The World of Elephants - International Congress, Rome 2001

"Gradual" evolution and molar scaling in the evolution of the mammoth

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SUMMARY: The assumption of gradual, directional change in molar morphology through the mammoth lineage has to be tested using samples dated independently of molar morphology itself. Moreover, lamellar frequency can be a misleading index of evolutionary advancement if molar size is changing at the same time. In the transition from *M. trogontherii* to *M. primigenius* in Europe, gradualistic increase in lamellar frequency is due to size reduction compressing molar plates. Plate number, a better index of evolutionary advancement, shows stasis around c. 500-200 ka BP, followed by a rapid shift to *M. primigenius* morphology.

Mammoths were continuously present in continental Eurasia from c. 2,6 Ma ago until the end of the Pleistocene. During that time they underwent very significant evolutionary change, including a shortening and heightening of the cranium and mandible, increase in molar hypsodonty, increase in plate number, and thinning of molar 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).

This evolutionary sequence, moreover, has frequently been presented as a paradigm of 'gradualistic evolution' (Gould & Eldredge 1977). Adam (1961), for example, assumed a sequence of ever-progressing 'transitional forms' between the three type species. 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. Most recently, Vangengeim and Pevsner (2000) have given an account of European mammoth evolution which represents an extreme case of gradualistic methodology. They take upper third molar samples from eight sites spanning the interval c. 2.5 – 0.02 Ma, and calculate mean lamellar frequency (LF) for each. On the assumption that the evolution of this character follows an 'area-cotangent law', a mathematical curve relating LF to geological age is fitted to three of the samples whose ages are regarded as independently known. The ages of the other samples are then calculated from their lamellar frequencies, using the equation of the curve, and they are plotted on the graph where, of necessity, they all fall precisely along the line. This procedure produces some unexpected ages for well-known Quaternary deposits, for example Mosbach (dated to the early Middle Pleistocene, c. 500 ka: Koenigswald & Heinrich 1999) at c. 270-300 ka; Ilford (dated to OIS 7, c. 200 ka: Bridgland 1994) at 80 ka; Balderton (dated to OIS 6, c. 150 ka: Brandon & Sumbler 1991) at 32 ka.

A feature of these and other studies has been the use of lamellar frequency (or its reciprocal, length-lamellar quotient) as an index of evolutionary progression. 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 & Joysey 1992). In the formula LF = N/L, where N is a 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 (Fig. 1).

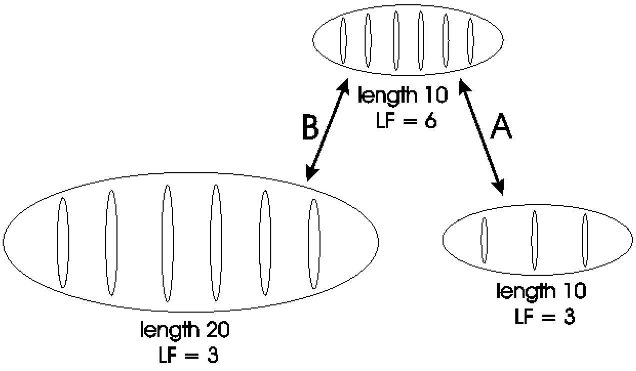

Fig.1 - Diagram illustrating how lamellar frequency (LF) can be altered both by (A) the addition or subtraction of plates, and (B) an increase or decrease in molar size. Lengths given in cm; LFs calculated as the number of plates in 10 cm of crown (10N/L).

A clear example of this is seen in Middle Pleistocene mammoths in Europe. The early Middle Pleistocene *M. trogontherii* was of extremely large size, and a progressive size decrease can be measured from Süssenborn and Mosbach (c. 600-500 ka), through Steinheim (c. 350 ka BP), to OIS 7 sites such as Ilford and Ehringsdorf (c. 200 ka), samples of the latter age being of unusually small molar size. 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 & Joysey 1992). This calculation shows that the LF increase through this part of the sequence (Fig. 2) is due entirely to size reduction; there is no residual effect attributable to increase in plate number.

This pattern of stasis through the Middle Pleistocene can be confirmed by plotting raw plate number (P) against time, based on independently dated samples, whence it is seen that there is little or no increase in P through the interval c. 600-200 ka (Lister & Joysey 1992; Lister & Sher, in press), the mean remaining constant at around 19 plates in M3 (Fig. 2). The increase in LF is a real phenomenon, and 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. Plate number is a more meaningful measure of evolutionary advancement, as it reflects genuine morphological and developmental change. Lamellar frequency can be a valuable index of plate num-

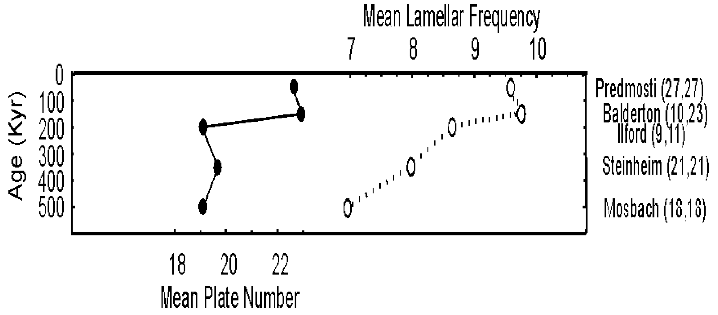

Fig.2 - Plot of mean plate number (P) and lamellar frequency (LF) of M^3s in the *Mammuthus trogontherii – M. primigenius* lineage. The stasis in plate number Mosbach – Steinheim – Ilford is evident, while lamellar frequency increases, due to size reduction. Sample sizes (P, LF) in brackets.

ber, as the latter requires complete molars whereas LF does not and is almost always measurable on a larger sample of teeth. However, it is a reliable index of evolutionary advancement *only if molar size remains constant*, or if size changes can be factored out (Lister & Joysey 1992).

The Late Middle Pleistocene interglacial age (cf. OIS 7, 200 ka) of the Ilford sample has been well-established on the basis of geomorphology (Bridgland 1994), amino-acid racemisation (Bowen *et al.* 1989) and mammalian biostratigraphy (Schreve, in press). Its unlikely reallocation to c. 82 ka by Vangengeim and Pevsner (2000) is based on an elevated LF which, according to our analysis, is produced entirely by size reduction. Plate number, the true index of evolutionary advancement, has remained at *M. trogontherii* levels.

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 *M. trogontherii* in both key aspects of molar morphology, differing mainly in reduced size. In most accounts (e.g. Dietrich 1912 for Steinheim; Gromov & Garutt 1975 for Ehringsdorf) they are regarded as early forms 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 '*Mammuthus trogontherii chosaricus*'.

After 200 ka, there is a switch in mammoth molar morphology, at least in NW 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.

Vangengeim and Pevsner (2000) challenge this finding, focussing in particular on the Balderton sample, since their model requires mammoth molars of this degree of advancement to be considerably younger than the published 150 ka age. They obtained a radiocarbon date of 29,600 +/- 600 BP (GIN-8734) on a mammoth bone from the locality, which fits their expectation of c. 32 ka calculated from lamellar frequency. However, three factors militate against this conclusion. First, the OIS6 age of the Balderton Sands and Gravels is strongly supported by an array of geological and biostratigraphic evidence, including geomorphology (its position in a terrace above Last Interglacial deposits), ESR dating of mammoth molar enamel, and biostratigraphy (fauna including Middle Pleistocene taxa) (Brandon & Sumbler 1991; Lister & Brandon 1991). Second, it is increasingly recognised that radiocarbon ages close to 30 ka can be obtained from samples which are in fact radiocarbon infinite (R.E.M. Hedges, pers. comm.). Third, a series of other European sites, independently dated to OIS 6, have also yielded fully-evolved *M. primigenius*. These include La Cotte, Jersey (Scott 1986); Zemst, Belgium (Germonpre *et al.* 1993); and Tattershall Thorpe, England (Holyoak & Preece 1980).

The presumed gradualistic 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 (little evolutionary change) before and after that date (Fig. 2). Lister and Sher (in press) argue that this rapid changeover in Europe reflects the origin of *M. primigenius* morphology in NE Siberia, followed by its spread to Europe, where it replaced that of *M. trogontherii*.

The danger of assuming a particular pattern of evolution, and then imposing on the data, is that we will never allow the fossils to reveal a pattern of change different from the one expected at the outset. It will also lead to bad biostratigraphy if the 'evolutionary level' of a sample is used to date it on the basis of an untested, preconceived idea of evolutionary trends. The trends have to be established on the basis of independently (geologically) dated samples; they can then be used to determine evolutionary pattern or geological age (Lister 1992).

The extreme gradualist view exemplified by Vanengeim and Pevsner (2000), with a species condemned to evolve 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. How could it be otherwise, if in the constantly changing world of the Quaternary a species managed to maintain an unstoppable, unidirectional evolutionary trajectory? Darwinian natural selection, on the other hand, an essentially externalist concept, would predict complex variations of rate and pattern in such a changeable environment.

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