James A. Burns[1], Charles G. Baker[2] & Dick Mol[3]
[1] Provincial Museum of Alberta, Edmonton
[2] University of Saskatchewan, Saskatoon
[3] Natuurmuseum Rotterdam

An extraordinary woolly mammoth molar from Alberta, Canada

Burns, J.A., C.G. Baker & D. Mol, 2003 - An extraordinary woolly mammoth molar from Alberta, Canada - in Reumer, J.W.F., De Vos, J. & Mol, D. (eds.) - ADVANCES IN MAMMOTH RESEARCH (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16-20 1999) - DEINSEA 9: 77-85 [ISSN 0923-9308] Published 24 May 2003

Unusual dental remains of a late Pleistocene woolly mammoth *Mammuthus primigenius* (Elephantidae, Proboscidea) were recovered from a gravel quarry near Edmonton, Alberta, Canada. The pair of teeth is unique because: (1) it comprises a morphologically normal left M6 and a true supernumerary M7; (2) the teeth are united by hypercementosis; and (3) the M7 is grossly malformed as the result of 'fabricational noise' (*cf.* Roth 1989) during its development. Identifying the fabricational anomalies and determining their etiologies led us to propose a model (to be described elsewhere) of elephantid dental progression that explains specifically the type of anomaly presented in our specimen. The Alberta specimen presents also an occlusal anomaly that occurred as a consequence of the initial fabricational anomaly.

Correspondence: James A. Burns, Curator, Quaternary Paleontology, Provincial Museum of Alberta, Edmonton, Alberta, Canada, T5N 0M6, e-mail Jim.Burns@gov.ab.ca; Charles G. Baker, College of Denistry, University of Saskatchewan, Saskatoon, Saskatchewan, Canada, S7N 5E5; Dick Mol, Natuurmuseum Rotterdam, P.O.Box 23452, NL-3001 KL Rotterdam, the Netherlands

Keywords: mammoth, *Mammuthus primigenius*, dentition, anomaly

INTRODUCTION

The zoological and paleontological literature has many references to supernumerary teeth in mammals (e.g., McDonald 1978, and references therein; Miles & Grigson 1990; Lucas & Schoch 1987). Lucas (1992) claimed that no notice had been made of such anomalies in extinct proboscideans until his report on a mastodont tooth from Oklahoma, USA. The following reports a most unusual dental anomaly in a woolly mammoth *Mammuthus primigenius* (Proboscidea, Elephantidae) from Alberta, Canada. It consists of a normal M6 (molar nomenclature of Laws 1966) to which is 'cemented' (concresced) a true supernumerary M7 whose crowning feature is the tortuous malformation caused by severe 'fabricational noise' (see Roth 1989). Determining the origin of the anomalies caused us to reexamine the mechanism of tooth progression in elephantids. Although previous scholars (e.g., Guenther 1955; Sikes 1971; Amand & Tinkelman 1985; Roth 1989) openly or tacitly accepted the idea that elephant teeth are pushed forward in the jaw, we have seen no convincing evidence in either the human or non-human dental literature to support the notion. Instead, we developed an alternative 'pull' model that accommodates current knowledge and plausibly explains the form of fabricational noise expressed in our specimen. However, such extension of this paper will be published elsewhere.

ORIGIN AND AGE OF THE SPECIMEN

In April 1990, Messrs. Richard and Bernard Johnston of Onoway, Alberta donated the mammoth tooth specimen to the Provincial Museum of Alberta (Quaternary Paleontology P90.7.1). It had been unearthed in a commercial gravel quarry operated by Alberta Concrete Products Ltd. near Villeneuve, 30 km northwest of Edmonton. The stratigraphic context is unknown. However, for some years gravel pits in the vicinity have sporadically yielded mid-Wisconsinan-age mammalian and plant macrofossils from below the only demonstrable glacial till in the central Alberta region (Shaw 1982; Young *et al*. 1994). Finite radiocarbon dates, corrected only for $^{13}C/^{12}C$ fractionation, from several local pits range from 2,730 to 39960 yBP on vertebrate bone collagen, and from 35500 to 42910 yBP on wood (Burns & Young 1994; Young *et al*. 1994). The only date from the Alberta Concrete Products pit is from a portion of caribou (*Rangifer tarandus*) antler dated at 27730 ± 1060 yBP (AECV-599c; corrected) which, by association, places the mammoth in a cool, dry grassland setting six or seven millennia before the local onset of late Wisconsinan glaciation (Burns & Young 1994).

METHODOLOGY

Most of the non-occlusal surface of our specimen is obscured by cementum. X-ray diffraction analysis showed samples from the crown and the roots to be hydroxyapatite, $Ca_5(PO_4)_3(OH)$, and no other crystalline compounds were observed (M.L. Wayman, personal communication 1994). The material was, therefore, not a product of soil diagenesis. Analysis was performed in a Rigaku x-ray diffractometer using a copper-target x-ray generating tube.

Visual inspection of the specimen was inadequate for assessment of the second tooth's tortuous morphology, making radiography necessary. Conventional plane radiographs failed to show sufficient detail of the interior of the specimen, it being very dense and structurally very complex; so, CT-scans were obtained. Taken in occlusal, transverse, and sagittal planes, forty 1- or 2-cm slices gave excellent results. A General Electric 9800 CT scanner at the Cross Cancer Institute, Edmonton was used. Voltage and current values ranged from 120-140kV and 120-170mA, respectively.

DESCRIPTION

The specimen is composed of two teeth united by hypercementosis (Fig. 1a - d). The anterior moiety is a fully developed left M6 whose anterior talon, consisting of the first root and associated lamellae, had been exfoliated. By the method of Maglio (1973), the tooth measures 280+ mm long and 108 mm wide. Crown height of the most recently occluded plate (#20) is about 180 mm, roughly measured on the tooth itself and also on the CT-scan (Fig. 2a). There were 23 lamellae, or plates, present (assuming 3 lamellae for the missing talon). The lamellar frequency, measured perpendicular to the vertical orientation of the plates, is about 7.5 plates per 100 mm. These data suggest identity with woolly mammoth (*M. primigenius*; Table 1). From the state of eruption and attrition of the M6, the animal was 46-48 years old (approximate age class XXV of Haynes 1991: table A8, based on mandibular dentition). A secondary occlusal facet, subparallel to the buccal edge of the tooth, measures 110 mm long and 25 mm wide at the widest point, and tilts at about 38° to the plane of the primary chewing surface (Fig. 1d). The deformed posterior entity is, therefore, a supernumerary M7. From CT-scan radiographs, it has about 17 plates (Fig. 2a, d), but due to extreme distortion of the latter tooth, meaningful measurements of occlusal length and width cannot be made. The entire specimen weighs 12.65 kg. The combination of a supernumerary M7 united with an M6, and the developmental anomaly of the M7 appear unique.

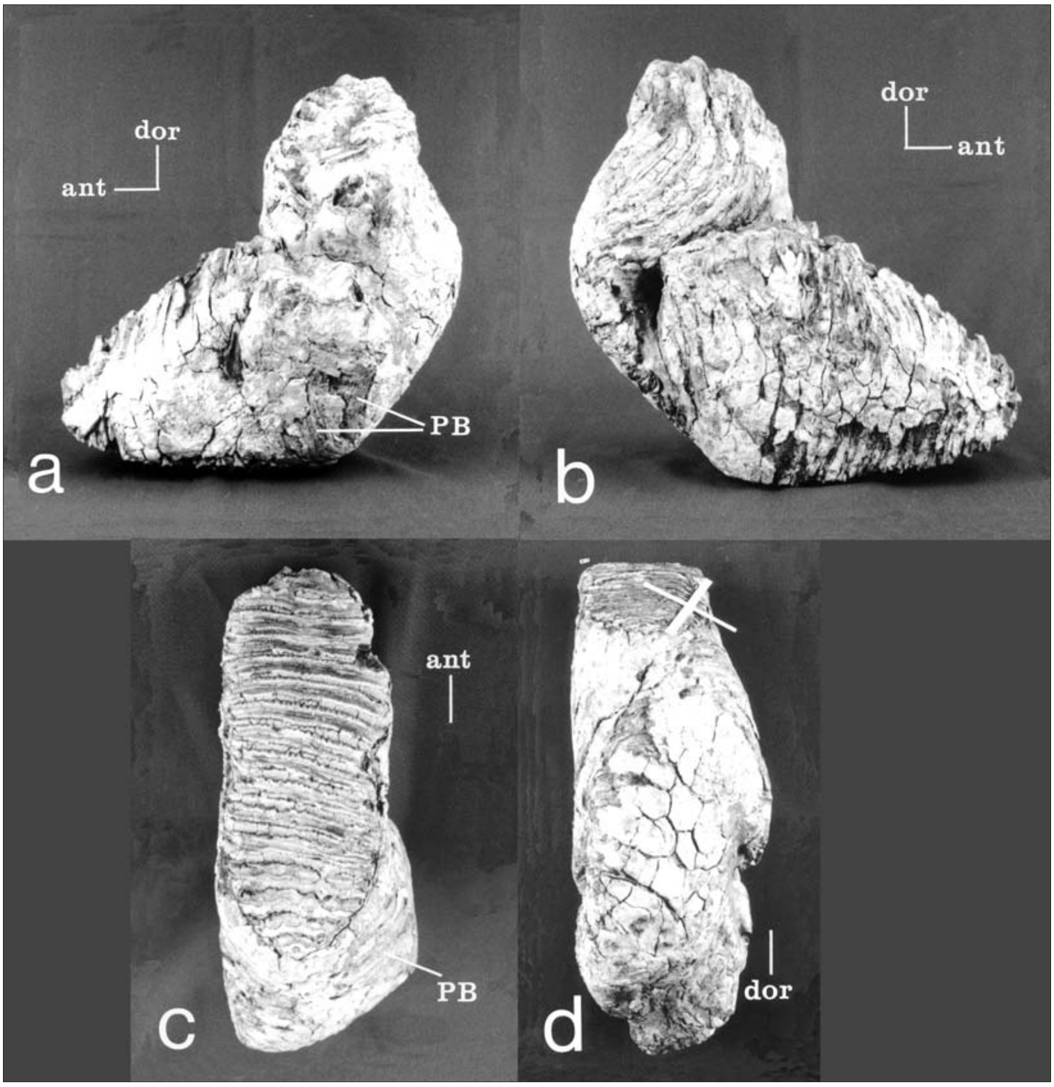


Figure 1 Left M6-7 (P90.7.1) from the Villeneuve, Alberta mammoth. (**a**) Buccal view: division between teeth is indistinct; PB indicates the posterobuccal area of thinned cementum described in text. (**b**) Lingual view: note distinct division between teeth and the tortuous curvature of M7 lamellae as they wrap around M6. (**c**) Occlusal view of M6 and the bulky apposition of M7 at bottom; PB as in Fig. 1a. (**d**) Posterior view: white 'X' indicates orientation (broad line) and angle (narrow line) of the secondary facet. Arrows indicate **ant**erior and **dor**sal.

SUPERNUMERARY MAMMOTH TEETH

The Villeneuve tooth is apparently the first reported instance of a true supernumerary M7 in a fossil elephantid (see Lucas 1992). Laws, in his landmark paper (1966), suggested that modern African elephants (*Loxodonta africana*) do produce supernumerary M7s on rare occasions. However, he hedged on the issue by further suggesting that such a tooth, usually diminutive, may consist of only a few lamellae separated from the back of the preceding tooth.

Table 1 Features of the Villeneuve M6 (P90.7.1) compared statistically to features of woolly mammoth (*M. primigenius*) M5 and M6 (data after Maglio 1973; see also Haynes 1991: Table A8). The Villeneuve M7 is not measurable, though it has about 17 plates.

	P90.7.1	woolly mammoth	
variable	M6	M5	M6
number of plates	23 (estimate)	15-16 (n=8)	20-27 (n=12)
tooth length (mm)	280+	154.0-172.0 (n=6)	226.0-285.0 (n=7)
tooth width (mm)	108	64.0-80.0 (n=7)	68.0-113.0 (n=17)
maximum Crown Height (mm)	180	127.0-151.0 (n=4)	135.0-188.5 (n=15)
lamellar frequency	7.5	9.4-11.5 (n=8)	6.5-11.1 (n=17)
enamel thickness (mm)	1.9-2.5	1.0-1.3 (n=7)	1.3-2.0 (n=17)
hypsodonty index (ht/width x 100)	166.7	198.4-228.8 (n=4)	164.6-211.8 (n=15)

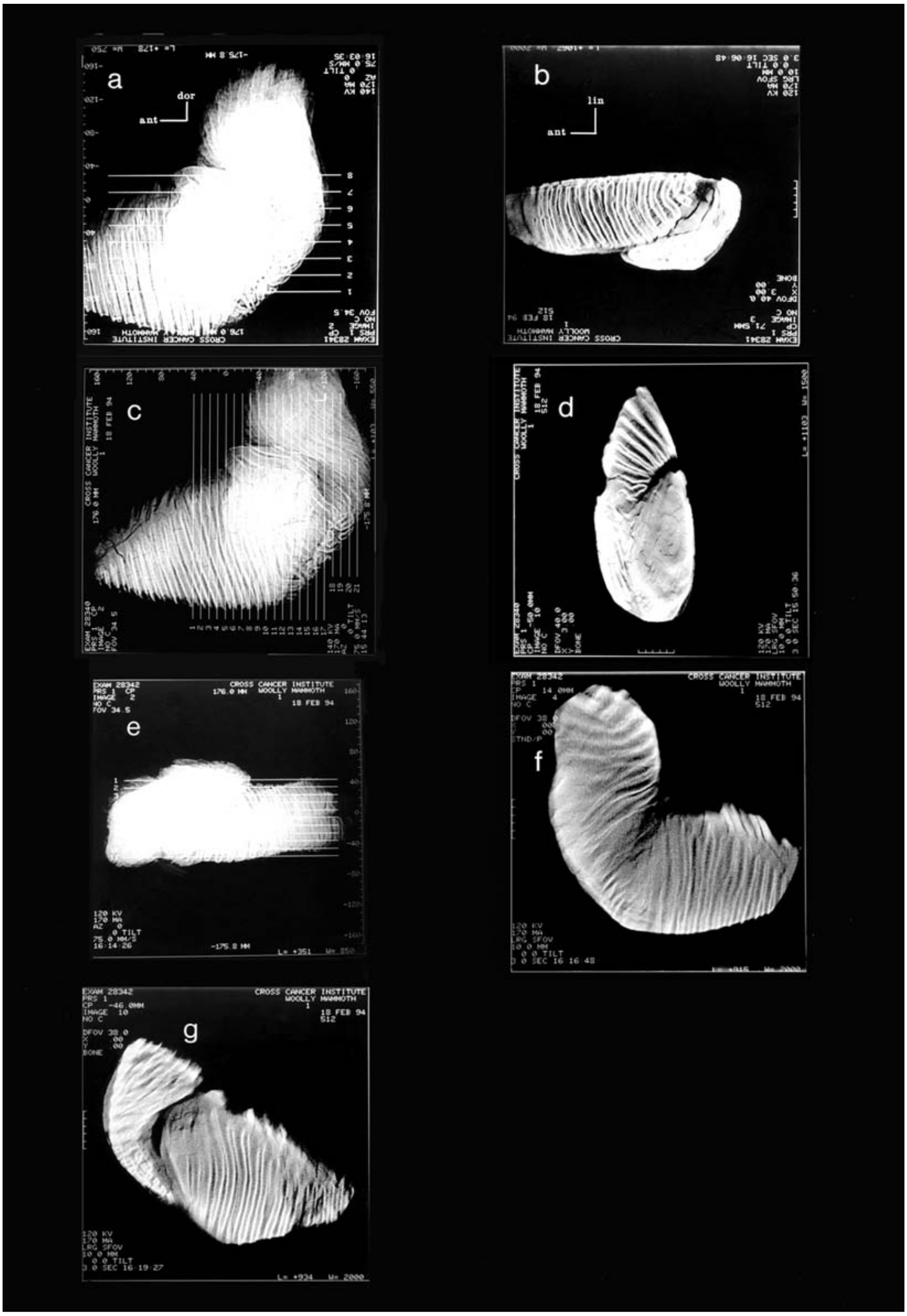
Pindborg (1970) outlined two other origins for supernumerary teeth which are produced by the fission of developing tooth buds, namely gemination and twinning. Gemination is the splitting of a single tooth bud to form two crowns with a common root; whereas, twinning produces two wholly separate, mirror-image teeth. A 30+ year-old, African elephant cow named Candy, from the Denver, Colorado zoo, possessed a twinned, supernumerary upper molar. Unfortunately, the exfoliated buccal twin was misplaced and is unavailable for study (L. Hooton, pers. comm. 1993). Radiographs (Fig. 2b, d, g) and simple observation show that the Villeneuve specimen is neither geminated nor twinned.

DENTAL UNION BY CONCRESCENCE

Roth (1989: fig. 10) figured the occlusal surface of two united cheek teeth in a specimen of Asian elephant, *Elephas maximus*. Enamel elements are shared but the roots are normal and separate. This specimen illustrates fusion, as defined by Pindborg (1970). CT radiographs of the Villeneuve specimen (Fig. 2b, d, g) show a clear line of demarcation between the crowns and roots of the united teeth, indicating union by concrescence, not fusion; the teeth are simply cemented together as a consequence of the thwarted eruption of the M7 by the presence of M6. Such acquired concrescence is a rare anomaly in elephantids, to judge by the literature; from the pre-CT-scan era, the maxillary teeth figured by Makiyama (1938: fig. 30) may be an example.

Characterising supernumerary and fused teeth as pathological entities (e.g., Lucas & Schoch 1987) is misleading, because lesions involve tissue changes due to disease or trauma. In the present instance, neither cause is demonstrable; describing it as anomalous is more realistic, being simply the result of a rare

Figure 2 Computed tomography radiographs of the Villeneuve specimen, presented in anatomical position; disregard orientation of text. (**a**) Lateral view 'scout' showing location of 8 CT slices in the occlusal plane. (**b**) Slice 3 from **a**; note the array of 17 normal plates in the M6 and the separated mass of the M7. (**c**) Lateral view 'scout' showing location of 21 vertical-transverse slices. (**d**) Slice 10 from **c**; light curved lines in lower right are acute-angled cuts through M6 lamellae, while cleft above shows separation from M7; note change of plate orientation in M7 down the left side. (**e**) Dorsal view 'scout' showing location of 11 vertical-longitudinal slices. (**f**) Slice 4 from **e**; note regular enamel folds in M6 at right, and fuzzy cross-cutting images of twisted plates in M7 at left. (**g**) Slice 10 from **e**; closer to the lingual side of the specimen, the separation of the teeth is clearer. Arrows indicate **ant**erior, **lin**gual, **buc**cal, and **dor**sal.


a
dor
ant
b
lin
ant
c
CROSS CANCER INSTITUTE
WOOLLY MAMMOTH
18 FEB 94
d
CROSS CANCER INSTITUTE
WOOLLY MAMMOTH
18 FEB 94
e
EXAM 28342
CROSS CANCER INSTITUTE
WOOLLY MAMMOTH
18 FEB 94
f
EXAM 28342
CROSS CANCER INSTITUTE
WOOLLY MAMMOTH
18 FEB 94
g
EXAM 28342
CROSS CANCER INSTITUTE
WOOLLY MAMMOTH
18 FEB 94

developmental circumstance. A complete, though distorted, tooth succeeding another tooth that meets the criteria for a *M. primigenius* M6 must be an anomalous, supernumerary M7 that developed from a seventh tooth bud.

DEVELOPMENTAL ANOMALY

The most conspicuous feature of the M7 in the Alberta specimen is its tortuous morphology, an example of what Roth (1989) termed 'fabricational noise in elephant dentition'. She reiterated the point that elephant teeth that are still developing in the capsule at the rear of the jaws can be plastically deformed before they are finally consolidated by mineralization. The Villeneuve specimen was undoubtedly deformed from a very early stage of its development because it is so thoroughly distorted. Enamel elements are twisted in multiple curves (Figs. 2d, f, g); virtually all lamellae were disengaged from their neighbours and later cemented at odd angles (Figs. 2b, c, f); roots are oriented in several directions (not too clear in Figs. 1a, b; Figs. 2a, b, c, g). It seems clear that the M6 was fully erupted when the M7 was forced into place, but the M6 functioned for some years before the M7 came to rest.

While we agree that we are dealing with fabricational noise, we differ with Roth on

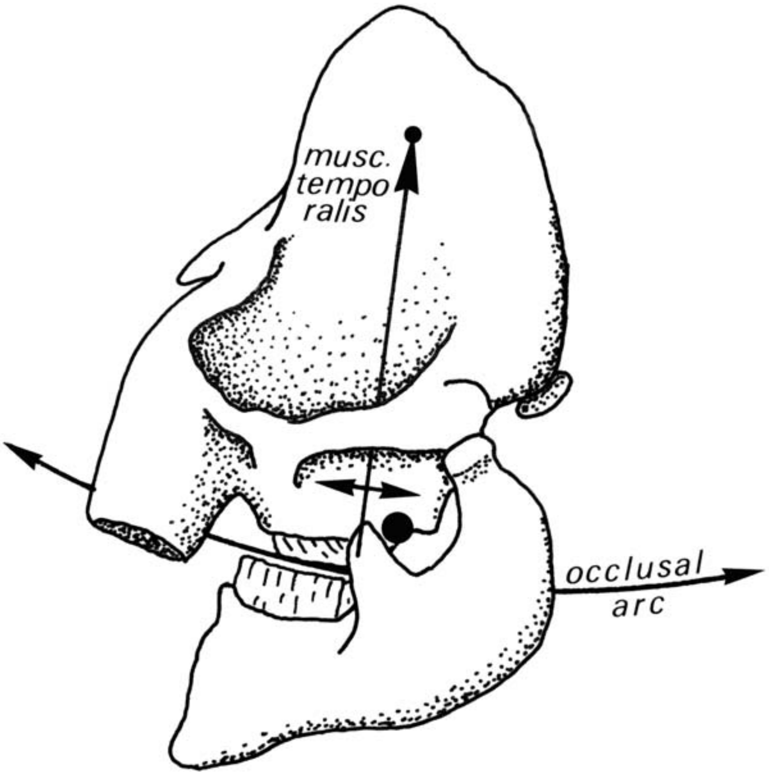


Figure 3 Diagrammatic representation of a mammoth skull showing the location and action of the Musculus temporalis in relation to the left maxillary alveolus. The black dot shows where the affected teeth were situated in the jaw. Painful abrasion of the muscle against the protruding alveolus during mastication was later reduced by the establishment of a new occlusal plane (Fig. 1d).

the mechanism that initiated and drove the deformation process. That said, her extensive studies of modern and fossil elephants suggest that many elephantid teeth have been deformed by fabricational noise.

IMPLICATIONS FOR THE ANIMAL

The Villeneuve mammoth was clearly in great pain due to a conspicuous bulging of the buccal alveolus, and it may be argued that it was the ultimate cause of death. The Musculus temporalis in elephants is largely responsible for suspending the massive mandible below the skull. Dental attrition, caused as the mandible swings through an occlusal arc with its radius pivoting on the origin of the temporalis (Fig. 3), produces the convex and concave surfaces of the upper and lower teeth, respectively. As the mandible swung through the arc during mastication, the muscle would have encountered the prominence on the left buccal aspect of the maxilla. The investment of cementum on the tooth is thin or non-existent where the temporalis would have passed over the prominence (Fig. 1a, c). Accordingly, one is tempted to speculate that a portion of the buccal lamina of the M6-7 alveoli—and of course the investing gingival tissue—had been compromised by the abrasive action of the temporalis muscle.

Normal chewing action was eventually rendered impossible. The secondary occlusal facet on the buccal edge of the molar suggests that the mammoth made an effort to avoid the painful passing of the muscle across the bulge. The animal was apparently able to shift the mandibular condyles in the temporomandibular joints to the left, just enough to initiate chewing at a 38° angle to the normal plane (Fig. 1d), thus avoiding the prominence (and the pain) to some extent. The minor facet was probably developed over a relatively short time, and the animal likely died of malnutrition shortly after cutting the new facet, at age 46 to 48 years, unable to process sufficient graze to survive.

DISCUSSION

The Villeneuve M7 is thoroughly distorted and suggests that deformation began early in its development. Under normal circumstances, the precedent M6 might be in occlusion for as much as 30 years, about half the animal's life (based on mandibular m6s; see Haynes 1991: 339). M6s migrate forward very slowly, so there would be no clear vacancy in the alveolus for the developing M7 to occupy. It would be forced into whatever space could be found, the lamellae plastically deformed by torsion and folding, and the tooth concresced to the anterior molar. In cases of human concrescence, normal eruption is impeded by the attached tooth; thus, dilaceration of unmineralized roots, held within anatomic boundaries, occurs.

Some members of the 'Sirenia' (Mammalia; Mirorder Tethytheria, which now also includes the Proboscidea, Hyracoidea, and the extinct Desmostylia) exhibit dental progression similar to that of the Proboscidea. Thus, the three extant species of manatees (genus *Trichechus*) have a series of low-crowned, enamelled, cross-crested, cuspidate cheek teeth (Nowak & Paradiso 1983: 1152) that erupt sequentially in a toothrow that is exfoliated anteriorly and replaced one-by-one from the capsule at the rear of the jaws. The series can number up to 20 or 30 teeth (see Husar 1978) - about six in occlusion at a given time, with a generally increasing size, and all but the first three are considered by most researchers as 'supernumerary' (Domning 1982). The mechanism of manatee tooth progression has not been studied histologically but there are likely to be similarities to the mechanism in the Proboscidea. It is tempting to speculate further about the somewhat tenuous phylogenetic connection between manatees and elephants (once included in the 'Subungulata'), given the occurrence now of a true supernumerary tooth in *Mammuthus primigenius*.

The secular human trend today towards crowded dental arcades and impacted wisdom teeth (third molars) is the result of a phenomenon analogous to the jaw-shortening observed in successively older mammoth individuals. Any dental practitioner (e.g., dentist, orthodontist) can attest to the fact that the human dental arcade exhibits forward movement of teeth within the alveolus; this is especially noticeable when an exfoliated or extracted tooth is not replaced by a prosthetic space-keeper. Even wisdom teeth, normal or impacted, progress anteriad, with no teeth behind them to push them in.

The supernumerary mammoth tooth we have described may be a very rare evolutionary throwback to the time when mammals possessed more than 44 teeth, although even the earliest known proboscidean, 50 million year-old *Moeritherium* from the Eocene of North Africa, had only six cheek teeth in each quarter of the dentition (Carroll 1988). This recalls the six occluding cheek teeth of the manatee. Or, it may be seen as a very rare mutation. Presumably, seventh molars would have increased the mammoth's longevity by extending its ability to process food. However, because the M7s would have appeared so late in life, normal mortality rates would have ensured that few mammoths appreciated the longer lifespan.

Moss (1988) suggested that African elephant cows reach menopause at about 55 years of age, and it appears that elephants can live to be about 60 - 65 years old (Moss 1988; Haynes 1991). This limit on longevity seems to reflect a nutritional deficit that is followed by bodily deterioration, then death, all triggered by the exhaustion of a six-tooth dental series. Perhaps elephants could live longer if more teeth were available. However, Darwinian fitness ends at 55, at least for females. Thus, the near contemporaneity of menopause (at 55) to death (at 60-65) suggests that elephant dentition evolved to function until the females' fertile years ended. After menopause, more teeth would only prolong life, not extend fitness which, from the point of view of bioenergetics, is nebulous. We interpret the occurrence of the M7 as a fluke with no clear adaptive evolutionary advantage.

ACKNOWLEDGEMENTS

The kind donation of the Villeneuve specimen to the Provincial Museum of Alberta by Messrs. R. and B. Johnston is gratefully acknowledged. For discussions and suggestions about the tooth we thank Drs. L.D. Agenbroad, C.R. Harington, (the late) E. Anderson, H.G. McDonald, V.L. Roth, R.R. Young, D.M. Stringham and G. Jakway. L. Hooton, keeper of the elephants at the Denver Zoo, kindly shared the information regarding the twinned molar in one of her animals. The CT-scans of the Villeneuve specimen were produced at the Cross Cancer Institute, Edmonton by radiology technician A. Anderson, with the kind permission of Acting Director Dr. T. Terry; we are pleased to acknowledge their efforts and fine results. X-ray diffraction analysis was kindly provided by Dr. M.L. Wayman, Department of Mining, Metallurgical and Petroleum Engineering, University of Alberta. We are indebted to Dr. L.D. Arnold, former head of the Alberta Environmental Centre's Isotopes Laboratory, Vegreville, Alberta for generously providing dozens of the radiocarbon dates, including the 'AECV' date on the *Rangifer tarandus* from the Alberta Concrete Products quarry. JAB photographed Fig. 1 and drafted Fig. 3. Financial support for reproduction of the CT-scans and photos (Fig. 2) was provided by the D.B. Stewart Radiology Research Fund of the University of Alberta's Faculty of Dentistry. We thank Dr. A.A. Sauks for translating Guenther's (1955) paper from German to English. T.A. Burns, MLIS, gave invaluable help in searching the literature and obtaining interlibrary loans of materials. Drs. G. Sperber, G. Haynes, H. van Essen and A. Lister read earlier drafts of the paper and improved it by their constructive comments. We thank all our 'collaborators' for their time, perceptiveness, and above all, patience.

REFERENCES

Amand, W.B. & Tinkelman, C.L., 1985 - Oral disease in captive wild animals - in: C.E. Harvey (ed.) - Veterinary Dentistry - pp. 289-311. W.B. Saunders Company, Philadelphia

Burns, J.A. & Young, R.R., 1994 - Pleistocene mammals of the Edmonton area, Alberta. Part I: the carnivores - Canadian Journal of Earth Sciences 31 (2): 393-400

Carroll, R.L., 1988 - Vertebrate paleontology and evolution - W.H. Freeman and Company, New York

Domning, D.P., 1982 - Evolution of manatees: a speculative history - J. Paleontology 56 (3): 599-619

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

Haynes, G., 1991 - Mammoths, mastodonts, and elephants: Biology, behavior, and the fossil record - Cambridge University Press, Cambridge

Husar, S.L., 1978 - *Trichechus manatus* - Mammalian Species 93: 1-5 (American Society of Mammalogists)

Laws, R.M., 1966 - Age criteria for the African elephant - East African Wildlife Journal 4: 1-37

Lucas, S.G., 1992 - Paleopathology of a mastodont molar - Texas Journal of Science 44 (3): 357-359

Lucas, S.G. & Schoch, R.M., 1987 - Paleopathology of early Cenozoic *Coryphodon* (Mammalia; Pantodonta) - Journal of Vertebrate Paleontology 7: 145-154

Maglio, V.J., 1973 - Origin and evolution of the Elephantidae - Transactions of the American Philosophical Society n.s. 63, Pt. 3: 1-149

Makiyama, J., 1938 - Japonic Proboscidea - College of Science, Kyoto Imperial University, Memoirs, Series B, 14(1): 1-59

McDonald, H.G., 1978 - A supernumerary tooth in the ground sloth, *Megalonyx* (Edentata, Mammalia) - Florida Scientist 41(1): 12-14

Miles, A.E.W. & Grigson, C. (eds.), 1990 - Colyer's variations and diseases of the teeth of animals - Cambridge University Press, Cambridge

Moss, C., 1988 - Elephant memories: Thirteen years in the life of an elephant family - Ballantine Books, New York

Nowak, J.M. & Paradiso, J.L., 1983 - Walker's mammals of the world, 4th ed., Volume 2 - Johns Hopkins University Press, Baltimore and London

Pindborg, J.J., 1970 - Pathology of the dental hard tissues - W.B. Saunders, Philadelphia

Roth, V.L., 1989 - Fabricational noise in elephant dentitions - Paleobiology 15 (2): 165-179

Shaw, J., 1982 - Melt-out till in the Edmonton area, Alberta, Canada - Canadian Journal of Earth Sciences 19 (8): 1548-1569

Sikes, S.K., 1971 - The natural history of the African elephant - Weidenfeld and Nicolson, London

Young, R.R., Burns, J.A., Smith, D.G., Arnold, L.D., & Rains, R.B., 1994 - A single late Wisconsin, Laurentide glaciation, Edmonton area and southern Alberta - Geology 22: 683-686

received 19 January 2001

DEINSEA - ANNUAL OF THE NATURAL HISTORY MUSEUM ROTTERDAM
P.O.Box 23452, NL-3001 KL Rotterdam The Netherlands