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Cement Furrows in the Dentition of *Mammuthus primigenius* and the Question of their Etiology

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Abstract**.** Linear furrows have been documented in the crown cement of *Mammuthus primigenius* molars from the late Pleistocene archaeological sites of Kraków Spadzista Street (B), Poland and Vogelherd, Germany. The high frequency of cement defects on these assemblages, 50% and 74% of the molars respectively, and on other fossil proboscidean teeth from Eurasia warrants investigation into their etiology. One possible cause of the furrows is a developmental defect such as hypoplasia, due to periodic physiological stress; such a causal factor could have broad implications for the life history of woolly mammoths. Other potential origins of the furrows include cement decay from infection or impaction of material in the gums and resorption of tooth cement. Apart from cause, the morphology of the cement furrows reflects regular rhythms of seasonal or annual formation.

Keywords. *Mammuthus primigenius*, tooth defects, Kraków Spadzista Street (B), Vogelherd, Pleistocene.

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I. INTRODUCTION

Cement furrows are exhibited in high frequencies in the molars of *Mammuthus primigenius* (BLUMENBACH, 1799) from the archaeological localities of Kraków Spadzista Street (B), Poland and Vogelherd, Germany. These defects are visible as thin bands in the upper crown cement, located most often on the lingual aspect of the tooth but often on other portions as well. Single furrows predominate but as many as four have been documented. The exact cause of these cement furrows is not clear but several possible causal factors are discussed here.

The mammoth dentition consisted of six sets of molars in their lifetime. New molars grew in and pushed worn ones out, with each successive molar becoming larger and in use for longer amounts of time. Constructed of enamel plates held together by cement, mammoth molars are characterized by high crowns that are adapted to their abrasive diet. Cement is deposited around the crown as the tooth develops and like other dental tissues, cement is layered in seasonal, monthly, or annual increments (GUENTHER 1955; KOCH et al. 1989; FISHER 2001). The long development period and use of the adult mammoth teeth in particular record a substantial window of the individual's life history, a detail that is applicable to this study.

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II. THE SITES AND MAMMOTH ASSEMBLAGES

The Kraków Spadzista Street (B) site is located on the top of Saint Bronisława hill (252 m asl) on the city limits. Discovered in 1967 and subsequently excavated in several campaigns over the past thirty years, Kraków Spadzista Street (B) is part of a larger archaeological complex consisting of five Upper Palaeolithic localities approximately 100 m from each other (KOZŁOWSKI et al. 1974; SOBCZYK 1995). Stone artifacts recovered in association with the mammoth assemblage belong to the Kostenki-Avdeevo type and radiocarbon assays of ca. 21 ka B. P. place the site in the Gravettian cultural complex of the Upper Palaeolithic (KOZŁOWSKI et al. 1974).

The archaeofauna from the site is made up of the remains of woolly mammoth (NISP = 5860) with the exception of 15 identified specimens from other Pleistocene taxa (LIPECKI & WOJTAL 1996; WOJTAL 2001). All skeletal elements are represented, including small and fragile hyoids, foetal limb bones, milk molars, and one milk tusk. A minimum number of individuals (MNI) was estimated at 71 based on lower molars, with 42% of individuals in the youngest age class (0-12 years) and other age classes represented in decreasing proportions (LIPECKI & WOJTAL 1996; WOJTAL 2001). Scarce butchery traces, extensive carnivore gnawing, and the representation of all skeletal elements suggest that the Kraków Spadzista Street (B) mammoths died in the place of their deposition. It is not clear whether these mammoths perished through natural causes, human hunting, or a combination of these factors.

The Kraków Spadzista Street (B) mammoth molar assemblage consists of 338 specimens including 55 mandibles. Many of these mandibles contain two or more teeth in alveolar bone. Of this total, 259 upper and lower molars were examined for the presence of cement furrows, while the remainder either have no cement due to poor preservation or were fragments and therefore not included in the quantification of defects. Cement furrows are visible on 50% (n = 130) of the molars and were observed on examples from the second milk molar to the third permanent molar (Table I, Figs. 1a, 1b). They are exhibited on both the lingual and buccal aspects of the teeth and notably, in some cases, on both aspects of the same molar (Figs. 1c, 1d). Six lower molar examples (M_1 and M_2) show furrows on their posterior ends and several specimens that are unworn or just beginning to wear also exhibit furrows (Fig. 2a). Overall, fewer upper molars contain cement furrows but this might be due to the smaller sample size of these cheek teeth (n = 103).

Vogelherd is one of several Palaeolithic cave sites located in the extensive limestone karst system of the Lone Valley in southwestern Germany. The cave was completely excavated in 1931 by Gustav Riek (RIEK 1934) and produced an enormous stone, bone, and ivory tool industry, early modern human remains, artwork in the form of ivory figurines, and a rich archaeofauna reflecting a broad spectrum of Pleistocene species. The largest deposit dates to the Aurignacian cultural complex with dates ranging from 29-36 ka B. P. (CONARD in press) and contains ~17,000 faunal specimens. *Mammuthus primigenius* is abundant in this deposit, with 28 individual animals represented by maxillary and mandibular molars (n = 147) and 12 individuals by skeletal bone (n = 770). Juvenile mammoths are most frequent, followed by relatively few old adults and smaller numbers of prime aged adults (NIVEN 2001). The remains of mammoth were transported by humans to Vogel-

Table I

Frequency and location of cement furrows on the Kraków Spadzista Street (B) mammoth molars

	N[1]	with furrows n (%)	Lingual n (%)	Buccal n (%)	Lingual/buccal n (%)	Proximal n (%)	Distal n (%)
dP_3	18	7 (38,9)	1 (14,3)	–	6 (85,7)	–	–
dP_4	28	16 (57,1)	6 (37,5)	7 (43,8)	3 (18,7)	–	–
M_1	45	25 (55,6)	7 (28)	11 (44)	6 (24)	1 (4)	–
M_2	36	23 (63,9)	5 (21,7)	5 (21,7)	8 (34,9)	5 (21,7)	–
M_3	14	10 (71,3)	5 (50)	1 (10)	4 (40)	–	–
dP^3	12	5 (41,7)	3 (60)	1 (20)	1 (20)	–	–
dP^4	1	1 (100)	–	–	–	–	–
M^1	17	13 (76,5)	10 (76,9)	1 (7,7)	2 (15,4)	–	–
M^2	17	9 (52,9)	6 (66,7)	–	2 (22,2)	1 (11,1)	–
M^3	14	4 (28,6)	2 (50)	1 (25)	1 (25)	–	–
unid.	57	17 (29,8)	3 (17,6)	4 (23,5)	10 (58,9)	–	–
Total	**259**	**130 (50)**	48 (36,9)	31 (23,8)	43 (33,1)	7 (5,4)	–

[1] N (of total assemblage) that were examined for cement furrows; this number does not include tooth fragments or specimens lacking cement due to preservation or damage, first milk molar, or milk tusks.

herd cave, with the possible exception of infantile or juvenile individuals that also could have been carried in by large carnivores. However, similar to Kraków Spadzista Street (B), the role of humans in the deaths of these mammoths is not clear.

Nearly all of the Vogelherd mammoth molars are isolated with the exception of one complete mandible and several specimens with portions of alveolar bone attached. Of the 147 molars, 61 were coated with enough cement to potentially exhibit furrows; first milk molars, milk tusks, and highly fragmented specimens were excluded. Of this total, cement furrows were documented on 74% (n = 45) of the specimens (Table II). The furrows are found in single or double bands ranging from well-

Table II

Frequency and location of cement furrows on the Vogelherd mammoth molars

	N[1]	with furrows n (%)	Lingual n (%)	Buccal n (%)	Lingual/buccal n (%)	Proximal n (%)	Distal n (%)
dP_3	3	1 (33,3)	–	1 (33,3)	–	–	–
dP_4	3	3 (100)	1 (33,3)	–	2 (66,7)	–	–
M_1	5	5 (100)	3 (60)	–	2 (40)	–	–
M_2	2	1 (50)	1 (100)	–	–	–	–
M_3	8	8 (100)	3 (37,5)	–	4 (50)	–	1 (12,5)
dP^3	3	1 (33,3)	1 (100)	–	–	–	–
dP^4	3	3 (100)	1 (33,3)	–	2 (66,7)	–	–
M^1	4	2 (50)	1 (50)	1 (50)	–	–	–
M^2	1	1 (100)	1 (100)	–	–	–	–
M^3	17	13 (76,5)	11 (84,6)	1 (7,7)	1 (7,7)	–	–
unid.	12	7 (58,3)	3 (42,9)	2 (28,6)	1 (14,3)	1 (14,3)	–
Total	**61**	**45 (73,8)**	26 (57,8)	5 (11,1)	12 (26,7)	1 (2,2)	1 (2,2)

[1] N (of total assemblage) that were examined for cement furrows; this number does not include tooth fragments or specimens lacking cement due to preservation or damage, first milk molar, or milk tusks.

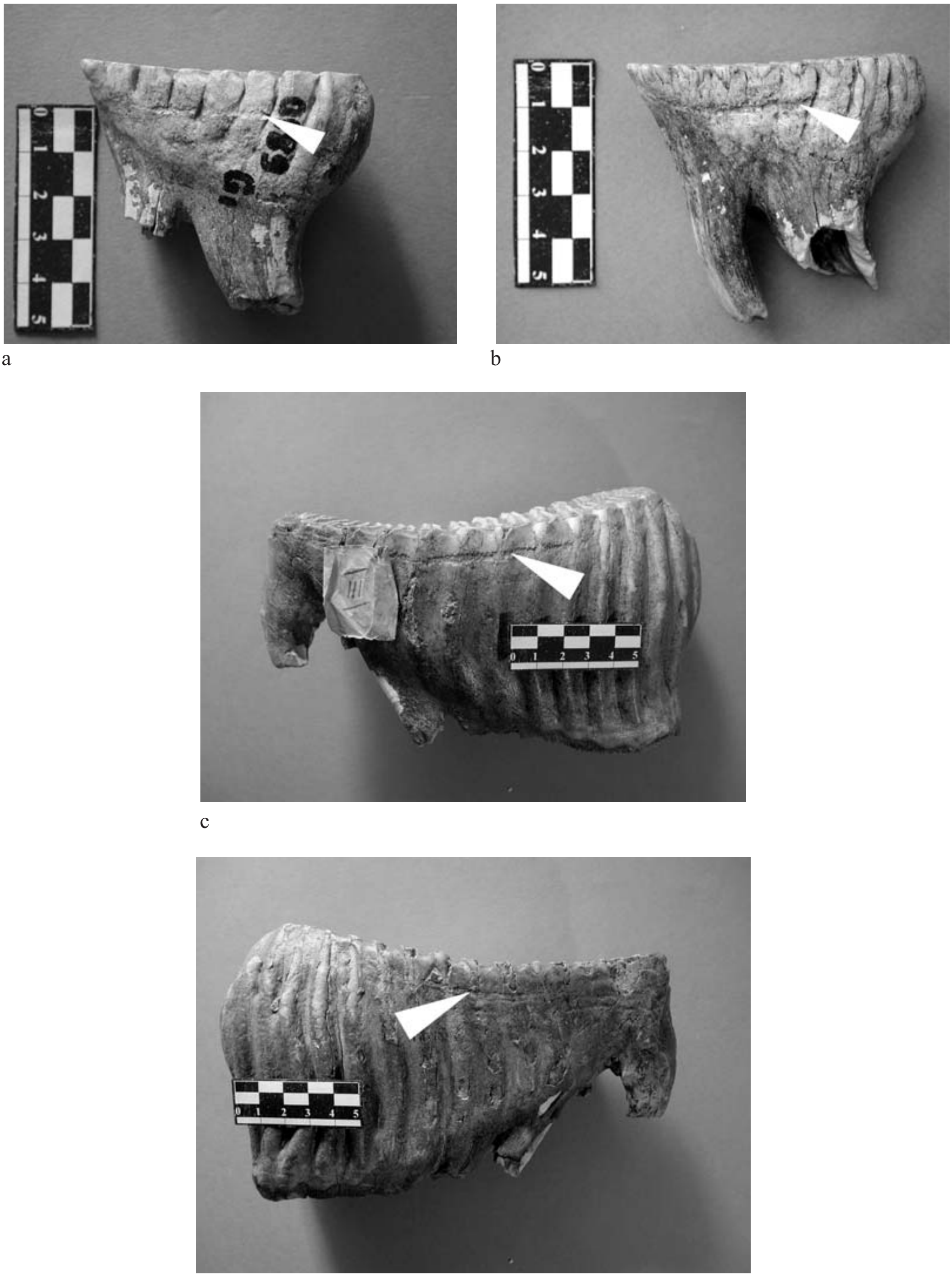

Fig. 1. a – Kraków Spadzista Street (B): right mm_2 with cement furrows on lingual aspect; b – Kraków Spadzista Street (B): left mm_2 with cement furrows on buccal aspect. This specimen belongs to the same individual as that shown in Fig. 1a; c – Kraków Spadzista Street (B): right M_2 with cement furrows on both aspects of the tooth crown, lingual aspect shown here; d – Kraków Spadzista Street (B): right M_2 (same as in Fig. 1c) with cement furrows on both aspects of the tooth crown, buccal aspect shown here.

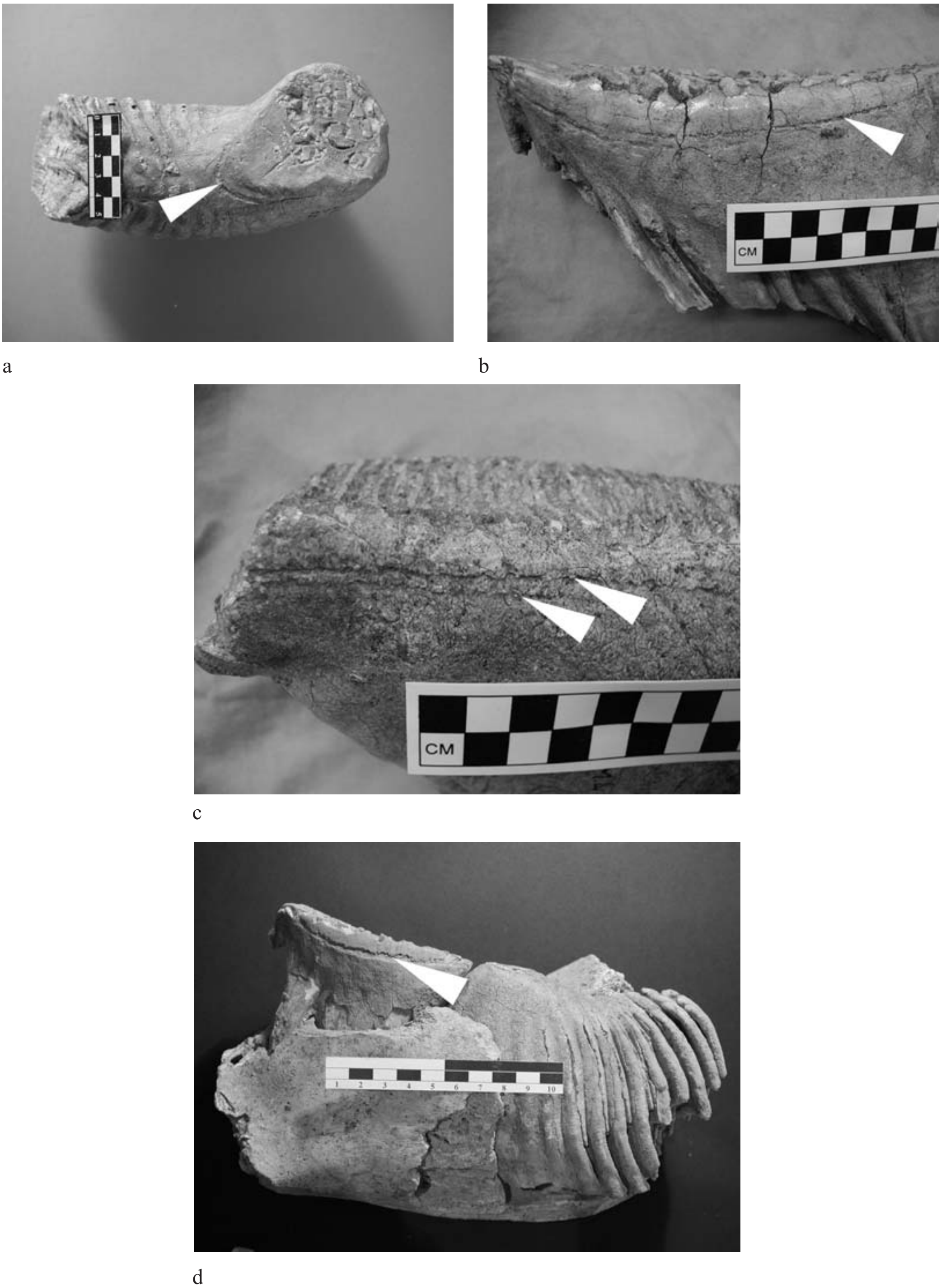

Fig. 2. a – Kraków Spadzista Street (B): right M_3 with cement furrows on posterior aspect; b – Vogelherd: left M_3 with cement furrows on lingual aspect; c – Vogelherd: left M^3 with cement furrows on lingual aspect; d – Kraków Spadzista Street (B): mm_3 and M_1 in alveolar bone, with well-developed cement furrows on lingual aspects.

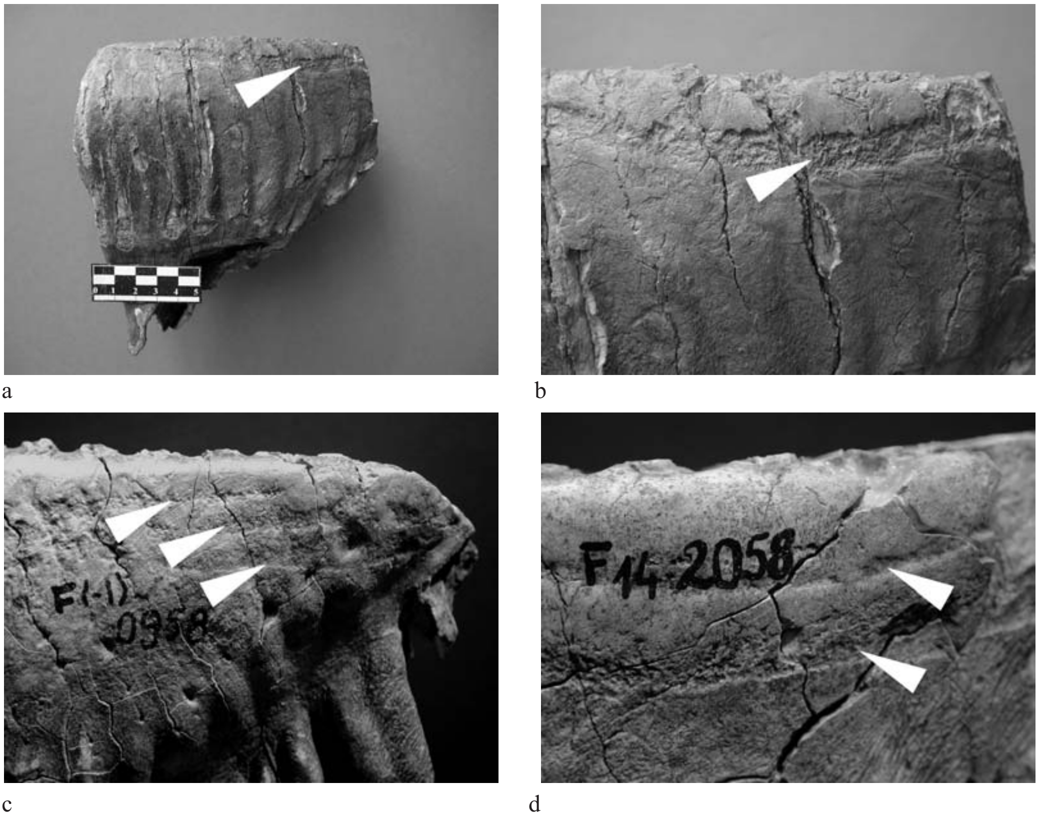

Fig. 3. a – Kraków Spadzista Street (B): left M_3 with particularly wide cement furrow (~ 1 cm) on lingual aspect; b – Closeup of molar in Fig. 3a; c – Kraków Spadzista Street (B): closeup of molar with triple cement furrows; d – Kraków Spadzista Street (B): closeup of molar with double cement furrows.

formed grooves (~ 1,5 – 4 mm width) to wider, more subtle bands (~ 4,5 – 8 mm width) (Figs. 2b, 2c). The furrows formed primarily on the lingual aspect of the teeth but are also visible on the buccal, distal, and proximal aspects. Occasionally furrows are discernible around the entire tooth crown but not always in equal distances from the occlusal surface. The defects do not seem to favor any particular tooth (e.g., upper M^3) but are more common on adult molars.

There are some notable differences in morphology and location of furrows between the Kraków Spadzista Street (B) and Vogelherd molars. Several of the Kraków Spadzista Street (B) molars exhibiting furrows are unworn or just beginning to wear. The furrows appear more strongly developed on many of the Kraków Spadzista Street (B) specimens (Fig. 2d, Figs. 3a-d) although this observation has not yet been methodically documented. It is not surprising that the Kraków Spadzista Street (B) assemblage shows more variation in morphology and location of furrows than the Vogelherd molars, since the former is a much larger sample. The distinct characteristics of each assemblage might also be a factor of the etiology of the furrows.

III. TOOTH DEFECTS: FORMS AND ETIOLOGY

Hypoplasia is a defect in the growth of tooth tissue and is thought to represent a visual record or general systemic stress and nutritional status of an individual or group of individuals (GOODMAN & ARMELAGOS 1985; SKINNER 1996). Although numerous factors may be involved, such as disease, vitamin or mineral deficiency, or ingestion of toxins (HILLSON 1986; NEIBURGER 1990), nutritional stress during the formation of the tooth is thought to be the most common cause. Hypoplasia is most often seen in tooth enamel and is exhibited in linear furrows, small pits, or patches (HILLSON 1986). Although these forms of hypoplasia can be seen with the naked eye or under minimal magnification, these defects are also marked on a microscopic level (HILLSON & BOND 1997).

Most of what is known about hypoplasia comes from extensive research on human dentition but a body of work conducted on fossil and extant nonhuman primates has expanded our knowledge of these tooth defects (e.g., MACHO et al. 1996; SKINNER 1996; GUATELLI-STEINBERG 2001; LUKACS 2001). In addition, studies of enamel hypoplasia in domestic suids (DOBNEY & ERVYNCK 2000), rhinoceros (*Teleoceras*) (MEAD 1999), giraffe (*Sivathere*) (FRANZ-ODENDAAL et al. n.d.), and North American bison (WILSON 1988; NIVEN 2000) have revealed information on the life histories of these animals.

Tooth cement is a bone-like tissue (HILLSON 1986:9) that is layered in increments from the upper crown moving towards the roots of a proboscidean molar, a process that continues throughout the life of the molar resulting in a rugged jacket (GUENTHER 1955). Deposition of cement in all mammals seems to follow an annual rhythm although increments are not necessarily of the same amount, which might be related to the degree of tooth wear or other systemic factors (GUENTHER 1955; HILLSON 1986). Proboscidean dental tissues reflect seasonal variation, repeated annually, in their deposition and these increments in tusk and tooth dentine have been successfully analyzed for their life history information (KOCH et al. 1989; FISHER 2001).

Defects of various types are relatively common in mammalian teeth, including such forms as developmental defects, caries, malformations, and malocclusions. Detailed discussions of tooth defect forms and etiology can be found in HILLSON (1986) and MILES and GRIGSON (1990), the latter focusing on animals. Tooth defects in mammoths have been discussed primarily by GUENTHER (1955, 1956) and KUBIAK (1965) with much attention given to deformities, tumors, and malocclusion. In addition to these authors, other researchers have noted the presence of furrows in Eurasian mammoth molars (Table III). German paleontologist Ekke Guenther documented linear furrows in the cement on molars of several species of fossil proboscideans and discussed their morphology and possible causes (GUENTHER 1955, 1956). He noted that the furrows varied in width, depth, and length as well as location on the tooth; that in some cases, multiple furrows were exhibited but seldom more than four; there were differences in distance from the furrow to occlusal surface, depending on which side of the molar; and that a series of pits, as opposed to furrows, were sometimes present. Guenther remarked that the furrows appear in rhythmic, regular distances on the majority of examples, which he thought could be caused by physiological changes such as infectious disease of the intestine that inhibits metabolism of calcium and results in persistent deficiency of this needed mineral; stress of pregnancy and associated metabolic changes; or general nutritional deficiency (GUENTHER 1955:30-32). The influence of climate on both biological rhythms and food availability/quality is also discussed. For instance, cold periods would have brought sand and dust that was ingested with forage and resulted in a faster rate of tooth wear in mammoths. According to GUENTHER (1955:35), the teeth respond to this abrasion through an increase in cement deposition, but when the forage quality improves during another season, tooth wear decreases and so does cement deposition. Such cycles might be one cause of irregularities in the layering of cement that Guenther saw in thin sections of *Palaeoloxodon antiquus* molar (GUENTHER 1955:30).

Using Guenther's ideas as a foundation, we suggest additional factors that might have caused physiological changes in mammoths, which in turn affected cement deposition on their molars. A dietary dependence on several macro- and microelements, especially sodium, is known to drive large herbivores to locations where they can replenish their deficiencies (MILEWSKI & DIAMOND 2000); modern African elephants are often found around sodium sources (REDMOND 1982; MOSS 1988; HAYNES 2001) and connections between fossil proboscidean bone deposits and mineral sources have been demonstrated (ABRACZINSKAS 1994; DEREVIANKO et al. 2000; LESHCHINSKIY 2001). Such evidence suggests that mammoths did suffer from occasional – probably seasonal – mineral deficiencies, a condition that can lead to metabolic and reproductive disorders and even

Table III

Paleontological and archaeological localities with reference to cement furrows in proboscidean molars

Site	Taxon	Reference(s)
Achenheim-Hangenbieten	*Mammuthus primigenius*	GUENTHER 1971
Bilzingsleben	*Palaeoloxodon antiquus*	GUENTHER 1991b
Burgtonna	*Palaeoloxodon antiquus*	GUENTHER 1978
Ehringsdorf	*Palaeoloxodon antiquus*	GUENTHER 1975
Kärlich	*Palaeoloxodon antiquus*	TURNER 1990; GAUDZINSKI 1997
La Brea	*Mammuthus primigenius*	GUENTHER 1987
La Brea	*Mammuthus imperator*	GUENTHER 1987
La Brea	*Mammuthus columbi*	GUENTHER 1987
Mosbach	*Mammuthus trogontherii*	GUENTHER 1968, 1969a
Mosbach	*Palaeoloxodon antiquus*	GUENTHER 1968, 1969a
Předmostí	*Mammuthus primigenius*	MUSIL 1968
Salzgitter-Lebenstedt	*Mammuthus primigenius*	GUENTHER 1981, 1991a
San River – Jarosław	*Palaeoloxodon antiquus*	KUBIAK 1965
Süßenborn	*Mammuthus trogontherii*	GUENTHER 1969b
Taubach	*Mammuthus primigenius*	GUENTHER 1977

death in other ungulates (JONES & HANSON 1985; MILEWSKI & DIAMOND 2000). Enamel hypoplasia in fossil and modern humans has been attributed to vitamin and mineral deficiencies (SKINNER 1996; GUATELLI-STEINBERG 2001), suggesting that similar deficiencies in needed nutrients could disrupt tooth development in other mammals.

Stress of pregnancy would have affected both cows and calves. Pronounced physiological stress is thought to be the cause of enamel hypoplasia formation in Miocene rhinoceros (*Teleoceras*) at the time of birth or just before birth (MEAD 1999). Such stress on mammoth calves might only be visible at a microscopic level, since the milk molars would not yet be coated in cement, but microscopic examination of mammoth milk teeth for defects in the enamel would be a worthwhile pursuit. Other reproductive factors that could induce systemic stress are periods of musth, when male proboscideans seek mates and often fight and decline in physical condition (MOSS 1988).

Poor food availability/quality or shortage of water during periods of drought, severe cold, or normal seasonal fluctuations during both glacial and interglacial periods were likely factors behind periodic metabolic stress in mammoths. Both cold and warm stage mammoths exhibit cement furrows on their teeth (see Table III) although we have little to no data from North American taxa (see GUENTHER 1987). Paleoclimatic data indicate a wildly fluctuating climate during much of the late Pleistocene. For example, OIS 3, the climate interval in which the Vogelherd mammoth assemblage was deposited, included frequent (~100-1000 years) cycles of warm to full glacial conditions (VAN ANDEL 2002:2) and aridity was especially severe during glacials (HOPKINS et al. 1982; GUTHRIE 1990, 2001; GUTHRIE & VAN KOLFSCHOTEN 2000). Although the "mammoth steppe" vegetation communities of the glacials were productive, it underwent seasonal periods when it was less so (GUTHRIE 1990) and such intervals might have been occasionally severe enough to cause nutritional stress in mammoths and other large grazing mammals. Climate conditions during the last interglacial were often marked by warmer and drier summers (VAN ANDEL & TZEDAKIS 1996; ZAGWIJN 1996), which might have resulted in periodic drought in localized areas. Whether mammoths migrated long distances (300 km) is not clear (GUTHRIE 1990; HAYNES 1991), but it is possible that seasonal fluctuations in food, water, and mineral availability spurred them to travel outside their home ranges to localities where these resources could be found (HAYNES 1991:96). Such nomadic movements would have put additional strain on weak animals, particularly pregnant or lactating females and young. Seasonal or semi-annual changes in climate and subsequent effects on health appear to play a role in many examples of enamel hypoplasia formation in both human and nonhuman primates (MACHO et al. 1996; GUATELLI-STEINBERG 2001), bison, (WILSON 1988; NIVEN 2000) and pigs (DOBNEY & ERVYNCK 2000) and might well have contributed to or caused the cement furrows on mammoths. Additional support for this argument can be found in studies of proboscidean tusk dentine, which reflect seasonal reduction in growth rates that might be environmentally related (KOCH et al. 1989; FISHER 2001).

The possibility of some sort of psychological stress affecting tooth development has only been speculated upon but it warrants further investigation. The strongest example is the Miocene *Teleoceras* (MEAD 1999), which exhibits enamel hypoplasia that formed at three to five years of age, an age that is not associated with a severe nutritional transition such as weaning. MEAD (1999:396) suggests cow-calf separation or exclusion from the herd (males) as possible stressors behind defects of the p4, but remains cautious in his interpretations. Offspring-mother separation and other dramatic social changes in the lives of nonhuman primates were shown to affect enamel development (GUATELLI-STEINBERG 2001:143). Predation pressure by humans or other predators might have been severe enough to cause distress in herd mammals such as mammoths, both in terms of separating closely related members such as cows and calves but also in disrupting feeding.

The above discussion shows that numerous factors can potentially affect the development of teeth in mammals, particularly in the formation of enamel. Deposition of tooth cementum on proboscidean molars occurs in increments and appears to be susceptible to changes in the animals' physiology (GUENTHER 1955). Although hypoplasia formation occurs at a microscopic level (HILLSON & BOND 1997), much of the time these defects are identified with the naked eye or minimal magnification on the visible surfaces of the tooth. Because of the unique morphology and development of proboscidean dentition, the most visible surface is the cement-jacketed crown, which is the location of the furrows. Developmental defects might well be in the enamel lamellae and dentine of proboscidean molars, but that possibility remains to be addressed in future microscopic studies. Whether the furrows seen in the Kraków Spadzista Street (B) and Vogelherd mammoth molars are cementum hypoplasia is not yet clear but there is acceptable support for this possibility.

An alternate possible cause of the furrows might be cement decay from bacterial infection or impaction of material in the gums. Such demineralization of tooth cement results in caries, which can be discernible in lesions, spots, bands, or cavities and is caused by low pH levels in dental plaque after the introduction of certain sugars (HILLSON 1986:283-287) or acidic substances (BAKER & BROTHWELL 1980:146-147). LISTER and BAHN (1994:90) mention dental decay that resulted from gumline bacterial buildup, but it is not clear whether these authors are referring to cementum furrows similar to what is seen on the Kraków Spadzista Street (B) and Vogelherd specimens. LISTER and BAHN (1994:90) discuss the low amount of sugars in mammoths' grass diet and hence the low frequency of gumline decay in a sample of mammoth teeth from Pleistocene Britain. If sugars in the diet caused the cement furrows, this would suggest that other mammoths such as those from continental Europe, including Kraków Spadzista Street (B) and Vogelherd, at times consumed different forage that was higher in sugar content and caused tooth decay. The diet of Siberian mammoths included grasses, sedges, mint, legume pods, poppies, moss, willow, birch, alder, and larch twigs (OLIVIER 1982:296-297; VERESHCHAGIN & BARYSHNIKOV 1982), evidence which shows that diet varied depending on availability and nutritional needs. Studies of extant elephant feeding strategies (OLIVIER 1982; MOSS 1988) also lend support to dietary variability in mammoths.

Another dental disease that afflicts mammals is periodontitis, which can affect cement, gums, and alveolar bone (HILLSON 1986:305-312). In most cases, periodontitis results in the loss of alveolar bone and tooth loss (HILLSON 1986:308), but we have seen no evidence of the former situation in the Kraków Spadzista Street (B) and Vogelherd assemblages, suggesting that periodontitis is not the cause of the cement furrows. Perhaps factors specific to proboscidean dentition and diet during the Pleistocene are responsible for cementum decay. For example, during the more arid stages, mammoths would have ingested more dust and grit, which could cling to the molars or get impacted between the tooth and gums. Additionally, if mammoths consumed bits of minerals or rocks in the process of replenishing their mineral deficiencies, as shown by the presence of minerals in the digestive tract of a Siberian mammoth and other fossil mammals (LESHCHINSKIY 2001), it is possible that traces of this material wedged along the gumline. Impaction of vegetal debris between the tooth and gum is not uncommon in animals but usually causes infection of the soft tissue and not the teeth (BAKER & BROTHWELL 1980); perhaps this situation had different effects in the mouths of mammoths. If the furrows in the mammoth teeth were caused by decay or disease, they would have formed in periodic stages, as the furrows appear to show a seasonal or annual cycle one or more times. This scenario is possible, considering the pronounced seasonality during much of the late Pleistocene and the likelihood of fluctuating forage quality and availability.

The furrows might reflect resorption of tooth cement. This possibility was also proposed by GUENTHER (1955) and KUBIAK (1965) who both attributed it to metabolic disturbances. Although all mammoth teeth begin to be resorbed as they wear, starting with the roots and followed by anterior lamellae, the fact that we do not see furrows on every molar suggests that they did not form through resorption of the cement. Resorption of the lamellae progresses with a seemingly regular pattern and amount, while the cement furrows are formed through brief or restricted periods. We also see furrows on unworn molars that show no other signs of normal resorption. Perhaps in some cases the furrows are actually the first trace of tooth resorption or are occasional occurrences related to an unknown physiological process or external factor. As discussed by GUENTHER (1955:30), even if the furrows are formed through resorption, they developed in a seasonal or annual cycle. This points to some kind of disturbance in cement formation in general, which in turn suggests metabolic changes.

Regardless of the cause of the cement furrows, their morphology reflects fairly regular rhythms of formation. This could be explained by most of the possible causal factors discussed above: fluctuations in both water and forage availability/quality, or vitamin or mineral deficiency; ingestion of grit or debris that was impacted along the gumline and caused erosion of the cement; additions in the diet of forage with a chemistry that resulted in gumline infections and decay of tooth cement; and localized resorption of cement. Considering the studies done on other mammalian dentition showing that multiple dynamics can be involved in developmental defects, a combination of causal factors should not be ruled out.

IV. DISCUSSION

Developmental defects such as enamel hypoplasia affect the teeth of many, if not all mammals and undoubtedly affected mammoths as well; the problem lies in determining whether the cement furrows are a type of hypoplasia or if these defects are recorded elsewhere. Thin sections of tooth enamel and dentine could be examined microscopically to answer this question. Mammoth molars are unique in their morphology and therefore unique in how they record systemic stress. Since the last three molars develop over longer periods of time and are in use for substantial portions of the animal's adult life, they record broad windows of the individual's life history in their hard tissues.

If these cement furrows are a developmental defect caused by systemic stress brought on by environmental conditions, their presence and frequency could have broad paleoecological implications. Defects such as hypoplasia are unique in that they reflect short-term conditions that affected populations in a localized area. Although large-scale paleoenvironmental data allow us to model, at least in a general sense, how animals might have responded to changing climatic conditions in the past, they do not necessarily apply to specific animal groups at specific times (BRYSON 1994). If such factors as drought, severe cold or seasonal fluctuations in forage availability/quality were responsible for single or recurrent episodes of nutritional stress in mammoths, then they are informative about regional paleoecology on a fine-grained timescale.

Such tooth defects also have implications for interactions between mammoths and hominids. For example, systemic stress from nutritional or vitamin and mineral deficiencies could have influenced the location of mammoth herds on the landscape. If mammoths were concentrated near patches of vegetation, water, or needed minerals, this would have presented prehistoric hunter-gatherers with possibilities for opportunistic hunting and access to natural death sites where bones could be collected. Hunting of proboscideans or scavenging of carcasses from natural deaths at such locations have been proposed at numerous prehistoric sites in both Eurasia and North America (e.g., ABRACZINSKAS 1994; HAYNES 1999; DEREVIANKO et al. 2000; LESHCHINSKIY 2001) and such scenarios might be reflected at Kraków Spadzista Street (B) and/or Vogelherd. Age profiles and skeletal element frequencies at both sites support this idea of animals tethered to localities where humans opportunistically foraged (WOJTAL 1997, 2001; NIVEN 2001).

The Kraków Spadzista Street (B) and Vogelherd mammoth molar assemblages provide a unique opportunity to examine cement furrows in detail. Although these two assemblages contain cement furrows in high frequencies, these defects are found in other fossil proboscidean dentitions, many of which were documented and thoughtfully discussed by Guenther (see especially GUENTHER 1955, 1956). But two critical questions remain: 1) why do some assemblages show cement furrows in high frequencies but not others? and 2) are the furrows exhibited in similar frequencies and morphology on North American mammoth assemblages? We have built upon Guenther's insightful work by expanding his arguments with data from fossil and modern primate or other mammalian dentition research, extant proboscidean behavior and biology, paleoecological studies, and the archaeological record in hopes of elucidating the morphology and causes of these tooth defects. In spite of our attempts at exploring this issue, a proper and thorough survey of both fossil and extant proboscidean molar assemblages worldwide would be the ideal approach towards understanding the etiology of these defects and in turn the implications for the life histories of these animals.

REFERENCES

ABRACZINSKAS L. M. 1994. The distribution of Pleistocene proboscidean sites in Michigan: a co-occurrence analysis of their relation to surface saline water. *Michigan Academician*, **27**:65-80.

BAKER J., BROTHWELL D. R. 1980. Animal diseases in archaeology. Academic Press, New York.

BRYSON R. A. 1994. On integrating climate change and culture change studies. *Human Ecology*, **22**: 115-128.

CONARD, N. J. In press. Chronostratigraphy of the Aurignacian in the Swabian Jura as a test of the Danube corridor and Kulturpumpe models. [In:] J. ZILHÃO, F. D'ERRICO (eds) – The chronology of the Aurignacian and of the transitional technocomplexes: dating, stratigraphies, cultural implications. Proceedings of the XIV^{e} Congress of the UISPP, Liège.

DEREVIANKO A. P., ZENIN V. N., LESHCHINSKIY S. V., MASHCHENKO E. N. 2000. Peculiarities of mammoth accumulation at Shestakovo site in west Siberia. *Archaeology, Ethnology & Anthropology of Eurasia*, **3**: 42-55.

DOBNEY K., ERVYNCK A. 2000. Interpreting developmental stress in archaeological pigs: the chronology of linear enamel hypoplasia. *Journal of Archaeological Science*, **27**: 597-607.

FISHER D. C. 2001. Season of death, growth rates, and life history of North American mammoths. [In:] D. WEST (ed.) – Proceedings of the international conference on mammoth site studies. *University of Kansas Publications in Anthropology* **22**, Lawrence. Pp. 121-135.

FRANZ-ODENDAAL T. A., CHINSAMY A., LEE-THORP J. A. Under review. Enamel hypoplasia in *Sivatherium hendeyi* (Giraffidae) from the Early Pliocene locality of Langebaanweg, South Africa. Submitted to Journal of Vertebrate Paleontology.

GAUDZINSKI S. 1997. Über die Komplexe Genese mittelpleistozäner archäologischer Fundstellen am Beispiel des Platzes Käarlich-Seeufer (Mittelrhein). *Eiszeitalter und Gegenwart*, **47**: 1-27.

GOODMAN A. H., ARMELAGOS G. J. 1985. Factors affecting the distribution of enamel hypoplasias within the human permanent dentition. *American Journal of Physical Anthropology*, **68**: 479-493.

GUATELLI-STEINBERG D. 2001. What can developmental defects of enamel reveal about physiological stress in nonhuman primates? *Evolutionary Anthropology*, **10**: 138-151.

GUENTHER E. W. 1955. Mißbildungen an den Backenzähnen diluvialer Elefanten. *Meyniana*, **4**: 12-36.

GUENTHER E. W. 1956. Zahnmissbildungen und die Frage des Aussterbens der diluvialen Elefanten in Mitteleuropa. *Geologische Rundschau*, **45**: 46-51.

GUENTHER E. W. 1968. Elefantenbackenzähne aus den Mosbacher Sanden. *Mainzer Naturwissenschaftliches Archiv*, **7**: 55-73.

GUENTHER E. W. 1969a. Elefantenbackenzähne aus den Mosbacher Sanden II. *Mainzer Naturwissenschaftliches Archiv*, **8**: 77-89.

GUENTHER E. W. 1969b. Die Elefantenmolaren aus den Kiesen von Süßenborn bei Weimar. *Paläontologische Abhandlungen*, **4:** 711-734.

GUENTHER E. W. 1971. Die Faunen von Achenheim-Hangenbieten im Elsass und ihre Aussage zur Altersdatierung der Lössprofile. *Quartär*, **22**: 55-71.

GUENTHER E. W. 1975. Backenzähne der Elefanten von Ehringsdorf bei Weimar. *Abhandlung Geologisches Institut Berlin*, **23**: 399-452.

GUENTHER E. W. 1977. Die Backenzähne der Elefanten von Taubach bei Weimar. *Quartärpaläontologie*, **2**: 265-304.

GUENTHER E. W. 1978. Die Elefantmolaren aus den Travertinen von Burgtonna in Thüringen. *Quartärpaläontologie*, **3**: 139-150.

GUENTHER E. W. 1981. Die Backenzähne der Mammute von Salzgitter-Lebenstedt. *Quartärpaläontologie*, **4**: 27-41.

GUENTHER E. W. 1987. Mammute und ihre Kümmerformen von Eurasien und Mexiko. *Quartär*, **37/38**: 13-51.

GUENTHER E. W. 1991a. Die Backenzähne von *Mammuthus primigenius* und *Mammuthus primigenius-trogontherii* von Salzgitter-Lebenstedt und Einigen Anderen Fundorten. [In:] R. BUSCH, H. SCHWABEDISSEN (eds) – Der altsteinzeitliche Fundplatz Salzgitter-Lebenstedt, Teil II. Böhlau Verlag, Köln. Pp. 101-147.

GUENTHER E. W. 1991b. Die Gebisse der Waldelefanten von Bilzingsleben. [In:] K. FISCHER, E. W. GUENTHER, W.-D. HEINRICH, D. MANIA, R. MUSIL, T. NÖTZOLD (eds) – Bilzingsleben IV. DVW, Berlin. Pp. 149-174.

GUTHRIE R. D. 1990. Frozen fauna of the mammoth steppe: the story of Blue Babe. University of Chicago Press, Chicago.

GUTHRIE R. D. 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews*, **20**: 549-574.

GUTHRIE D., VAN KOLFSCHOTEN T. 2000. Neither warm and moist, nor cold and arid: the ecology of the Mid Upper Palaeolithic. [In:] W. ROEBROEKS, M. MUSSI, J. SVOBODA, K. FENNEMA (eds) – Hunters of the golden age:the Mid Upper Palaeolithic of Eurasia 30,000 – 20,000 BP. University of Leiden, Leiden. Pp. 13-20.

HAYNES G. 1991. Mammoths, mastodonts, and elephants: biology, behavior, and the fossil record. Cambridge University Press, Cambridge.

HAYNES G. 1999. The role of mammoths in rapid Clovis dispersal. [In:] G. HAYNES, J. KLIMOWICZ, J. W. F. REUMER (eds) – Mammoths and the mammoth fauna: studies of an extinct ecosystem. Deinsea, Rotterdam. Pp. 9-38.

HAYNES G. 2001. Elephant landscapes: human foragers in the world of mammoths, mastodonts, and elephants. [In:] G. CAVARRETTA, P. GIOIA, M. MUSSI, M. R. PALOMBO (eds) – Le terra degli elefanti – The world of elephants: proceedings of the 1st international congress. CNR, Rome. Pp. 571-576.

HILLSON S. 1986. Teeth. Cambridge University Press, Cambridge.

HILLSON S., BOND S. 1997. Relationship of enamel hypoplasia to the pattern of tooth crown growth: a discussion. *American Journal of Physical Anthropology*, **104**: 89-103.

HOPKINS D. M., MATTHEWS J. V., SCHWEGER C. E., YOUNG S. B. 1982. Paleoecology of Beringia. Academic Press, New York.

JONES R. L., HANSON H. C. 1985. Mineral licks, geophagy, and biochemistry of North American ungulates. Iowa State University Press, Ames.

KOCH P. L., FISHER D. C., DETTMAN D. 1989. Oxygen isotope variation in the tusks of extinct proboscideans: a measure of season of death and seasonality. *Geology*, **17**: 515-519.

KOZŁOWSKI J. K., SACHSE-KOZŁOWSKA E., VLIET B., KUBIAK H., ZAKRZEWSKA G. 1974. Upper Palaeolithic site with dwellings of mammoth bone – Cracow, Spadzista Street B. *Folia Quaternaria*, **44**: 1-110.

KUBIAK H. 1965. Examples of abnormalities in the dentition of fossil elephants. *Folia Quaternaria*, **19**: 45-61.

LESHCHINSKIY S. V. 2001. The Late Pleistocene *beast solonetz* of western Siberia: "mineral oases" in the mammoth migration paths, foci of the Palaeolithic man's activity. [In:] G. CAVARRETTA, P. GIOIA, M. MUSSI, M. R. PALOMBO (eds) – Le terra degli elefanti – The world of elephants: proceedings of the 1st international congress. CNR, Rome. Pp. 293-298.

LIPECKI G., WOJTAL P. 1996. Mammoth population from Cracow Spadzista Street (B) site. *Acta zoologica cracoviensia*, **39**(1): 289-292.

LISTER A., BAHN P. 1994. Mammoths. Macmillan, New York.

LUKACS J. R. 2001. Enamel hypoplasia in the deciduous teeth of great apes: variation in prevalence and timing of defects. *American Journal of Physical Anthropology*, **116**: 199-208.

MACHO G. A., REID D. J., LEAKEY M. G., JABLONSKI N., BEYNON A. D. 1996. Climatic effects on dental development of *Theropithicus oswaldi* from Koobi Fora and Olorgesailie. *Journal of Human Evolution*, **30:** 57-70.

MEAD A. 1999. Enamel hypoplasia in Miocene rhinoceroses (*Teleoceras*) from Nebraska: evidence of severe physiological stress. *Journal of Vertebrate Paleontology*, **19**: 391-397.

MILES A. W., GRIGSON C. 1990. Colyer's variations and diseases of the teeth of animals. Cambridge University Press, Cambridge.

MILEWSKI A. V., DIAMOND R. E. 2000. Why are very large herbivores absent from Australia? A new theory of micronutrients. *Journal of Biogeography*, **27**:957-978.

MOSS C. 1988. Elephant memories: thirteen years in the life of an elephant family. University of Chicago Press, Chicago.

MUSIL R. 1968. Die Mammutmolaren von Předmostí (ČSSR). *Palaontologische Abhandlungen*, *A/*III: 1-198.

NEIBURGER E. J. 1990. Enamel hypoplasias: poor indicators of dietary stress. *American Journal of Physical Anthropology*, **82**: 231-233.

NIVEN L. B. 2000. Enamel hypoplasia in bison: paleoecological implications for modeling hunter-gatherer procurement and processing on the northwestern Plains. [In:] A. PIKE-TAY (ed.) Assessing season of capture, age, and sex of archaeofaunas: recent work. *Archaeozoologia* vol. XI: 101-112.

NIVEN L. 2001. The role of mammoths in Upper Palaeolithic economies of southern Germany. [In:] G. CAVARRETTA, P. GIOIA, M. MUSSI, M. R. PALOMBO (eds) – Le terra degli elefanti – The world of elephants: proceedings of the 1st international congress. CNR, Rome. Pp. 323-327.

OLIVIER R. C. D. 1982. Ecology and behavior of living elephants: bases for assumptions concerning the extinct woolly mammoths. [In:] D. M. HOPKINS, J. V. MATTHEWS, C. E. SCHWEGER, S. B. YOUNG (eds) – Paleoecology of Beringia. Academic Press, New York. Pp. 291-305.

REDMOND I. 1982. Salt mining elephants of Mount Elgon. *Swara*, **5**: 28-31.

RIEK G. 1934. Die Eiszeitjägerstation am Vogelherd im Lontal. Akademische Verlagsbuchhandlung, Tübingen.

SKINNER M. 1996. Developmental stress in immature hominines from Late Pleistocene Eurasia: evidence from enamel hypoplasia. *Journal of Archaeological Science*, **23**: 833-852.

SOBCZYK K. 1995. Osadnictwo wschodniograweckie w dolinie Wisły pod Krakowem. *Rozprawy habilitacyjne UJ*, No. 303. Kraków. (In Polish).

TURNER E. 1997. Ariendorf: Quaternary deposits and Palaeolithic excavations in the Karl Schneider gravel pit. Römisch-Germanisches Zentralmuseum, Mainz.

VAN ANDEL T. H. 2002. The climate and landscape of the middle part of the Weichselian glaciation in Europe: the Stage 3 project. *Quaternary Research*, **57**:2-8.

VAN ANDEL T. H., TZEDAKIS P. C. 1996. Palaeolithic landscapes of Europe and environs, 150,000 – 25,000 years ago: an overview. *Quaternary Science Reviews*, **15**: 481-500.

VERESHCHAGIN N. K., BARYSHNIKOV G. F. 1982. Paleoecology of the mammoth fauna in the Eurasian Arctic. [In:] D. M. HOPKINS, J. V. MATTHEWS, C. E. SCHWEGER, S. B. YOUNG (eds) – Paleoecology of Beringia. Academic Press, New York. Pp. 267-279.

WILSON M. C. 1988. Bison dentitions from the Henry Smith site, Montana: evidence for seasonality and paleoenvironments at an Avonlea bison kill. [In:] L. B. DAVIS (ed.) – Avonlea yesterday and today: archaeology and prehistory. *Saskatchewan Archaeological Society*, Saskatoon. Pp. 203-225.

WOJTAL P. 1997. The number of mammoths (Mammuthus primigenius/Blumenbach) at the site Cracow Spadzista Street B. *Anthropozoologica*, **25-26**: 803-805.

WOJTAL P. 2001. The woolly mammoth (Mammuthus primigenius) remains from the Upper Palaeolithic site Kraków Spadzista Street (B). [In:] G. CAVARRETTA, P. GIOIA, M. MUSSI, M. R. PALOMBO (eds) – Le terra degli elefanti – The world of elephants: proceedings of the 1st international congress. CNR, Rome. Pp. 367-372.

ZAGWIJN W. H. 1996. An analysis of Eemian climate in western and central europe. *Quaternary Science Reviews*, **15**: 451-469.