The Pleistocene easternmost distribution in Eurasia of the species associated with the Eemian *Palaeoloxodon antiquus* assemblage

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ABSTRACT

1. The *Palaeoloxodon antiquus* large-mammal assemblage was typical of the late middle and late Pleistocene interglacials in Europe. This review examines the assemblage's origins, dispersal and cohesiveness in Eurasia.
2. During the more climatically equable middle-Pleistocene periods, the *Palaeoloxodon* assemblage (or closely related) species occurred across central Eurasia almost simultaneously. In Central and Western Europe, these species responded to climatic changes together as an unvarying interglacial assemblage, whereas in Eastern Europe and Siberia, they occurred in diverging assemblages. The boundary of the *Palaeoloxodon* assemblage can be drawn roughly from Poland to Romania.
3. In Central and Western Europe this interglacial assemblage last occurred during the Eemian. During this period many of the *Palaeoloxodon* assemblage species may also have co-occurred in south-eastern Europe and, except for *Bubalus murrensis* and *Hippopotamus amphibius*, further eastwards. The extinct species of the *Palaeoloxodon* assemblage disappeared in Siberia and Central Asia prior to Europe and the Caucasus whereas the extant species were already present in their modern distribution areas.
4. A quantitative study of faunal associations across Eurasia, following much-needed comprehensive systematic reviews, would further elucidate the patterns of faunal change associated with local and global climatic changes during the middle to late Pleistocene.

Keywords: aurochs, *Bubalus*, Eemian, giant deer, *Hippopotamus*, interglacial, *Palaeoloxodon*, *Stephanorhinus kirchbergensis*, USSR

INTRODUCTION

The *Palaeoloxodon antiquus* faunal assemblage was the typical interglacial fauna of the late middle and late Pleistocene, mainly of Cromerian/Galerian origin (Kahlke, 1986; Azzaroli *et al.*, 1988; Stuart, 1991; von Koenigswald & Heinrich, 1996, 1999; Bradshaw, Hannon & Lister, 2003). It permanently resided in the Mediterranean region and is well recognized from Western and Central Europe where it alternated with the woolly mammoth glacial steppe assemblage during glaciations (Currant, 1989; Stuart, 1991; von Koenigswald, 1999, 2003; Mol, van den Bergh & de Vos, 1999). The interglacial assemblage was represented by straight-tusked elephant *Palaeoloxodon antiquus*, Merck's and the narrow-nosed rhinoceroses *Stephanorhinus kirchbergensis* and *S. hemitoechus*, aurochs *Bos primigenius*, hippopotamus *Hippopotamus amphibius*, giant deer *Megaloceros giganteus*, fallow deer *Dama dama*, roe

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deer *Capreolus capreolus*, wild boar *Sus scrofa*, and, in Central Europe, water buffalo *Bubalus murrensis*. Kahlke (1986) called this assemblage the Western European fauna with Mediterranean and African affinities, boundary of which was marked by the easternmost distribution of the hippopotamus.

In Eastern Europe and Siberia the *Palaeoloxodon* assemblage as a whole is considered practically unknown or rather unusual owing to a more continental climate (Scheglova, 1963; Kalinovskij, 1983; Markova, 1984, 2000; Kowalski, 1989). Interest is usually concentrated on the distribution of the glacial-steppe fauna, because the interglacial environments in Eastern Europe and Siberia were extensively more open than in the rest of Europe and the fauna more similar to the fauna of glaciations (Sher, 1971, 1992, 1997; Kowalski, 1980). Intriguingly though, a great deal of information buried in the former-USSR literature apparently reveals that the characteristic species of the *Palaeoloxodon* assemblage (or in some cases species closely related to them) had much wider distribution in Eurasia as far as the Russian Far East and on occasion with typical glacial and steppe species (Kozhamkulova, 1969; Gromov, 1972; Garutt, 1972, 1986; Vangengeim & Sher, 1972; Vangengeim, 1977; Alexeeva, 1980; Vereshchagin & Baryshnikov, 1980, 1985; Vangengeim & Zhegallo, 1982; Svistun, David & Nesin, 1989; Khromov, Arkhangelskij & Ivanov, 2001). The majority of these species appear to have been more abundant during the middle Pleistocene and thereafter become restricted to Europe until their final extinction, probably because during the early late Pleistocene (Eemian), a pronounced maritime climate affected only Western and Central Europe (Zagwijn, 1996), allowing these species to persist longer.

Given that the species' responses to changing environments could occur separately in response to their own climatic and environmental tolerances, even though at times they were together characteristic of the same assemblage (Graham & Lundelius, 1984; Webb & Barnosky, 1989), here I concentrate on the easternmost geographical ranges of the species associated with the *Palaeoloxodon* assemblage and discuss their temporal distributions with a particular interest in the territory of what was the former USSR.

METHODS

The data were mostly obtained from published Russian literature and existing databases (the Neogene of the Old World (http://www.helsinki.fi/science/now/), European Quaternary Mammalia (Pangaea, http://www.pangaea.de/, Western Europe), the marine oxygen isotope stage 3 project (OIS3; European Russia and Europe) (van Andel, 2002). The dataset consists mainly of the middle and late Pleistocene sites from Western and Central Europe and the former USSR, along with several type localities from Eastern Europe and the Mediterranean. Occurrences of the typical Central European Eemian interglacial species were traced back to their first appearances. The Holocene localities are less well represented. South-eastern Asia for the most part was avoided because of controversial taxonomy for many of their species (Chinese), high endemicity (Japanese, Indian) or lack of data. Although several Chinese and Japanese species occurrences are mentioned, the main emphasis was made on the former-USSR territory.

Fossil record localities were chronostratigraphically correlated using marine oxygen isotope stage records (MIS, OIS), continental mammalian biochronology, absolute dating (radiocarbon, thermoluminescence (TL), electron spin resonance (ESR), uranium u-series methods) or palaeomagnetic dating and sometimes archaeological cultural stages (Gerbova & Krasnov, 1982; Azzaroli *et al.*, 1988; Kahlke, 1999; van Kolfschoten, 2000; Currant & Jacobi, 2001; Khromov *et al.*, 2001; Lister & Sher, 2001; Stuart & Lister, 2001; Vangengeim,

Pevzner & Tesakov, 2001; Vasil'ev *et al.*, 2002; Lister *et al.*, 2005a; Sher *et al.*, 2005; Markova, 2007) (Table 1).

GEOGRAPHICAL DISTRIBUTION
Straight-tusked elephant *Palaeoloxodon antiquus* and related species

The straight-tusked or forest elephant was adapted to a mild humid and warm climate (Garutt & Vangengeim, 1982; Stuart, 1991). It inhabited forested areas where it fed on leaves, branches and soft grass (Garutt, 1972, 1986). In Western and Central Europe the straight-tusked elephant appeared during the early middle Pleistocene, the Galerian (Azzaroli *et al.*, 1988; Kahlke, 2001), and more precisely OIS15 in Britain (Stuart & Lister, 2001; Bradshaw *et al.*, 2003) or the late Cromerian complex in Germany (von Koenigswald & Heinrich, 1999; Stuart & Lister, 2001). *P. antiquus* was common during the Holsteinian (OIS11) and Eemian (OIS5e) interglacials, and became extinct during the late Eemian in Central Europe and the early Weichselian (OIS4) in the Mediterranean (Italy) (Stuart, 1991, 2005; Mol *et al.*, 1999; van Kolfschoten, 2000; Bedetti, Palombo & Sardella, 2001; Bradshaw *et al.*, 2003). A remarkably late dating of an assumed *P. antiquus* in the middle Weichselian (OIS3) is also reported from the Netherlands (Bosscha Erdbrink, Brewer & Mol, 2001).

Most recent and well-identified remains of *P. antiquus* are known from Europe and Asia south of 55°N and west of 50°E (Fig. 1). In Eastern Europe it has been identified in Croatia (Malez, 1986), Poland (Kowalski, 1989; Kubiak, 2001), Moldova (David & Lungu, 1972; David, 1985), Ukraine (Kahlke, 2001) and European Russia (Alexeeva, 1980; Markova, 2000, 2007). In European Russia *P. antiquus* or *P.* cf. *antiquus* have been reportedly found in several sites on the lower and middle Volga River (Khromov *et al.*, 2001; Markova, 2007), in Moscow during construction work and in Bojets (60°30′N; 57°E) at the Kolva River in the Urals (Perm region) (Garutt, 1972, 1986; Yakhimovich & Chigurjaeva, 1972). Finds of *P. antiquus* or *P.* cf. *antiquus* were also suggested in the Caucasus (Vereshchagin, 1959), in Kazakhstan at about 75°E (Kozhamkulova, 1969, 1990) and Tajikistan (Forsten & Sharapov, 2000). A definite find of *P. antiquus* is described from Iran at 33°30′N, 48°25′E (Farchad & Sahabi, 1961; confirmed by A. Lister, personal communication).

In Central Asia *Palaeoloxodon turkmenicus* was reported from the early middle Pleistocene (Baku-Khazarian deposits) in Turkmenia in the Palaeo Amu-Darja (ancient) river valley at around 60°E (Garutt & Vangengeim, 1982; Dubrovo *et al.*, 1996). In Eastern Siberia (Yakutija) *Palaeoloxodon* cf. *namadicus* was recorded from the Aldan River basin at about 60°N, which is the northernmost occurrence of a *Palaeoloxodon* elephant (Garutt, 1972, 1986; Vangengeim, 1977). Both *P. namadicus* and its descendant *P. naumanni* are known from China (Kahlke, 1975b; Dong *et al.*, 1996) and Japan (Dubrovo, 1981, 1985; Kamei, 1981), where *P. naumanni* survived into the middle Weichselian (OIS3) (Kamei, 1981; Dong *et al.*, 1996; Kondo *et al.*, 2001; Tong & Patou-Mathis, 2003). In China there is even the Last Glacial Maximum (LGM) record of *P. naumanni* (Xue *et al.*, 2000).

It was suggested that *P. antiquus* occurred in Europe and Western Siberia, while *P. namadicus* replaced it in Eastern Siberia and the Russian Far East during the early middle Pleistocene (Gromov, 1972; Kahlke, 1975b; Vangengeim, 1977; Garutt & Vangengeim, 1982; Garutt, 1986). According to Mol *et al.* (1999) the south-east Asian *P. namadicus* is conspecific and a senior synonym of *P. antiquus*, while according to Palombo, Anzidei & Arnoldus-Huyzendveld (2003), it is a distinct but closely allied species. Alternatively, the Southern mammoth (or Southern elephant) *Mammuthus meridionalis* (*M. m. meridionalis* = *Archidiskodon gromovi*) and Steppe mammoth (or Steppe elephant) *M. trogontherii* (*M. t. trogontherii* = *Archidiskon wüsti*) are also known from Yakutija (Dubrovo, 1985,

Table 1. A summarizing stratigraphical table of Northern Eurasia. Note: The name Khazarian faunal complex, derived from the Turkic name of the Caspian Sea – the Khazarian Sea, was used here as in Dubrovo *et al.* (1996) to seperate from the species names, e.g. *M. trogontherii chosaricus*; The name is written sometimes as Khozarian and Chozarian

Stratigraphy	Geochron	Mammal ages	OIS	absolute ages (ka)		Western climatostrat	Eastern Europe/Siberia	Faunal complexes and fossil bearing horizons	Alpine scale
Brunhes	Holocene	Oldenburgian			0	Flandrian	Holocene	'Modern'	
	Pleistocene Late		OIS2		10	Weichselian	Valdaj (Sartanian, Karginian, Zyrjanian)	Mammoth or upper Palaeolithic: Sartanian (late Weichselian); 0.3–0.11 Zyrjanian (early–middle Weichselian)	*Wurm*
			OIS3	11	20				
				24	60				
			OIS4	57	70				
			OIS5ad	71	115			*Shkurlat (Eastern Europe) (0.075–0.128)*	
			OIS5e	115	125	Eemian	Mikulino/Kazantsevo	Shkurlat (Eastern Europe) Karangat (Black Sea) upper Khazarian (Caspian Sea)	*Riss–Wurm*
	Middle		OIS6	129	190	Saalian Glaciation	Moskovian/Tazovian	early Mammoth or upper Palaeolithic (Pavlovian)	*Riss*
			OIS7	186	240		Odintsovian	Khazarian	
			OIS8	242	300		Dneprovian/Samara	Priirtyshskij (Kazakhstan)	
			OIS9	301	330		Likhvin/Tobolian	Singilian	*Mindel–Riss*
		Biharian	OIS10	334	360	Holsteinian interglacial			
			OIS11	364	430	Elsterian Glaciation			
			OIS12	427	470				
			OIS13	474	530	Cromerian (Galerian)	Oka	Tiraspolian (European Russia, Ukraine) Koshkurgan (Kazakhstan)	*Mindel*
			OIS14	528	570		Muchkapian	Vyatkinskij (Western Siberia)	
			OIS15	568	620		Donskoj	late Olyorian (north–eastern Siberia)	
			OIS16	621	660		Kolkotovian	– Aldan/Viljuj fauna	*Gunz–Mindel*
			OIS17	659	710		Platovian		
			OIS18	712	760		Mikhajlovian		
			OIS19	760	790		Michurin		
							Petropavlovian		
Matuyama	Early			800	1.1	Bavelian (Galerian)		Tamanian (European Russia, Ukraine), Odessa (0.95–1.8) Khorgoss suite 0.73–0.1, Ilijskij (Kazakhstan)	
				1.1	1.8	Menapian/Waalian/Eburonian (Villafranchian)		Razdoljinskij (Western Siberia) Early Olyorian (0.8–1.2) (north–eastern Siberia) – Aldan/Viljuj fauna	
Gauss	Pliocene	Villanyan		1.8	2.5	(Villafranchian)		Khaprovian 1.5/1.8–2.5	
				2.5	3.4			Moldavian 2.5–3.4	

OIS, oxygen isotope stage.

1990). A more advanced *M. trogontherii* was already present in Siberia before 800 000 years ago during the early Olyorian where its succession of *M. meridionalis* preceded that in Europe at 700 000 years (Lister & Sher, 2001). Remains of *P. antiquus* could have been mistaken with those of *M. meridionalis* or an aberrant form of *M. trogontherii*, as their isolated teeth resemble each other's (Garutt & Vangengeim, 1982). For instance, *P.* cf. *antiquus* finds from the Caucasus (Georgievsk, Girej) were later attributed to *M. meridionalis* and *M. trogontherii*, respectively (Kahlke, 2001). *M. trogontherii* has been also discovered in association with *S. kirchbergensis* on the Viljuj River in Yakutija in the Aldan-Viljuj fauna correlated to the Olyorian (Vangengeim & Sher, 1972; Fig. 2, Table 1).

   P. antiquus was considered to occur during the early middle Pleistocene in Kazakhstan (Koshkurgan faunal complex) and in the Ukraine (Tiraspolian complex) (Kozhamkulova, 1969, 1990; Garutt & Vangengeim, 1982), along with the more widespread *M. t. trogontherii* (Kozhamkulova & Kochenov, 1989; Dubrovo, 1990). The majority of the rare straight-tusked elephant discoveries in European Russia, Northern Caucasus and Southern Siberia seem to be associated with the Holsteinian or Likhvin interglacial (Singilian complex) (Garutt & Vangengeim, 1982; Khromov *et al.*, 2001) and possibly the early Saalian (Khazarian
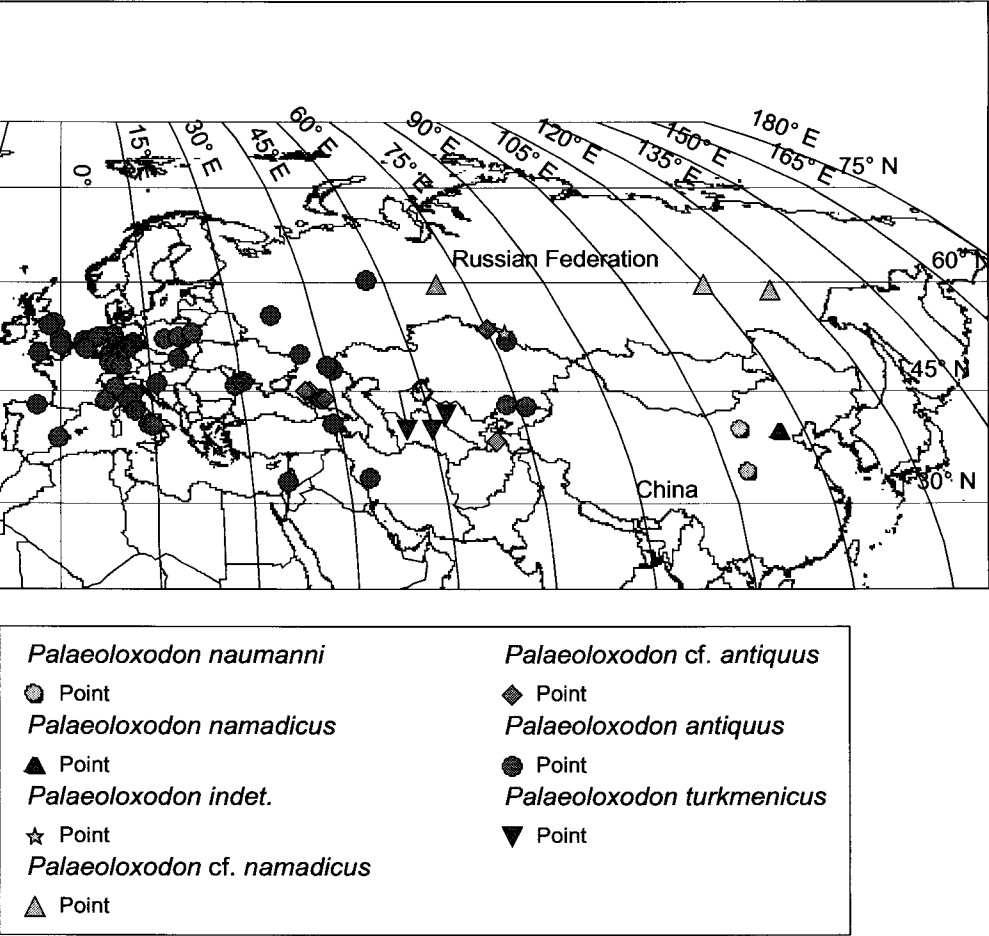

Fig. 1. Easternmost distribution of *Palaeoloxodon antiquus* and related species during the middle and late Pleistocene.
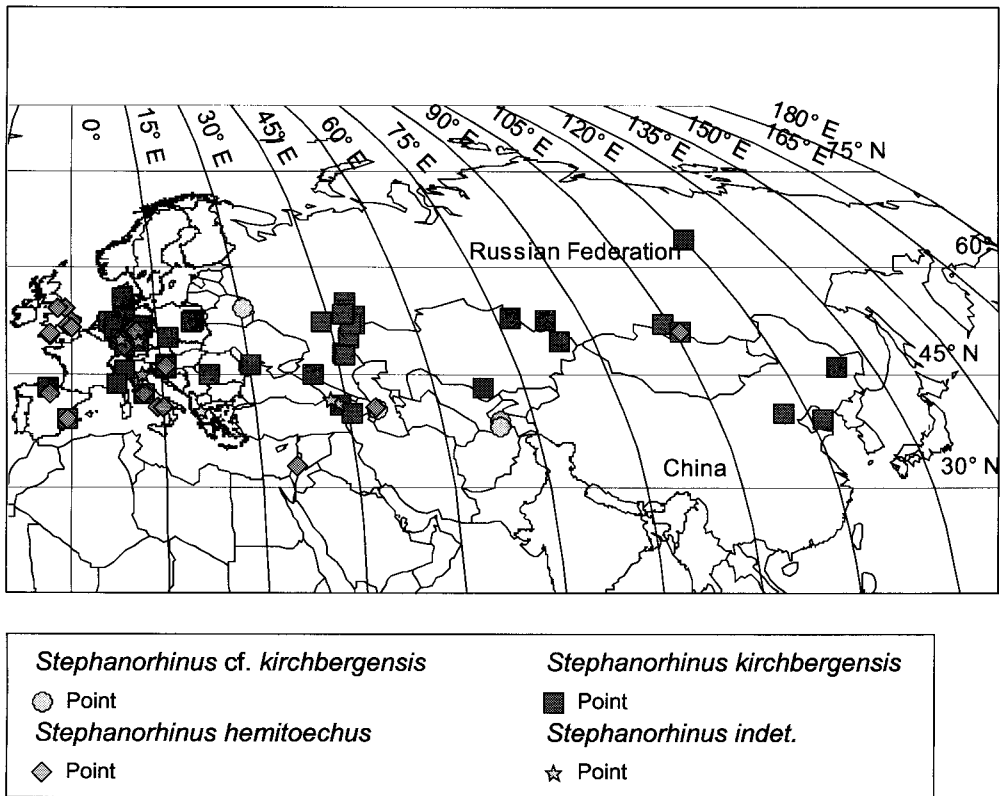
Fig. 2. Easternmost distribution of *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus* during the middle and late Pleistocene.

complex) (David, 1985; Khromov *et al.*, 2001). *P. antiquus* occurred along with the main component of the Khazarian *M. trogontheri chosaricus* (Garutt & Vangengeim, 1982; Dubrovo, 1990; Khromov *et al.*, 2001). Later *M. primigenius* appeared and became the dominant species over the vast periglacial landscape (Dubrovo, 1990; Markova *et al.*, 1995). The straight-tusked elephant's distribution contracted enormously during glaciations when steppes spread through Siberia and most of Europe, and apparently expanded northwards along the river floodplains during warmer periods (and seasonally) along with the distributions of broad-leaved forests (Garutt, 1972, 1986; Vangengeim, 1977; Markova, 1984; Stuart, 1991). Yet, even during the Eemian, *P. antiquus* never overcame the steppe barrier in Central Asia (Garutt, 1986). In Eastern Europe the last occurrence of *P. antiquus* is recorded during the Eemian in Poland (Kowalski, 1989; Kubiak, 2001), former Yugoslavia (Malez, 1986) and in the Shkurlat complex in European Russia (Alexeyeva & Tikhomirov, 1989; Markova, 2000, 2007).

Strictly speaking, *P. antiquus* was restricted to Europe and replaced by related species in Siberia, China and Japan, although a systematic review of *Palaeoloxodon* fossils across Eurasia is essential. Seemingly inappropriate dates and localities beyond 60°E and 60°N could result from the varying histories of origin and dispersal. Large species are less susceptible to minor climatic oscillations and extremes (Hone & Benton, 2005; Isaac, 2005) and during optimal conditions could disperse over long distances to appear in very unusual

places. If all dubious records of *P. antiquus* and related species beyond European Russia are included, the *Palaeoloxodon* elephants could have occupied vast humid forested areas across central Eurasia during the middle Pleistocene.

Merck's *Stephanorhinus kirchbergensis* and narrow-nosed steppe *Stephanorhinus hemitoechus* rhinoceroses

Merck's rhinoceros preferred closed forest or woodland habitats, whereas the smaller narrow-nosed rhinoceros was better adapted to more open habitats (Stuart, 1991; Fortelius, Mazza & Sala, 1993). Curiously, Merck's rhinoceros appeared to be more common (or 'better' identified) across Eurasia than the straight-tusked elephant. Both Merck's and narrow-nosed rhinoceroses first appeared in Europe during the early middle Pleistocene (Fortelius *et al.*, 1993), the Galerian (Azzaroli *et al.*, 1988) and more precisely the late Cromerian complex in Germany (von Koenigswald & Heinrich, 1999; Stuart & Lister, 2001) and the Holsteinian in Britain (Schreve, 2001; Bradshaw *et al.*, 2003; Bridgland *et al.*, 2004). Possibly, *S. hemitoechus* appeared earlier than *S. kirchbergensis* (von Koenigswald & Heinrich, 1999). Both species became widespread during the middle Pleistocene (Azzaroli *et al.*, 1988; Fortelius *et al.*, 1993), typical during the Eemian, and subsequently became extinct following the latest occurrences in the Mediterranean (Spain) for *S. kirchbergensis* and the Balkans for *S. hemitoechus* during the middle and early late Weichselian (Aurignacian industries), respectively (Stuart, 1991; von Koenigswald, 1999). Peculiarly, in Western and Central Europe, *S. hemitoechus* disappeared earlier than *S. kirchbergensis* (von Koenigswald & Heinrich, 1999; Schreve, 2001; Bradshaw *et al.*, 2003) and in the Mediterranean later (Stuart, 1991). In Italy *S. hemitoechus* is still known from the OIS4 (Stuart, 2005). Bedetti *et al.* (2001) suggested the last appearance for the genus in Italy during the OIS3.

Neither Merck's nor the narrow-nosed rhinoceros were recorded in more open and arid landscapes beyond 55°N (Fig. 2). An exceptional find of *S. kirchbergensis*, discovered with *M. trogontherii* (see above) on the Viljuj River at about (63°30'N; 120°E), suggested that Merck's rhinoceros penetrated northwards along river valleys and floodplain forests during climatic optima (Yakutija, the Urals) as did the straight-tusked elephant (Vangengeim, 1977). The eastward limit for both species appears to be around 105°E as far as Lake Baikal (Kahlke, 1975a; Stuart, 1991). *S. kirchbergensis* is better represented in the fossil record in China (Dong *et al.*, 1996; Qiu, 2006) and not found in the south of the Russian Far East, possibly due to a small sampling area. The numerous mountain ranges and elevated landscape that cover the south- and north-east of Russia, starting at the border with Mongolia, were probably the barrier that prevented these large species from spreading further east. From Lake Baikal the rhinoceros could have spread into China along river valleys or possibly appeared there via the southern route around the Tibetan plateau.

Surprisingly, *S. hemitoechus* remains are rather scarce. Apart from the two records in the Caucasus and near Lake Baikal, most of the narrow-nosed rhinoceros finds were recorded west of 16°E in Europe (Fig. 2). In Syria and Israel the species was present up to 36°E during the early middle Pleistocene (Tchernov *et al.*, 1994; Kahlke, 2001). In Russia there is only one late Pleistocene locality, Troitskosavsk near Lake Baikal, where Merck's and the narrow-nosed rhinoceroses were apparently encountered together (Imetkhanov & Kalmykov, 1988).

Regional variations in mammalian faunas could result in *S. hemitoechus* having been more common in Britain (Currant, 1989; Currant & Jacobi, 2001) and, perhaps, the Caucasus (Vereshchagin & Baryshnikov, 1980; Baryshnikov, Geren & Mezhlumjan, 1989). The Caucasus rhinoceros was originally identified as a closely related species, *S. binagadensis*

(Vereshchagin & Baryshnikov, 1980; Baryshnikov *et al.*, 1989; M. Fortelius, personal communication, 2004).

In Central Asia *Elasmotherium sibiricum*, a rhinoceros adapted to a rather dry continental climate, was common during the middle Pleistocene (Kozhamkulova, 1969, 1990; Kahlke, 1975b; Kozhamkulova & Kochenov, 1989; Khromov *et al.*, 2001) or even the late Pleistocene in Manchuria (Vereshchagin & Baryshnikov, 1984). Most widespread in European Russia and Siberia was the cold-adapted woolly rhinoceros *Coelodonta antiquitatis*. At the Tunguz peninsula in the middle Volga River, associated with the Khazarian complex, *S. kirchbergensis* was found together with *C. antiquitatis* and *E. sibiricum* (Khromov *et al.*, 2001) where they are believed to have coexisted.

In Eastern Europe, Central Asia and Siberia, Merck's rhinoceros appears to have occurred during the middle Pleistocene in the faunal complexes of Koshkurgan/Tiraspol (Kozhamkulova, 1969, 1990; Khromov *et al.*, 2001), the Singilian where it was most common (Vangengeim & Zhegallo, 1982; Baryshnikov, 1987; Khromov *et al.*, 2001) and the Khazarian (Khromov *et al.*, 2001). In Eastern Europe *S. kirchbergensis* disappeared from the fossil record earlier than *P. antiquus* (Alexeyeva & Tikhomirov, 1989), supposedly during the earliest late Pleistocene (early Shkurlat complex) (Khromov *et al.*, 2001). *S. kirchbergensis* is last recorded during the Eemian in Poland (Kowalski, 1989) and possibly Croatia (Malez, 1986), whereas *S. hemitoechus* is recorded in Croatia during the early late Weichselian (see the Balkans above). On the Russian Plain Merck's rhinoceros is probably not recorded outside the middle Pleistocene (Baryshnikov, 1987) or even the Likhvin interglacial (Vangengeim & Zhegallo, 1982), but possibly survived in the forests of the Caucasus (Azerbaijan) during the early Weichselian (Mousterian) (Baryshnikov, 1987). For example, a middle Pleistocene European *S. hundsheimensis* was discovered there from the middle Weichselian (Mousterian) (Baryshnikov *et al.*, 1989), suggesting that the Caucasus could have been a refuge for many archaic species (Baryshnikov, 1987).

Hippopotamus *Hippopotamus amphibius*

A semi-aquatic hippopotamus *H. amphibius* survives to the present day, but became restricted to Africa (Stuart, 1986, 1991). The hippopotamus cannot tolerate severe and long-lasting frost, requires higher precipitation, milder temperatures, and is dependent on the availability of rivers and lakes with bordering grasslands (Stuart, 1986, 1991; van Kolfschoten, 2000). Two hippopotamus species are recognized in the Pleistocene of Europe, *Hippopotamus major* (or syn. *H. antiquus*, Kahlke, 1987) and *H. amphibius* (Petronio, 1995). The former is known from Europe during the late early and early middle Pleistocene (late Villafranchian and Galerian) (Azzaroli *et al.*, 1988; Petronio, 1995) and the Cromerian complex in the British Isles (Stuart, 1986). *H. amphibius* occurred during the Eemian in Western and Central Europe (Currant, 1989; Mol *et al.*, 1999; von Koenigswald, 1999; van Kolfschoten, 2000; Currant & Jacobi, 2001) and in the Mediterranean (Stuart, 1991; von Koenigswald, 2003). It appeared sometime during the middle Pleistocene (Petronio, 1995) and the earliest find is known from Greece (Kahlke, 1987).

The two species probably overlapped in time. In south-western Europe the hippopotamus was common and sometimes referred to as *Hippopotamus amphibius antiquus* (Stuart, 1991; Kahlke, 2001). *H. antiquus* was described in the Netherlands from the late early Pleistocene (Bavelian) and is almost indistinguishable from the Eemian hippopotamus, except for its larger size (Mol *et al.*, 2003). In Britain *H. amphibius* was particularly common during the middle part of the Eemian (Ipswichian) in association with *P. antiquus* (Stuart, 1986; Mol *et al.*, 2003), and was seemingly absent during the previous Holsteinian (Stuart, 1986;
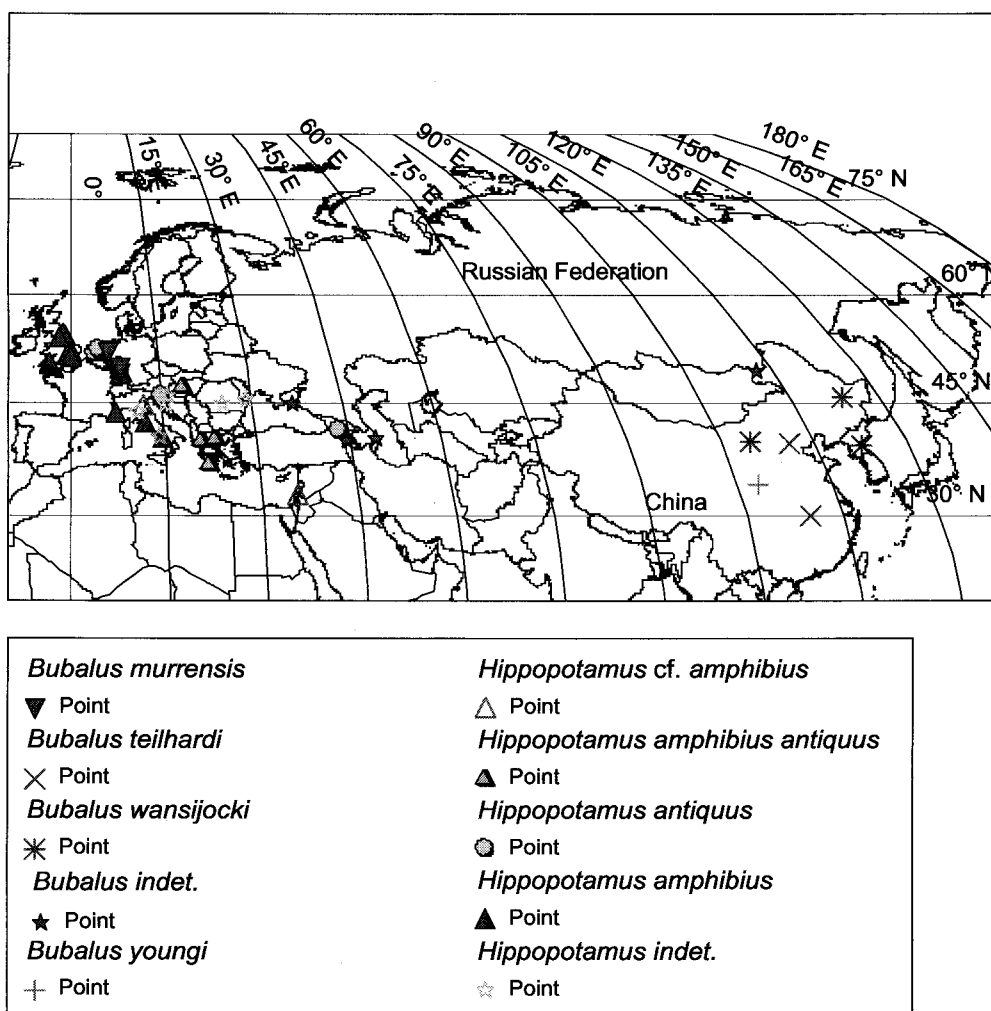
Bubalus murrensis
▼ Point
Bubalus teilhardi
✕ Point
Bubalus wansijocki
✷ Point
 Bubalus indet.
★ Point
Bubalus youngi
+ Point

Hippopotamus cf. amphibius
△ Point
Hippopotamus amphibius antiquus
▲ Point
Hippopotamus antiquus
◎ Point
Hippopotamus amphibius
▲ Point
Hippopotamus indet.
☆ Point

Fig. 3. Easternmost distribution of *Hippopotamus amphibius, Bubalus murrensis* and related species during the Pleistocene. (Two Armenian sites with unidentified *Bubalus* genus are from the Holocene).

Currant, 1989; van Kolfschoten, 1995; Schreve, 2001). In Germany this hippopotamus is known from assumed Eemian localities in the Rhine Valley that may be mixed with the preceding OIS7 and early Weichselian temperate deposits (von Koenigswald & Heinrich, 1996, 1999; von Koenigswald, 1999, 2003; van Kolfschoten, 2000). In the Mediterranen (Italy) *H. amphibius* survived into the early Weichselian (Vereshchagin & Baryshnikov, 1980; Stuart, 1991), until apparently OIS5 (Bedetti *et al.*, 2001) or even OIS4 (Petronio, 1995).

The distribution of both hippopotamuses was probably restricted to south of 55°N and west of 10°E in Western Europe (Stuart, 1986) (Fig. 3). Eastern populations apparently inhabited Croatia, Slovenia, Hungary, Romania, Moldova (Malez, 1986; Kahlke, 1987, 2001) up to 30°E and the Northern Caucasus (Georgia) (Vereshchagin & Baryshnikov, 1980), Turkey (Kahlke, 1987), Israel and Syria (Tchernov *et al.*, 1994) up to 45°E. Assuming correct identification, there is a find related to hippopotamus from an unknown locality (probably

Yunnan) in China with an estimated late Pliocene – early Pleistocene age (Zhou, 1962). A hippopotamus was recorded in Moldova (Bessarabia) during the late Pliocene (Borissiak & Belyaeva, 1948). Svistun *et al.* (1989) described a dwarf hippopotamus that occurred together with *M. meridionalis* in the middle Pliocene Moldavian faunal complex in south-western Moldova. *H. antiquus* is known from the early Pleistocene in Moldova and the early middle Pleistocene in Georgia (Vereshchagin & Baryshnikov, 1980). In Georgia, *H. antiquus* was originally referred to as *H. georgicus* (Vereshchagin & Baryshnikov, 1980; Kahlke, 1987). In Eastern Europe, Slovenia is probably the only country where the hippopotamus has been recorded during the assumed Eemian (Malez, 1986).

European water buffalo *Bubalus murrensis*

Morphologically and anatomically the water buffalo is well adapted to hot and humid climates, and muddy and swampy terrain (Shafie, 1993) with ecological demands similar to those of the hippopotamus. In Western and Central Europe, *B. murrensis* is recorded along river valleys in Germany (von Koenigswald, 1999, 2003) and the Netherlands (van Dam *et al.*, 1997) from suggested Eemian deposits (van Kolfschoten, 2000). Elsewhere, except south-eastern Asia where modern water buffalo (*Bubalus*) species are still found (Shafie, 1993), water buffalo remains are extremely rare.

B. murrensis was restricted to south of 52°N and west of 9°E (Fig. 3). The water buffalo could have populated Moldova (Bessarabia) along with the hippopotamus and possibly Manchuria (G. F. Baryshnikov, personal communication, 2006), but there are no verified records of the water buffalo anywhere in the former USSR (Vereshchagin & Baryshnikov, 1980). The only rather uncertain fragment of the water buffalo's left horn core from the Taman' peninsula in Russia was discovered in early or early middle Pleistocene deposits of Mount Tsimbala near Sennaja along with *M. meridionalis* and a horse with teeth similar to those of *Equus stenonis* (Burchak-Abramovich, 1952, 1957; Vereshchagin, 1959). Other species known from this site are *Bos* spp., a rhinoceros and a transitional *Mammuthus meridionalis/trogontherii* (Lister *et al.*, 2005a) that was originally described as *Palaeoloxodon* cf. *antiquus* (Burchak-Abramovich, 1952).

Fossils of the genus *Bubalus* are frequently found in Eastern China (Xue & Li, 2000). Many species are described, among which are *B. youngi*, *B. wansijocki*, the oldest *B. teilhardi* and the domesticated *B. bubalis* (Xue & Li, 2000; Qiu, 2006). The latter was derived from the wild progenitor, *B. arnee* from south-eastern Asia (India, Nepal, Malaysia) (Nowak, 1991; Shafie, 1993), which appears to be more closely related to *B. youngi* than *B. wansijocki* (Xue & Li, 2000). In China *B. youngi* and *B. wansijocki* were encountered together with the straight-tusked elephant and the woolly mammoth (Xue & Li, 2000). In Georgia *Eosyncerus ivericus*, a water buffalo related to the African buffalo, *Syncerus caffer* is known from the late Pliocene (Vereshchagin & Baryshnikov, 1980). In Armenia the Holocene buffalos (Vereshchagin, 1959) (Fig. 3) are probably domestic (G. F. Baryshnikov, personal communication, 2006).

DISCUSSION

Species of the *Palaeoloxodon* assemblage originated during the period from the Cromerian to Holsteinian and spread as far as climatic conditions allowed, suggesting that species that originated earlier could spread further probably experiencing speciation on the way. A similar pattern of replacement to that in Central European interglacials/glaciations was also found during the late Pleistocene in Japan (Takahashi *et al.*, 2003) and China (Kahlke, 1986; Xue & Li, 2000).

In northern China a mild climate was recorded during the middle Pleistocene at 600 000–480 000 years ago (Qiu, 2006). In continental Siberia the middle Pleistocene (MIS 15–11) was very mild with a weak climatic contrast between the Elsterian Glaciation and Holsteinian interglacial (Prokopenko *et al.*, 2002). The Holsteinian was sufficiently long and warm (Howard, 1997) to allow the temperate species to disperse further east. For example, the late early and early middle Pleistocene (post-Villafranchian or Galerian) fauna, with the associations of *Praeovibos* and *Soergelia* covered a wide range throughout the middle and high latitudes of Eurasia (Kahlke, 1975b, 1986; Azzaroli *et al.*, 1988) from Central Europe (France, Germany) (Mol *et al.*, 1999) to north-eastern Siberia (Sher, 1971), although it originated in Europe over an extended period of time (Sher, 1992). These species were part of the Euro-Siberian palaeozoogeographical region during the early middle Pleistocene (Udvardy, 1969; Kozhamkulova & Kochenov, 1989). In Europe this fauna was temperate (Mol *et al.*, 1999), although in Siberia it became adapted to severe climatic conditions (Sher, 1992).

Today similar biogeographical distribution patterns exist across Eurasia from Europe to China throughout the deciduous woodland corridor along the taiga–steppe boundary (Udvardy, 1969). The Holsteinian climate is suggested to have been more similar to the Holocene climate (Howard, 1997). Theoretically, the species that appeared during the Holsteinian could have survived until now if not perturbed. Several extant species inhabited already their modern distribution areas. However, among the largest, only *B. primigenius* and *M. giganteus* survived in Europe till the later Holocene. The *Palaeoloxodon* assemblage has left no analogues in the Holocene (Graham & Lundelius, 1984; Sher, 1997). The last occurrence of the interglacial assemblage as a whole in Central and Western Europe is recognized during the last Pleistocene interglacial Eemian (von Koenigswald, 1999, 2003; Bradshaw *et al.*, 2003), which can be related to this period having been more climatically unstable in both Siberia and Europe (Granoszewski *et al.*, 2005). In Siberia and Central Asia the now-extinct species of the *Palaeoloxodon* assemblage disappeared earlier than in Europe and the Caucasus. During the Eemian many species of the *Palaeoloxodon* assemblage could have co-occurred in south-eastern Europe (the Balkans) (Malez, 1986; Spiridonov & Spassov, 1998). At least the straight-tusked elephant, Merck's rhinoceros, roe deer, aurochs and red deer appear to have been found in Poland (Kowalski, 1989), whereas in European Russia the advanced form of *P. antiquus* is suggested to have occurred alongside the glacial large-mammal community (Markova, 2000, 2007).

Nevertheless, the temperate refugia were not only restricted to the Mediterranean region, but also present in south-eastern Europe (Hungary) during the late Pleistocene (Stewart & Lister, 2001). The Caucasus (Baryshnikov, 1987), the Urals (Stuart *et al.*, 2004) and southern Russia (Volga river region) could have accommodated warm-adapted species along with the region around Lake Baikal, with its moderating effect on climate, so that the *Palaeoloxodon* assemblage species, except for *B. murrensis* and *H. amphibius*, could have been separately present somewhere in the former USSR during the Eemian.

The *Palaeoloxodon* assemblage is much harder to identify in the east because of often less severe climatic changes, geographical barriers, possible divergence of fragmented populations during glaciations, the influence of other species in Asia, and uncertainties over identification and taxonomy. Central and Western Europe is a small biogeographical region where mammalian faunas maintained a greater cohesion in response to climatic and environmental changes forming an unvarying *Palaeoloxodon* assemblage. In comparison, more regional variation in communities has been identified in the rest of Eurasia with its environmental fragmentation as each species tended to respond separately and differently in nonanalogous diverse assemblages. The boundary of the *Palaeoloxodon* assemblage's existence as a whole can be roughly drawn from Poland to Romania. Possibly, after taxonomic revision, some of the related large species described here will be recognized as the same species as those of the *Palaeoloxodon* assemblage or as local subspecies unless they were geographically or biologically isolated. Widely distributed species may diverge greatly, and sympatric and other non-allopatric modes of speciation are more difficult to determine (Vangengeim, 1977; Cox & Moore, 2000). However, in order to further elucidate the degree of breakdown of this assemblage towards the north and east of Asia, a specialist systematic review is required of the species of the *P. antiquus* assemblage across Eurasia.

CONCLUSIONS

Although I cannot rule out all stratigraphical and/or nomenclatural confusion and errors, it appears that the species of the European *P. antiquus* interglacial assemblage were independently present in different assemblages across central Eurasia during the late middle Pleis-

tocene and possibly the Eemian, with some surviving into the Holocene. The middle part of the middle Pleistocene appears to have been more climatically equable than either before or after allowing for temperate species to diversify and disperse. During the latest part of the middle Pleistocene and late Pleistocene these species were squeezed out of central Eurasia and became fragmented into smaller biogeographical zones, possibly similar on both sides of the continent. Further research on systematics and geographical variation in these species, and their possible dispersal routes is necessary to facilitate quantitative research on the similarity of mammalian assemblages across Eurasia during the Pleistocene and early Holocene.

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