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Holocene survival of Late Pleistocene megafauna in China: a critical review of the evidence

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ABSTRACT

Late Quaternary megafaunal extinction chronologies are poorly understood across eastern and south-east Asia. Previous radiometric studies suggested that surprisingly many extinct Late Pleistocene large mammal species survived into the Holocene in northern China (*Bos primigenius*, *Coelodonta antiquitatis*, *Mammuthus primigenius*) and southern China (*Ailuropoda baconi*, *Crocuta* [*crocuta*] *ultima*, *Megatapirus augustus*, *Stegodon orientalis*, *Sus* cf. *xiaozhu*), indicating that Chinese megafaunal extinctions may have been "staggered" across the Late Quaternary. We critically re-examined all radiometric evidence suggesting Holocene survival of Chinese Late Quaternary megafauna, and conducted new dating of mammal material from reportedly Holocene sites containing characteristically Late Pleistocene faunas. Evidence for Holocene survival of any Chinese Late Pleistocene megafaunal species is weak or untenable. No previous radiometric dates used to support Holocene megafaunal survival represent direct bone dates for species of interest, and stratigraphic association between material yielding Holocene dates and megafaunal remains is dubious at most sites. Concerns over accurate identification of faunal material further confuse claims for Holocene survival of many species. Robust radiometric last-occurrence dates for extinct Chinese megafauna are all restricted to the Late Pleistocene, similar to the timing of many other Late Quaternary megafaunal species extinctions elsewhere in Eurasia and the Americas.

1. Introduction

The disappearance of a large proportion of the world's megafaunal mammal taxa during the Late Quaternary (two-thirds of all mammal genera, and half of all species, with body masses >44 kg) is the subject of considerable scientific interest (Martin and Klein, 1984; MacPhee, 1999; Barnosky et al., 2004). The great majority of research into Late Quaternary extinctions has focused on megafaunal species losses in the continental regions of North America, northern Eurasia, and Australia. Although many questions remain, this research has led to an increasingly sophisticated understanding of the timing and dynamics of megafaunal extinction in response to both anthropogenic impacts and environmental change in each of these regions (e.g. Stuart et al., 2004; Turney et al., 2008; Gill et al., 2009; Rule et al., 2012; Stuart and Lister, 2012). In contrast, megafaunal extinction chronologies remain far more poorly constrained elsewhere, notably across much of eastern and south-east Asia (Louys et al., 2007; Turvey, 2009). Clarifying the magnitude, timing and causation of Late Quaternary extinctions in this region is of particular significance because, apart from Africa, it is the only part of the world with surviving representatives of "truly" megafaunal (sensu Owen-Smith, 1988, i.e. >1000 kg) proboscidean and rhinocerotid taxa (*Dicerorhinus*, *Elephas*, *Rhinoceros*). It is also recognized as having the world's highest number of currently threatened large land mammal species, making attempts to understand the dynamics and drivers of past regional mammal extinction of considerable conservation relevance (Schipper et al., 2008).

China possesses the richest known Late Quaternary palaeontological and zooarchaeological record in the eastern/south-east Asian region, and spatial and temporal variation in the species composition of Chinese Late Quaternary mammal faunas has long been recognized. This vast country spans substantial portions of both the Palaearctic and Oriental zoogeographic realms. The northeastern Chinese Late Pleistocene mammal fauna is interpreted as an extension of the northern Eurasian fauna that was also

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distributed in Europe, the Russian Federation, Kazakhstan, Mongolia and Japan, and contained several characteristic representatives of this fauna such as woolly mammoth *Mammuthus primigenius* and woolly rhinoceros *Coelodonta antiquitatis* (Dong et al., 1996; Tong and Patou-Mathis, 2003; Stuart and Lister, 2012), with mammoths occurring as far south as Shandong Province during Marine Oxygen Isotope Stage 3a (Takahashi et al., 2007). The more warm-adapted straight-tusked elephant *Palaeoloxodon naumanni* was also distributed in northeastern China during the Late Pleistocene, where it is known from more than 30 localities, often in apparent stratigraphic association with *Coelodonta* (Xue et al., 2000; Tong and Patou-Mathis, 2003). Other extinct megafaunal taxa associated with the Eurasian *Palaeoloxodon* assemblage (e.g. *Bos primigenius*, *Stephanorhinus*, megacerine deer) are also known from northeastern China during the Late Pleistocene (Dong et al., 1996; Pushkina, 2007; Tong and Wu, 2010). The subtropical area of China and neighbouring south-east Asia south of the Yellow River–Qinling Mountains, the traditional biogeographic boundary between the Palaearctic and Oriental Realms (Tong, 2007), was defined during much of the Pleistocene by the regionally distinctive *Stegodon–Ailuropoda* fauna (Colbert and Hooijer, 1953; Kahlke, 1961; Wang and Ouyang, 1982; Yang et al., 1995; Long et al., 1996; Louys et al., 2007). This fauna was characterized by the extinct proboscidean *Stegodon orientalis* and the “giant” giant panda *Ailuropoda baconi*, formerly considered to be a subspecies of the extant *Ailuropoda melanoleuca* but now often interpreted as a distinct chronospecies (Jin et al., 2007). It also contained a relatively high diversity of anthropoid primates (including archaic hominins that may be specifically distinct from *Homo sapiens*; Curnoe et al., 2012), as well as several other regionally endemic extinct large mammals such as *Megatapirus augustus*, *Rhinoceros sinensis*, *Sus xiaozhu*, and *Crocuta* [*crocuta*] *ultima* (which may also represent a distinct species; Rohland et al., 2005) and also extant taxa such as the Asian elephant *Elephas maximus*.

The *Stegodon–Ailuropoda* fauna has been interpreted as a general category of fossil assemblages rather than an ecologically consistent fauna, and may mask important spatial and temporal variation in large mammal species composition in southern China across the Late Quaternary (Wang and Ouyang, 1982; Wang et al., 2007). For example, cold-adapted northern taxa such as Merck’s rhinoceros *Stephanorhinus kirchbergensis* are now known to have also been present at high altitudes in the Yangtze region of southern China during the Late Pleistocene (Tong and Wu, 2010). The respective spatiotemporal distributions of cold-adapted and warm-adapted megafaunal taxa in northern China during the Pleistocene are also incompletely resolved (Tong, 2007). However, although some terminal Pleistocene dates for Chinese megafaunal taxa are considered questionable (Kuzmin, 2010), direct AMS ^{14}C dating, ESR and U-series analyses demonstrate that most of the characteristic megafaunal representatives of the different regionally distinctive assemblages persisted into the Late Pleistocene in both northern China (Xue et al., 2000; Takahashi et al., 2007; Lorenzen et al., 2011; Stuart and Lister, 2012) and southern China (Wu et al., 2006; Louys et al., 2007; Wang et al., 2007; Pei et al., 2013).

In contrast, although the Chinese Holocene record also contains several megafaunal mammal taxa that no longer occur in the region, most of these are species that are known to have survived into the historical period either in China (Père David’s deer *Elaphurus davidianus*) or elsewhere in south-east Asia (kouprey *Bos sauveli*; Malayan tapir *Tapirus indicus*; Sumatran rhinoceros *Dicerorhinus sumatrensis*; Javan rhinoceros *Rhinoceros sondaicus*) (Teilhard de Chardin and Young, 1936; Hoffmann, 1986; Wei et al., 1990; Xu, 2000; Cao, 2005; Rookmaaker, 2006; Zhu et al., 2008). These regional extirpations probably represent an early phase of the ongoing and escalating series of severe range contractions, regional extirpations and global extinctions of Chinese large mammals, including elephants (Xu, 2000; Elvin, 2004), ungulates (Yang et al., 2005; Wen, 2009), carnivores (Tilson et al., 2004; Yang et al., 2005; Jablonski et al., 2012), primates (Zhang et al., 1989; Li et al., 2002; Grueter et al., 2009; Chatterjee et al., 2012), and endemic freshwater cetaceans (Turvey et al., 2007), associated with extreme levels of human overpopulation, natural resource overexploitation and habitat modification throughout the development of Chinese civilization.

Only one globally extinct and taxonomically valid Chinese mammal species, the short-horned water buffalo *Bubalus mephistopheles*, is known with certainty to have disappeared during the Holocene before the recent historical era. Although no direct radiometric dates are available, this species is present in a series of well-dated early–middle Holocene (Neolithic–Bronze Age) zooarchaeological deposits across southern, central and eastern China (from Yunnan to northern Henan), in association with representatives of the modern Holocene Chinese large mammal fauna (Teilhard de Chardin and Young, 1936; Wei et al., 1990; Zhang et al., 1992; Ji et al., 2004; Liu et al., 2004). Ancient DNA analysis demonstrates that it is phylogenetically distinct from domesticated water buffalo *Bubalus bubalis* present in China today (Yang et al., 2008).

However, it has also been suggested that a surprisingly large number of globally extinct representatives of China’s Late Pleistocene megafauna survived well beyond the Pleistocene–Holocene transition in both northern and southern China (Table 1; Figs. 1 and 2). A series of radiometric dates was put forward by Ma and Tang (1992) and Tong and Liu (2004) as evidence for the early–middle Holocene persistence of *Bos primigenius, Coelodonta antiquitatis* and *Mammuthus primigenius* in northern China, and *Ailuropoda baconi, Crocuta* [*crocuta*] *ultima, Megatapirus augustus, Stegodon orientalis* and *Sus cf. xiaozhu* in southern China. More recently, Li et al. (2012) reassigned two allegedly mid-Holocene elephant molars from northern China from *Elephas maximus* to *Palaeoloxodon* sp., and proposed that this extinct proboscidean also survived until around 3000 years ago in China. Many of these dates have been reported again in wider reviews of Late Quaternary extinction and faunal turnover (e.g. Saegusa, 2001; Tong and Patou-Mathis, 2003; Louys et al., 2007; Wu, 2007; Van Den Bergh et al., 2008; Corlett, 2010, 2011; Louys, 2012). If these Holocene records are accurate, then they would represent the latest known continental or global records of several characteristic Late Pleistocene megafaunal taxa that disappeared from all other continental regions by the end of the Last Glacial or earlier (Stuart, 2005; Louys et al., 2007; Pushkina, 2007; Stuart and Lister, 2012), and would suggest a radically different pattern of faunal turnover and extinction in China compared to the rest of the world during the Late Quaternary.

Chinese ecosystems experienced large-scale climatically-driven environmental shifts and habitat redistributions during the Late Pleistocene–Holocene transition, comparable in magnitude to those seen elsewhere in the world, and which are implicated in driving extinctions in other large mammal faunas (Lorenzen et al., 2011). Climates during the Last Glacial Maximum were 7–10 °C lower than today in northern China and 4–6 °C lower in southern China, with taiga extending southwards to c. 43°N, steppe and desert vegetation replacing temperate forest in eastern regions, tropical forests excluded from the country, and broadleaved evergreen/warm mixed forest present only in tropical latitudes (Zheng et al., 1998; Yu et al., 2000). Modern humans were present in China by at least 40 ka (Fu et al., 2013), with fragmentary human fossils showing some modern characters also recorded from the initial Late Pleistocene >100 ka (Liu et al., 2010). Evidence for prehistoric human exploitation of large mammals in China is demonstrated in many archaeological sites across the Late Pleistocene and Pleistocene–Holocene transition (Liu and Chen, 2012;

Table 1
Radiometric or other dates from previous publications and this study for globally extinct Chinese large mammal species that are proposed to have survived into the Holocene.

Species	Dating method	^{14}C date (yr BP)	Material	Lab number	Reference
1. Zhoujiayoufang					
Bos primigenius, *Coelodonta antiquitatis*, *Mammuthus primigenius*	Indirect ^{14}C	7380 ± 100	Wood	PV-96	Li et al. (1980)
Coelodonta antiquitatis	Direct ^{14}C	31,800 ± 900	Bone (unspecified element)	Not reported	Sun et al. (1981)
Coelodonta antiquitatis	Direct ^{14}C	30,900 ± 875	Bone (unspecified element)	WB78-46	Radiocarbon Dating Society of Chinese Quaternary Research Association (1987)
Mammuthus primigenius	Direct ^{14}C	28,910 ± 1185 (recalculated as 28,880 ± 1220)	Bone (unspecified element)	WB78-45	Radiocarbon Dating Society of Chinese Quaternary Research Association (1987); Kuzmin et al. (2003)
Mammuthus primigenius	Direct ^{14}C	30,810 ± 1385	Femur	Not reported	Liu et al. (1988)
Mammuthus primigenius	Direct ^{14}C	39,400 ± 250	Incisor	Not reported	Liu et al. (1988)
Mammuthus primigenius	Direct AMS ^{14}C	51,600 ± 1400	Molar	OxA-21001	This study
2. Dingjiabu					
Bos primigenius, *Coelodonta antiquitatis*, "*Palaeoloxodon* sp." (=*Elephas maximus*)	Indirect ^{14}C	3630 ± 90	Wood	PV-34	Jia and Wei (1980); Radiocarbon Dating Society of Chinese Quaternary Research Association (1987)
Bos primigenius, *Coelodonta antiquitatis*, "*Palaeoloxodon* sp." (=*Elephas maximus*)	Indirect ^{14}C	3830 ± 85	Wood	Not reported	Jia and Wei (1980)
Bos primigenius	Direct AMS ^{14}C	Failed due to no collagen yield	Mandible	–	This study
"*Palaeoloxodon* sp." (=*Elephas maximus*)	Direct AMS ^{14}C	>50,300	Molar	OxA-26337	This study
3. Shuanglong Cave					
Ailuropoda baconi, *Crocuta* [*crocuta*] *ultima*, *Megatapirus augustus*, *Stegodon orientalis*, *Sus* sp. (cf. *xiaozhu*)	Indirect ^{14}C	7815 ± 385	*Bubalus* sp. bone (unspecified element)	Not reported	Ma and Tang (1992)
Sus scrofa	Direct AMS ^{14}C	Failed due to no collagen yield	Molar	–	This study
Sus scrofa	Direct AMS ^{14}C	Failed due to no collagen yield	Molar	–	This study
Cervus ?nippon	Direct AMS ^{14}C	Failed due to no collagen yield	Molar	–	This study
Dicerorhinus sumatrensis or *Rhinoceros sondaicus*	Direct AMS ^{14}C	Failed due to no collagen yield	Molar	–	This study
4. Wushan					
"*Tapirus* sp." (*Megatapirus augustus*?)	Indirect ^{14}C	7500 ± 130	Wood	Not reported	Fourth Science Research Team (1975)
"*Tapirus* sp." (*Megatapirus augustus*?)	Indirect ^{14}C	6740 ± 120	Wood	Not reported	Fourth Science Research Team (1975)
"*Tapirus* sp." (*Megatapirus augustus*?)	Indirect ^{14}C	6550 ± 120	Wood	Not reported	Fourth Science Research Team (1975)
"*Tapirus* sp." (*Megatapirus augustus*?)	Comparison to ^{14}C dates from other sites	Between 5600 ± 105 and 4235 ± 95	–	–	Fourth Science Research Team (1975)
5. Xiaohe Cave					
Stegodon sp.	Non-radiometric estimate	c. 4100	–	–	Huang (1979)
6. Tangzigou					
Ailuropoda ?baconi	Indirect AMS ^{14}C	9000 ± 40 to 8745 ± 60	Charcoal	BA04271–BA04275	Jin (2010)

Pei et al., 2012). However, it has been suggested that the longer-term coexistence of hominins and megafauna in eastern and south-east Asian ecosystems may have permitted behavioural adaptation in response to early hominin hunting strategies and the evolution of a "non-naïve" megafauna more resilient to later impacts by modern humans (Louys et al., 2007; Corlett, 2010). Conversely, intensive anthropogenically-driven environmental modification and habitat degradation may have begun in China much earlier during the prehistoric Holocene than in most other global regions (Goldewijk et al., 2011), and there were also relatively substantial climatic and environmental shifts in China during the early–middle Holocene associated with changing monsoon patterns (Zheng et al., 1998; An et al., 2000; Yu et al., 2000; Yang and Scuderi, 2010; Yang et al., 2011). It is therefore possible that megafaunal extinctions in China may indeed have displayed a "staggered" temporal pattern across the Late Pleistocene and Holocene, rather than only taking place close to the Pleistocene–Holocene boundary as in regions such as North America.

The chronology of Late Quaternary extinctions in China therefore represents an important subject for rigorous further investigation, in order to accurately identify causal drivers responsible for mammal species loss during this interval, and to provide a more robust temporal framework for understanding similarities and differences in patterns of megafaunal turnover between different continents. We address this research priority by critically examining all of the radiometric evidence previously used to support claims for Holocene survival of different Late Pleistocene megafaunal mammal species, and by conducting new radiometric dating

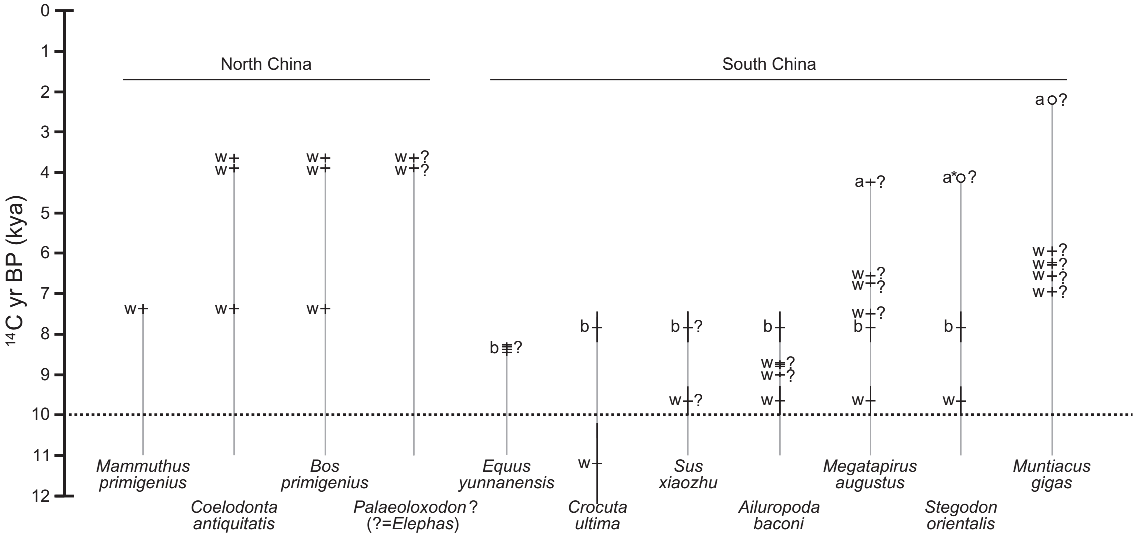

Fig. 1. Summary of putative evidence for persistence of globally extinct large mammal species into the Holocene in China, based on data from previously published radiometric and other studies. The extinct short-horned water buffalo *Bubalus mephistopheles* is not shown, as this species is considered to represent a valid prehistoric Holocene extinction. Dates are shown with 95% ranges where reported. Legend: w, indirect ^{14}C date (wood/charcoal); b, indirect ^{14}C date (bone from different species); a, ^{14}C date from different archaeological site presumed by earlier authors to be stratigraphically coeval; a*, estimated archaeological age not based on ^{14}C dating. A question-mark next to a specific record indicates that species-level or higher-order taxonomic identification of large mammal material associated with this date is not secure.

on available mammal material from reportedly Holocene sites containing characteristically Late Pleistocene faunas.

2. Materials and methods

The original radiometric dating studies and available data on the taxonomic identification and stratigraphic context of all putatively Holocene samples of Chinese Late Pleistocene megafaunal taxa were reviewed. Where possible, original samples or other faunal material from the same horizon or site were relocated in Chinese institutional collections and re-dated. Ultrafiltered AMS dating was carried out at the Oxford Radiocarbon Accelerator Unit (ORAU). Dates are quoted in uncalibrated radiocarbon years BP except where indicated, when the IntCal09 curve implemented in OxCal version 4.1 (https://c14.arch.ox.ac.uk/) was used.

Institutional or laboratory abbreviations are as follows: BA, Peking University Radiocarbon Laboratory, Beijing; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese

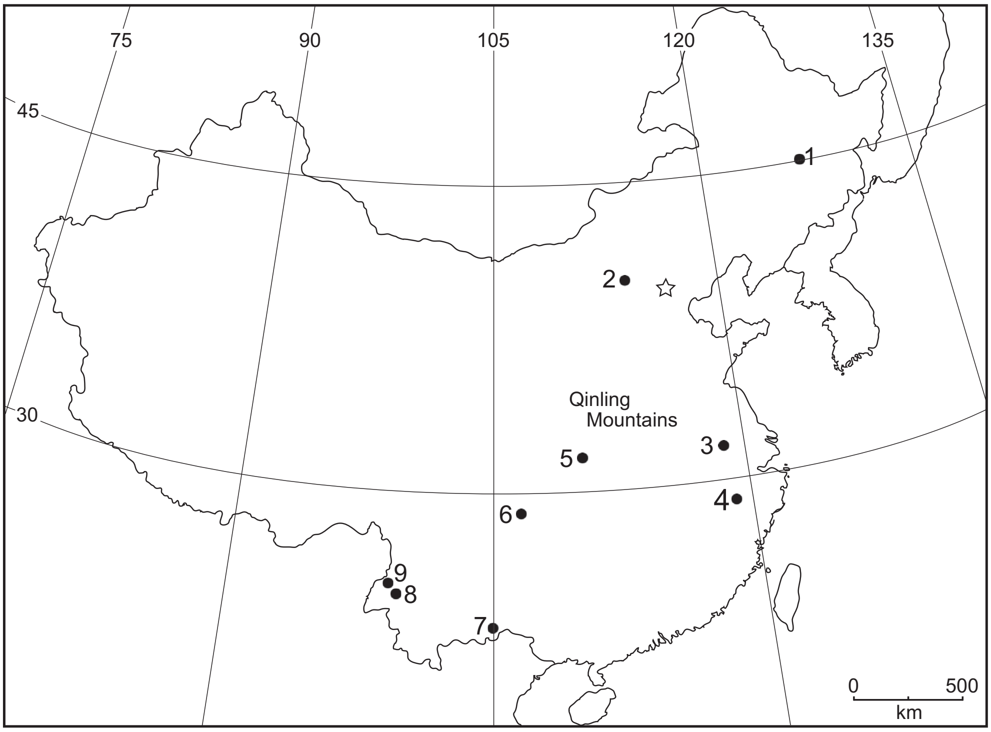

Fig. 2. Map of China, showing locations of key fossil and zooarchaeological sites for which Holocene occurrence of globally extinct large mammal species has been proposed. The locations of Beijing (star) and the Qinling Mountains (approximate biogeographic boundary between distribution of northern and southern Chinese faunas) are also shown. Legend: 1, Zhoujiayoufang; 2, Dingjiabu; 3, Lishui; 4, Shuanglong Cave; 5, Wushan; 6, Gulin; 7, Xiaohe Cave; 8, Tangzigou; 9, Jiangdong Mountain.

Academy of Sciences, Beijing; OxA, Oxford Radiocarbon Accelerator Unit; PV, Radiocarbon Laboratory of the IVPP; WB, Institute for Preservation Technology of Cultural Relics, Beijing.

3. Northern Chinese sites

3.1. Zhoujiayoufang, Yushu County, Jilin Province (44°44′N, 126°21′E)

Li et al. (1980) reported a series of 38 ^{14}C dates for a range of different Chinese palaeontological and archaeological samples and sites, all of which were dated between December 1978 and November 1979. This dating series included three Holocene dates for pieces of wood from the Tantu Formation at Locality 2 of Zhoujiayoufang (PV-70: 6060 ± 100 yr BP; PV-71: 7300 ± 100 yr BP; PV-96: 7380 ± 100 yr BP); the oldest of these dates, PV-96, was from wood that was reported to be stratigraphically associated with remains of *Mammuthus primigenius, Coelodonta antiquitatis* and *Bos primigenius*. This indirect date has been used to suggest regional Holocene survival of *Mammuthus* and *Coelodonta* by Tong and Liu (2004), and represents the only supposed evidence for Holocene occurrence of *M. primigenius* in China.

Zhoujiayoufang is a well-known Paleolithic site containing stone and bone implements characteristic of the early Late Palaeolithic associated with a diverse fossil assemblage (comprising 35 species) and a large number of bones of *Mammuthus* and *Coelodonta* (Sun et al., 1981; Liu and Li, 1984). The site is stratigraphically complex, containing multiple Quaternary horizons spanning the mid-Pleistocene to the Holocene (Liu and Li, 1984). Further ^{14}C dating by Sun et al. (1981) provided a fourth Holocene date of 7250 ± 140 yr BP on wood from the Tantu Formation at Locality 2, but direct dating of *C. antiquitatis* bone from the Tantu Formation at this locality by these authors returned a much older date of 31,800 ± 900 yr BP (lab numbers unreported). Sun et al. (1981) concluded that megafaunal and cultural remains present in the Tantu Formation at Locality 2 had been reworked from the older underlying Late Pleistocene Guxiangtun Formation. Subsequent direct ^{14}C dating of *M. primigenius* bones and teeth returned dates of 28,910 ± 1185 yr BP (unidentified element, WB78-45; recalculated as 28,880 ± 1220 yr BP using a ^{14}C half-life of 5568 years by Kuzmin et al., 2003), 30,810 ± 1385 yr BP (femur, lab number unreported), and 39,400 ± 250 yr BP (incisor, lab number unreported), and direct ^{14}C dating of *C. antiquitatis* material returned a date of 30,900 ± 875 yr BP (unidentified element, WB78-46) (Radiocarbon Dating Society of Chinese Quaternary Research Association, 1987; Liu et al., 1988). Most researchers have therefore considered *Mammuthus* and *Coelodonta* material from Zhoujiayoufang to be Late Pleistocene in age, with stratigraphically late specimens likely to have been redeposited from older horizons.

New direct AMS ^{14}C dating of two further mammal specimens from Zhoujiayoufang for this study provided further radiometric evidence that the site contains both Pleistocene and Holocene material, and that there was no support for post-Pleistocene mammoth survival. A red deer *Cervus elaphus* metacarpal (IVPP RV 2139.1) returned a date of 3500 ± 300 yr BP (OxA-20917), whereas a *M. primigenius* molar (IVPP RV 2009) returned a date of 51,600 ± 1400 yr BP (OxA-21001).

3.2. Dingjiabu, Yangyuan County, Hebei Province (40°06′N, 114°20′E)

Jia and Wei (1980) reported the discovery of a fossil assemblage associated with numerous tree trunks 10 m below the bed of the Sangganghe River at Dingjiabu Reservoir. Mammal remains from this site were identified as *Bos primigenius, Cervus elaphus, Coelodonta antiquitatis, Elephas maximus, Equus przewalskii* and *Nyctereutes procyonoides*. Dating of fossil wood from this site returned two ^{14}C dates of 3630 ± 90 yr BP (PV-34; lab number reported in Radiocarbon Dating Society of Chinese Quaternary Research Association, 1987) and 3830 ± 85 yr BP (lab number unreported), leading Jia and Wei (1980) to suggest that the mammal assemblage from Dingjiabu was mid-Holocene (Late Xia Dynasty or Early Shang Dynasty) in age. The authors drew particular attention to this apparent evidence for the Holocene survival of *B. primigenius* and *Coelodonta* in northern China.

Recently, Li et al. (2012) referred two proboscidean teeth from Dingjiabu to *Palaeoloxodon namadicus* or *P. naumanni* instead of *Elephas*; together with questionable taxonomic identification of proboscideans represented on highly stylized Xia, Shang and Zhou Dynasty bronzes dating from 4100 to 2300 bp, these authors suggested that *Palaeoloxodon* had survived until around 3000 yr BP in northern China. However, re-examination of one of these molars (IVPP RV 80005, an almost complete right upper M3 with a width of 96 mm; Fig. 3) indicates that it is indeed referable to *E. maximus*, as originally stated by Jia and Wei (1980) and by Stuart and Lister (2012). This specimen has 21 preserved enamel lamellae plus a posterior talon, with two additional lamellae worn to the root at the front; the likely total of 23 is typical for *E. maximus* (Roth and Shoshani, 1988; Lister et al., 2013), and reflected in the tightly-packed appearance of the lamellae in medial view, but is above the known range for *Palaeoloxodon* where lamellar number does not normally exceed 19 (Osborn, 1942; Maglio, 1973). Lamellar frequency in this specimen is approximately seven (estimated following the method of Maglio, 1973), a value typical for *E. maximus* M3 in specimens of this width (Lister et al., 2013); the value of 5.5–6 given by Jia and Wei (1980) and quoted by Li et al. (2012) was probably taken on the occlusal surface, lowering the apparent value because of oblique wear of the tooth. The widenings shown in the anterior lamellae and cited by Li et al. (2012) as ‘loxodont sinuses’ characteristic of *Palaeoloxodon* are in fact common in lamellae of many elephantid species in advanced wear, and are not present in the more posterior (less worn) plates of the Dingjiabu molar as would be expected if these were true loxodont sinuses. The folding of the enamel bands is regularly distributed across the width of the band, like the condition in *E. maximus* but unlike *Palaeoloxodon* where the main median fold is typically flanked by parasagittal folds. Finally, the tripartite subdivision of the early-wear posterior lamellae is not the extreme dot-dash-dot pattern common in *Palaeoloxodon* but is consistent with *E. maximus*.

IVPP RV 80005 was sampled and submitted for dating, returning an AMS ^{14}C date of >50,300 yr BP (OxA-26337). Even if this specimen had been identifiable as *Palaeoloxodon*, it would therefore not indicate Holocene persistence of that genus in northern China as Li

Fig. 3. Right upper M3 of *Elephas maximus* from Dingjiabu, Yangyuan County, Hebei Province (IVPP RV 80005). Scale bar = 2 cm.

et al. (2012) contended; however, this date is of value in demonstrating the presence of *E. maximus* in the region during Marine Oxygen Isotope Stage 3. A mandible of *B. primigenius* from Dingjiabu (IVPP RV 80007) was also submitted for dating, but failed to return an AMS ^{14}C date due to having no collagen. The only available *Coelodonta* specimen from Dingjiabu, a right M3 (IVPP RV 80004), was heavily fossilized in appearance in comparison to the other available material from the site. This specimen has also been considered to display a somewhat 'primitive' morphology in comparison to specimens of known Late Pleistocene age, e.g. absence of central fossette (Zhanxiang Qiu, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, personal communication, 2013). This specimen was considered extremely unlikely to be of Holocene age and was not dated.

4. Southern Chinese sites

4.1. Shuanglong Cave, Jinhua County, Zhejiang Province (29°12′N, 119°37′E)

A diverse Late Quaternary fossil assemblage comprising 47 mammal species was described from Shuanglong Cave by Ma and Tang (1992). Most of the species present in the assemblage are still extant, although some of the taxa identified at Shuanglong Cave have become extirpated in eastern China (e.g. *Cuon alpinus*, *Rhinopithecus* sp.) or more widely across the country (e.g. *Dicerorhinus sumatrensis*, *Rhinoceros sondaicus*). However, Ma and Tang (1992) reported that the Shuanglong Cave assemblage also contained several large mammals otherwise characteristic of the Pleistocene *Stegodon*–*Ailuropoda* fauna: *Ailuropoda baconi*, *Megatapirus augustus*, *Sus* sp. (cf. *xiaozhu*), and *Stegodon orientalis*. A left P4 from Shuanglong Cave was assigned to *Crocuta* [*crocuta*] *ultima* by Ma and Tang (1992), but may instead be referable to *Homotherium* on the basis of the almost vertically oriented wear facets on the parastyle, paracone, and metastyle, and its lack of a protruding protocone (Zhanxiang Qiu, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, personal communication, 2013). The majority of the fossil material from Shuanglong Cave was collected from the lower part of the second of six stratigraphic beds in the Inner Cavern, which was made up of clay, gravel and sand; *A. baconi* was also recorded from the younger clay bed, and *Sus* sp. (cf. *xiaozhu*) was recorded from the top five beds. It is probable that all of the animal bones were transported into the cave by an underground river. A ^{14}C date of 7815 ± 385 yr BP (lab number unreported) was provided by Ma and Tang (1992) for *Bubalus* sp. bone from the fossil-rich second stratigraphic bed, and was interpreted by these authors as evidence for a coeval early Holocene age for the entire faunal assemblage at Shuanglong Cave. This date has been widely accepted as evidence for Holocene survival of several components of the *Stegodon*–*Ailuropoda* fauna in China.

Shuanglong Cave has been developed as a tourist cave, and a visit by IVPP staff in 2010 revealed that all of the fossiliferous beds in the Inner Cavern have now been cleared out, making further excavation at the site impossible. None of the fossil material excavated from Shuanglong Cave is still kept in the collections of Beijing Normal University, but a small collection of mammal fossils from the site is retained in the private collection of Ma Ancheng, senior author of the 1992 study. Unfortunately this surviving collection does not contain any material referable to extinct representatives of the *Stegodon*–*Ailuropoda* fauna, meaning that direct re-dating of these taxa to investigate their proposed persistence into the Holocene is impossible. The collection also lacks any associated stratigraphic information, although it may be assumed that much or all of it is from the fossil-rich lower second stratigraphic bed of the Inner Chamber. We submitted four samples from the surviving Shuanglong collection for AMS ^{14}C dating: two *Sus scrofa* molars, one *Cervus* molar probably referable to *C. nippon*, and one lower molar fragment from a rhinoceros (either *Dicerorhinus sumatrensis* or *Rhinoceros sondaicus*, and representing the only surviving rhinoceros sample from the site). However, unfortunately all of these samples failed to return an AMS ^{14}C date, due to yielding no collagen.

4.2. Wushan Town, Wushan County, Chongqing Municipality (31°06′N, 109°53′E)

An open-air excavation in 1972 in Wushan County town, close to the confluence of the Daning River and the main Yangtze channel in the Three Gorges region, yielded a partial modern human skull and Neolithic artifacts as well as a small amount of animal remains including fish bones, deer, pig, porcupine, and two lower molars initially identified as *Tapirus* sp. (Fourth Science Research Team, 1975). It is not possible to diagnose the specific identity of the tapir teeth from Wushan on the basis of the single poor-quality photograph published in the original site report, and several tapir species are known from the Late Quaternary of central and southern China. In addition to *Megatapirus augustus,* the extant *Tapirus indicus* has been recorded from the Shang Dynasty archaeological site of Anyang in Henan province (Teilhard de Chardin and Young, 1936), and the extinct *Tapirus sinensis* was also present during the Late Pleistocene (Wang et al., 2007). However, the Wushan tapir material has been interpreted by subsequent authors as representing *M. augustus* (Ma and Tang, 1992; Huang et al., 2000). The tapir teeth were found approximately 30 m away from the Neolithic artifacts.

Three ^{14}C dates of 7500 ± 130 yr BP, 6740 ± 120 yr BP and 6550 ± 120 yr BP on ebony wood were reported for the site (lab numbers unreported), but the authors also suggested that the human remains were likely to date from between 5600 ± 105 yr BP and 4235 ± 95 yr BP on the basis of comparison with then-available ^{14}C dates from other Neolithic sites (Daxi and Yidu) in the Yangtze region of Chongqing and Hubei (Fourth Science Research Team, 1975). Subsequent authors have interpreted the youngest of these suggested dates for the human remains at Wushan (4235 ± 95 yr BP) as representing a last-occurrence date for *M. augustus* (Ma and Tang, 1992; Huang et al., 2000; Tong and Liu, 2004), although this date is several thousand years younger than the series of ^{14}C dates available from the Wushan excavation, and even the indirect dates from the site are not necessarily associated with the faunal material. The site has now been flooded following construction of the Three Gorges Dam, and the faunal samples cannot currently be located (Chen Shaokun, Three Gorges Museum, Chongqing, personal communication, 2010).

Wushan County contains numerous important Pleistocene–Holocene palaeontological and archaeological sites (Huang et al., 1995; Zheng et al., 2008), with *M. augustus* otherwise recorded from characteristic *Stegodon*–*Ailuropoda* faunal assemblages in the region (Huang et al., 1995, 2000; Pei et al., 2013). We sampled *M. augustus* material from Yumi Cave, Wushan County, in the collections of the Three Gorges Museum in Chongqing, but initial screening for collagen indicated a very low yield, and so it was not submitted for further radiometric dating.

4.3. Xiaohe Cave, Malipo County, Yunnan Province (approx. 23°09′N, 104°42′E)

In an early review of the age of Chinese cave faunas, Huang (1979) stated that some characteristic Late Pleistocene taxa had persisted into the Holocene, citing unpublished data on Xiaohe Cave provided by Zhang Xingyong (Yunnan Provincial Museum, Kunming) to support this suggestion. Huang (1979) reported that Xiaohe Cave was a Neolithic site approximately 4100 years old, which contained a molar of *Stegodon* sp. as well as the remains of horse, domestic dog, bear and deer. The date of 4100 yr BP for Xiaohe Cave given by Huang (1979) is not a radiometric date for the site, and apparently constitutes an estimated age based on inference from other Neolithic sites in southern China. The suggestion that *Stegodon* was recorded from deposits dating from 4100 yr BP in Xiaohe Cave was repeated by Ma and Tang (1992) in their review of possible Holocene survival of Late Pleistocene megafaunal species in China, but these authors did not provide a direct citation to Huang (1979) in association with this comment, leading subsequent authors to attribute the data for mid-Holocene survival of *Stegodon* in southern Yunnan directly to Ma and Tang (1992).

A full site description for Xiaohe Cave was provided by Zhang and Qiu (1983). In the main text of this paper, these authors listed domesticated horse, black bear, deer, wild boar, tiger, and bamboo rat as the mammal remains found in the same stratigraphic context as Neolithic implements (e.g. stone scraping tools, engraved pottery shards). No radiometric or even estimated dates were provided for the site. The only mention of *Stegodon* was in a footnote at the end of the paper, where the authors reported that “in the excavation mound, the team found half a *Stegodon* molar which was only superficially fossilised, but whether or not this specimen came from the cultural layer cannot easily be determined.” Unfortunately there is no possibility for further investigation of the true age of this potentially important specimen, as it has reportedly now been lost (Ji Xueping, Yunnan University Archaeology Research Centre and Yunnan Institute of Cultural Relics and Archaeology, Kunming, personal communication, 2011).

4.4. Tangzigou, Baoshan Prefecture, Yunnan Province (25°02′N, 99°00′E)

Tangzigou is a well-known archaeological site in western Yunnan that has yielded abundant mammalian remains and Palaeolithic-Neolithic artifacts as well as human remains (Zhang et al., 1992; Jablonski et al., 2003; Ji et al., 2004; Jin, 2010; Jin et al., 2012). Older reports suggested that the site is early Holocene (8000–6250 yr BP) in age, and contained *Ailuropoda baconi* (Ma and Tang, 1992; Zhang et al., 1992; Geng, 1995). Following further excavations, Ji et al. (2004) reported the presence of *A. baconi* [as *A. melanoleuca baconi*] at Tangzigou, but suggested that based on the composition of the mammal fauna, the site was more likely to be Late Pleistocene rather than early Holocene in age. However, the most recent and thorough assessment of the Tangzigou mammal fauna, based on excavations in 2003 and 2006, constrained the age of the site's bone bed using AMS ^{14}C dating of charcoal to a narrow interval during the early Holocene, between 9000 ± 40 yr BP and 8745 ± 60 yr BP (BA04271–BA04275), and reported the presence only of *A. melanoleuca* rather than *A. baconi* (Jin, 2010).

Tangzigou therefore represents the only Late Quaternary site with proposed evidence of late survival of representatives of the Late Pleistocene megafauna that has been relatively securely dated to the Holocene using modern techniques (although with associated charcoal dates rather than direct bone dates), but conversely has uncertainty over the taxonomic identity of its megafaunal material. Other subfossil panda material recovered from a sinkhole at Jiangdong Mountain, southwestern Yunnan, that has been directly dated to 8470 ± 45 yr BP using AMS ^{14}C dating (BA06229) and so is extremely close in both age and location to the Tangzigou panda material, was also recently identified as *A. melanoleuca* (Jablonski et al., 2012), and the sympatric occurrence of two relatively similar panda sister-taxa in Yunnan during the early Holocene may be ecologically unlikely. The taxonomic relationship between Late Quaternary fossil and zooarchaeological material assigned to *A. melanoleuca* and *A. baconi* therefore requires further investigation using modern quantitative systematic techniques before the survival of *A. baconi* into the Holocene can be assumed.

5. Other proposed evidence for Holocene megafaunal extinctions in China

Several further examples of Holocene survival of Late Pleistocene megafauna in both northern and southern China have been proposed, but can either be more easily discounted, or cannot be further assessed without detailed taxonomic review of the original material. Li and Lei (1980) reported a ^{14}C date of 11,200 ± 1000 yr BP (lab number unreported) for a cave deposit from Lishui, Jiangsu Province, containing *Crocuta* [*crocuta*] *ultima*, which has been interpreted by several subsequent authors (Ma and Tang, 1992; Tong and Liu, 2004; Tseng and Chang, 2007) as evidence for early Holocene survival of this taxon. However, this represents a calibrated age of 16,623–10,717 bp, and so is highly likely to represent a Late Pleistocene rather than an early Holocene date. Similarly, Yang et al. (1995) provided two indirect ^{14}C dates of 13,810 ± 560 yr BP and 9640 ± 360 yr BP (lab numbers unreported) for a *Stegodon*–*Ailuropoda* faunal assemblage from Gulin, Sichuan Province, containing *Ailuropoda baconi, Megatapirus augustus, Rhinoceros sinensis, Stegodon orientalis* and *Sus* cf. *xiaozhu*, and considered that this represented evidence of a Holocene age for the fauna; however, the older date is unquestionably Late Pleistocene rather than Holocene in age, and the younger date represents a calibrated age of 12,382–10,175 BP (95% probability range), which also overlaps the terminal Late Pleistocene.

Several other reported Holocene occurrences of globally extinct large mammal species in China represent taxonomic uncertainties or errors. Two rhinoceros metacarpals from a 7300–7000 BP zooarchaeological horizon at Guantaoyuan, Shaanxi Province, were originally identified as *Coelodonta antiquitatis* but later reassigned to the living Sumatran rhinoceros (Tong and Liu, 2004; Hu and Li, 2006). A large muntjac described as a distinct species, *Muntiacus gigas*, is known from several Neolithic–Bronze Age zooarchaeological sites in Hubei and Zhejiang provinces (Wei et al., 1990; Wu and Zhou, 2005; Wu, 2007), but this species has not been taxonomically assessed in relation to the diversity of more recently described extant muntjacs from continental south-east Asia (Groves and Grubb, 2011), and its status remains unclear; it is possible that the material on which it is based may be referable to an extant species. Jablonski et al. (2012) questionably reported *Equus yunnanensis*, a small extinct equid species otherwise known from the Early Pleistocene (Qian and Zhou, 1991; Huang et al., 1995; Louys et al., 2007), from the upper chamber of a sinkhole at Jiangdong Mountain, southwestern Yunnan, that also contains other large mammal remains directly dated to the early Holocene (~8470–8290 yr bp) using AMS ^{14}C dating (BA06229–06230, 06232–06233); however, the extant Asiatic wild ass *E. hemionus* has also been recorded from Late Pleistocene sites in nearby western Guangxi Province (Wang and Mo, 2004; Wang et al., 2007), and without more confident identification or proper description of the undated equid material from Yunnan, it is possible that this may instead represent the living species. It has also been suggested that some of the early–middle Neolithic zooarchaeological cattle remains from northern China originally referred to domestic cattle *Bos taurus* may instead represent wild aurochs *B. primigenius*, which persisted in Europe until AD 1627, but this possibility has not yet been systematically investigated (Flad et al., 2007; Liu and Chen, 2012). Further research is needed to assess the taxonomic status of these specimens and their significance for understanding Late Quaternary faunal turnover in China. Similar taxonomic reassessment is also required for China's Holocene small mammal fauna, notably into the validity of putative now-extinct species of *Hystrix* and *Rhizomys* that have been reported from Holocene zooarchaeological and fossil deposits (Teilhard de Chardin and Young, 1936; van Weers, 2005).

6. Discussion and conclusions

Our analysis of available radiometric data and new dating of surviving samples from key Late Quaternary sites in both northern and southern China demonstrates that evidence for the Holocene survival of any representatives of China's Late Pleistocene mammalian megafauna is weak or untenable. However, opportunities for further investigation and critical reassessment of the ages of these key sites and their faunas are now unfortunately limited.

None of the initial radiometric dates put forward as evidence for Holocene occurrence of Chinese megafaunal taxa represent direct dates on bone samples from species of interest, and at most sites the stratigraphic association between material or horizons yielding Holocene dates and megafaunal remains is not clearly demonstrated or is dubious because of the possibility of reworking. Indeed, the widely reported Holocene last-occurrence dates for *Megatapirus augustus* and *Stegodon* sp. from Wushan and Xiaohe are based on radiometric dates or more general archaeological ages inferred from similar deposits at other sites, and so are of extremely limited reliability. Such dates would typically be rejected by modern radiometric auditing studies that use standardized evaluation criteria to improve quality control of ^{14}C data (cf. Pettitt et al., 2003; Graf, 2009; Lister and Stuart, 2013). Attempts to re-date megafaunal material from Zhoujiayoufang and Dingjiabu directly have yielded Late Pleistocene rather than Holocene dates, and relevant faunal material from Wushan and Xiaohe is no longer available for study, with the Wushan site also no longer accessible, preventing further critical analysis of the true ages of these important samples. The original radiometric dates for Zhoujiayoufang, Dingjiabu and Wushan were also all obtained before 1980, before exclusive use of collagen and adequate pretreatment (especially cleaning) came into regular use (Stafford et al., 1987); modern radiometric auditing studies will typically reject pre-1980 dates because of their known higher potential for unreliability, with the use of ultrafiltration and single amino acid dating now representing the 'gold standard' for dating studies (e.g. Stuart and Lister, 2012). Concerns over accurate taxonomic identification of faunal material also further confuse the interpretation of claims for Holocene survival of Late Pleistocene megafauna at Wushan, Tangzigou, and other sites.

The only site for which we cannot definitively rule out Holocene survival of Late Pleistocene megafauna is Shuanglong Cave, due to the unavailability of any remaining samples of key megafaunal taxa from this site for dating, but even here evidence for Holocene survival is weak. The original radiometric dating of the site was made on a bone sample of *Bubalus* sp., a genus known from other sites to have occurred in China during both the Late Pleistocene and Holocene. Although stratigraphic association between the early Holocene *Bubalus* sample and other megafaunal remains from Shuanglong Cave was reported by Ma and Tang (1992), our failure to obtain new radiometric dates from any of the surviving faunal samples from this site, due to no collagen yield, suggests that the original Holocene date may be an artefact of contamination or erroneous laboratory procedure. Without the opportunity to reassess the stratigraphy of Shuanglong Cave, due to clearance of Quaternary deposits from the site, we also cannot rule out the possibility that the bone bed may have represented a water-mixed horizon containing some redeposited faunal material, as suggested by the original site description and by the presence of species characteristic of both Late Pleistocene and Holocene Chinese faunas (Ma and Tang, 1992).

Our critical re-appraisal of Late Quaternary radiometrically-determined extinction chronologies for a range of extinct Chinese large mammals demonstrates that past claims for Holocene survival cannot be substantiated, and robust last-occurrence dates in China for *Ailuropoda baconi, Bos primigenius, Coelodonta antiquitatis, Crocuta [crocuta] ultima, Mammuthus primigenius, Megatapirus augustus, Palaeoloxodon* sp., *Stegodon orientalis* and *Sus xiaozhu* are all now restricted to the Late Pleistocene. Whilst a detailed review of Late Pleistocene records for these species in China is outside the scope of the current study, this revised pattern of substantial regional disappearance of large mammal species before the Holocene is similar to the pattern and timing of much of the megafaunal diversity loss seen in other continental areas of Eurasia and the Americas for which detailed radiometric data are available (MacPhee, 1999; Steadman et al., 2005; Gill et al., 2009; Lorenzen et al., 2011; Stuart and Lister, 2012). Indeed, it is even possible that some members of the Late Pleistocene Chinese megafauna may have disappeared from much or all of their ranges before the Pleistocene–Holocene boundary, as suggested by the absence of many extinct taxa from several recently dated end-Pleistocene sites containing diverse mammal faunas (Tong and Liu, 2004; Wang et al., 2007). This could match the "staggered" pattern of extinction shown by successive warm-adapted and cold-adapted megafaunal taxa in Europe across the Late Quaternary (Stuart, 2005; Stuart and Lister, 2007, 2012); however, considerable further investigation into the age and distribution of Late Quaternary megafaunal fossils across China is required to control for sampling bias and other errors in reconstruction of both temporal and spatial faunal dynamics.

The exclusion of early radiometric dating studies allegedly demonstrating regional Holocene persistence of megafaunal taxa, following more critical auditing of data quality and re-dating, has now followed the same pattern in China as previous revisions of extinction chronologies for North and South American Late Quaternary megafaunas (Stuart, 1991; Steadman et al., 2005). However, several post-1980 direct ^{14}C and AMS dates are still proposed to demonstrate Holocene survival for a range of now-extinct South American megafaunal mammals (e.g. Borrero et al., 1998; Auler et al., 2006; Hubbe et al., 2007), suggesting that temporal staggering of megafaunal extinctions across the Pleistocene–Holocene boundary in this region cannot yet be ruled out (Turvey, 2009; Barnosky and Lindsey, 2010). Some characteristic representatives of the northern Eurasian Late Pleistocene megafauna (*Equus hydruntinus*, *Mammuthus primigenius*, *Megaloceros giganteus*, *Ovibos moschatus*) are also known to have persisted into the mid or late Holocene on the basis of well-resolved radiometric studies (MacPhee et al., 2002; Stuart et al., 2004; Campos et al., 2011; Stuart and Lister, 2012). It is therefore necessary to investigate Late Quaternary population dynamics and extinction trajectories of different species within the Chinese mammalian megafauna in terms of their likely responses to prehistoric environmental change and anthropogenic pressures (cf. Lorenzen et al., 2011).

Considerable further research is required to reconstruct robust extinction chronologies for different Chinese megafaunal mammals across the Late Quaternary within well-resolved radiometric frameworks. Other studies have also put forward supposed evidence for Holocene survival of Late Pleistocene megafauna in China on the basis of non-radiometric evidence, e.g. amino acid racemization (Chen et al., 1995), which also require critical re-evaluation. However, we emphasize the crucial importance of direct AMS ^{14}C dating and auditing of previously published radiometric dates for extinct taxa, in order to develop a more meaningful understanding of patterns of Late Quaternary faunal turnover in China and to prevent the further perpetuation of errors in radiometric analysis or site interpretation.

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