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Epiphyseal fusion and postcranial age determination in the woolly mammoth *Mammuthus primigenius*

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The long-bone epiphyses of the woolly mammoth fused, as in living elephants, over an extended period of the animal's life. A series of associated male skeletons has been examined, and the state of epiphysis fusion plotted against ontogenetic age determined from dental progression and wear. This shows a consistent sequence of fusion from the distal humerus at around age 10 to the distal radius/ulna at around age 45. The pattern is similar to that of living elephants with a few minor differences. This provides a means of roughly ageing woolly mammoth postcrania when dental remains are unavailable, and also provides data for the investigation of growth patterns among elephantid species. The Columbian mammoth fused its epiphyses in a similar order to the woolly mammoth, but circumstantial evidence suggests that, with a longer lifespan, the successive fusions may have occurred at earlier dental stages.

Epiphyse-vergroeiing en postcraniale leeftijdsbepaling in de wolharige mammoet Mammuthus primigenius – De epiphysairschijven in de wolharige mammoet vergroeiiden, net als bij de recente olifanten, gedurende een lange periode van het leven van de mammoet. Een serie mannelijke skeletten is onderzocht, en de mate van epiphyse-vergroeiing is uitgezet tegen de ontogenetische leeftijd op basis van de gebitsmorfologie. Er blijkt uit dat de vergroeiingen in volgorde plaatsvonden, beginnend bij distale humerus-schijf rond 10-jarige leeftijd en eindigend bij de distale ulna/radius rond het 45e levensjaar. Dit patroon lijkt sterk op dat van recente olifanten. Het levert dus een methode om mammoetskeletten grofweg op leeftijd te brengen wanneer gebitselementen afwezig zijn. Bij de Amerikaanse ('Columbian') mammoet vergroeiiden de schijven in een vergelijkbare volgorde als bij de wolharige mammoet, maar er zijn aanwijzingen dat, als gevolg van een langere levensduur, de verschillende vergroeiingen bij jongere gebitsstadia plaatsvonden.

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INTRODUCTION

Elephants are unusual among mammals in that the skeleton continues to grow well into adult life (Laws *et al.* 1975). As in all mammals, increase in length of the postcranial bones effectively ceases when their epiphyses become fused to the shaft (diaphysis) by ossification of the cartilaginous growth zone which previously separated them. In

elephants, however, this process continues well beyond sexual maturity, and may take up to 30 years to accomplish, as the different epiphyses of the skeleton fuse at different times. It has been shown for living elephants that the different limb bone epiphyses fuse in a fairly predictable order and rate through life, with some differences of pattern between

the two living species (Roth 1984). In the present paper, an attempt is made to establish the order and timing of fusion in an extinct elephantid, the woolly mammoth *Mammuthus primigenius* (BLUMENBACH 1799). This is of interest for two reasons. First, it will enable comparison of growth patterns between mammoths and the two living elephant species, ultimately helping to explain the ontogeny of their different body forms. Second, it will enable the state of epiphysis fusion to be used as a proxy for age determination in mammoth postcranial fossils.

MATERIALS AND METHODS

The essential methodology of this study is to utilise a series of complete or nearly-complete mammoth skeletons (*Mammuthus primigenius*), of differing ontogenetic ages determined from associated dentitions (Tables 1 & 2). It is therefore possible to plot the progression of epiphysis fusion through life. The yardstick of ontogenetic age used in this study, as in many previous studies of fossil elephantids, is the stage of tooth eruption and wear, by comparison with the known patterns of dental progression in living elephants (Laws 1966,

Table 1 Mammoth skeletons utilised in this study. Key to collections: DMH, Dick Mol, Hoofddorp; GML, Geological Museum, Lausanne; GPIUM, Geologisch-Palaeontologisch Institut, Münster; ISEAC, Institute for the Systematics and Evolution of Animals, Cracow; IQW, Institut für Quartärpaläontologie, Weimar; MNHN, Museum National d'Histoire Naturelle, Paris; MZM, Museum of Zoology, Moscow; NMWC, National Museum of Wales, Cardiff; PIN, Palaeontological Institute, Moscow; RSB, Rathaus, Siegsdorf, Bavaria; SMN, Schloss Monrepos, Neuwied; SMNS, Staatliches Museum, Stuttgart; ZIN, Zoological Institute, St. Petersburg.

Site	Country	Collection	References
Arlow	Ukraine	ISEAC	Medvedev 1959
Alfoche	Russia	DMH	-
Bessunyka	Russia	ZIN	Zakovsky 1993
Bozovozu	England	GPIUM	Laws 1966
Chesovka	Belarus	DMH	Adri 1986
Cyca II	Russia	ZIN	Medvedev 1972, Gerasim 1981, p. 35
Elzevaya	Russia	ZIN	Vertebrate & Zoology 1987
Lou II	Russia	ZIN	Tobias & Gerasim 1984, Gerasim 1986, p. 12-17
Ludlow Is.	Spain	MNHN	Yakovlev 1964, Coppens 1968
Mudjanyakh	Russia	ZIN	Kutsumov 1962, Gerasim 1981, p. 36
Neumack-Nord	Germany	DMH	R. J. Wallis, 1982, 1983
Pala	Germany	DMH	von Sarnowskij 1970
Pre-Rosta	Soviet Union	GML	Wentmann 1965
Reas, Deyach	Russia	ZIN	Medvedev 1969, Gerasim 1964, p. 25-16
Roch	Russia	DMH	Medvedev 1967
Sarguel	Germany	DMH	Ziggen 1991
Sarona	Ukraine	ISEAC	Nicolajewski 1974
Sarshina	Ukraine	ISEAC	Medvedev 1972
Teitel	Russia	ZIN	Gerasim & Pospelov 1973
Verzigi beam	Italy	DMH	Sighe 1985, p. 17
Walden	Russia	ZIN	Tobias 1982

Table 2 State of epiphysis fusion in skeletons of *Mammuthus primigenius*. Site details and references in Table 1. Gender indicated only where certain (Lister 1996b). Condover includes a male and a female, each aged six, with identical epiphysis states. Tooth eruption and wear: **e** early; **m** middle; **l** late; **v** very; **-** to. Age classes based on Laws (1966). African Equivalent Years based on Laws (1966), Jachmann (1988), Haynes (1991). Asian Equivalent Years based on Roth & Shoshani (1988). Epiphyses: **O** unfused; **(X)** fusing or recently fused; **X** fused; **-** fusion state not visible.

Locality	Sex	Dental Stage	Laws' age class	Dental age (African EY)	Dental age (Asian EY)	Dist hum	Prox tibia	Dist tibia	Prox ulna	Dist fem	Prox hum	Prox scap	Prox fem	Dist rad	Dist ulna
Condover	M+F	dP4	VII	6	6	O	O	O	O	O	O	O	O	O	O
Neumark-Nord	M	-	-	-	-	(X)	O	O	O	O	O	O	O	O	O
Yuribei	F	M1	XI	12	11-13	(X)	O	O	O	O	O	O	O	O	O
Gewande	M	-	-	-	-	X	O	O	O	O	O	-	O	O	O
Starunia		M2 (e-m)	XV-XVI	22	23-27	-	O	O	-	O	-	-	-	-	-
Condover	M	M2 (m-l)	XVIII	26	28	X	X	X	O	O	O	O	O	O	O
Ahlen	M	M2 (l) - M3 (e)	XX	34	31-33	X	X	(X)	X	(X)	O	O	O	O	O
Khatanga		M2 (vl) - M3	XXII	39	37-39	X	X	X	X	X	O	O	O	O	O
Praz Rodet	M	M2 (vv1) - M3	XXIII-XXIII	41	40-46	X	X	X	X	X	(X)	?X	O	O	O
Mochovaya R.		M3 (e-m)	XXIII	43	44-48	X	X	X	X	X	X	X	O	O	O
Yenisei basin	M	M3 (m)	XXIII-XXV	43-47	45-50	X	X	X	X	X	X	(X)	?O	O	O
Allaicha	M	-	-	-	-	X	X	X	X	X	X	(X)	(X)	O	O
Taimyr	M	M3 (m)	XXIII-XXV	43-47	45-50	X	X	X	X	X	X	(X)	(X)	O	O
Steinheim	M	M3 (m)	XXIII-XXV	43-47	45-50	X	X	X	X	X	-	-	X	O	O
Lena R.	M	M3 (m)	XXIII-XXV	43-47	45-50	X	X	X	X	X	X	X	X	X	X
Gyda R.	M	M3 (lm)	XXIV-XXV	45-47	45-50	X	X	X	X	X	X	X	X	X	(X)
Siegsdorf	M	M3 (m-l)	XXVI	49	>52	X	X	X	X	X	X	X	X	X	X
Sanga-Jurjach	F	M3 (l)	XXX	60	>55	X	-	-	-	X	X	-	X	-	-
Polch	M	M3 (vl)	XXX	60	>55	-	X	X	-	X	-	-	X	-	-
Sievsk	F	M3 (vv1)	>XXX	>60	>55	X	-	-	X	X	X	-	X	X	X

Roth & Shoshani 1988). Some details of this methodology will first be provided.

The living species, and all fossil elephantids as far as can be determined, share a horizontal progression of six molariform teeth which are anatomically dP2-dP4 and M1-M3, although some authors name them M1-M6 for convenience. The identity of the teeth in a given mandible or skull can generally be determined from the size, shape and plate number, though problems occasionally arise in separating dP4 from M1 or M1 from M2 (Musil 1968, Sher & Garutt 1985). Published schemes of ageing, based on the living elephants, rely on the identity of the teeth in use, the number of enamel plates in wear, and the deduced number of plates lost anteriorly or still unworn posteriorly. The pioneering study on African elephant (*Loxodonta africana*) was undertaken by Laws (1966), but was subsequently found to overestimate ages in mid-

life, so has been refined by Jachmann (1988) and Craig (Haynes 1991). A scheme for the Asian elephant (*Elephas maximus*) was presented by Roth & Shoshani (1988).

The mammoth skeletons were aged on their mandibular dentitions, independent estimates being obtained using Laws' (1966) and Jachmann's (1988) African elephant scheme on the one hand, and Roth & Shoshani's (1988) scheme for Asian elephant on the other. Since mammoths have many more enamel plates in each molar than African elephants, the number of plates worn in each age class of the African elephant scheme was converted to a proportion of the total plate count for use with mammoth teeth. For example, Laws' (1966) scheme indicates a total of 9 plates in a typical M2 of *L. africana*, whereas this figure is typically 15 in *M. primigenius*. In Laws' wear stage XXI, seven plates of M2 remain, so for *M. primigenius*, a jaw was

adjudged to be in wear stage XXI if $(15/9) \times 7 = 12$ plates remained. In the case of *E. maximus*, the number of plates per unworn tooth is very similar to that in *M. primigenius* (Maglio 1973, Roth & Shoshani 1988), so the scheme of the latter authors could be directly applied.

The dental stage of the mammoth skeletons, based on mandibular teeth, allowed the specimens to be placed in an order of relative age, and this was then tied to the absolute age scale provided by studies on the living species. As Laws (1966) correctly pointed out, such age estimates are strictly speaking on a relative scale, and he recommended the use of the term 'African Elephant Equivalent Years' (AEY) for age estimates based on his standard *Loxodonta* sequence. However, the ages of the mammoth skeletons are here taken to be similar in an absolute sense to those of the modern samples on which they are based, for two reasons: (1) The body size of Eurasian *M. primigenius*, though itself covering a significant range (Lister 1996a) is similar to that of modern *E. maximus* and *L. africanus*, suggesting a similar total life-span of c. 60 years. With six molariform teeth, of sizes again similar to those of living elephants, it is likely that the absolute ages at which each tooth succeeded its predecessor, was similar. (2) Very similar age estimates were obtained by ageing mammoths using the African elephant scheme on the one hand, and the Asian elephant scheme on the other. Since the two living species are believed to be more distantly related to each other than one of them is to the mammoth (Maglio 1973, Yang *et al.* 1996), it is likely that a similar relationship of age to dental progression is preserved in all three.

RESULTS

The skeletons utilised in this study are listed in Table 1, and the ageing and fusion data shown in Table 2. For each skeleton, the epiphyses of each major limb bone were scored as O (unfused), X (fused to the diaphysis), or (X) (just fusing or recently fused).

The latter condition was scored when the epiphysis and diaphysis were joined by at least some ossified growth, but the line dividing them was still clearly visible. Additional subdivisions of the fusion process, such as those scored by Roth (1984), could not reliably be separated on the fossil material. Care also had to be taken in scoring specimens which had been treated with filler, paint or other substances which tended to obscure the true state of fusion. Other parts of the postcranial skeleton (ribs, vertebrae, pelvic girdle and foot bones) also have epiphyses, but these were not sufficiently preserved on enough skeletons to be scored in the present study.

In Table 2, the skeletons have been ranked in order of dental age, and the different epiphyses listed according to their order of fusion as revealed by this study. One group of six skeletons, all with the last molar in mid-wear, are of similar age to each other and could not be reliably ordered on tooth wear, in part because the tooth crowns were buried in the mandible, making crown height difficult to observe. These specimens have been listed in Table 2 in order of age as suggested by their epiphysis fusion. This does not circularise the deduction on relative ages of fusion of the epiphyses: only three epiphyses fuse within this time interval, and their ordering is quite clear from the postcranial skeletons themselves (proximal femur after proximal scapula, shown by three skeletons; distal radius + ulna after proximal femur, shown by three skeletons). Similarly, three skeletons (Neumark-Nord, Gewande and Allaicha) lack dental remains, but fit conformably within the scheme. Indeed, the entire relative fusion sequence can be deduced without recourse to dental ages. It is significant that it has been possible, through the entire Table, to order the epiphyses such that no skeleton shows a X-O-X or O-X-O pattern. This clearly indicates that the order of epiphysis fusion follows a very regular and constant pattern; this pattern is illustrated in Table 3. The absolute ages of fusion

Table 3 Chart highlighting the similarities and differences in order of epiphysis fusion among the three genera of elephantids. The order of fusion is from left to right. Epiphyses listed in the same box fuse simultaneously. For a diagrammatic presentation of these data, see Lister 1994: fig. 98.

<i>Elephas</i>	dist hum	prox r-u	dist fem, prox tib, dist tib	prox hum	prox fem	dist r-u	prox scap
<i>Loxodonta</i>	dist hum	dist fem, prox tib, dist tib	prox r-u	prox hum	prox fem	dist r-u	prox scap
<i>Mammuthus</i>	dist hum	prox tib, dist tib	prox r-u, dist fem	prox hum, prox scap	prox fem	dist r-u	

of proximal scapula, proximal femur, and distal radius + ulna cannot, however, be accurately determined from the material available. Within the sequence, three pairs of epiphyses seem to fuse at the same time, or at least are inseparable on the basis of the data available. These are the proximal tibia / distal tibia; the proximal humerus / proximal scapula; and the distal radius / distal ulna (cf. Table 2). For the proximal and distal tibia epiphyses, this question can be addressed by looking at large samples of isolated tibiae of different ages. In all *M. primigenius* tibiae observed to date [including the sample of many tens of specimens from Berelekh, Siberia at the Zoological Institute, St. Petersburg (Vereshchagin 1977)], proximal and distal epiphyses are either both fused, or both unfused. No specimen with only one end fused has ever been seen, suggesting that the two epiphyses do fuse at exactly the same age. Fibulae have not been included in Table 2, but where observed on the same skeletons, their fusion state parallels that of the tibiae, to which they are closely associated anatomically. A similar situation pertains to the radius and ulna (Table 2). The data on proximal humerus and proximal scapula is a little ambiguous (Table 2); clearly these two epiphyses fuse at a similar age, but may be separable if further material in the late M2 / early M3 age range becomes available.

SEXUAL VARIATION

An important question which needs to be addressed is whether there are gender differences in growth rate and timing of epiphysis fusion. Among living elephants, males continue to increase in body height to a greater age than females. In *L. africana*, females have largely ceased growth in height by the age of 25, while males continue until around 45 (Laws *et al.* 1975: fig. 8.9). In *E. maximus*, female growth in height asymptotes in the mid-twenties, males in the mid-thirties (Sukumar *et al.* 1988: figs. 1 & 2). This implies that females may fuse their epiphyses at earlier ages than males, and Haynes (1991) shows for *L. africana* that the various long-bone epiphyses fuse anything between 6 and 12 years later in males than females.

The sample used in the present study comprises almost entirely males, determined from body size, skeletal robusticity and pelvic shape (Lister 1996b). Few of the available skeletons are clearly females, and these are either very young with few or no epiphyses fused (Condover and Yuribe) or very old with all epiphyses fused (Sanga Juryach and Sevsk). The scheme outlined in Tables 2 and 3 is therefore a valid representation of fusion sequence in the male woolly mammoth. Further female skeletons of differing ages

(especially in the critical mid-life period) will be required to establish a scheme for the female woolly mammoth, and to determine the extent of differences between the genders.

EXCEPTIONS TO THE RULE

Two skeletons, not included in Table 2, appear to show somewhat anomalous epiphysis fusion (Table 4; see also Haynes 1991). These skeletons, from Beresovka and Liakhov Island, have almost identical dental ages, with M2 in late wear and M3 in early wear, indicating an age of about 39, similar to the skeleton from Khatanga (Table 2). However, unlike the latter specimen, the epiphysis fusion in these two individuals is retarded, with the proximal and distal tibia, and distal femur, still unfused. They are thus about 10 years behind schedule. Tichonov (1997) has suggested that the Liakhov mammoth is only 25-30 years old, based on the supposition that its two teeth are M1 and M2, which he deduces from the length of the occlusal surface in comparison with a sample of *Elephas maximus*. This dental allocation would better fit the unfused state of the epiphyses, but cannot be upheld. In both upper and lower jaws of the Liakhov skull, observed in the Paris Museum, the posterior tooth has 22 plates visible, with more plates buried in the jaw behind. This plate count is well beyond the range of M2 and clearly indicates the third (last) molar.

The reason for the anomalous unfused state of the Beresovka and Liakhov mammoths is unknown. Possibly they result from illness, malnourishment or hormonal malfunction. Hatting (1983) indicates that for sheep, fusion may be delayed by castration. In humans,

fusions that are missed at the normal time because of one of these causes can be delayed a very long time, or may never happen (C. Duhig personal communication). The Liakhov and Beresovka skeletons do, however, show incipient fusion of the proximal ulna, ahead of the tibia (as in *Elephas*: Roth 1984). This sequence, if not due to abnormality in these animals, may suggest that the fusion of the tibia before the proximal ulna (as in *Loxodonta*: Roth 1984, Haynes 1991), clear in the Condover skeleton (Table 2) but observable only on that individual, might not be an invariable rule. Further skeletons of this age range are required.

SPECIES VARIATION

In Table 3, the sequence of epiphysis fusion in *M. primigenius* is compared with that in the two living elephant species (Lister 1994). The three species have many points in common, with a few differences. Distal humerus is the first epiphysis to fuse in all species, followed by both ends of the tibia and then proximal ulna, although the latter two are reversed in *E. maximus*. Proximal humerus is the next to fuse in all species. The most significant difference is that while proximal scapula fuses at around the same time as proximal humerus in the mammoth, this is the very last long-bone epiphysis to fuse in both living species, according to Roth (1984). But all three species agree in the remaining order: proximal femur, then distal radius and ulna.

The only other mammoth species with a sufficiently large number of preserved skeletons to examine order of epiphysis fusion, is the North American *Mammuthus columbi*. Lister (1994) scored a series of partial skeletons from the

Table 4 Two individuals of *Mammuthus primigenius* with retarded epiphysis fusion. Symbols as in Table 2. See text for discussion.

Locality	Sex	Dental Stage	Laws' age class	Dental age (African EY)	Dental age (Asian EY)	Dist hum	Prox tibia	Dist tibia	Prox ulna	Dist fem	Prox hum	Prox scap	Prox fem	Dist rad	Dist ulna
Beresovka	M	M2/M3	XXII	35	37-39	X	O	O	(X)	O	O	O	O	O	O
Liakhov Is.	M	M2/M3	XXII	35	?		O	O	(X)	O	-	O	O	O	O

Hot Springs Mammoth Site, South Dakota and concluded that, so far as the data allowed, there was no difference between the order of epiphysis fusion in *M. columbi* and *M. primigenius*. However, there was circumstantial evidence that epiphysis fusion may occur at earlier dental stages in Columbian than in woolly mammoth. Only two skeletons at Hot Springs have definitely associated dentitions and postcrania, and both show fully fused skeletons at a dental 'age' of about 44-49 AEY, consistent with the woolly mammoth scheme. But eight other associated postcrania also have largely or fully fused epiphyses, in contrast to the total dental sample from the site, which indicates only 6% of individuals with a dental age of 40 AEY or older, and 85% in the 10-29 AEY category (Agenbroad 1994). Unless due to chance taphonomic factors, the situation at Hot Springs may indicate that the relationship of fusion sequence to tooth eruption is different in *M. columbi* and *M. primigenius* (Lister 1994). A possible reason for this could be the larger body size of *M. columbi*. Typical male body weights in this species have been estimated at 10 tonnes, compared to 6 tonnes for *M. primigenius* (Lister & Bahn 1995). Extrapolating from the general rule among mammals (Wootton 1987), this size difference would suggest a significantly longer lifespan for *M. columbi* compared to *M. primigenius*. Suppose that *M. primigenius* lived to c. 60 years (as in living elephants, which are of approximately the same body size), but that *M. columbi* lived to, say, 100 years. The progression of six teeth in the larger species would then be 'stretched out' over a longer period of time, so that any given dental stage (in AEY) corresponded to a higher absolute age than the same dental stage in the smaller species. Bone growth and fusion might also be expected to

occur later in the larger species, but if this 'stretching out' were less prolonged than that of the dental progression, similar stages of bone fusion would appear at earlier (apparently 'younger') dental stages in the larger species than in the smaller. Some support for this idea is given by the Lange-Ferguson mammoth described by Mol & Agenbroad (1994). This male individual of *M. columbi* has a dental stage of c. 38 AEY, but all of its limb epiphyses are fused, a situation which is not seen in *M. primigenius* until dental ages of c. 47 AEY (Table 2). On the other hand, Haynes (1991) stated that his studies of *M. columbi* and *M. primigenius* indicated that 'the correspondence of fusion to dental stage is nearly identical'. The examination of additional *M. columbi* skeletons with associated dentitions should resolve this question.

CONCLUSION

This study has demonstrated the sequence of epiphysis fusion in the male woolly mammoth, *Mammuthus primigenius*, and related it to absolute age of the animal. This allows rough assessment of individual age to be made from postcranial remains when the dentition is absent. Order of fusion is similar to that in living elephants, with minor differences. There is circumstantial evidence that epiphyses fused at earlier dental stages in *M. columbi* than in *M. primigenius*, perhaps because of a longer life-span in the former species.

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