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The pattern and process of mammoth evolution in Eurasia

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Abstract

Mammoth evolution in Eurasia represents one of the best-studied examples of evolutionary pattern and process in the terrestrial fossil record. A pervasive belief in the gradual transformation of chronospecies in Europe is giving way to a more complex model incorporating geographical variation across the whole of northern Eurasia. This in turn casts doubt on biostratigraphic deductions which assume gradual transformation of molar morphology, simultaneous across the species' range. The earliest European elephantids, *Mammuthus rumanus*, occur in the interval 3.5–2.5 Ma, and are distinctly more primitive than the better-known *M. meridionalis.* The species '*M. gromovi*', identified in the interval c. 2.6–2.2 Ma, appears to be a junior synonym of *M. meridionalis*. *M. meridionalis* dispersed widely and, in the interval 2.0–1.5 Ma, gave rise to *M. trogontherii* in eastern Asia, probably in China, spreading to NE Siberia by 1.2 Ma. Between that date and c. 600 ka, flow of genes and/or individuals westwards produced an interaction with European *M. meridionalis* which led to a network of populations in time and space and the eventual supplanting of that species by *M. trogontherii*. This conclusion is based principally on the earlier appearance of *M. trogontherii* morphology in eastern Asia, supplemented by complex morphological patterns in Europe during the time of transition. Subsequently, *M. trogontherii* did not undergo a gradual transformation into *M. primigenius* (woolly mammoth) in Europe, but remained in stasis (apart from size reduction) until 200 ka. In NE Siberia, however, *M. trogontherii* began a transformation into primitive *M. primigenius* morphology as early as 700 ka, and that species continued its evolution in the same region through the Middle and Late Pleistocene. The incursion of *M. primigenius* into Europe appears to have occurred soon after 200 ka, and its 'replacement' of *M. trogontherii* there probably included some introgression from the latter species.

1. Introduction

Fossil elephants have long been a favourite subject of study, not only for elucidating their phylogenetic relationships, but also for illustrating patterns and processes of evolution (e.g. Osborn, 1942; Maglio, 1973). In recent years, the mammoth lineage has attracted particular attention, because of the profound changes it shows in a relatively short period of time, many of them evidently adaptive to Quaternary environments, and because of the increasingly impressive array of well-dated samples from across the broad range of the genus.

Continuously present in continental Eurasia from at least 3.0 Ma until the end of the Pleistocene, mammoths underwent very significant evolutionary change, including a shortening and heightening of the cranium and mandible, increase in molar hypsodonty index (HI), increase in plate number (*P*), and thinning of dental enamel. Based on these changes, European mammoths have conventionally been divided into three chronospecies: Early Pleistocene *Mammuthus meridionalis*, Middle Pleistocene *M. trogontherii* and Late Pleistocene *M. primigenius* (Maglio, 1973; Lister, 1996). In the following account, all data are our own except where stated. The term 'M3' refers to the third (last) molar, whether upper or lower, while M^3 and M_3 signify upper and lower M3, respectively. Fossils are described as being the 'typical' form of each of these species when

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they are statistically indistinguishable from the sample of the type locality.

2. Theoretical considerations

The evolutionary sequence of the mammoth has frequently been presented as a paradigm of 'gradualistic evolution' (cf. Gould and Eldredge, 1977). Numerous authors, from Adam (1961) to Vangengeim and Pevsner (2000), have assumed a sequence of ever-progressing 'transitional forms' between the three classic species, with Europe generally considered the locus of transformation. There are also many examples in the literature where the logic is inverted and fossil deposits are dated on the basis of the evolutionary 'level' of the mammoths. At its extreme, the gradualistic model, with a species evolving relentlessly in one direction over long periods of time, implies an 'internalist' view of evolution, recalling the orthogenesis of the 19th century, in which the motive force for change comes from within the animal. Darwinian natural selection, on the other hand, an essentially externalist concept, would predict complex variations of rate and pattern in the constantly changing environment of the Quaternary. In fact no particular pattern of change among the mammoths should be assumed a priori, but has to be determined from fossil samples dated independently of their 'evolutionary level' (Lister, 1992, 2001).

In addition, it is essential to take account of geographical variation and migration. The cardinal importance of these factors in species-level evolution is axiomatic in the world of evolutionary biology research, but is only recently becoming a subject of study among palaeontologists, including those working in the Quaternary (e.g. Polly, 2003). Most species today exist as a 'metapopulation'—a complex of geographically separated populations linked by restricted gene flow through migration (Barton and Whitlock, 1997). The origin of novel features in one area, followed by their spread by a combination of gene flow, migration or selection, has been extensively modelled in terms of population genetics. Theories of species origin, such as the classic allopatric model of Mayr (1963), can be seen as variants of this general paradigm. In the allopatric model, a population becomes isolated from the main range of the parent species, and there evolves into a new species, aided by the genetic effects of small population size (Fig. 1a). The newly formed species can expand from its small peripheral range to co-exist with, or possibly supplant, the parent species. Equally likely, however, the allopatric population may not have become completely reproductively isolated from the parent species, and on expanding to meet it, forms a hybrid zone (Harrison, 1993). Here, the second stage of the speciation process may occur, by selection against interbreeding driven by the relative inviability of hybrids—a process known as reinforcement. Recent work has tended to emphasise the power of local habitat variation, rather than mere isolation, in driving peripheral populations to speciation via adaptive natural or sexual selection (Schneider, 2000). The divergence of abutting populations without isolation (parapatric speciation) can also be modelled if the species' ranges are large enough to allow selection to dominate over gene flow (Jiggins and Mallet, 2000).

The common thread to all these models is that geographical variation plays a fundamental part in driving species-level evolution. Moreover, the raw material for this process is abundantly evident in living species, where geographical variation among populations and subspecies is ubiquitous. A recent revival of interest in sympatric speciation indicates the theoretical possibility of species formation without geographic separation in some cases (Doebeli and Dieckmann, 2000), but it requires relative immobility and assortative mating between different phenotypes or genotypes, and seems unlikely for large, mobile mammals such as the mammoth.

Transferred into the fossil record, some of these processes, at least, should have predictable signatures which can be used to test between different models of evolution. The gradual transformation of one morphology into another through a chronological series of fossils, coincident in correlated samples across the geographical range, would suggest anagenetic evolution (transformation of a lineage without splitting) over a wide area (Fig. 1b). On the other hand, if change is found in a small area while elsewhere the ancestor remained little-changed, it would suggest that one is sampling in the very area where an allopatric isolate is speciating (cladogenetic evolution) (Figs. 1a and c). Sampling of later deposits over a wider area may then show the process of spread of the new form. A further important line of evidence is the finding that 'ancestral' and 'descendent' forms co-occur at a single time and place, implying that their ranges have come to overlap (Fig. 1c). This is inconsistent with purely anagenetic change and implies that a cladogenetic event has occurred, presumably outside the sampling area. The identification of possible 'hybrid' individuals in the fossil record is a subtle and understudied topic of research. Identifying any of these patterns requires an exceptionally complete and finely-divided biostratigraphy, statistical samples of fossils, and reliable chronological correlation over wide areas. It therefore stretches the resolution of the fossil record to its limits, and will be possible only in relatively few instances. Most published examples (e.g. Malmgren et al., 1984; Cheetham, 1987) have come from continuous marine sequences; meeting these requirements in the more fragmentary terrestrial record is a considerable challenge.

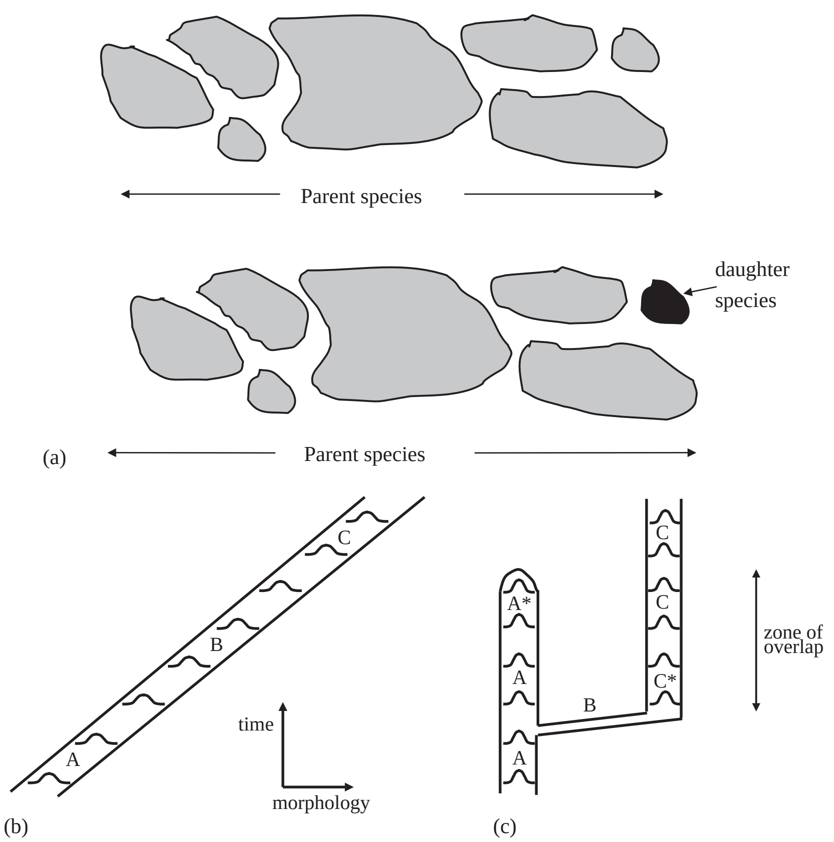

Fig. 1. Schematic representation of (a) allopatric speciation; (b) anagenetic evolution: morphological change A > B > C occurs across the whole species, and produces a shifting but unimodal distribution of morphology at successive levels. There is no temporal overlap between A, B or C; (c) cladogenetic evolution: corresponding to the situation in (a), morphological change A > B > C occurs in a geographically separated population while the parent population remains at level A. If the two resulting lineages then come to occupy the same geographical area, a bimodal distribution of morphology, A and C, will be observed, with the possibility of an apparent temporal 'inversion' of morphologies between the samples marked by an asterisk. The early phase of contact may also be marked by limited hybridisation, producing some individuals of intermediate or mosaic morphology. Eventually, the two populations may merge, or come to coexist as separate species, or (as shown) one may replace the other.

Aside from their inherent assumption of gradualistic change, many published models of mammoth evolution are based on a sequence of samples restricted to Europe—a small peninsula of a vast continental landmass, and a relatively small area of the total distribution of mammoths. They thereby run the risk of extrapolating local patterns of change into broad evolutionary scenarios. A notable exception is the work of Foronova and Zudin (1999), who have examined mammoth molar morphology across Eurasia, and have described various aspects of clinal and chronological variation, although they tend to regard all geographic variation as autochthonously derived rather than incorporating migration or gene flow as in our model. In the present review we examine the European evidence in the light of important recently described mammoth material from Arctic Siberia (Lister and Sher, 2001), central Siberia (Foronova, 1998), China (Wei et al., 2003) and Japan (Taruno, 1999; Takahashi and Namatsu, 2000). We focus on the pan-Eurasian evidence; North America is an important part of the complete picture, but further research is required to clarify the evolutionary sequence there (Agenbroad, 2003; McDaniel and Jefferson, 2003).

3. Early mammoths in Eurasia: *M. rumanus* and '*M. gromovi*'

Mammoth evolution began in Africa, where the Pliocene species *M. subplanifrons* and Pleistocene *M. africanavus* have been named (Maglio, 1973; Kalb and Mebrate, 1993). The former taxon incorporates the earliest known mammoth material, at around 4 Ma, but probably includes fossils which should be referred to other species, and is in need of re-study (H. Saegusa, pers. comm. to AML, 2001).

In recent syntheses (e.g. Lister, 1996), mammoth material dating from around 2.6–2.5 Ma has been assumed to be the earliest in Europe, based on material from sites such as Montopoli (Italy) and the Red Crag (England). However, Radulesco and Samson (1995, 2001) referred elephantid molars from the Dacic Basin, Romania, to mammalian biozone MN16a, correlated to the Triversa faunal unit of Italy, and placed by palaeomagnetic data in the middle Gauss subchron, c. 3.5–3.0 Ma. This material includes the type specimen of *Elephas antiquus rumanus* Ştefănescu 1924—an incomplete M^3 from Tuluceşti, and a complete M_3 from Cernăteşti (Fig. 2a). Until recently, the holotype specimen was believed to be lost, leading Lister and van Essen (2003) to propose the Cernăteşti specimen as the neotype of *rumanus*. However, the holotype specimen has now been rediscovered by HvE in Bucharest. Lister and van Essen (2003) indicated that metrically, the molars from Cernăteşti and Tuluceşti form a homogeneous group with those from the Red Crag and Montopoli (Fig. 2b), which taken together is distinctly more primitive than the type sample of *M. meridionalis* from the Upper Valdarno, Italy (c. 2.0–1.77 Ma). The early group has 8–10 plates in M3 (excluding talons and platelets), while typical *M. meridionalis* has 12–14, rarely 11 or 15 (see also Fig. 3 of Lister and Sher, 2001). Another primitive feature in the early group is the retention of strong median folds on the enamel loops, although there is no evidence of a significantly lower hypsodonty index compared to *M. meridionalis*. Material from some other localities may be referable to the '*rumanus* group' (Lister and van Essen, 2003; Markov and Spassov, 2003; Palombo and Ferretti, 2004). In the absence of cranial material, referral of the Dacic material to *Mammuthus* is provisional. Markov and Spassov (2003) compare it to *M. subplanifrons* (of which it might be an advanced derivative, with an elevated hypsodonty index) and to *Elephas planifrons* (referral to that genus being possibly supported by enamel crenulation we have observed in the Romanian material). The generic identity of the Montopoli and Red Crag material as *Mammuthus* is less problematic, with relatively uncrenulated enamel and a partial skull at Montopoli. Although existing samples are too small to be sure whether there was any evolutionary transformation or replacement between the earlier Romanian, and later Italian and British, samples, on available evidence we provisionally ascribe the Romanian material to *M. rumanus* and the Montopoli and Red Crag samples to *Mammuthus* cf. *rumanus.*

The *rumanus* taxon has been recently utilised, for the original Romanian material, by Garutt and Tichonov (2001) as '*Archidiskodon*' *rumanus*, by Titov (2001) as '*Archidiskodon*' *meridionalis rumanus*, and by Markov and Spassov (2003) as *M. rumanus*. Maglio (1973), however, did not recognise this taxon; he divided *M. meridionalis* into three informal chronological and morphological groups, each named after a locality where key material was found: the 'Laiatico Stage', 'Montevarchi Stage' and 'Bacton Stage'. He included in the early, Laiatico Stage, the Montopoli remains here referred to *M.* cf. *rumanus*, as well as remains from some other localities which we believe to be of uncertain morphology and/or age (Lister and van Essen, 2003 and in prep). Palombo and Ferretti (2004) provisionally retain the Montopoli material as an early form of *M. meridionalis*, although they recognise its more primitive morphology than the typical form.

Another name which has gained currency for the earliest European mammoths is *M. gromovi*, coined by Alexeeva and Garutt (1965) for remains from the Khapry Faunal Complex, in the south of European Russia and now dated to MN17, c. 2.6–2.2 Ma (Titov, 2001). These remains (Fig. 2c) are therefore intermediate in age between those here referred to *M.* cf. *rumanus* and typical *M. meridionalis*. The mammoths were regarded as more primitive than *M. meridionalis* on the basis of molar morphology, cranial proportions, and the presence of a supposed atavistic fourth true premolar (P4) in one skull (Alexeeva and Garutt, 1965). However, measurements on the type sample of *M. gromovi* from Khapry show that in the key features of plate formula and hypsodonty index, it shows no significant difference from typical *M. meridionalis,* with 12–14 full plates in M3 (Dubrovo, 1989; Lister, 1996; Lister and Sher, 2001; Lister and van Essen, 2003). In addition, recent research by Maschenko (2002) has discounted the presence of a true P4, regarding the element in question as an abnormal second deciduous premolar (dP2) in one individual. In lamellar frequency and enamel thickness, the Khapry teeth seem slightly more primitive on average than *M. meridionalis* from the Upper Valdarno (Lister, 1996; Lister and van Essen, 2003), but to a degree consistent with intraspecific variation.

Dentally at least, the type material of *M. gromovi* therefore appears synonymous with *M. meridionalis* (Fig. 3). Regarding skulls, there is a difference between primitively low-peaked crania at sites such as Liventsovka (Khapry faunal complex, c. 2.6–2.2 Ma, '*M. gromovi*') and Chilhac (c. 2.0 Ma) on the one hand, and the higher-peaked type *M. meridionalis* crania from Italy (c. 2.0–1.77 Ma), on the other (Azzaroli, 1977; Lister, 1996; Titov, 2001; Figs. 4a–c). Palombo and Ferretti (2004), however, point out that the Upper Valdarno sample includes at least one skull of morphology similar to that of Liventsovka and Chilhac. On this basis, the evidence for the existence of '*M. gromovi*' as a taxon distinct from *M. meridionalis* seems weak on craniological as well as dental grounds. By the same token, Lister and van Essen (2003) discounted the extension of the name *M. gromovi* to dental specimens such as those from Montopoli (e.g. Azzaroli, 1977), since this material, here referred to *M.* cf. *rumanus*, is both older and more primitive than the type sample of *M. gromovi* from Khapry (Fig. 3).

There is evidence that the *M. rumanus* stage of evolution spread as far as China (Fig. 5). In sediments of the Mazegou and Youhe Formations from the Yushe

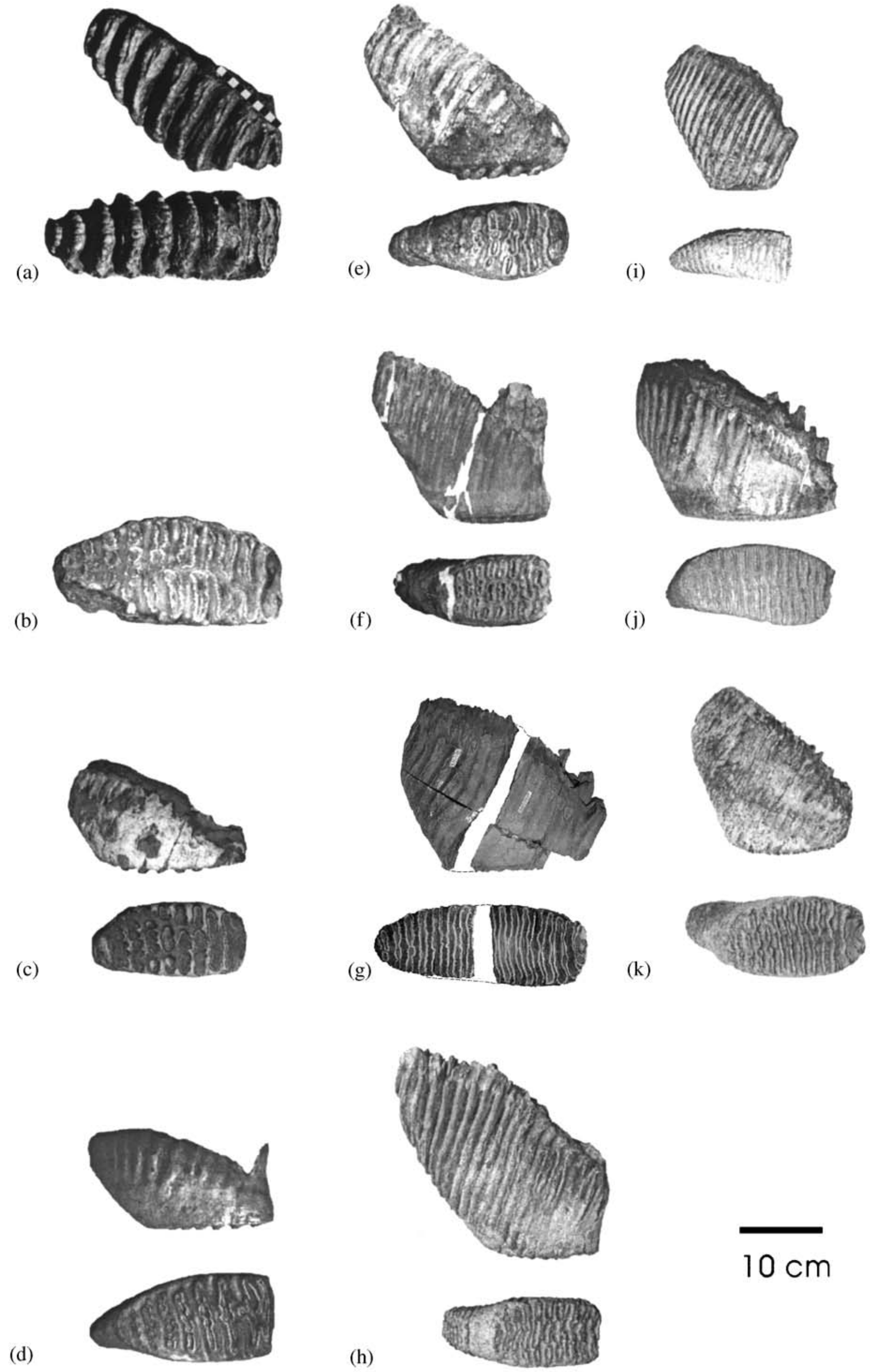

Fig. 2. Examples of mammoth third upper molars representing different evolutionary stages discussed in the text. All teeth shown in medial or lateral, and occlusal views (except Montopoli, occlusal only). (a) *M. rumanus*, Cernăteşti, Romania, Institute of Speleology 'Emil Racoviţă' Bucharest no. Cr007-8/1001, right; (b) *M.* cf. *rumanus,* Montopoli, Italy, Museum of Geology and Palaeontology, Florence no. 1077, right; (c) *M. meridionalis* (ex '*M. gromovi*'), Khapry, Russia, Geological Institute, Moscow no. 300-120, left, reversed; (d) *M. meridionalis* (type sample), Upper Valdarno, Italy, Museum of Geology and Palaeontology, Florence no. 46, right; (e) 'mosaic' specimen, *M. meridionalis/trogontherii* transition, Sinyaya Balka, Taman' peninsula, Russia, Palaeontological Institute, Moscow no. 1249/256, left, reversed; (f) early trogontherioid mammoth, Majuangou, China, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing no. V13610, right; (g) early trogontherioid mammoth, Bolshaya Chukochya R., Loc. 23, Early Olyorian, Kolyma Lowland, Russia, Palaeontological Institute, Moscow no. 3100-784, right; two plates have been lost from the middle of the tooth; (h) *M. trogontherii* (type sample), Süssenborn, Germany, Institute for Quaternary Palaeontology, Weimar no. 1965/3224, right, reversed; (i) late trogontherioid mammoth, Brundon, England, Natural History Museum London no. 15506, right; (j) early primigenioid mammoth, Bolshaya Chukochya R., Loc. 34, Late Olyorian, Russia, Palaeontological Institute, Moscow no. 3100-411, left, reversed; (k) *M. primigenius*, Balderton Terrace, England, Royal Scottish Museums Edinburgh no. 6A/16, left.

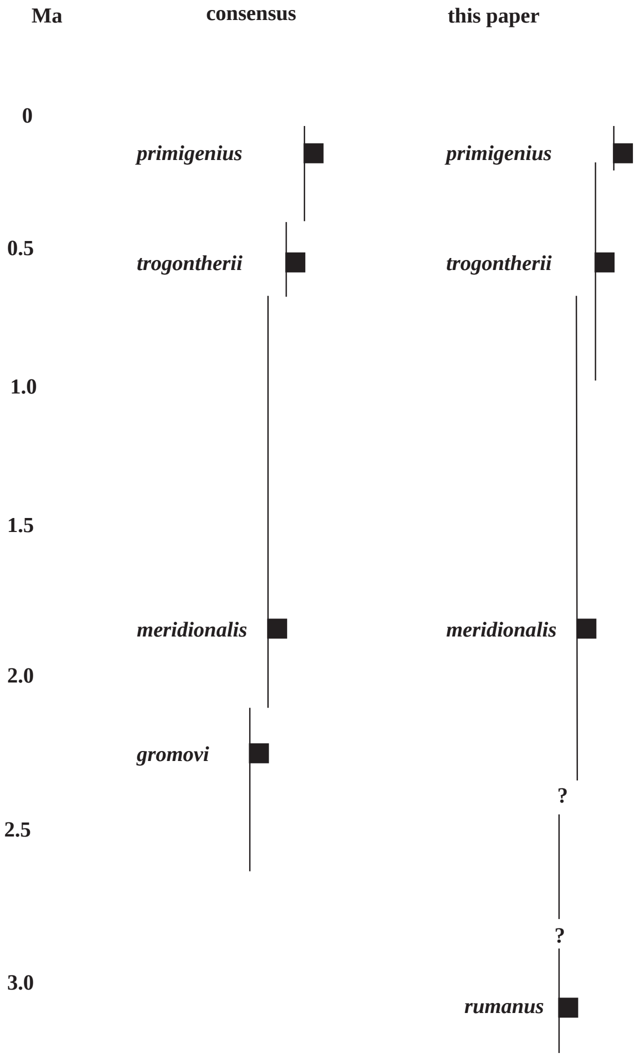

Fig. 3. Taxonomy and time-span of mammoth species in Europe. Filled squares mark approximate age of type material of each species. Left side: simple chronospecies series, based on a variety of sources. Right side: based on data presented in this paper, with recognition of *M. rumanus*, redetermination of the type material of '*M. gromovi*' as *M. meridionalis*, chronological overlap between *M. meridionalis* and *M. trogontherii*, recognition of *M. trogontherii* both earlier and later than the usual restriction to the early Middle Pleistocene, a short period of overlap between *M. trogontherii* and *M. primigenius*, and relatively late appearance of *M. primigenius*. The horizontal displacement between the range lines represents advancement in features such as molar plate number and hypsodonty index.

Basin and its neighbourhood, primitive teeth of a morphology comparable to European *M. rumanus* and *M.* cf. *rumanus* occur (Wei and Taruno, unpublished observations). Some of this material was formerly referred to '*Archidiskodon planifrons*' (Teilhard de Chardin and Trassaert, 1937) or '*Elephas youheensis*' (Xue, 1981). The age of the Yushe deposits, similar to the occurrence of *M. rumanus* and *M.* cf. *rumanus* in Europe, is 3.4–2.5 Ma.

4. *M. meridionalis* and the origin of *M. trogontherii*

M. meridionalis was defined on the basis of material from the Upper Valdarno, Italy (Fig. 2d); most of the material is from the Matassino and Tasso Faunal Units, now dated to c. 2.0–1.77 Ma on the basis of magnetostratigraphy (Palombo and Ferretti, 2004). The typical form of the species persists in central and western Europe until at least 1.4 Ma (e.g. at Pietrafitta, Italy: Ferretti, 1999; Lister and Sher, 2001), perhaps to 1.2 Ma. By 0.6 Ma, at Süssenborn (the type locality) and elsewhere, this species has been completely replaced by *M. trogontherii* (Fig. 2h). Fortunately, both the Upper Valdarno and Süssenborn deposits have yielded large samples of mammoth teeth, providing a statistical basis for comparison (Lister, 1996; Lister and Sher, 2001). In M3, average plate count has increased from around 13 to 19, and average hypsodonty index in M^3 from about 1.25 to 1.75. Cranial changes are difficult to trace because of a shortage of well-preserved early *M. trogontherii* specimens, but probably included an antero–posterior shortening, flattening of the facial concavity, and deepening of the cheek to accommodate the higher-crowned molars (Lister, 1996). The mandibular rostrum shortened and the horizontal ramus also deepened.

In the interval 1.0–0.7 Ma, a series of samples in Europe illustrates a complex and fascinating transitional period, which has been discussed in some detail by Ferretti (1999) and Van Essen (2003). The largest samples are those from St-Prest (France), and Sinyaya Balka on the Taman' peninsula (southern European Russia; Fig. 2e), both dated to around 1.0 Ma. Other, smaller and/or more fragmentary samples in Europe have been the subject of extensive discussion, but are more difficult of interpretation. Some of the key samples, with their approximate ages, are shown in Table 1. This table is simplified and is intended only to give a broad indication of a more complex series of morphologies and sample distributions.

Mammoth molars from some of the localities, such as Untermassfeld (Germany) and Oriolo (Italy), fall within the metric range of the Upper Valdarno sample. At St-Prest, according to our data, the molars have added around one plate on average compared to the typical form from Upper Valdarno, to produce an average of 14. In hypsodonty index, most specimens fall within the Valdarno range, although some lie significantly above it (indicated by the double entry in Table 1). The St-Prest form was named *M. m. depereti* by Coppens and Beden (1980). Other samples showing varying degrees of advancement in plate count and/or hypsodonty index over typical *M. meridionalis* include the limited material from Rio Pradella, Imola (Italy), from Edersleben (Germany), and some of the specimens from Dorst (The Netherlands). The advanced nature of some of the

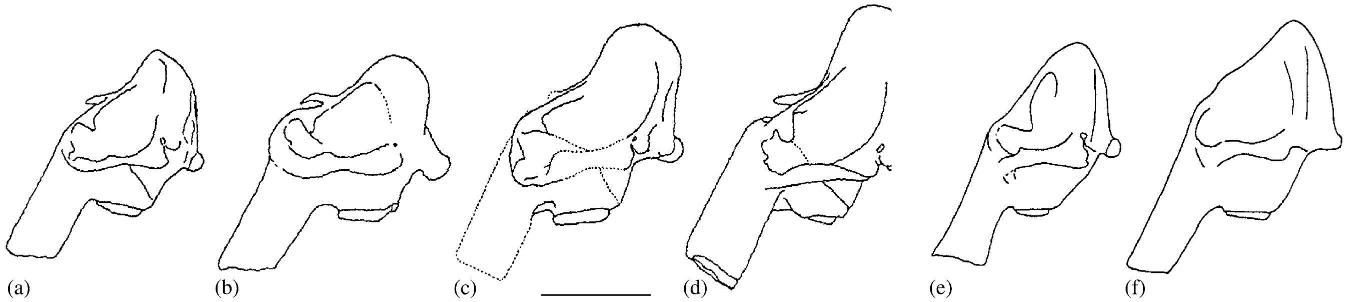

Fig. 4. *Mammuthus* crania from (a) Liventsovka, Russia, c. 2.3 Ma, type locality of '*M. gromovi*' (after Azzaroli, 1977); (b) Chilhac, France (*M. meridionalis*, c. 1.9 Ma, after Boeuf, 1990); (c) Upper Valdarno, Italy (*M. meridionalis* type locality, c. 1.8 Ma, after Azzaroli, 1966); (d) Scoppito, Italy ('*M. meridionalis vestinus*', c. 1.2 Ma, after Maccagno, 1962); (e) Cherny Yar, Russia, type of '*M. trogontherii chosaricus*', after Dubrovo, 1966); (f) Debica, Poland (typical *M. primigenius*, after Kubiak, 1980). Scale bar 50 cm. Note the apparent increase in cranium height between (b) and (c).

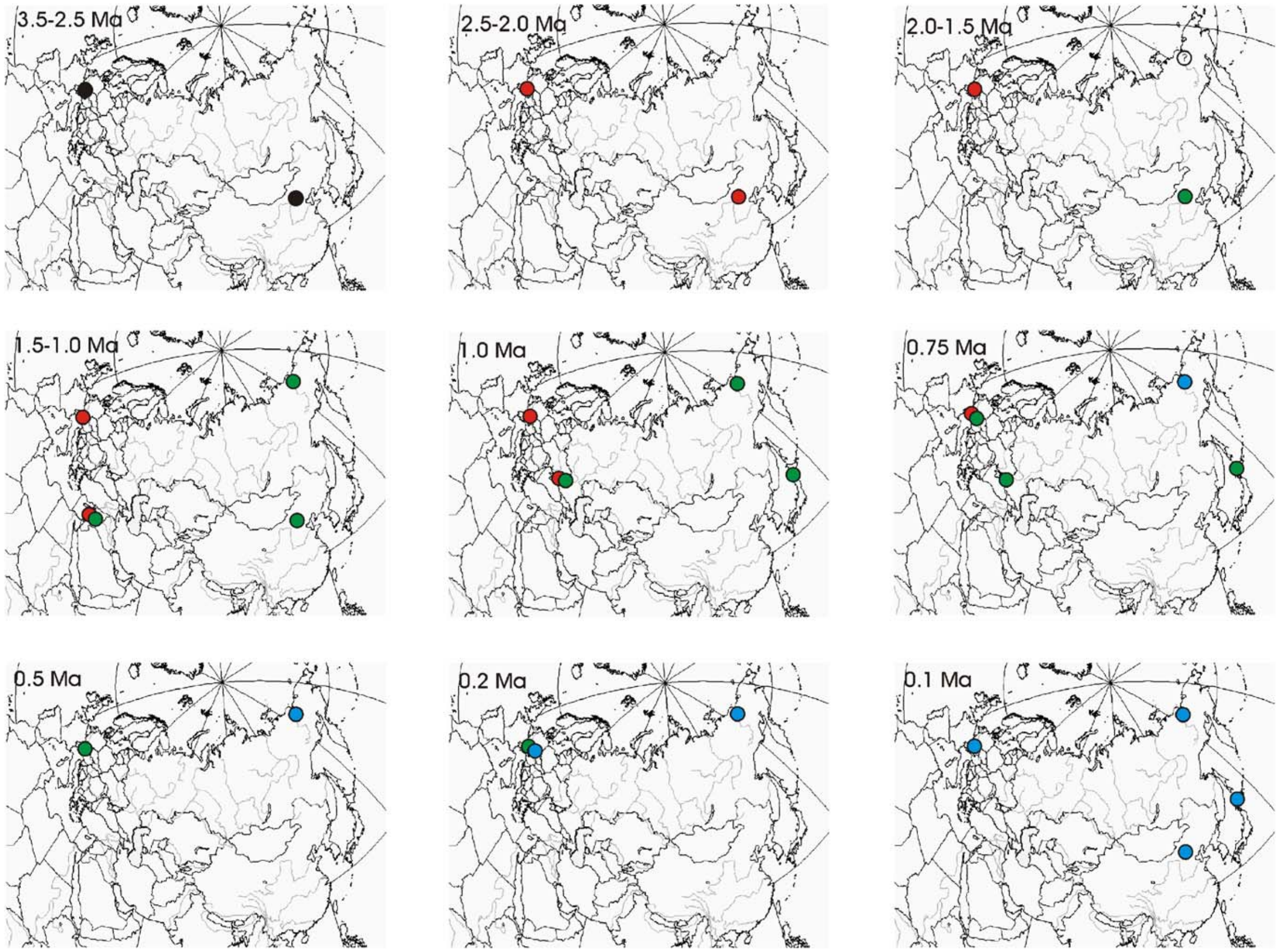

Fig. 5. Regional occurrence of named species of *Mammuthus* in Eurasia, based on localities discussed in the text. Black, *M. rumanus* and *M.* cf. *rumanus*; red, *M. meridionalis*; green, *M. trogontherii*, blue, *M. primigenius*.

named 'late' subspecies from other sites is open to question, however, as the type material may not depart significantly from typical *M. meridionalis*. This includes '*M. meridionalis vestinus*' from Italy (Palombo and Ferretti, 2004; see below) and Maglio's (1973) 'Bacton Stage' from the Cromer Forest-bed Formation (England) (Lister, 1996).

Over the same interval, however, there is evidence of even more advanced mammoths, conforming to typical *M. trogontherii* (Table 1; Fig. 3). The type Cromerian

Table 1
European localities with mammoth remains spanning the replacement of *M. meridionalis* by *M. trogontherii*

Ma	*M. meridionalis* typical or marginally advanced	*M. meridionalis* advanced	*M. trogontherii* primitive	*M. trogontherii* typical
0.6				Süssenborn
				(Voigtstedt G)
		(Voigtstedt R) ----------------	(Voigtstedt R)	(West Runton)
		(Edersleben)		
		(Imola)		(Beeston)
0.8				
		(Dorn-Dürkheim 3)		(Dorn-Dürkheim 3)
	(Dorst) ---------------------	(Dorst)		(??Kärlich)
	St-Prest -----------------	(St-Prest)		
1.0	(Oriolo)	Sinyaya Balka	Sinyaya Balka	
	(Oosterhout)			
	(Untermassfeld)			

This simplified representation summarises a complex array of morphologies, but illustrates the apparent chronological overlap between populations or species at different levels of advancement (cf. Fig. 1). The attribution of samples to each column is based on molar characters only. Samples in brackets comprise a small number of individuals (<10). Geological ages are approximate; see Ferretti (1999), Lister and Sher (2001, supplement) and Van Essen (2003) for details. Curly brackets indicate samples at approximately the same age. Voigtstedt R, the 'red group', may be contemporaneous with, or (as shown) slightly older than, the 'grey group' (Voigtstedt G); see text for discussion. Voigtstedt R specimens are referable either to advanced *M. meridionalis* or to primitive *M. trogontherii* (dashed line). For several localities, material is listed under two categories. When joined by a dashed line, this indicates a range of variation whose position is uncertain because of small sample size. Where unjoined, there is apparent bimodality indicating co-occurrence of discrete morphologies in a single assemblage; see text for discussion.

West Runton Freshwater Bed, England, which recently yielded a complete skeleton of *M. trogontherii* with high-crowned molars and 22 plates in M^3, belongs in the very early Brunhes (Stuart and Lister, 2001); the type Beestonian gravels, England, underlying the type Cromerian though still normally magnetised (West, 1980), yielded a complete mandible with M_3s bearing 19 plates. Deperet and Mayet's (1923) *M. meridionalis cromerensis* from Kessingland, also in the Cromer Forest-bed Formation, is referable to typical *M. trogontherii* (Stuart and Lister, 2001; Lister and van Essen, in prep.). A single molar fragment, of clearly *M. trogontherii* (or even *M. primigenius*) morphology from Kärlich, Germany, is thought to have come from Unit Ba, below the Brunhes/Matuyama boundary, though its provenance is unfortunately not wholly secure (M. Street and E. Turner, pers. comm.; Van Essen, 2003).

Among the mammoth samples, two were suggested by Lister and Sher (2001) to indicate co-existence of significantly different morphotypes in a single horizon, apparently too distinct to have been drawn from the same statistical population, and therefore directly implying cladogenesis. At the first, Voigtstedt, one group of specimens has been regarded as the latest stage of *M. meridionalis* evolution (*M. m. voigtstedtensis*; Dietrich, 1965), although some incomplete specimens can alternatively be reconstructed as primitive *M. trogontherii* (Ferretti, 1999; Lister and Sher, 2001; Van Essen, 2003). A second group of specimens is indistinguishable from *M. trogontherii* of typical form. Voigtstedt is regarded as very close in age to W. Runton (Stuart, 1981; Stuart and Lister, 2001), and the finds were originally described as having been recovered from a single horizon, the Hauptfundschicht (Kahlke, 1965).

Van Essen (2003), however, has pointed out a correlation between preservation type and morphology (advanced *meridionalis* or primitive *trogontherii*—the 'red group'—on the one hand; advanced *trogontherii*—the 'grey group'—on the other), leading to the suggestion that remains of the latter might have come from a slightly younger deposit than those of the former.

At the second site, Sinyaya Balka (Fig. 2e), the molars span a range of morphologies encompassing 14–19 in P and c. 1.3–1.8 in M^3 HI. This corresponds roughly to the 'advanced' end of typical *meridionalis* morphology and the 'primitive' end of typical *trogontherii* morphology. In terms of mean measurements, this sample appeared to form an almost perfect intermediate between typical *M. meridionalis* and *M. trogontherii* (Dubrovo, 1964, 1977; Lister, 1996), and was codified as the advanced subspecies *M. meridionalis tamanensis* Dubrovo. However, both plate number and hypsodonty index of M3 are distributed bimodally, suggesting that the sample was the product of more complex populational processes (Sher, 1999; Lister and Sher, 2001). The possibility of the Sinyaya Balka assemblage being 'mixed' is difficult to imagine, since all the fossils, with a range of preservation uncorrelated with morphology, were recovered from a deposit which had been reworked, apparently rapidly, en masse (Sher, 1999). Any hypothesis of mixing, while not impossible, would require the unlikely, simultaneous reworking of two separate, differently dated deposits, each extremely rich in elephantid remains.

To these two sites can be added Dorn-Dürkheim 3 (Germany), a lacustrine bone-bed dated by biostratigraphy and palaeomagnetism to c. 800 ka (Franzen et al., 2000). Although this large sample is only partly prepared for study, reappraisal of available material (HvE) indicates both *M. meridionalis* (e.g. M2s with 8–9 plates and hypsodonty index in the upper end of the Valdarno range) and *M. trogontherii* (M2s with 11–12 plates and hypsodonty within the Süssenborn range).

The repeated occurrence of bimodal morphology in mammoth molars at various European sites in this interval, not described for other mammalian taxa, is suggestive of an evolutionary rather than a taphonomic explanation. It is almost impossible to be absolutely certain from a fossil assemblage, however, that two taxa were in the same place at exactly the same time. As discussed by Lister (1996) and Van Essen (2003), populations of *M. meridionalis* and *M. trogontherii* morphology might, for example, have occupied different areas of the European continent for much of the interval 1.0–0.7 Ma, perhaps shifting their distributions seasonally or with short-term climatic cycles and so both coming to be represented in deposits which are to some extent time-averaged. Modern studies show that even a hybrid zone between adjacent populations can move its position through time (Dasmahapatra et al., 2002). If hybridisation did take place between the mammoth populations (see below), periods of geographical overlap between the two morphotypes must have occurred, even if episodically.

Potentially more decisive than simultaneity in a single deposit is a chronological inversion of the two forms, which need not be at a single locality provided dating and correlation are reliable. Such 'inverted' records are predicted by any model (such as allopatry or parapatry) where only part of a species' geographical range undergoes evolutionary transformation (Fig. 1a, c). Although many of the individual sample sizes are small, current evidence suggests that the series of European mammoth populations 'transitional' between typical *M. meridionalis* and *M. trogontherii*, do not follow each other in an orderly chronological succession, but overlap in time (Table 1, Fig. 3). This suggests a complex of populations, some of them possibly at the level of subspecies or species, and implying one or more episodes of geographical separation and independent evolution. The idea of an allochthonous, cladogenetic origin for *M. trogontherii* was first suggested by Azzaroli (1977), on the basis of cranial morphology among the Italian specimens, since skulls of late *M. meridionalis* from Farneta and Scoppito (*M. m. vestinus*) showed exaggerated, specialised features which appeared to preclude ancestry of *M. trogontherii* from this European stock (Figs. 4c, d). Ferretti and Croitor (2001) suggest that the dorsally expanded crania of *M. m. vestinus* might have been a mechanical adaptation linked to very large tusk size. It is unclear, however, whether this was a local phenomenon of a population in the Italian peninsula, or more widespread across Europe, and Palombo and Ferretti (2004) advise caution in its recognition as a subspecies, in view of the small number of preserved skulls of *M. meridionalis*.

Strong support for the origin of *M. trogontherii* morphology outside Europe has come from recent studies of mammoth material in eastern Asia. Sher (1986a) illustrated molars of *M. trogontherii* morphology from the Early Olyorian of NE Siberia (Fig. 2g), dated by palaeomagnetism and microfauna to the interval 1.2–0.8 Ma (Fig. 5). They have high crowns (mean M^3 hypsodonty c. 1.75), and 19–22 plates in M3, similar to typical European *M. trogontherii* from Süssenborn (Lister and Sher, 2001; Sher and Lister, in prep.). The earliest specimens, from below the Jaramillo event, pre-date the appearance of *M. trogontherii* in Europe, and led to the suggestion that this morphology had arisen allopatrically from a population of *M. meridionalis* in NE Siberia, subsequently spreading south and west into Europe (Lister and Sher, 2001). Fossils of *M. meridionalis* are not known from Arctic Siberia, but the mammal fauna of the stage preceding the Olyorian, the Kutuyakhan, is poorly known in general and so far includes small mammals only (Sher, 1986b).

Recently, the description of remains referable to *M. trogontherii* in China, suggests an elaboration of this model. Two molars recovered in situ from lacustrine sediments of the Nihewan Formation at Majuangou, Hebei Province, have high crowns and 17–18 plates in M3 (Wei et al., 2003; Fig. 2f). Based on rodent biostratigraphy, Cai and Li (2003) placed the mammoth horizon at 2.0–1.8 Ma. Since the Majuangou site is stratigraphically lower than the nearby Xiaochangliang site which has been dated by palaeomagnetism to c. 1.36 Ma (Zhu et al., 2001), this provides an upper limit for the Majuangou mammoths (Wei et al., 2003). This suggests a model whereby *M. trogontherii* arose from *M. meridionalis* in China some time in the interval 2.0–1.5 Ma, thence spreading to Siberia by 1.2 Ma (Fig. 5), where it underwent further evolution to more advanced *M. trogontherii* and ultimately to *M. primigenius* (see below). The continental climate of China in the Early Pleistocene, and the existence of steppic as well as forest vegetation (Min and Chi, 2000; Cai and Li, 2003), provide a selective force for the origin of *M. trogontherii,* and a suitable ancestor is available in the form of *M. meridionalis*, known by remains from the Haiyan Formation of the Yushe Basin (2.5–1.9 Ma) (see above; Wei et al., 2003). *M. trogontherii* evidently persisted in China until at least 1 Ma: dental remains attributable to *M. trogontherii* have also been found at the Donggutuo site (1.1 Ma), as well as the Xiaochangliang site (1.36 Ma) (Wei, in prep.). There is no apparent overlap in the ages of dated *M. meridionalis* and *M. trogontherii* in China, consistent with this area being the locus of change.

This hypothesis suggests that the morphology of European *M. trogontherii*, starting from c. 1.0 Ma (Table 1), could be derived from immigrants either from Siberia or from China, or that the latter two regions might have formed an essentially continuous distribution which contributed to European (and other) populations (Fig. 5). The earliest European specimens showing *M. trogontherii* morphology, at Sinyaya Balka on the eastern fringes of the continent, have a low modal value of 18 plates, but this could be derived either direct from an ancestor with plate count centred around this value (like the Chinese specimens), or by founder effect (a small random sample) from the lower end of the range of a more advanced population (like that of the early Olyorian), or, finally, by some introgression from European *M. meridionalis* into an immigrant form such as that of the early Olyorian (Lister and Sher, 2001; see below).

The allochthonous model is best described in terms of the transfer of 'morphology' from eastern Asia to Europe, rather than simple replacement of 'species'. The first stage in the process, the origin of the new form in the East, may well have corresponded to an allopatric or parapatric event under a conventional speciation model. However, as pointed out by Lister and Sher (2001), the complexity of European forms in the transitional period does not support a 'clean' allopatric replacement whereby the European ancestor (*M. meridionalis* of typical form, Fig. 2d) was simply displaced by an incoming daughter species (*M. trogontherii* of typical form, Fig. 2h). First, samples such as Sinyaya Balka and Voigtstedt represent populations of individuals more advanced than Valdarno, and/or more primitive than Süssenborn (Table 1; Fig. 2e). This is evident not only in the mean and range of important characters, but in the existence of individual molars which are 'intermediate' in form between typical *meridionalis* and *trogontherii* in particular characters (e.g. $P = 16$ forms 23% of the Sinyaya Balka sample of M3s, but is absent in the Upper Valdarno and barely exists at Süssenborn: Lister and Sher, 2001). Second, a number of the samples listed in Table 1 include individuals showing a mosaic morphology of, for example, high (*trogontheriii*-like) hypsodonty index but low (*meridionalis*-like) plate number (seen particularly at Voigtstedt, red group: Van Essen, 2003), or vice versa (seen particularly at Sinyaya Balka: Fig. 2e; Lister and Sher, 2001). One interpretation of this finding is that the Sinyaya Balka sample (and possibly the Voigtstedt red group) were the result of genetic mixing between two populations. Such inbreeding could occur in a hybrid zone, which is expected to produce a proportion of mosaic or intermediate individuals as well as those which correspond to the parent populations in all characters; such character distributions are well-known from studies of hybrid zones in modern organisms (Jiggins and Mallet, 2000). In the case of the Sinyaya Balka sample, any such hypothesis would imply either hybridisation between populations already at the 'advanced' end of *meridionalis* morphology and the 'primitive' end of *trogontherii* morphology, or else that the interbreeding had already averaged these metric characters to some extent. An alternative explanation for intermediate and mosaic morphology, corresponding to the traditional interpretation of Sinyaya Balka or Voigtstedt as an anagenetic intermediate, remains theoretically possible, but sits less well with the observed bimodality in key characters which suggests, rather, the contribution of more than one source population.

It is useful to apply a cladistic perspective to the problem. Under this methodology, a close relationship between European *M. trogontherii* morphology and the known eastern populations is the most parsimonious hypothesis, since it requires this form to have evolved only once. Further, the greatest similarity in dental morphology is between typical European *M. trogontherii* and that of the Early Olyorian (Lister and Sher, 2001; Sher and Lister in prep.), which under a cladistic algorithm would identify the NE Siberian population as the closest relative of its European successor. The alternative hypothesis, maintaining an autochthonous origin of *M. trogontherii* in Europe, would require two or three similar, parallel evolutionary events in Europe, China and/or Siberia, and is therefore less parsimonious.

Cladistics would therefore identify the derived morphological features of '*trogontherii*' as synapomorphies uniting Early Pleistocene east Asian mammoths on the one hand, and early Middle Pleistocene European mammoths on the other. Nonetheless, these deductions are based largely on a few metric variables of molar morphology which, viewing elephantid evolution as a whole, are highly susceptible to parallel evolution or the common inheritance of a primitive condition. Choosing between different models of mammoth evolution will be greatly facilitated when other parts of the skeleton become available, especially suitably dated and well-preserved crania from the various regions, allowing the identification of derived characters linking European *M. trogontherii* with either the Asian forms, or endogenous European *M. meridionalis*, or both. Other parts of the skeleton which show interesting transitions from *M. meridionalis* to *M. trogontherii* include the mandible and forefoot (Lister, 1996 and references therein). Unfortunately, there is too little material associated with the major dental samples for a thorough analysis, but available specimens suggest that characters changed in a mosaic pattern, again implying a complex evolutionary and taxonomic scenario. For example, the Edersleben skeleton (near Voigtstedt and of similar age) has a low molar plate count (15 in M3) like *M. meridionalis*, but an 'aserial' carpal structure like *M. trogontherii* (Dubrovo, 1977; Garutt and Nikolskaya, 1988); Ferretti and Croitor (2001) pointed to similar variation in *M. meridionalis* from Italy. The general observation of the shortening and heightening of the mandibular ramus is also subject to variation which does not seem always to correlate tightly with other characters or taxonomic attribution (Lister, 1996; McDaniel and Jefferson, 2003).

Taking all the evidence together, it is likely that the whole Eurasian *M. meridionalis*—*M. trogontherii* complex had a 'metapopulation' structure (a series of populations with greater or lesser degrees of connection between them: Hanski and Gilpin, 1997), and that the transition between the two species in Europe was achieved by input from the East, either in the form of migrating herds, and/or by gene flow without the long-distance movement of individual animals. There must also have been selection in Europe, on an individual and/or population level, resulting ultimately in the dominance of the incoming morphology. Such processes could have been continuous or episodic, and as the Siberian and Chinese evidence illustrates, from various source areas, leading to a complex of morphologies in time and space which are difficult to unravel from the fossil record.

In view of the long-distance movement of individuals or genes from eastern Asia to Europe implied by the above model, considerable interest attaches to mammoth samples from intervening regions. Foronova (1986, 1998, 2001) has described a series of mammoth fossils from deposits of the Kuznetsk Basin, south central Siberia, dated by small mammals and palaeomagnetism. The taxonomic sequence she describes is broadly similar chronologically to that of Europe, with a transition from *M. meridionalis* to *M. trogontherii* around the Early/Middle Pleistocene boundary. This might imply that the eastern populations of *M. trogontherii* morphology, whether in China or NE Siberia, did not spread far west until roughly the time of their appearance in Europe. However, the published sample sizes are small, and Foronova (1998, 2001) comments that the Early Pleistocene *M.* cf. *meridionalis* from the Kuznetsk Basin are advanced in some ways over those of Europe, especially in hypsodonty. While Foronova interprets this in terms of local adaptation in central Siberia, it could, if corroborated, suggest gene flow from further east and a complexity of interaction similar to that found, later, in Europe.

Another sample of interest came from the site of 'Ubeidiya in the Jordan Valley, Israel (Beden, 1986). Dated to c. 1.4–1.5 Ma on the basis of an extensive mammalian fauna (Tchernov, 1987; Belmaker et al., 2002), a sample of mammoth molars is clearly advanced over typical *M. meridionalis.* Several little-worn molars show hypsodonty indices intermediate between the latter and typical *M. trogontherii.* In plate counts, two M^2s reach *M. trogontherii* levels ($P = 11$) while two M_3s are apparently still at *M. meridionalis* level ($P = 14$–15). The M^2s occur slightly higher in the section than the M_3s, but the age difference is thought to be minimal (M. Belmaker, pers. comm.). Whether this represents two taxa or a mosaic morphology is unclear, but in either case, it indicates advancement ahead of Europe, and given the geographical position, further evidence of possible early 'leakage' of advanced morphology from the East.

In the opposite geographical direction, the appearance of mammoths similar to *M. trogontherii* in Japan, in the interval 1.0–0.5 Ma, very likely also represents a migration from China or Siberia. The molars, described by Takahashi and Namatsu (2000), are of rather small size and narrow crown, and are referred to *Mammuthus protomammonteus* Matsumoto, but are in other respects similar to *M. trogontherii*, with typically 19 plates in M3. According to Konishi and Yoshikawa (1999) and Taruno (1999), the species may have made its appearance even earlier, at 1.2 Ma, while Takahashi et al. (2001) indicate dispersal as far south as Taiwan.

5. The origin and evolution of Mammuthus primigenius

Mammuthus trogontherii of typical form persists through the Cromerian Complex and early Elsterian glaciation in Europe (together c. 800–500 ka). Typical woolly mammoth, *M. primigenius*, is best known from the Weichselian (Last) glaciation (c. 100–10 ka). The transition between the two has been the subject of considerable discussion. The majority of authors assume the gradual transformation of a single lineage in Europe, sometimes dividing it chronologically into a series of subspecies. Some researchers, however, have seen a variety of evolutionary levels among European Late Middle Pleistocene mammoths, not necessarily 'advancing' in chronological order, and have suggested a complex multi-population model or even allopatric speciation (Kotsakis et al., 1978; Lister, 1996).

The debate on this issue has been partly clouded by the use of 'lamellar frequency' (LF) as an index of evolutionary change. Very broadly, as the number of plates in mammoth molars increased through time, their packing became denser, and so lamellar frequency increased. But the way in which LF is defined means that it can be influenced not only by the number of plates but also by the size of the tooth (Lister and Joysey, 1992; Lister, 2001). In the formula $LF = N/L$, where N is the number of plates and L the length of molar they occupy, LF will increase if N goes up but also if L goes down. In other words, samples with the same number of plates in the molar will show altered LF if molar size varies.

This effect is particularly significant through the Middle Pleistocene, when European mammoths underwent a marked reduction in body size. Early Middle Pleistocene *M. trogontherii* was of extremely large size, and a progressive size decrease can be measured from there (Süssenborn and Mosbach, c. 600–500 ka), through Steinheim, Germany (c. 350 ka BP), to OIS 7 sites such as Ilford and Brundon, UK, and Ehringsdorf, Germany (c. 200 ka), samples of the latter age being of unusually small molar size (Fig. 2i). It is possible to calculate, from the degree of size reduction alone, the expected compression effect on the plates and hence the expected elevation of LF (Lister and Joysey, 1992). This calculation shows that the LF increase through this part of the sequence (Fig. 6) is due entirely to size reduction; there is no residual effect attributable to increase in plate number. The increase in LF may have had implications in terms of molar function—shearing adaptation is affected by closeness of lamellar packing (Maglio, 1973). But it does not, when caused by size reduction, represent evolutionary change in the morphological or developmental sense. The later, smaller teeth are merely isometrically scaled replicas of the earlier, larger ones. The true pattern of stasis (little evolutionary change) through the Middle Pleistocene is confirmed by plotting P against time, whence it is seen that there is little or no increase through the interval c. 600–200 ka (Lister and Joysey, 1992; Lister and Sher, 2001), the mean remaining constant at around 19 plates in M3 (Fig. 6).

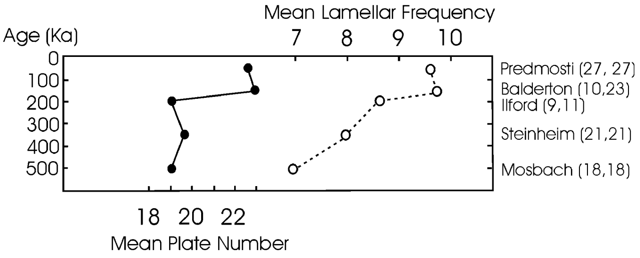

Fig. 6. Plot of mean plate number (P) and lamellar frequency (LF) of M^3s in Middle to Late Pleistocene *Mammuthus* samples from Europe. The stasis in plate number Mosbach—Steinheim—Ilford is evident, while lamellar frequency increases, due to size reduction. Conversely, the further increase in LF between Ilford and Balderton genuinely reflects increased plate number. Sample sizes (P, LF) in brackets.

Adherence to lamellar frequency has also led to debatable biostratigraphic deductions (Lister, 2001). For example, the Late Middle Pleistocene interglacial age (cf. OIS 7, 200 ka) of the Ilford sample (Fig. 6) has been well-established on the basis of geomorphology (Bridgland, 1994), amino-acid racemisation (Bowen et al., 1989) and mammalian biostratigraphy (Schreve, 2001). Its surprising reallocation to c. 82 ka by Vangengeim and Pevsner (2000) is based on an elevated LF which is produced entirely by size reduction.

Since the other main variable in mammoth molar evolution, hypsodonty index, had reached its full and final extent by late *M. trogontherii* c. 500 ka (Lister, 1996), late Middle Pleistocene mammoths in Europe (c. 450–200 ka) resemble typical *M. trogontherii* in both key aspects of molar morphology, hypsodonty and plate count, differing mainly in reduced size (Fig. 2i). In most accounts (e.g. Dietrich, 1912 for Steinheim; Gromov and Garutt, 1975 for Ehringsdorf) this assemblage is regarded as an early form of *M. primigenius*, based on elevated LF. A late survival of *M. trogontherii* was, however, presaged by Dubrovo (1966) in her concept of late Middle Pleistocene '*M. trogontherii chosaricus*', based on a cranium from supposedly Holsteinian to early Saalian deposits (c. 0.4–0.2 Ma) of the Khasar faunal assemblage at Cherny Yar, in the SE of European Russia. As discussed by Lister (1996), the morphology of the cranium is similar to that of *M. primigenius* (Figs. 4e, f), or at most slightly more 'primitive', as are those of other late Middle Pleistocene specimens with '*trogontherii*' dentition such as Ilford, England (Adams, 1887–1881) and Via Flaminia, Italy (Ambrosetti, 1964; Palombo and Ferretti, 2004). However, this may well be true of *M. trogontherii* as a whole; we lack well-preserved crania from the 'typical', early middle Pleistocene stage. In sum, the survival of *M. trogontherii* in Europe until c. 200 ka is not contradicted on current evidence.

After 200 ka, there is a switch in mammoth molar morphology in Europe, to forms of typical *M. primigenius* morphology, with mean plate number of 23 or so in M3. Various samples of OIS 6 age (c. 150 ka) are indistinguishable from those of the Weichselian (last) glaciation. These include Balderton, England (Figs. 2k and 6; Lister and Brandon, 1991); La Cotte, Jersey (Scott, 1986); Zemst, Belgium (Germonpré et al., 1993); and Tattershall Thorpe, England (Holyoak and Preece, 1980); see Lister and Sher (2001, supplement) for stratigraphic details, Pevzner and Vangengeim (2001) for a gradualistic counterargument, and Lister (2001) for a response. Palombo and Ferretti (2004) indicate a similar replacement of late '*trogontherii*'—like mammoths with the first advanced *M. primigenius* at around the same time (OIS 7–6) in Italy.

The presumed gradual transition in mammoth molars through the Middle and Late Pleistocene therefore appears instead rather rectangular in shape, at least in these characters, with a rather sudden replacement of *M. trogontherii* morphology by that of *M. primigenius* some time between c. 200–150 ka, but stasis before and after that date (Fig. 3 of Lister and Sher, 2001). In an earlier account (Lister, 1996), *M. primigenius* was thought to be evidenced in Europe as early as c. 450 ka, and again at c. 300 ka, alternating with more primitive populations such as Steinheim and Ilford. This conclusion was due in part to the use of lamellar frequency, as discussed above, but also to some stratigraphic attributions which have now been altered; in particular, molars from the Homersfield site, England, formerly dated to the Anglian glaciation c. 450 ka, are now regarded as being of later, uncertain date (Schreve, in Benton et al., 2003). According to plate number of currently available samples, *M. trogontherii* morphology appears to have been consistently present in Europe through the interval 600–200 ka (Lister and Sher, 2001).

The pattern of stasis (apart from size) in dental morphology in Europe, first in *M. trogontherii* in the interval c. 600–200 ka, and then in *M. primigenius* c. 200–10 ka, fulfils one of the predictions of the 'punctuated equilibrium' model of evolution (Gould and Eldredge, 1977), and suggests either that the transition between the two was due to very rapid evolution in Europe, or that it represents a replacement event due to immigration from outside. Lister and Sher (2001) showed that NE Siberia is a strong candidate area for the origin of *M. primigenius*. Following the Early Olyorian (1.2–0.8 Ma) presence of *M. trogontherii*, samples dated to the Late Olyorian (0.8–0.6 Ma) show an increase in plate number to 22–24 (Fig. 2j), and by the late Middle Pleistocene (c. 400 ka) a further small but significant increase in both plate number and hypsodonty index to typical *M. primigenius* values (Fig. 3 of Lister and Sher, 2001). This sequence of forms, culminating in full *M. primigenius* morphology some 200 ka before its appearance in Europe, leads to the deduction of an allopatric origin of the species in NE Siberia (or, more broadly, Beringia), followed by its subsequent spread to the south and west (and east into North America). As discussed by Sher et al. (2003), the evolutionary transition was very likely driven by environmental conditions in the Beringian region, for which proxy data indicate a consistently cold, xeric grassland throughout the Pleistocene.

In Europe, a single sample directly suggests the replacement of indigenous *M. trogontherii* by incoming *M. primigenius.* This is from the Lower Channel at Marsworth, England, where the distribution of plate counts is bimodal, the two modes corresponding in morphology to those of earlier *M. trogontherii* and later *M. primigenius* (Fig. 3 of Lister and Sher, 2001). The age of the Lower Channel is regarded, on the basis of biostratigraphy and absolute age measurements, as either late OIS 7 (c. 200 ka), or early OIS 6 (c. 190–160 ka) (Murton et al., 2001). As discussed previously, it is impossible in any situation of 'associated' fossils to be absolutely certain that the two types of mammoth were exactly contemporaneous. They were collected in situ from a single horizon, with no apparent difference in preservation, but the possibility of time-stratigraphic mixing can never be entirely ruled out. If such mixing had occurred, the evidence it might have obliterated is more likely to have been of oscillating population movements (analogous to those discussed above for *M. meridionalis*/*M. trogontherii*) than of the extremely rapid in situ evolutionary change that would be required on an autochthonous model.

There is circumstantial evidence that a complex of populations persisted in Eurasia throughout the Late Pleistocene. Foronova and Zudin (1999) and Foronova (2001) identify thick- and thin-enamel morphs which they believe correspond to warmer and colder habitats, respectively. Among our own material, some Weichselian samples retain molar morphologies reminiscent of *M. trogontherii* (Lister, in prep.); others display a wide range of variation encompassing values typical of both species. For example, at Předmostí (Czech republic), the sample of M3s dated to c. 25 ka has a range of plate counts from 20–27, while in the Lea Valley Gravels, England, of similar age, the range is 20–28 (Lister and Sher, 2001). This could be explained by genetic input from ancestral populations of both *trogontherii* and *primigenius* type. Interestingly, and expected if it is the locus of transformation, such late retention of primitive morphology does not occur in NE Siberia. Instead, Siberian mammoths underwent a further and final increase in plate count between the Late Middle and Late Pleistocene, taking their mean above that of European *primigenius* (Fig. 3 of Lister and Sher, 2001), and presumably forced by the persistently more extreme climatic conditions in NE Siberia than in Europe.

6. Conclusion

Sampling across the whole geographical range of Eurasian mammoths, utilising dating evidence which is independent of the mammoths' morphology itself, and emphasising statistical sample sizes in morphological comparisons, has led to a model of mammoth evolution which appears complex in time and space, but which corresponds to processes understood by evolutionary biologists working on present-day organisms. The key elements of mammoth history in Eurasia which, taken together, point to the geographical model suggested here, are: (1) the appearance of successive stages of evolution earlier in eastern Asia than in Europe, and (2) the complexity of inter- and intra-sample variation, including bimodality, in Europe during the periods of transformation. To these can be added (3) the argument from parsimony, requiring *trogontherii* and *primigenius* morphologies to have each evolved once, rather than twice or more convergently; and (4) the palaeoenvironmental logic, especially for *M. primigenius*, that the adaptive changes occurred in areas of persistently cold, open habitat.

Although many questions remain, the following scenario seems plausible on current evidence (Fig. 5). Elephantids tentatively referred to *Mammuthus* had entered Europe, apparently from Africa, no later than 3 Ma. The earliest stage, *M. rumanus*, spread across Europe and eastwards to China. In the interval 2.6–2.0 Ma, this taxon was replaced by mammoths which were dentally more advanced, *M. meridionalis*, but the details of this transition, including the question of where it occurred and whether by anagenesis or cladogenesis, are unknown. From an indigenous population of *M. meridionalis*, *M. trogontherii* morphology arose in eastern Asia, probably in China, and spread to NE Siberia in the interval 2.0–1.2 Ma. Gene flow or incursion of individuals into Europe occurred from 1.0 Ma or even earlier, progressively supplanting indigenous *M. meridionalis*. This was not a linear process homogeneous across Europe, however, but produced populations at different levels of advancement which were occasionally contemporaneous. The boundaries between different populations moved and on occasion probably met in hybrid zones. European *M. trogontherii* then suffered little change except size reduction in the interval 600–200 ka, but a population in NE Siberia advanced to the *M. primigenius* stage, in turn seeding Europe some time after 200 ka. There is again evidence of a complex interplay between populations in the Late Pleistocene of Europe, and the retention of both *trogontherii* and immigrant *primigenius* genes within them. Overall, in both the *meridionalis–trogontherii* and *trogontherii–primigenius* transitions, the advanced form originated in a peripheral area in a way corresponding to the first stage of an 'allopatric speciation' model, but its subsequent spread more closely approximates a multi-population, gene-flow model.

The fossil record of mammoths undoubtedly represents one of the better-resolved examples of species-level evolution among the vertebrates. This has come about largely because of improvements in excavation technique, dating, and geological correlation. Even so, there are still many uncertainties and unresolved questions, which will only be answered with the accumulation of further dated finds, especially skulls, from across the geographic range of the lineage.

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