Pleistocene (Guérin, 1982). While the most recent study shows the arrival time of *Coelodonta* in Europe is earlier, and the Bad Frankenhausen *Coelodonta* record indicates the initial formation of a pan-Eurasian *Mammuthus-Coelodonta* Faunal Complex at the time 460 kyr BP (Kahlke and Lacombat, 2008).

North America had early mammoth records, but they are later than the Eurasian ones; bisons also occurred in North America, but it's in quite late time; meanwhile, the woolly rhino never crossed the Bering land bridge. In the late Quaternary, the Holarctic realm shared a same ecosystem, that's the mammoth steppe (Guthrie, 1982; Zimov et al., 2012; Kahlke, 2015), but the woolly rhino was absent in North America. Although the arrival time of mammoth and bison in North America is still debatable, they are unquestionably later than the Eurasian records.

It's worth mentioning that the species *Rhinoceros platyrhinus* Falconer and Cautley, 1846 was once referred to *Coelodonta* by Colbert (1935), which was followed by a couple of authors (Badam, 1979; Patnaik and Nanda, 2010); however, further study shows it lacks such derived states of the *Coelodonta* lineage as facial elongation, cloison and incisor loss (Groves, 1983). Therefore, the report of *Coelodonta* in the Siwalik fauna can be definitely denied. Meanwhile, the early bison was definitely derived from Siwalik or somewhere else in South Asia according to the current knowledge. In China, the tribe of Bovini and the elephantid group appeared in the North first, which means they were immigrators from South Asia either via the Plateau or central Asia. Moreover, the evolutionary relationships between the North China fauna and the Siwalik fauna is not yet well understood.

The Tibetan Plateau region was regarded as one of the origin centers for the cold-adapted Quaternary ice age fauna (Wang et al., 2014, 2015, 2016; Deng et al., 2019). The Nihewan Basin is one of the most important gathering areas for the boreal mammals, from where the cold-adapted mammals dispersed to other parts of the continental Eurasia and even to North America for some taxa.

7. Conclusions

The general appearance of the Nihewan Fauna demonstrates a Palearctic type. According to fossil discoveries, Nihewan Basin yielded the richest and the best-preserved fossil specimens of Early Pleistocene *Coelodonta* and *Bison*; it also has the earliest *M. trogontherii* and the richest and best-preserved juvenile fossils of its kind. The nearly complete skull and mandibles as well as the deciduous teeth of *M. trogontherii* from SSMZ site shows they are generally larger than the true woolly mammoth *M. primigenius*. The complete skull of *C. nihowanensis* from YNP represents the closest ancestor for the later woolly rhinos, which has already had its nasal septum fully ossified and its occiput strongly backwardly inclined; but it's still primitive in its triangular upper M3 and larger zygomatic width as well as some other characteristics; the complete juvenile skull and mandible with complete milk dentitions represents the only sample for early woolly rhinos. The partial skulls with complete horn-cores of *B. palaeosinensis* from XSG and YNP represent the richest and best-preserved fossil collection for Early Pleistocene bison; the early bisons are relatively small and have shorter distance between temporal fossae at the caudal end as well as slender limb bones. The three most important iconic taxa of the *Mammuthus - Coelodonta* Faunal Complex, i.e. *Mammuthus*, *Coelodonta* and *Bison*, had concurrently appeared in the Early Pleistocene at Nihewan, which made great contributions to the Mid-Late Pleistocene *Mammuthus - Coelodonta* Faunal Complex.

Data availability

Data are included within the submitted article and supplementary materials.

CRediT authorship contribution statement

Haowen Tong: Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Xi Chen:** Writing – review & editing, Investigation. **Bei Zhang:** Writing – review & editing, Investigation.

Declaration of competing interest

There's no financial/personal interest or belief that could affect our objectivity.

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