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A supernumerary tooth and an odontoma attributable to *Mammuthus primigenius* (BLUMENBACH, 1799) (Mammalia, Proboscidea) from The Netherlands, and various related finds

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Abstract. Two dental anomalies referable to *Mammuthus primigenius* (BLUMENBACH, 1799) are described. The first is a unilateral supernumerary tooth in a mandible with M_3 in advanced wear (part I). A mandible with two supernumerary teeth from Otterstadt (Germany) was published earlier, but interpreted as an anomalous replacement of M_2 by M_3 (ADAM 1994). The discussion therefore focuses on the implications of this alternative theory and the arguments against it. On the basis of specimens in mandibles, some isolated finds of mammoth teeth from various locations in western Europe are tentatively presented as supernumerary. The second anomaly is a compound odontoma that developed around a normal M_3. Previously published elephantid odontomas are discussed and a preliminary survey of their macroscopic characteristics as opposed to those of supernumerary teeth is presented. Some terminological problems arising from the imperfect morphological analogy between anomalies in human and elephantid dentitions are discussed.

Key words: *Mammuthus primigenius*, dental anomalies, supernumerary tooth, odontoma.

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I. INTRODUCTION

Elephants in general and especially woolly mammoths are known for a wide range of dental anomalies (e.g., GUENTHER 1955; ROTH 1989), which is by no means exhausted by the following survey.

Many deformities are caused by the pressure that builds up between teeth whose normal progression in the jaw is somehow delayed or hampered. BURNS et al. (2003) rightly remark that the way in which pressure between elements of the elephantid dentition is generated has hitherto been treated superficially and announce a theory on the subject. The present text does not assume their results and simply accepts pressure as an important cause of dental anomalies. As far as mechanical deformation is concerned, it is the longer duration of the formation and full calcification of M3s that keeps especially their posterior parts vulnerable for quite some time. The same applies to supernumerary teeth of sufficiently large dimensions. A post-M^3 specimen that belongs to a woolly mammoth from Villeneuve, Canada (BURNS et al. 2003), is much distorted.

In other cases, damage to or loss of one of the teeth that form a grinding pair causes some degree of deformation and/or dislocation in the other (e.g., HEINRICH 1982).

Finally, certain so-called odontogenic anomalies result from disruptions of the normal process of tooth formation. They originate at its very beginning as epithelial aberrations on the dental laminae, but usually appear at some later stage. Odontomas and other tumorous forms as well as more or less (ab-)normal supernumerary teeth all belong to this heterogeneous group. (For explanations of these concepts, see the terminology sections of parts I and II below).

To judge by extant elephantid specimens, supernumerary teeth as well as odontomas may reach a stage of comparatively early wear (e.g., ADAM 1994; RAUBENHEIMER et al. 1989). Further development and wear of anomalous elements behind or around M3 was presumably cut short by the death of their bearers, already well past their prime as the extra element developed. It is not clear whether odontomas in elephantids could have lethal effects or just contribute to the overall health decline of old age. Generally speaking, there will be many variants of the anomalous tooth types mentioned.

In the majority of cases where tooth development and replacement in fossil and living elephants was a cause of morphological anomalies, the hindmost permanent molars were affected. This does not only relate to the fact that the majority of individuals reached the mature age at which the M3s were functional, but also to the circumstance that at this stage many formerly hidden anomalies become manifest. LAWS (1966: 15) reported that four *Loxodonta africana* (BLUMENBACH, 1797) mandibles in a sample of 385 had developed additional teeth and observed that such an element "would not make its appearance until at least group xxv". At this wear stage only M_3 is present in the mandible and has an occlusal surface of about maximal length, but is not yet worn down to the crown base anteriorly. According to LAWS (1966: 30) this stage corresponds to an estimated age of 47 ± 2 years. G. CRAIG arrived at 46-48 years (HAYNES 1991: 339). When restricted to *L. africana* individuals of this age/wear class or older ones, the incidence of additional teeth within the said sample rises to 10.5%, and to 8.0% in another (LAWS 1966: 15). An analogous percentage for *M. primigenius* is unknown and in fact would be hard to produce in retrospect. The main reason is that in living species some anomalies seem to be typical of certain populations (LAWS 1966: 16), which may imply some regional environmental or hereditary factor. According to ROTH (1989, 172, 174), such a factor could be population stress. In sufficiently large accumulations of mammoth teeth – for example that in the southern North Sea basin – many generations of migrating herds are probably represented. This would rule out any distinctions with regard to the percentages of anomalies per population.

Serious dental aberrations that precede M3 seem to be less common in elephants. An interesting example is provided by the famous Jumbo (captive *L. africana*), whose disorderly dentition was figured by OSBORN (1942: 1200). According to HUNTER & LANGSTON (1965: 679) it may contain "several massive odontomas". To name but a few other cases: POHLIG (1888: 85, fig. 26; 1891: 441/442, fig. 144) mentioned a morphologically anomalous dP_2 [an atavistic dP_1?] of *M. primigenius*, the only element in an anomalous foetal mandible fragment from Oelsnitz. PONTIER (1930) interpreted a molariform growth between the roots of a cf. dP^4 of *M. trogontherii* (POHLIG, 1885) as an atavistic premolar, but according to HUNTER & LANGSTON (1965: 678) it might be a compound odontoma. BUSS (1990: 66) figured an M_1 of *L. africana*, much deflected to the buccal side of the mandible by the remains of the dP_4 in front of it and deformed in the process. Similar cases regarding M_1 and M_2 were mentioned by LAWS (1966).

Because supernumerary teeth need not differ all that much from deformed M3s, several have presumably passed into collections unrecognized. Some candidates are presented at the end of part I of this paper.

Odontomas in various forms appear to be much rarer. HUNTER & LANGSTON (1965) were inclined to confirm only four occurrences in fossil elephants. None of these was European, although GUENTHER (1955: 28/29, pl. 6, fig. 2) had described and figured a tumorous anomaly in a tooth from Germany as an odontoma. It seems possible, however, that in older literature the term 'odontoma' was sometimes too readily applied or served as a kind of bag into which all sorts of anomalies could be thrown (see the section on application problems below). The first odontoma discovered in an African elephant mandible was described by RAUBENHEIMER et al. as late as 1989. To judge by the short record to date, it seems that elephantid odontomas are preferentially mandibular phenomena. It has been known for a long time that this certainly applies to odontomas in humans (e.g., EULER 1929: 442). The extant specimens also suggest that the parallel between man and elephant extends still further, so that elephantid odontomas are likely to be predominantly linked with the permanent teeth. No finds that testify to a simultaneous occurrence in both mandible halves or in both upper and lower jaws of elephants have so far been made.

The mandible with the supernumerary tooth was dredged from the Ketelmeer (between the Noordoostpolder and Oostelijk Flevoland, 52°36'N/05°45'E) in 1953. In the text it shall be referred to with "the Ketelmeer mandible". It is now kept in the museum on the former island of Schokland in the Noordoostpolder and bears the number MS 1953-1-32/f.

The odontoma – ac no. 517/R1660 – was dredged from deposits of the Kreftenheye Formation in the Rhederlaag sand and gravel concession (right bank of the river IJssel near Giesbeek, 52°00'N/06°03'E) by the dredger Kaliwaal 17 in September 1994. Dredging depth at the time was 16-18 m (VAN RAAY, pers. comm.).

It is highly probable that both specimens are of Weichselian age, just as the vast majority of Dutch *M. primigenius* finds.

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X - r a y d a t a. The X-rays of the Ketelmeer mandible were kindly provided by the Dr. J. H. JANSEN Hospital at Emmeloord, represented by Mrs. H. L. BERKHUIJSEN. The jaw regrettably proved too large for a CT scan and was subsequently X-rayed on a bucky-table by means of a single field Philips Optimus machine at 110 kV (Figs. 2a and 2b).

A b b r e v i a t i o n s. ac – author's collection; AEY – African elephant years; e – estimate(d); ET – enamel thickness; FSFQ – Forschungsinstitut Senckenberg, Forschungsstelle für Quartärpaläontologie; H – height; indet – indeterminable; L – length; LF – lamellar frequency; LWI – Length-Width Index; M^3, etc. – upper teeth; M_3, etc. – lower teeth; M3, etc. – both upper and lower teeth; NAT – Naturalis; nm – not directly measurable; NHM – Natural History Museum; P – plate number; p – platelet; SM – Sedgwick Museum; SMN – Staatliches Museum für Naturkunde; W – width; x(!) – (large) talonid [in M_3 plate formulas]

II. THE KETELMEER MANDIBLE

Figs 1-3, 5-7; table I

Terminology

The term "supernumerary" indicates any tooth that exceeds the standard number in a given species. The degree to which supernumerary teeth resemble the normal ones is variable. Specimens that look normal are sometimes called "supplemental" (SCOTT & SYMONS, 1961; PINDBORG 1970) because they enlarge the typical mammalian number of three permanent molars to four. For this reason the short characterization 'M4' is also often found. However, with respect to elephantid teeth it is not always clear where the boundary between normal and abnormal should be placed, because in elephants some degree of abnormality and/or deformation is likely to occur in supernumerary teeth that seem normal otherwise. The term "supernumerary" is therefore used throughout the text.

Description

The mandible is near-complete. Both condyles are lost, and the coronoid processes as well as the posterior border of the right ascending ramus are damaged. The compact outer wall of the left corpus mandibulae is broken away in two areas of limited extent. The frontal parts of the mandibular corpora are rather rounded – a condition often seen in specimens with M_3 in wear – and there is a slender symphyseal rostrum. The interalveolar crests are pronounced, and there is a marked asymmetry in the distribution of the mental foramina. The right interalveolar crest obscures two of these, whereas the frontal area of the right corpus does not show any, but for a small one immediately below the upper edge of the corpus, in front of the anteriormost preserved root alveolus. In front of the alveolus of the right M_3 there is but one foramen in the lingual wall of the corpus, whereas there are three in the opposite lingual wall, in front of the left M_3. These correspond with two large ones in the frontal area (Fig. 1b).

Two teeth are present in the left mandible half: the complete remains of an M_3 in advanced wear and a somewhat deformed supernumerary tooth. The latter is in touch with the posterior part of the M_3, and the specimens are apparently histologically separate from each other, as if engaged in normal tooth replacement. By contrast, the maxillary elements from Villeneuve, Canada, are united by hypercementosis (BURNS et al. 2003).

The occlusal surface of the M_3 has a lamellar formula of ∞ 10 in 166. mm. The length of the dentine platform (∞, with lingual cement islet) equals that of two lamellae. The dentine platform had started developing from the lingual side, and the lingual dentine of the two lamellae behind it is already confluent. As the X-ray (Fig. 2a) suggests, another two lamellae and a subnormal platelet probably complete the posterior end within the jaw, so that the plate formula of this M_3 would be best represented by ∞ 12 (p). (Note: A "platelet" (p) is the name adopted for the hindmost plate structure in an M3 if it is markedly smaller than the lamella that precedes it. A platelet may be plate-like or just consist of one or a few (thick) digitations. Its position and size render it more or less equivalent to the posterior talon(id)s in the teeth that precede M3, but there is an essential difference between the two categories because the base of a platelet, unlike that of a talon(id), does not merge with the base of the preceding lamella. In this sense, platelets are independent structures).

The pronounced basal bend in the medio-posterior lamellae that is usually observed in M_3s of all advanced species is visible here, too, and the hindmost part of the crown rapidly decreases in height. The lamellar frequency (LF), measured at square angles to the vertical axis of the central plates, is about 6.2, the posteriormost plates excluded. The maximum remaining crown width at the occlusal surface is 69. mm (lam. VIII, excl. cover cement; note: Roman numerals are used if lamellae are counted from the posterior to the anterior part of the tooth. This is the standard procedure for anteriorly incomplete specimens). The modal enamel thickness (ET) is 1.5, the maximum 1.8 mm.

The right mandible half is empty. A supernumerary tooth never developed here, and the right M_3 was at some time lost. Its alveolus is completely closed at the back, and the dental canal behind it is

Fig. 1. *M. primigenius*. The Ketelmeer mandible, with left M_3 in advanced wear and left supernumerary tooth at the point of eruption; a – superior view, b – anterior view, c – left lateral view. Ketelmeer, Flevoland, The Netherlands (Schokland Museum, no. MS 1953-1-32/f).

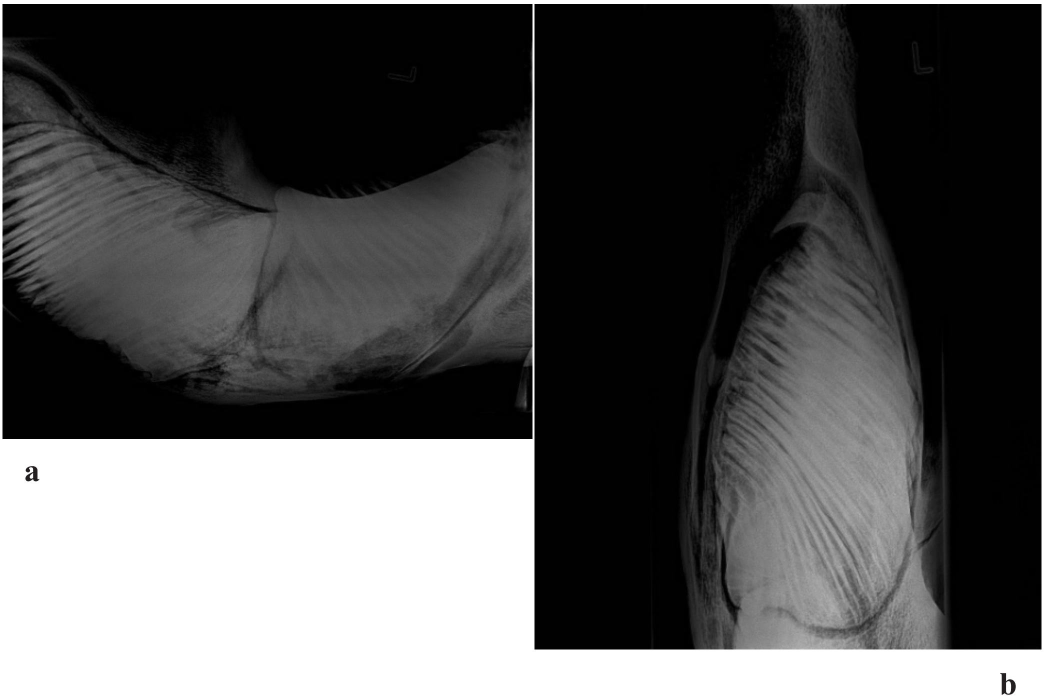


Fig. 2. *M. primigenius*. The Ketelmeer mandible; a – lingual view of left mandible half with worn M_3 (to the right) and supernumerary tooth, b – oblique superior view of left supernumerary tooth. X-rays provided by the radiology department of the Dr. J.H. Jansen Hospital, Emmeloord.

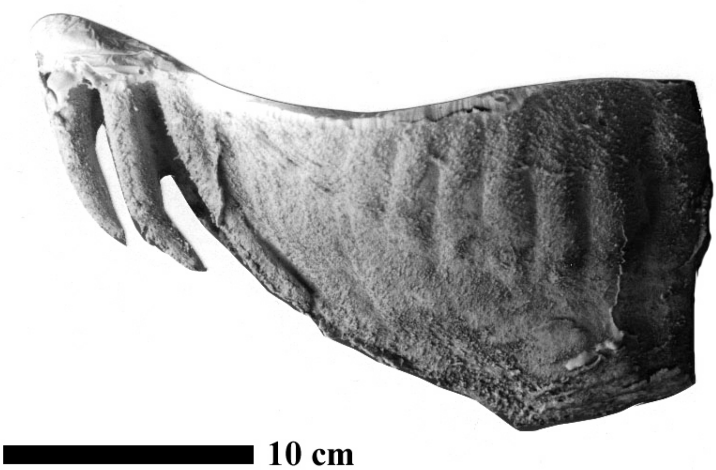


Fig. 3. *M. primigenius*. The Ketelmeer mandible; cast of right M_3 alveolus up to its superior edge; lingual view. Cast by Kennis & Kennis, Arnhem.

empty, but for an irregular layer of materia spongiosa lining its anterior part. Within this space, no traces of lamellar structures are visible, neither as threedimensional fragments nor as imprints.

A cast of the right alveolus shows that the shape of the lost tooth was typically that of an M_3 in advanced wear (Fig. 3). The wear stage of this specimen is approximately XXVII/XXVIII according to LAWS (1966: 11). The corresponding individual age is about 53 to 56 AEY (LAWS 1966: 30; CRAIG in HAYNES 1991: 339). Abrasion had proceeded further than in the left specimen and probably also touched the hindmost plates. This is essentially a normal situation because the formation of right mandibular molars is generally slightly ahead of that of left ones, and the wear process on the right therefore starts a little earlier. Comparison with the X-ray shows that the eruption angle was more acute in the right M_3. This means that the right occlusal surface was less steeply inclined with respect to the original sagittal axis of the crown. Its length was about 236. mm, 70. mm greater than that of the left one. An approximation of the degree of wear in both M_3s is indicated in Fig. 4. The right M_3 still had some individual roots in front, but behind these a keel-shaped complex with a lengthwise extended pulp cavity had developed (Fig. 3). This is essentially the same situation as in the left M_3.

In the anterior bases of the ascending rami, above the rear ends of the M_3s that have entered the occlusal area, the retromolar foramina are still visible. The left one is filled with fine gravel and cannot be sounded. The right retromolar canal opens onto the dental canal behind it, but a sounding device emerged from a narrow dorsal space between the outer mandible wall and the lining of materia spongiosa mentioned above. The bony floor underneath the left retromolar foramen was in danger of being annihilated by the erupting supernumerary tooth, which had already started to widen the alveolus behind the M_3.

Because of damage to the lingual part of the left angulus mandibulae, the basal front of the supernumerary tooth can be inspected (Fig. 5). The anteriormost part – nearly equivalent to the area of the first root – is covered by an uninterrupted, undulating layer of dentine. The corresponding lingual crown wall suggests the presence of a talonid and three lamellae here. Behind this area, six more or less regular lamellar pulp cavities can be counted, but between their medio-lateral axis and the frontal plane of the tooth there is an abnormally wide angle of about 70°. The basal enamel is rather thickly covered with dentine, so that the pulp cavities have already narrowed. Through the foramen mandibulare the posteriormost lamellae are visible from above. The distance from the damaged part is so short that more than five or six lamellae over and above the nine already accounted for seem unlikely. The lingual view of Fig. 2a likewise suggests about 14 or 15 lamellae in total.

The crown base is turned obliquely towards the lingual/posterior side instead of the expected ventral or buccal side. The anterior lamellae therefore point upwards in buccal direction. The frontal top of the crown reaches the posterior end of the occlusal surface of the M_3, but not its level, so that the supernumerary tooth itself is not touched by wear. Originally it was presumably still covered by the gingiva (Fig. 6). Since the M_3 extends slightly further to the rear than the posterior end of its occlusal surface (Fig. 2a), contact of the two teeth takes place within a larger area below the crown apexes. A small pressure scar may have developed there. Part of the front of the supernumerary tooth has come to lie on the buccal side of the narrow, crest-like hindmost part of the M_3. This becomes evident from the X-ray (Fig. 2a) as well as in occlusal view (Fig. 6), where the cement-covered apexes of the anteriormost plates can be seen behind the rear part of the occlusal surface of the M_3. The frontal plane of the supernumerary tooth is therefore somewhat concave and suggests that it reached the posterior end of the M_3 in an incompletely calcified state, whereas there is no apparent posterior deformation in the latter. The advanced wear stage of the M_3 suggests that it had been completed much earlier. (Note: A time gap between the development of M_3s and supernumerary teeth may be a common phenomenon. LAWS (1966: 15/16) observed that M_3s in *L. africana* had remained quite normal in each case an additional tooth had developed. The same applies to the M_3s of the African elephant cow Beira from the Basel Zoo, published by LANG et al. (2000 [quoted in more detail below]).

Behind the supernumerary tooth, higher up in the ascending ramus, a conical, cap-shaped ossified structure is visible through the foramen mandibulare (Fig. 7) as well as in the X-ray (Fig. 2b). Such structures are commonly interpreted as the remains of the enamel organ (see TOEPFER 1957, 11-12, pl. IV).

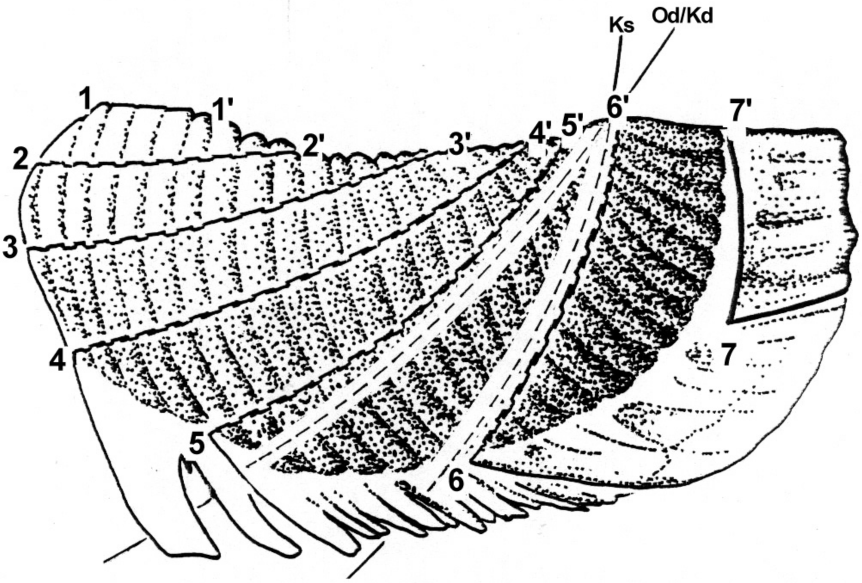


Fig. 4. Seven arbitrary wear stages in an M_3 of *M. primigenius* showing the effects of its arcuate path through the mandible on the shape of the crown. Development of a keel-shaped root portion after stage 5-5'. Ks, Kd – Approximate wear stages of respectively left and right M_3 in the Ketelmeer mandible.; Od – Approximate wear stage of right M_3 in the Otterstadt mandible.

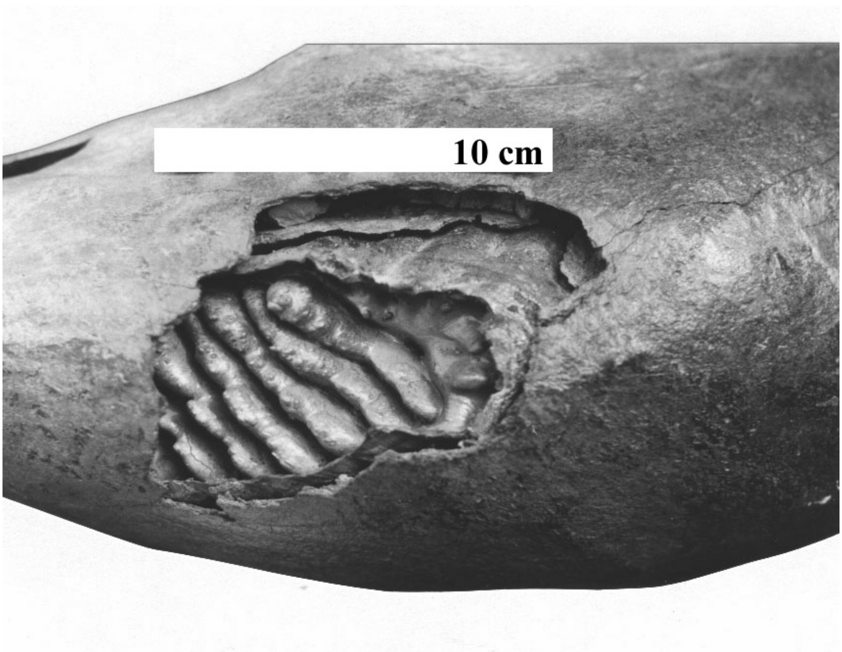


Fig. 5. *M. primigenius*. The Ketelmeer mandible; oblique lingual view of basal anterior portion of left supernumerary tooth in the area of the angulus mandibulae.

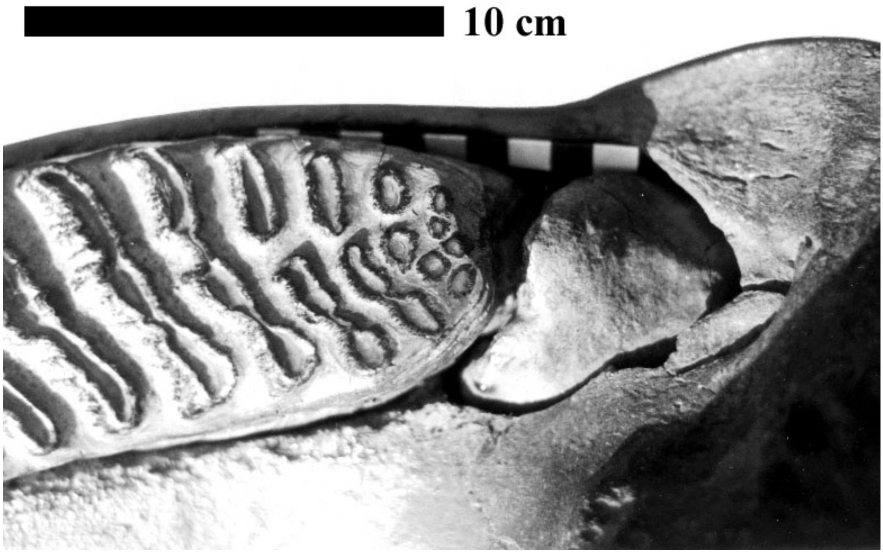


Fig. 6. *M. primigenius*. The Ketelmeer mandible; close-up of left corpus mandibulae with worn M_3 and unworn apical part of anterior extreme of supernumerary tooth in occlusal view. Note development of buccal lobe in the latter.

Fig. 7. *M. primigenius*. The Ketelmeer mandible; superior/lingual close-up of left ramus ascendens; in the foramen mandibulare the enamel organ and the posteriormost plate bases of the supernumerary tooth are visible.

Table I

Measurements of the Ketelmeer mandible (in mm; measurement definitions after BEDEN 1983: 104)

Superior surface				
A	maximum width incl. mandibular condyles	nm	e	540.
B	intercondyloid width of mandible	nm	e	380.
C	transverse width of condyle	nm		–
D	anteroposterior length of condyle	nm		–
E	width between coronoid processes			400.
F	width of mandible at base of ascending rami			425.
G	width between corpora mandibulae (in same plane as F)			90.
H	width of corpus mandibulae (in same plane as F)			153.
J	width between corpora mandibulae at anterior alveolar border			77.
K	width of corpus mandibulae (at same point as J)			111.
L	length of symphysis			144.
M	width of symphyseal beak			22.5
N	width between superior edges of interalveolar crests			78.
Lateral surface				
A	length of (left) interalveolar crest			203.
B	horiz. length between symphyseal beak and level of ant. alveolar border			146.
C	horiz. length between ant. alveolar border and base of ascending ramus			187.
D	horiz. length between base and posterior edge of ascending ramus			241.
BCD	maximum length mandible			574.
E	height of corpus mandibulae at anterior alveolar border			186.
F	height of corpus mandibulae at base of ascending ramus			152.
G	maximum height of mandible incl. condyle	nm	e	460.
H	length of posterior part ascending ramus behind mandibular condyle			30.
J	maximum length ascending ramus			160.
K	height between dental foramen and base of mandibular condyle (measured from basal extreme of dental foramen)			220.

An analogue from Germany

A very similar mandible from Otterstadt (Upper Rhine Graben, Germany) was published by ADAM (1994). This magnificent specimen (Staatliches Museum für Naturkunde in Stuttgart, no. 6616.4.12.87.4) shows about the same peculiarities as the Ketelmeer mandible (see the comparison below), but generally further developed and observable in both mandible halves (Fig. 8). Prof. ADAM, however, holds a different view on the Otterstadt mandible. In his interpretation it displays an anomaly in the replacement of M_2 by M_3. He explains the M_3-like morphology of the anterior tooth pair – M_2s according to him – as the result of lacking pressure by the following M_3s, because these failed to make the normal median contact with the posterior ends of their predecessors. Instead of the blunt posterior end otherwise bestowed on M_2s by M_3s, he argues, one now observes basal antero-posterior divergence of lamellae and even lengthening of the crown in the M_2s. He therefore

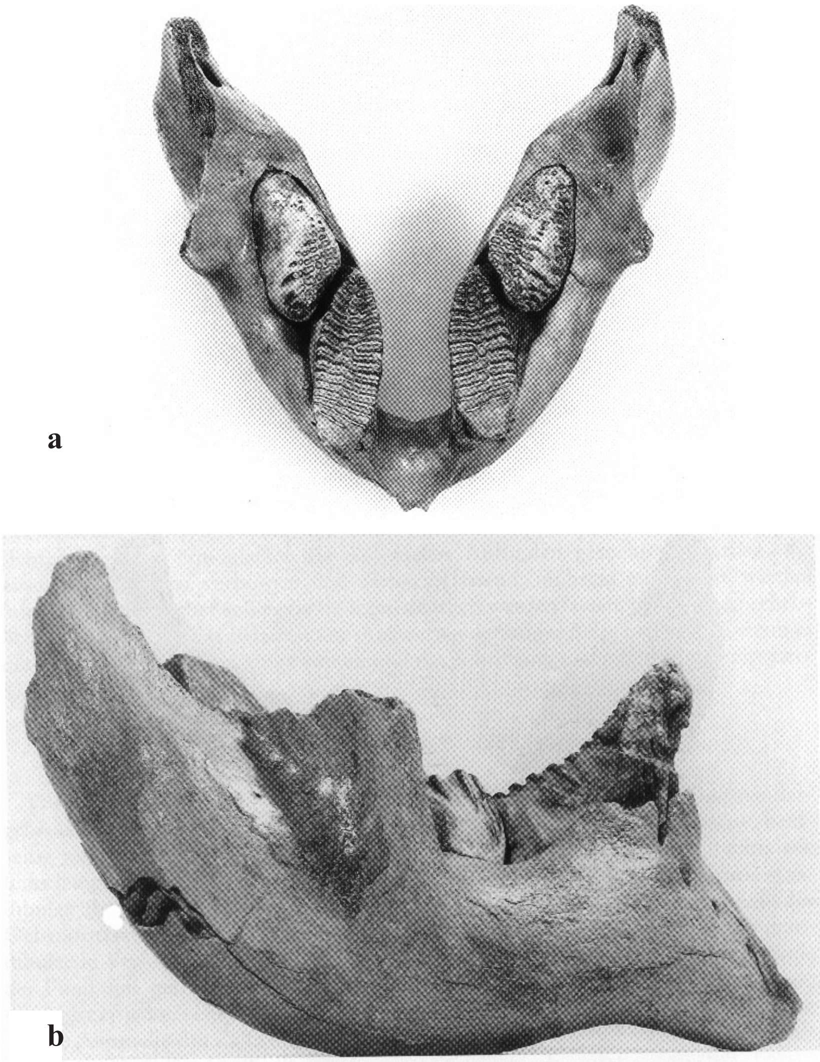


Fig. 8. *M. primigenius*. The Otterstadt mandible; a – superior view, b – right lateral view. Otterstadt, Rheinland-Pfalz (Upper Rhine Graben), Germany (SMN in Stuttgart, no. 6616.4.12.87.4). Photos: H. Lumpe, originally published in Adam 1994; reproduction with kind permission by the editors of the Stuttgarter Beiträge zur Naturkunde.

diagnoses a general problem with regard to the accurate attribution of isolated finds to either M3-shaped M2s or true M3s. Conversely, an M3 followed by a supernumerary tooth is believed to develop M2-like characteristics through the pressure exerted from behind. The arguments against this alternative interpretation are given below.

Discussion

The concept of the development of M_3-shaped M_2s through the absence of posterior pressure (ADAM 1994) is based on the idea that M_3s possess basally divergent or 'fanning' posterior plates because they are not followed by yet another tooth that generates pressure against their posterior ends. In the present author's view, however, the characteristics of M_2 and M_3 are predetermined and not interchangeable in such a way that the former could take over the role of the latter and become unrecognizable as an M_2, or the reverse. The arguments that support the interpretation of the anterior teeth in the Otterstadt mandible as M_3s rather than M_2s are the following:

– First of all there is a morphological difference that is not likely to be effaced just through lack of pressure: As explained above, M_2s have posterior talonids, often more than one in *M. primigenius*. A posterior talonid is therefore a minor plate structure borne by the last lamella or a larger talonid, i.e., it merges with the base of its predecessor at a certain level above the root. By contrast, M_3s have platelets ('p' in plate formulas) in posteriormost position. These are minor plate structures as well, but make their own full contact with the posterior root complex and are therefore essentially lamellar. This difference speaks for predetermined crown details, as does the plate number.

– The basic assumption is that shape is gradually imparted to each molar crown through the calcification of one lamella after the other, during which process changes in lamellar shape occur. These changes likely relate to the part of the dental canal where the lamellae of the continually erupting tooth develop. An M_3 has to become considerably longer than an M_2, and hence the formation area of its posterior lamellae shifts backward to the less spacious part of the dental canal. This brings about a steady decrease in height and width of the posterior plates, as well as basal anteroposterior divergence and a backward bend of their basal thirds (i.e., a further height reduction in the posterior part of the crown).

Weight is considered one of the mechanical forces that influence teeth (ROTH 1989: 168). This suggests that the weight of the dental matter involved plays a role in the generation of the abovementioned effects, because the calcification of the tooth proceeds from the apical to the basal region. The relatively less dense and weaker base of a lower tooth will therefore be loaded by the higher part of the crown, which is ahead in its development. In combination with the progression of the tooth, its weight would also create greater counteracting forces in its wider basal part. Hence the basal region would be susceptible to deformation to the same degree as it had remained unfinished. This mechanism affects the posterior part of an M_3 crown most. It could be called a 'dragging effect' and may partly account for the basal bend.

As a result, the posterior end of an M_3 crown clearly contrasts with the high, wide, and about perpendicular posterior lamellae in an M_2. These may show minor basal dragging effects as well, but are not at all likely to develop tapering and basal divergence if pressure by the M_3 should be absent: In order to mimic a posterior M_3 portion, they would actually have to shrink by various and increasing degrees, because in a normal M_2 the hindmost lamellae are the highest and widest. As for divergence, an M_2 is rather short, and by the time it is becoming fully calcified does not extend far back into the dental canal, so that there is no analogous situation with respect to M_3s. Already calcified lamellae, on the other hand, could hardly undergo the alledged change in their array anyway.

In addition to this, M_2s do not experience posterior pressure continuously. There is a period (wear stages XV-XVI; LAWS 1966: 8) during which M_1 is in very advanced wear and M_2 fully formed, calcified, and in earliest wear. At the same time, the M_3 is still in an early germinal, largely uncalcified state and certainly in no position yet to exert significant pressure. An M_2 at this particular stage therefore does not show the slightest pressure scar. Yet it retains its typical shape and does not show any lengthening of the crown. The likely cause of this shape retention is the presence of the ossified and comparatively large enamel organ behind the tooth until shortly after its complete calcification. It is the enamel organ also that absorbs the minor posterior pressure exerted through the apical part of the M_3 germ, by which it may be dented (VAN ESSEN, personal observation). TOEPFER (1957: 11-12) succinctly interprets the ossification of the enamel organ as the creation of a counterpoise for its tooth, believed to be functional within the system of the so-called horizontal tooth replacement in elephants. By implication, this function would shift from one enamel organ to the next in the course of the resorption of the earlier and the growth of the later one, while at the same time the tooth between them would have to become calcified to a degree that would enable it to pass on the forces generated by the system. This scenario seems somewhat failure-prone and might explain some of the spatial deformations encountered in elephantid teeth. At any rate, the proposed shift from the M_2 model to that of M_3 through the mere absence of pressure would involve categorial feature changes that do not occur during the normal replacement of M_2 by M_3, which is – at least temporarily – not essentially different where lack of pressure is concerned.

– A similar argument can be used with regard to the roots. In M_2 the root system is comparatively simple, and the posterior section fuses into a single large and squarish root that maintains a short pulp cavity for a long time. The wide posterior face of this root is flat or concave and lies in the same plane as the posteriormost plate and its talonid(s). As the time approaches at which the posterior remains of the tooth must be shed, the root portion is resorbed as far as necessary to let this happen. In M_3, on the contrary, no such preparation for shedding takes place: Anterior roots disappear with the anterior portion of the crown, but the last permanent molar is scheduled to stay in the jaw as long as possible. From a certain stage of advanced wear, the posterior part of its crown is carried by the long and keel-shaped root complex already mentioned above (wear stage 6-6' in Fig. 4). It may likewise be observed in M_3s that belong to other proboscidean taxa. Its anterior and posterior limits are usually fairly acute, and it extends downward to the floor of the corpus mandibulae for greater stability as the crown becomes shallower. The pulp cavity is narrow and long at first, and shortens along with the keel itself as wear proceeds. If the individual lives on long enough, the last traces of plates and cement intervals disappear, the pulp cavity dwindles, and an occlusal surface without any relief develops on the hindmost part of the root dentine (wear stage 7-7' in Fig. 4; note: this is a stage slightly beyond no. XXX in the LAWS system. LAWS may not have encountered it in his samples, but among large quantities of *M. primigenius* molars it is not very uncommon). An M_3 therefore holds on to the very last, and it is exactly the M_3 type of root formation that is observed in the anterior Otterstadt specimens. A causal link between the presence or absence of pressure and the categorial root characteristics described does not seem plausible (see also the discussion of a posteriorly dented M_3 under 'Some Aspects…' below).

– Furthermore, if the anterior teeth are interpreted as near-complete M_2s, the usually rather thick first root should be visible on the median line – even in the arrangement of the dentine at the fracture surface if it should have been broken off – but it is not (ADAM 1994: figs. 8, 9).

– Again, if the tooth is an M_2, the width maximum (74. mm) is too small in relation to the reconstructed length of 260. mm (ibid., 26), which gives a LWI of 351. The average M_2 LWI value in western European *M. primigenius* is about 240. (VAN ESSEN, unpublished data). As shown above, the alledged lengthening of the anterior teeth through lack of pressure is not encountered in M_2, although at a certain stage of development lack of pressure occurs. Lengthening therefore cannot serve as an explanation of the about 46% surplus over the normal M_2 LWI value. Instead, the difference indicates that the anterior teeth in the Otterstadt mandible are M_3s.

– A very important feature that often allows one to discern between tooth generations is the plate number (P). The present author differs with prof. ADAM on the reconstruction of P in the anterior teeth of the Otterstadt mandible. Thanks to the excellent photos by mr. H. LUMPE (ADAM 1994: figs. 2-15) it proved possible to present an alternative to the published reconstruction of the longer right specimen. It is reported to have a lamellar formula of ∞ 9 ½ 8 x, which is reconstructed as x! 9 ½ 8 x (ibid.: 26). The dentine platform (∞) is therefore interpreted as representing a large anterior talonid (x!) only, and with 17 full lamellae the tooth would show the maximum number possible for an M_2 of *M. primigenius*. However, the anteriormost part of a dentine platform that indicates the loss of the anteriormost plates of a tooth always represents the anterior talon(id) and the first lamella together, because the bases of these two plate structures merge. For this reason alone, there would have been 18 full lamellae instead of 17. The total length of the dentine platform suggests the number of lamellae that were worn down below the level of their basal enamel, so that the root dentine was exposed. In the tooth considered here, the platform has a length of approximately 20. mm (ibid.: 8 fig. 7; 28), about the equivalent of two lamellae. The dentine of the next lamella is already laterally confluent with that of the platform. Then there are 16 lamellae (excl. '½') visible within the occlusal surface, the last one only as the top of a single digitation. The occlusal surface including the anterior dentine platform therefore represents 19 lamellae. In the lingual view of Fig. 10 the count may be resumed from the enamel that represents the first laterally intact lamella (in fact the fourth from the front). This leads to the count 4 through 19, plus space for a posterior platelet. Because the posterior lamellae can be traced in the lingual crown wall, the same result is obtained from the baseline of the crown. The tooth therefore had more lamellae than an M_2 (range in *M. primigenius*: 15-16 [MAGLIO 1973]/14-17 [VAN ESSEN, unpublished data]) and hence may be considered to be an M_3 with 19+ plates. Since wear has proceeded barely beyond the line 5-5' in the present Fig. 4, about 4 or 5 lamellae and the anterior talonid were lost by wear, so that an original plate formula of x 23 p or x 24 p is plausible. The posterior teeth therefore must be supernumerary.

Both M_3s in the Otterstadt mandible can be lifted from the jaw (ADAM 1994: figs. 6-15) and show M_3 characteristics only. In summary these are:

– a plate number that is too high for an M_2;

– the lack of evidence for a true posterior talonid;

– the fact that the greatest remaining width lies at about half the original plate height in the medial crown portion, i.e., near the middle of the occlusal surface; the elongate occlusal surface is therefore acutely oval;

– the steadily decreasing width (and presumably height) in the posterior part of the crown;

– the basally divergent posterior plates, the lower portions of which are markedly bent to the rear;

– a long dentine platform;

– the development of an almost smooth, keel-shaped root portion with a very elongate, narrow pulp cavity.

The Ketelmeer and Otterstadt mandibles. A comparison

The basic similarity between the two jaws is that both contain M_3s in advanced wear that are followed by supernumerary teeth of considerable size. All three of these had started wedging in between the buccal crown sides of the M_3s and the buccal walls of the mandibular corpus. There are some differences in degree, however:

– The left M_3 in the Ketelmeer mandible (KM) has reached a more advanced wear stage than the Otterstadt (OM) specimens, but in length and number of preserved plates the right M_3 in the KM was apparently close to these (Fig. 4).

– The supernumerary tooth in the KM is a unilateral phenomenon; in the OM the anomaly is bilateral.

– The supernumerary tooth in the KM is on the verge of erupting; in the OM both specimens have erupted and are in initial wear.

– Because the wear stages of the M_3s in both mandibles are essentially the same and the eruption stages of the supernumerary teeth differ, the supernumerary tooth in the KM seems to have made its appearance later than the specimens in the OM.

– The M_3 in the left half of the KM is in a normal position with respect to both the upper and the anterior limits of the mandibular corpus. In the OM the occlusal surfaces of both M3s as well as those of the supernumerary teeth have markedly risen above the mandible. The frontal portions of the M_3s project well beyond the interalveolar crests (which may be the cause of the apparent superficial damage these frontal portions incurred).

– The posterior crown base of the left supernumerary tooth in the KM is turned towards the lingual/posterior side; that of the right specimen in the OM is turned towards the buccal/posterior side (ADAM 1994: fig. 4); the left specimen could not be checked in this respect, but might present a mirror image.

– The supernumerary teeth in the OM had progressed to such an extent that they partly 'overtook' the M_3s on the buccal side, and as a result made contact with their buccal posterior ends only, where they caused extensive pressure scars (ADAM 1994: figs. 14 & 15). In the KM the supernumerary tooth had only just started on its course to the buccal side of the M_3.

– Alveolar space in the OM was much enlarged. In the KM post-M_3 alveolar widening had only just begun.

– The P of the supernumerary teeth in the OM is unknown, but greater than that in the specimen in the KM because at least 15 closely spaced plates can be counted on the buccal side of the erupted part of the left specimen (ADAM 1994: fig. 2), and there are probably some more. The germ in the KM presumably started developing at a later stage and for that reason not more than 14 or 15 lamellae had yet been completed.

From the details described above, the following deductions regarding initial situations and later developments were made:

– Both mandibles originally contained fully calcified M_3s that were in wear and occupied a normal position within the jaw.

– Relative to M_3 development, the supernumerary teeth in the OM were the first to develop (simultaneously).

– Because M_3s are large and stay in the mandibular corpus for a very long time, the specimens in the KM as well as in the OM started impeding the progression of the supernumerary teeth while these were still growing, largely encased in the conical dental canal within the ascending ramus. Dislocation and deformation of the supernumerary teeth was the result. (Note: The main aspect of deformation in the specimen in the KM is the warping of the crown. In addition, however, it seems possible that the undulate layer of dentine at the base of its anteriormost plates is the dentine originally intended for the outer wall of the first root, whose further development may have been halted by the collapse of the Sheath of Hertwig as this was squeezed against the floor of the mandible before the eruption of the tooth could create the necessary space. In the supernumerary specimens in the OM, the condition of the anterior roots is hidden by the jaw).

– Because of the blockade, an upward vector began to contribute to the course of progression in the OM, and the supernumerary teeth erupted prematurely. In the KM this development had scarcely been initiated.

– The posterior ends of the M_3s in the OM being fully calcified and wedge-shaped, the anterior portions of the supernumerary teeth were first dented and then deflected to the buccal sides of the jaws. With a buccal lobe of the supernumerary tooth extending just beyond the posterior border of the M_3, the situation in the KM represents an earlier stage of this development. The preference of the supernumerary teeth for the buccal side of the M_3 crowns in spite of their different orientation within the dental canal may be explained by the fact that anteriorly the antero-posterior axis of the ascending ramus angles away in buccal direction from the sagittal axis of the M_3. The space on the buccal side of posterior parts of M_3 crowns is therefore much larger than on the lingual side, where there is virtually no space at all.

– Especially in the OM, upward and forward pressure mounted to such an extent that the retromolar triangles were resorbed to give room to the rising anterior portions of the prematurely erupting supernumerary teeth, so that the retromolar foramina were destroyed in the process. The anterior portions of the supernumerary teeth became increasingly wedge-shaped buccally. In the KM, the bone around the left retromolar foramen was on the brink of being resorbed.

– At the same time, the posterior crown portions of the M_3s in the OM experienced forces that were directed lingually, forward, and upward. This resulted in a posterior dislocation in lingual direction (as observed by ADAM [1994]). At their frontal ends, where they used to be closest to each other, the rigid M_3s were therefore turned away from each other in buccal direction. M_3s and supernumerary teeth were apparently so much pressed together that the upward as well as the forward course components of the erupting supernumerary teeth were imparted to the M_3s. While these were lifted up, a net forward displacement was caused by a force exerted obliquely on the convex buccal posterior crown sides. It was gradually pressing the M_3s out of the jaw, so that they already stuck out in front (Fig. 8b). This was probably made easier through their backward-slanting root portions.

– In the OM the rate of wear in the M_3s was obviously not high enough for the above-mentioned horizontal and vertical displacement of their crowns to be counterbalanced by the loss of part of the apical tooth volume. In the KM, however, the length difference between the M_3s is more conspicuous than usual and was probably influenced by the advance of the supernumerary tooth on the left. The front of the left M_3 could well have been forced upward because the supernumerary tooth bore on its hindmost plates. The X-ray (Fig. 2a) seems to suggest exactly this. Just as in the OM, the backward-slanting root portion would have facilitated the uplift. If the rate of wear sufficed to counteract the anterior uplift at this early stage, this could explain the degree of shortening observed in the occlusal surface. The pressure exerted by the supernumerary tooth probably moved the left M_3 forward while it was being shortened, so that the total length difference between the two specimens is now indicated by the positions of their posterior ends only.

Some aspects of replacement by supernumerary teeth

The variable time span between the completion of an M_3 and the formation of a supernumerary tooth is in itself an indication that the latter does not belong to the normal dentition. In both mandibles mentioned here, the supernumerary teeth had caught up with the M_3s and started overtaking them, because these were not worn quick enough to get out of the way in time. Since there are no signs of delayed wear in the M_3s, the relatively high and persistent velocity of the supernumerary teeth could indicate that one is indeed dealing with duplicated M_3s that behaved as if they were replacing comparatively rapidly disappearing M_2s. True M_3s, however, do not behave as M_2s, so that they blocked the progression of the supernumerary teeth in the Otterstadt and Ketelmeer mandibles. This situation is another argument in favour of predetermined characteristics and behaviour.

The fact that some post-M3 supernumerary teeth are to some extent worn – as in the Otterstadt mandible, and possibly in the absence of a corresponding supernumerary specimen in the opposite jaw – is likely to be the result of 'overtaking' and/or a forward displacement of the M3s caused by the advance of the supernumerary teeth, as described above. The latter could then for some time be functional in combination with an M3 in normal position within the opposite jaw.

In those cases where M3 is followed by a supernumerary tooth, prof. ADAM (1994: 13, table 1) expects that the shape of the M3 will forcibly be altered into that of an M2, characterized by a posteriorly widened crown. As far as categorial changes are implied – e.g., from posterior platelet into talonid(s), from keel-shaped into block-shaped root, from divergent and tapering plates to parallel ones of equal height and width – this seems as unlikely as the reverse. Nor would any other deformation than a pressure scar have to be expected if the M3 happened to have been completed well before the arrival of the supernumerary tooth at its posterior end (Ketelmeer and Otterstadt mandibles). The lack or occurrence of a time lapse between the development of the two elements is therefore crucial: Only an early close conjunction could indeed have the alledged effect, because then the posterior part of the M3 would already be affected while it was still uncalcified and vulnerable. This also implies that it actually was the M3's enamel organ that was made to cause the deformation, because it would still have been present as long as the M3 was unfinished (see below). Fig. 9 (ac no. 018, M_3 of *M. primigenius* from the Rhederlaag concession, Giesbeek, The Netherlands) is here presented as a probable example of such a case. Although the posterior face of the tooth is concave – presumably through pressure exerted by a supernumerary element, and via the enamel organ – it is characterized by a marked relief (including a deep sinus to the right of the label in Fig. 9c) and there is no posterior pressure scar whatsoever. This speaks for deformation in an uncalcified state. Possibly in part because the enamel organ was squeezed between the M_3 and the supernumerary tooth and therefore malfunctioning, the posterior plates in this M_3 have spatially disintegrated, and the parts

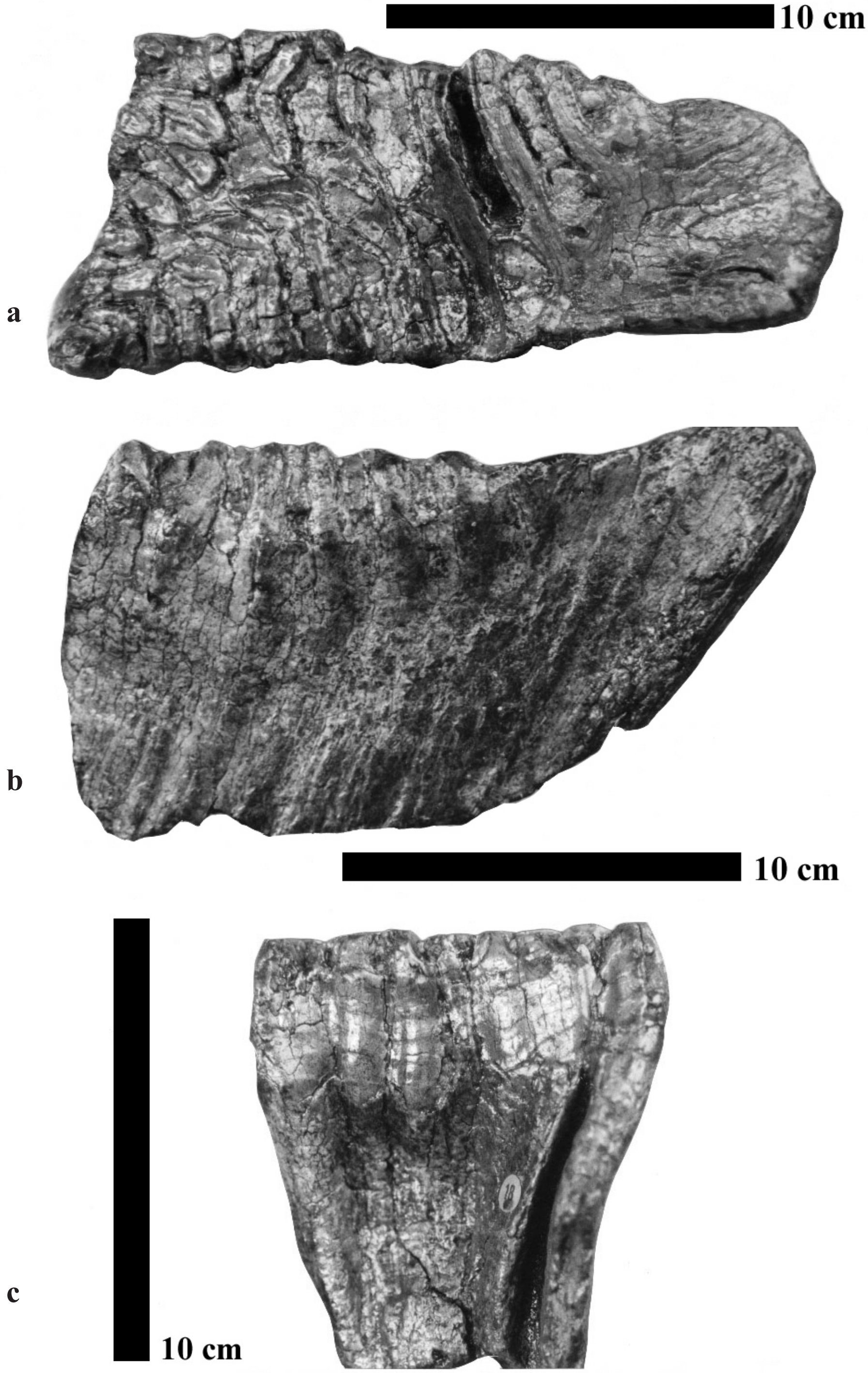


Fig. 9. *M. primigenius*. Complete remains of M_3 cf. sin.; a – occlusal view, b – cf. lingual view, c – posterior view. Note development of keel-shaped root and lack of pressure scar on dented posterior surface. Rhederlaag concession, Giesbeek, Gelderland, The Netherlands (ac, no. 018).

were rearranged into a quite disorderly configuration that subsequently calcified. The later development of a keel-shaped root underneath the deformed crown has yet taken place and shows that M_3s will always be recognizable by this feature. The posteriormost part of the tooth is indeed the widest, but the altered features of the crown are only of a spatial, not of a categorial nature. Difficulties in telling an isolated worn M3 apart from an M2 are therefore not to be expected, even if the M_3 was followed by a supernumerary element.

On the incompleteness of supernumerary teeth

In cases where one has to decide whether or not a tooth had been completed, the presence or absence of the enamel organ may to some extent facilitate the interpretation. In a mandible (ac 336/R762/772, not figured) from the Rhederlaag concession, for example, the posterior end of the right M_1 in earliest wear had just been completed and the adjoining enamel organ – still covering the total height of the posterior plates of M_1 – had already reached a position over the angulus mandibulae, within a few centimetres from the point where it would have become visible from the outside if the teeth had progressed any further. Since no enamel organ has so far been observed within the occlusal area while still being stuck between two advancing molars, the described situation implies that enamel organs in elephants are fairly rapidly resorbed after the completion of their tooth. Hence it is understandable that the enamel organ that belonged to the left M_3 in the Ketelmeer mandible had not been turned into an instrument of deformation before it disappeared completely: the fossilized configuration reflects a point in time well after the complete calcification of the M_3.

The presence of the enamel organ behind the supernumerary element in the Ketelmeer mandible then leaves two possibilities: The tooth had either just been completed or was still under construction. The former possibility at first glance appears to be more likely because all plates present seem to be connected and there are no loose plate germs. Some uncertainty remains, however, since plate germs of sufficiently small dimensions might have been lost post mortem via the foramen mandibulare in spite of the presence of the enamel organ. The original X-ray (Fig. 2a) shows a fragment of a basal enamel joint – presumably broken away from a pair of lamellae in the anterior part of the crown – to be stuck against the concave face of the enamel organ (presumably because the mandible was preserved with thinned linseed oil [database Schokland Museum]). This indicates that there is some space between the posteriormost plate visible and the organ.

Because nothing is so far known about the enamel organs in the Otterstadt mandible, the evidence for completion of the three supernumerary teeth in the jaws here discussed is poor, although each of them comes comparatively close to being an M_3 replica. As an average M_3 – possibly developed from a reduplicated bud – the Ketelmeer specimen would be lacking about seven or eight lamellae, for which space would probably never have become available: The dental canal was nearly filled up to the foramen mandibulare and the M_3 formed a blockade in front that was likely to give way only very slowly. Further development would possibly have resembled that in the Otterstadt mandible, but the plate formula of its two partly erupted supernumerary teeth could not be determined (ADAM 1994: 10, 27).

From a tentative theoretical point of view, the plate number of a supernumerary tooth could be influenced by various factors:

The death of the animal

On the assumption that a tooth approaching an M3 replica is under construction, an incomplete tooth would be the result if death interfered at any stage before a normal M3 plate number was reached. With about 15 plates, the Ketelmeer specimen could be an example of such a case. Its posteriormost lamellae seem to be lower than the preceding ones (Fig. 2a), but since the crown is warped it is not possible to establish a complete morphological parallel with the posterior end of an M_3 on the basis of the X-ray. In some isolated specimens tentatively interpreted as supernumerary teeth, however, the shape of the posterior end is indistinguishable from that in a normal M3 (see category I, below). This suggests that a complete tooth is mapped out, however small its plate number may be, and that formation stopped by death would indeed result in a tooth that looks incomplete posteriorly.

The limited space behind M3

If the available space would be the limiting factor and thus lead to supernumerary teeth with varying plate numbers and lengths, there would generally be no cause for excessive deformation. The plate number of the supernumerary teeth in the Otterstadt mandible is not in tune with the available space, nor did the formation of the Villeneuve specimen stop when space ran out. This appears to be consistent with those cases in which plates keep being added, especially to M3s, while the situation is derailing and deformation ensues (see, e.g., ROTH 1989: 173, fig. 6). In her discussion of the problem of variable plate numbers with respect to elephantid teeth in general, ROTH (ibid.: 177) states that this variability is likely the result of both predetermination and available space, because tooth formation and progression as well as the growth of the jaw are interrelated processes. The above examples, however, suggest that 'predetermined plate number' overrules 'available space' instead of the reverse (if the reverse is at all biologically or logically possible). As long as a tooth goes through the earliest stages of formation and calcification within a comparatively small space, a perhaps uncomfortably high plate number is likely to lead to an enhanced lamellar frequency first (see also LISTER & JOYSEY 1992; VAN ESSEN 2003: 482/483). If this compaction should not solve the problem, deformation is about to start. Another hint in this direction is the fact that in diminutive mammoth molars it is the size of the plates that is adapted, not their number. Whereas smallness is likely to be a developmental feature of the entire organism in the case of diminutive mainland mammoths, the plate number appears to be fixed by inheritance and to remain subject to selective pressure. High lamellar frequencies therefore commonly occur in late *M. primigenius* populations such as those of Berelekh and Wrangel, whose relatively small body and tooth sizes are possibly to be interpreted as symptoms of approaching extinction (LISTER 1996: 211).

In the fossil record, supernumerary teeth and other odontogenic anomalies in elephants are not observed in great numbers, although the true frequency of their occurrence may hitherto have been underestimated. In view of their occasional appearance, they are likely the result of a somehow disrupted interaction of genes, the outcome of which generally leads to recurrent types of malformation that may reflect more or less fixed 'weak spots' in the system. Yet the larger supernumerary specimens are essentially formed as any other element of the dentition, and in spite of their not having been 'foreseen' by the system, so that suitable space for a regular development will often be denied them, may approach a normal M3 plate number. If it is not the death of the animals that keeps them from reaching this, nor spatial limitations, the possibility has to be considered that predetermination plays a part here as well as in normal teeth, albeit as a corollary of the disruption. This factor then could be termed:

Defectiveness of the supernumerary germ

In spite of its tortuousness, the maxillary Villeneuve specimen looks as if it had been completed, but it only has about 17 plates (BURNS et al. 2003: 78, 79 fig. 1b). This could mean that it developed according to plan and was by chance deformed for lack of space. A few isolated teeth are listed below as presumed supernumerary specimens (category I). Since they likely developed within the reduced space behind M3, some possess the tapering posterior ends of the M3 model. If the classification as supernumerary teeth is correct, a few completed specimens with very low plate numbers attract attention and are – perhaps exactly because they have so few lamellae – hardly deformed. This might confirm that at least some supernumerary elements are essentially subnormal in plate number in comparison with M3, which they resemble in other respects (Figs. 10, 11, 15). The more odd-looking category II specimens described below do not or hardly at all possess complete lamellae, so that in this respect there is no good reason for comparison.

The mechanism by which the actual plate number in supernumerary teeth is predetermined is likely to act on the cellular level during the earliest stages of tooth formation. The way in which aberrations in the supernumerary tooth buds come into being – perhaps through mechanical or biochemical influences – is speculative, and apparently there are gradations in malformation. For the time being it is important that more examples are gathered and to establish the limits within which the seemingly random plate numbers are realized. The preliminary list of fossil specimens preserved within their jaws comprises:

– The Villeneuve maxillary specimen; P≈17 (BURNS et al., 2003)
– The Otterstadt mandible; two specimens; P>15 (ADAM 1994; this paper)
– The Ketelmeer mandible; one specimen; P≈15 (this paper)

Isolated specimens tentatively presented as supernumerary are listed below and may have even fewer plates.

Characteristics of supernumerary teeth and possible examples

Because especially some larger post-M3 supernumerary teeth were probably distorted while developing within a part of the jaw that proved too narrow for them, one may expect that the normal distinctive features of upper and lower teeth were either enhanced or to some extent obliterated. The enamel thickness of the specimens in the jaws compared above is not known, but if the isolated teeth tentatively listed below as Category I specimens are indeed supernumerary, the enamel thickness apparently stays within the M3 range representative of the species concerned.

Based on the mandibular Otterstadt and Ketelmeer specimens as well as on the maxillary Villeneuve specimen (BURNS et al. 2003), a preliminary set of characteristics emerges that could help to identify isolated finds that belong to this group of supernumerary teeth:

Category I – Teeth with an M3-like appearance that show (combinations of):
– normal-looking plates;
– slight to severe distortion of the crown;
– incompleteness of the crown / a lower plate number in comparison with M3;
– the presence of a concave frontal face;
– absence of wear or early wear;
– suppressed or stunted growth of the anterior root(s);
– signs of hypercementosis (exceptional).

Apart from the M3-like Category I specimens, some smaller-sized anomalies exist that are rather remote from the standard tooth model. They have one or more roots and show some kind of imperfect lamellar build, which usually is so abnormal that it could hardly or not at all be expressed in a plate formula. This group is here named:

Category II – Elements with an extremely subnormal crown build, composed of
– minor rooted clusters of plates, pillars, or digitations, possibly in combination.

This is probably the type that LAWS (1966) encountered in his *L. africana* sample of mandibles. He stated that “three of the specimens appear to be equivalent to a single lamella, but the fourth has four lamellae massively fused” (ibid.: 16). Because these elements were found in jaws whose M_3s looked quite normal, he dismissed the idea that they had somehow been separated from the M_3 germ and believed they sprang from a separate seventh tooth bud.

A very interesting example of this category occurred bilaterally behind the M_3s of the African elephant cow Beira in the Basel Zoo (LANG et al. 2000). These specimens were unworn as the animal died at the age of 48 years, and according to the authors would never have reached occlusion because there are no maxillary counterparts. The weights are 0.62 kg (left) and 0.78 kg. The crown lengths and widths are 52. and 62. mm respectively in the left specimen, and 72. and 60. mm in the right one. Apically concave fronts, possibly with pressure scars, indicate where they made contact with the M_3s. The horizontal cross section of the right supernumerary tooth shows but one complete lamella in the centre of the crown, surrounded by some scattered pillars and digitations. The left specimen has two roots, and the right one four, all with spacious pulp cavities. The longest roots measure 156. mm on the left and 164. mm on the right. Their tips reach the area of the angulus mandibulae.

The main difference between the categories I and II lies in the size and composition of the crown. Mutual extrapolation of each set of characteristics leads to forms that have not actually been encountered yet: M3-shaped crowns with no more than about four or five normal plates on the one hand, and very large, even M3-sized irregular clusters of digitations and lamellar pillars on the other. Hence it seems likely that the arrangement in two categories is not merely artificial and preliminary, but reflects basic developmental differences.

There is an intermediate group of malformed specimens that used to be looked upon as odontomas (see Part II). They are found attached to or partly fused with the anterior parts of M3s and are composed of relatively few plates that characteristically allow identification of the species. This type could provisionally be called Category III**.** There is one example from Japan (MAKIYAMA 1938: fig. 25) and one from Poland (KULCZYCKI 1955: pl. IV, fig. 3a-d). Perhaps one of the specimens mentioned by LAWS (1966) – the one with four lamellae massively fused – belongs here as well.

A number of isolated specimens in European collections of mammoth remains fit the above descriptions of either Category I or II and may tentatively be classified as supernumerary teeth (Tables IIa, 2b).

As M3s with somehow decreased plate numbers the specimens in Category I do not convince, since in that case there would generally be no cause for distortion, and the examples so far observed in mandibles show many similarities. A relapse of M3s into a more primitive condition is equally unlikely because then the plate number would be the only morphological feature that had changed, apart from size.

Table IIa

Six isolated specimens attributed to the supernumerary tooth category I

COLLECTION	FSFQ Weimar	**REMARKS** Various distortions/altered size relations;
NUMBER	1965/2445	plate formula: about x 13 p; in very early wear;
SPECIES	*M. trogontherii*	abnormal position of occlusal surface.
SITE	Süßenborn, GFR	
JAW	upper	Figure 10
COLLECTION	FSFQ Weimar	**REMARKS** Slightly distorted posteriorly;
NUMBER	1965/2410	plate formula: x 1 ½ 10 p; in early wear.
SPECIES	*M. trogontherii*	
SITE	Süßenborn, GFR	
JAW	upper	Figure 11
COLLECTION	SMN Karlsruhe	**REMARKS** Much distorted;
NUMBER	QP/599	plate formula: about 15 or 16 (p); unworn.
SPECIES	*Mammuthus* sp.	
SITE	Eggenstein, GFR	
JAW	indeterminable	Figure 12

COLLECTION	NHM London	**REMARKS** Much distorted;
NUMBER	37274	plate formula: about x 10 p; unworn.
SPECIES	*M.* cf. *trogontherii*	
SITE	North Sea off Cromer, GB	
JAW	upper?	Figure 13
COLLECTION	SM Cambridge	**REMARKS** Various distortions; plate formula: (x) 16;
NUMBER	D 31863	unworn; concave frontal face; L 230. mm; W 94. mm
SPECIES	*M.* cf. *primigenius*	(lam. 11); H 171. mm (lam. 4); HI 182.; ET 1.5-1.7 mm;
SITE	North Sea off Cromer, GB	LF 7.39.
JAW	indeterminable	Figure 14
COLLECTION	Naturalis, Leiden	**REMARKS** Slightly distorted;
NUMBER	RGM 146796	plate formula x 1 ½ 11 p; in early wear; occlusal
SPECIES	*M. primigenius*	surface concave; L 206. mm; W 81. mm (lam. 2);
SITE	North Sea,	H e120. mm (lam. 2); HI e148.; ET 1.4-1.6 mm;
	S. of Brown Bank	LF 8.77.
JAW	probably lower	Figure 15

Table IIb

Three isolated specimens attributed to the supernumerary tooth category II

COLLECTION	NHM London	**REMARKS** Small cluster of digitations;
NUMBER	1232 (Savin coll.)	single root with oval cross section and wide pulp
SPECIES	*Mammuthus* sp.	cavity; unworn; cover cement largely intact.
SITE	Trimingham, GB	
JAW	indeterminable	Figure 16
COLLECTION	author	**REMARKS** Cluster of at least nine digitations, six of
NUMBER	154	which are slightly worn or damaged apically;
SPECIES	*M. primigenius*	fairly thick cement cover damaged; broad single
SITE	North Sea	root with triangular / oval cross section and
	(no coordinates)	conical pulp cavity; modal ET 1.4 mm.
JAW	indeterminable	Figure 17
COLLECTION	VAN der Bok	**REMARKS** Tubular cluster of (half) plates that radiate
	Ouddorp, NL	from the central axis; unworn; height equivalent to M2
NUMBER	–	or M3; root broken off at the crown base.
SPECIES	*M. primigenius*	
SITE	North Sea	
	(no coordinates)	
JAW	indeterminable	Not figured.

The three specimens attributed to Category II have a more or less central plan and a single tubular root in common. LAWS (1966: 16) did not discuss the presence or absence of roots, but the similarity to the specimens he found in *L. africana* seems obvious, since the majority of these were characterized as “equivalent” to a single plate. This is here interpreted as ‘consisting of isolated ele-

a

b

Fig. 10. *M . trogontherii*. Presumed post-M^3 right supernumerary tooth; a – oblique lingual view, b – occlusal view. Süßenborn, Thüringen, Germany (FSFQ Weimar, no. 1965/2445). Photos: T. KORN.

a

b

Fig. 11. *M. trogontherii*. Presumed post-M^3 right supernumerary tooth; a – lingual view, b – occlusal view. Süßenborn, Thüringen, Germany (FSFQ Weimar, no. 1965/2410). Photos: T. Korn.

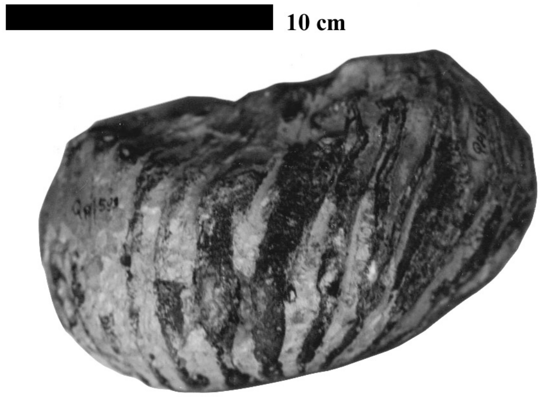


Fig. 12. *M.* cf. *primigenius*. Unworn presumed post-M3 supernumerary tooth; occlusal view. Eggenstein, Baden-Württemberg (Upper Rhine Graben), Germany (SMN in Karlsruhe, no. QP/599).

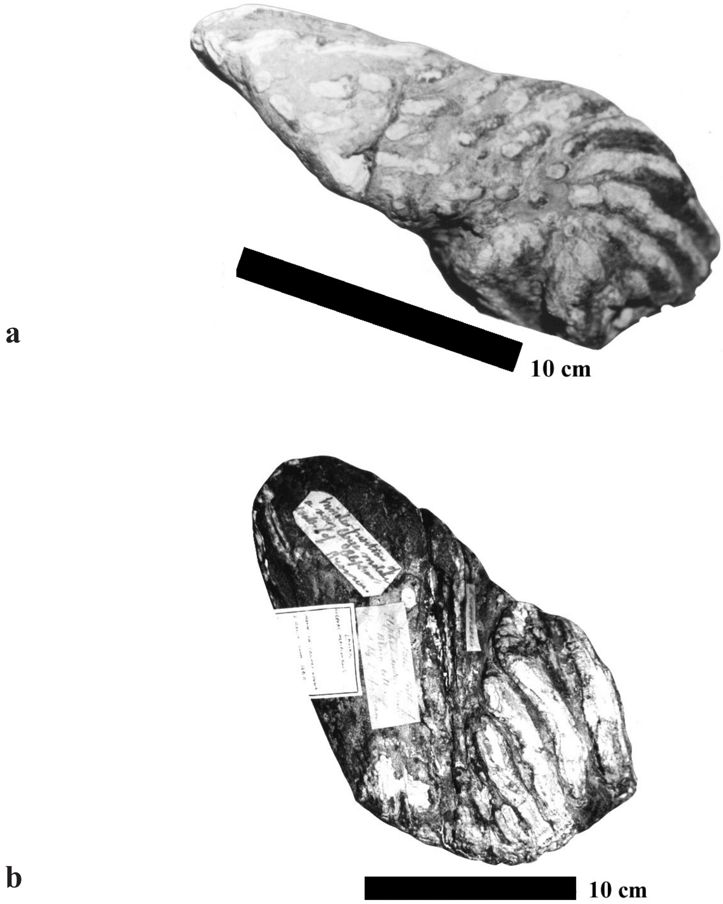


Fig. 13. *Mammuthus* sp. (*trogontherii* or *primigenius)*. Unworn presumed post-M^3 supernumerary tooth; a – occlusal view, b – lateral view. Southern North Sea off Cromer, Norfolk, England (NHM London, no. 37274).

a

b

c

d

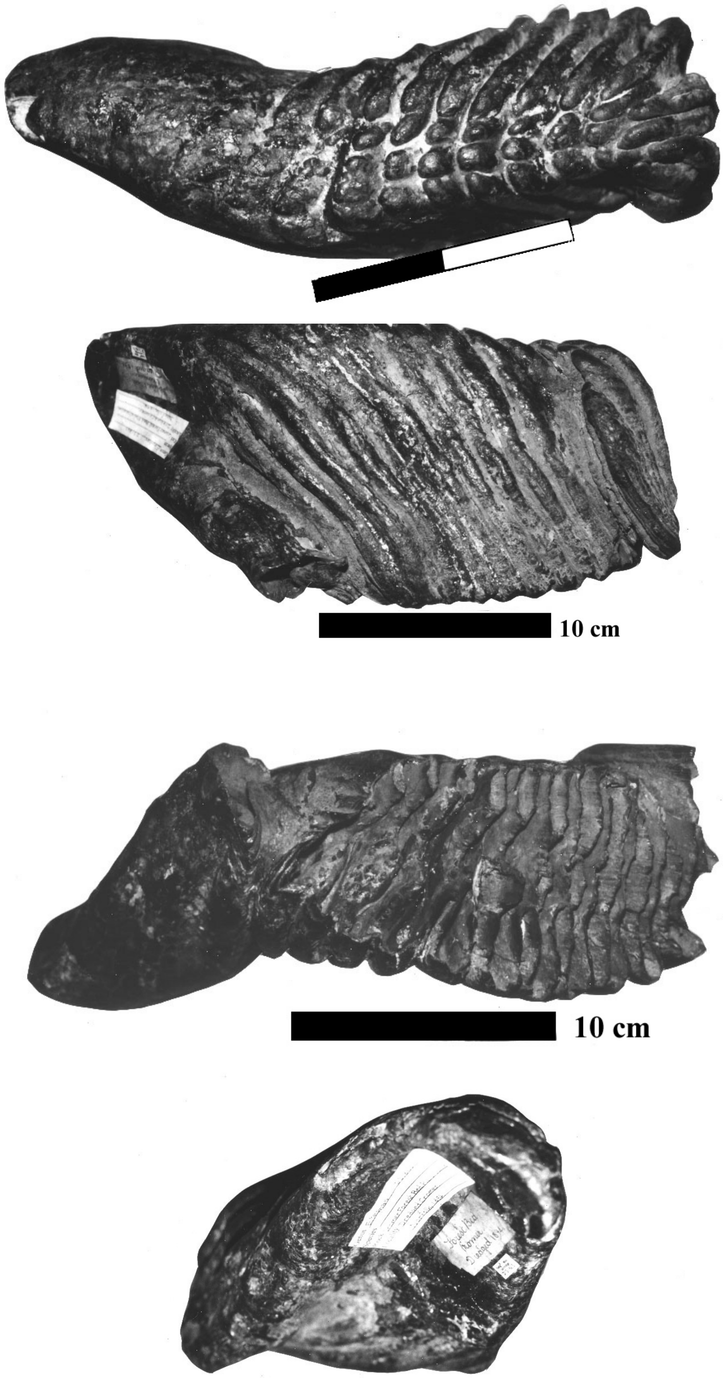


Fig. 14. *M*.cf. *primigenius*. Unworn presumed post-M_3 supernumerary tooth; a – occlusal view, b – lateral view, c – basal view, d – oblique anterior view. Note concave anterior surface. Scale bar is 10 cm. Southern North Sea off Cromer, Norfolk, England (SM Cambridge, no. D 31863).

ments that together could constitute one plate', viz., digitations or combinations of these. The supernumerary teeth found in the mandible of the cow *Beira* in the Basel Zoo are only slightly more organised in that the right specimen shows one small lamella and a few lamellar fragments instead of a mere bundle of digitations, and more than one root. The left specimen was left entire (LANG et al. 2000).

It is possible that some would prefer to classify these malformed elements as odontomas. A similar specimen from China was indeed published as such (TAKAI 1939), but it seems questionable whether such anomalies could be called tumorous – as required by the current definition of an odontoma. This problem is further discussed in part II below.

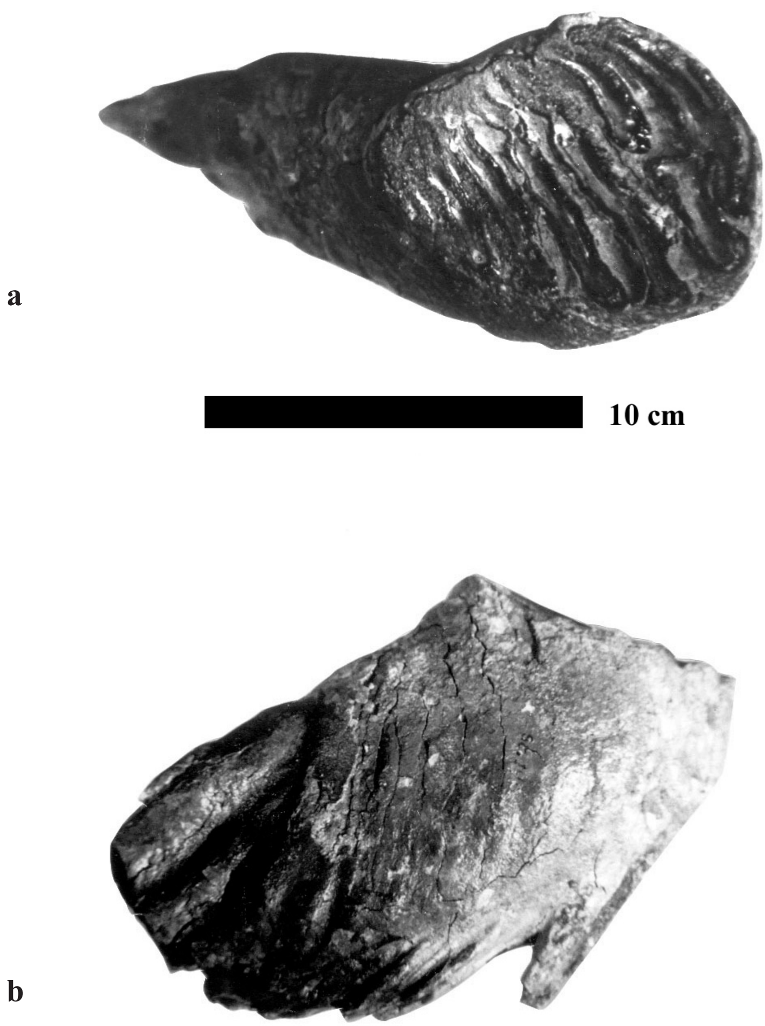


Fig. 15. *M. primigenius*. Presumed post-M_3 supernumerary tooth in early wear; a – occlusal view, b – lateral view. Southern North Sea, S. of Brown Bank (NAT Leiden, no. RGM 146796).

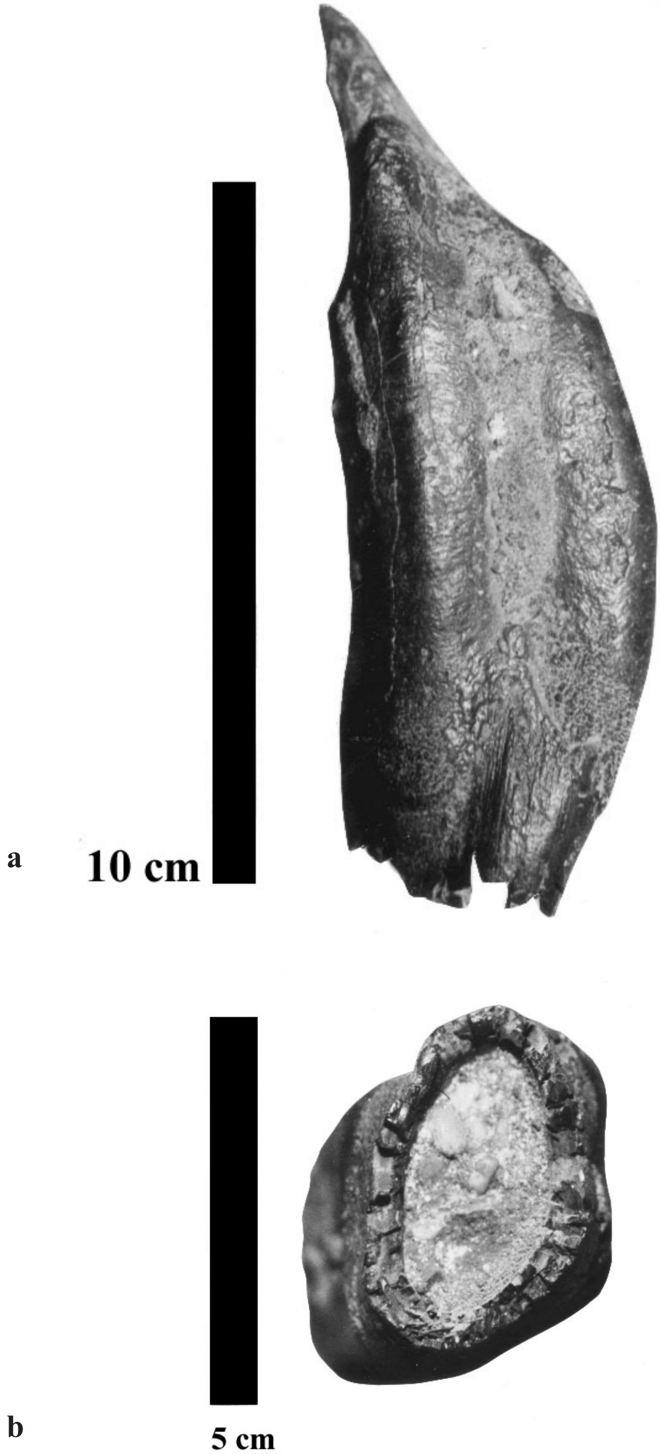


Fig. 16. *Mammuthus* sp. (*trogontherii* or *primigenius*). Unworn presumed (post-M3?) supernumerary element; a – lateral view, b – basal view. Trimingham, Norfolk, England (NHM London, Savin collection no. 1232).

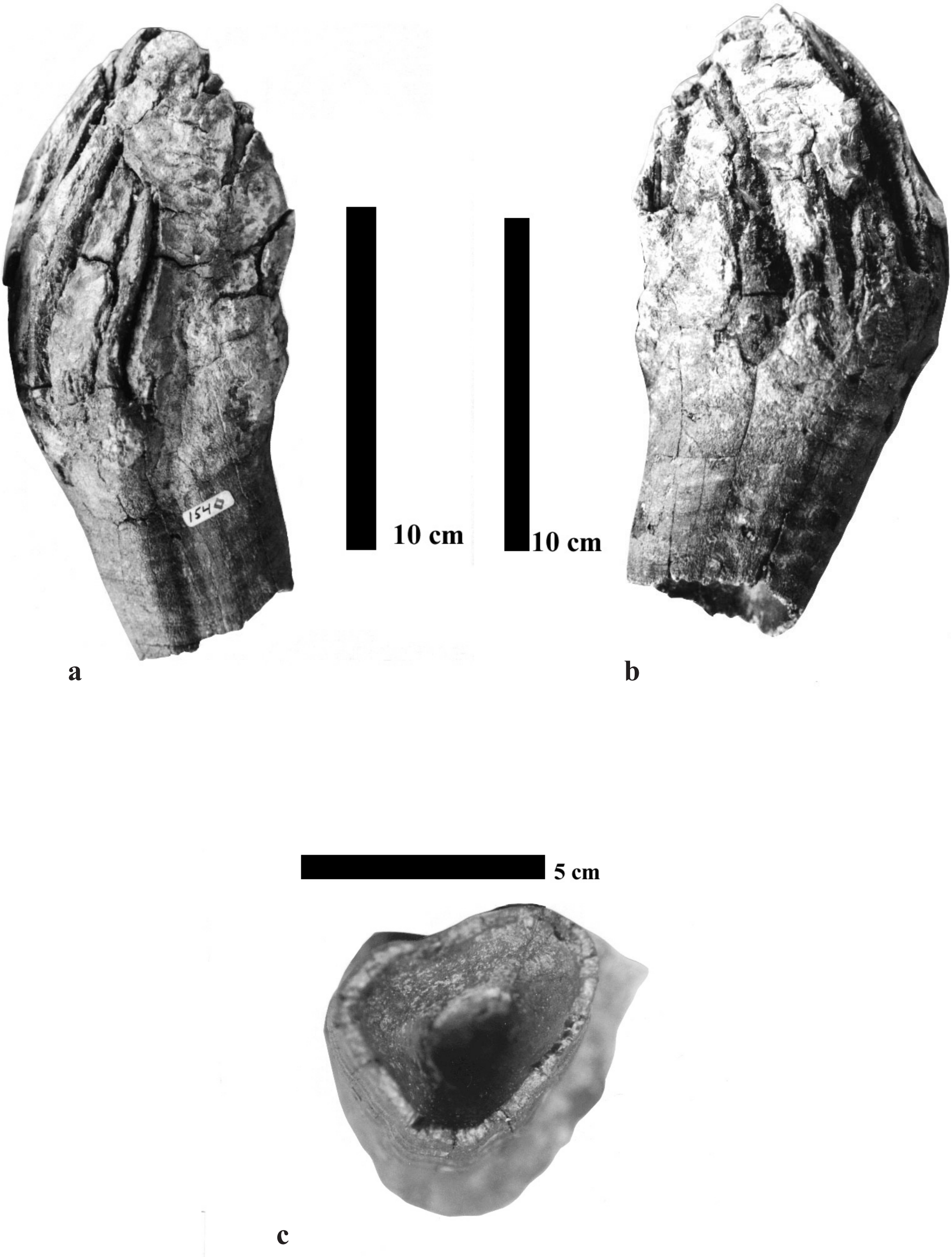


Fig. 17. *M. primigenius*. Slightly worn (damaged?) presumed post-M3 supernumerary element; a and b – lateral views, c – pulpal cavity of root. Southern North Sea (ac, no. 154).

III. M3 WITH ODONTOMA

Figs 18a-e; Table 3

Terminology

According to SCOTT & SYMONS (1961: 77) the term "odontoma" covers a number of lesions that develop from abnormal proliferations of the odontogenic epithelium. Some of these produce "single or multiple masses of the calcified dental tissues arranged in irregular and haphazard fashion". The terms coined for these varieties were "complex composite" and "compound composite" odontoma respectively. (Older terminologies may differ, but are not summarized here). In the revised terminology by PINDBORG (1970: 368), odontomas belong to a group of benign tumours that induce changes in connective tissue. They may be characterized as slowly growing odontogenic tumours which contain enamel and dentine (i.e., in humans), and the above-mentioned varieties appear simplified to "complex" and "compound" odontoma. The former is considered a true tumour (neoplasm), whereas the latter is more differentiated and interpreted as a malformation (usually attached to permanent teeth, preferably M_3s). If the full set of normal teeth is present, a compound odontoma could also be considered a malformed supernumerary tooth. The special nature of dental replacement in elephants, however, leads to uncertainty about the completeness of the tooth series. Meanwhile, the basic possibility of a dual interpretation has a complicating effect on the classification of various anomalous elements in elephantid dentitions, which is unsatisfactory.

Problems of application

HUNTER & LANGSTON (1965: 674) characterized odontomas as "a loosely knit group of lesions". The implied diversity of forms is certainly found if one compares the published elephantid examples, but the usefulness of the term seems questionable if it does not differentiate between all varieties observed. The nomenclature of odontomas is based on examples found in humans. As long as definitions are general, the interpretation of macroscopic characteristics found in some elephantid specimens need not pose special problems. When it comes to details, questions may arise as to whether certain anomalous forms should be named odontomas or not, or, if so, whether they should be called complex or compound: Variations with regard to the differentiation of the dental hard tissues cause some human complex odontomas to look very similar to compound ones (PINDBORG 1970: 400), so the same may in principle apply to elephants. Furthermore, it seems possible that some elephantid odontomas were called supernumerary teeth in the past, and vice versa. In spite of the fact that both categories may be united under the heading 'odontogenic anomalies', this situation is not a contribution to clarity.

Especially with respect to elephants, it would therefore be important to define the degree of differentiation and spatial organization to which a compound odontoma may proceed without losing its tumorous character. In other words: How is the word 'tumorous' defined and how far can this definition be stretched? In view of the fact that a complex odontoma is really equivalent to a tumour, i.e., to an independent local increase of tissue by way of cell division, the definition of a compound odontoma should preferably add no more than the greater differentiation already mentioned. A very unorganized, lobular build reminiscent of a cauliflower would then be a basic characteristic. If any other anomalous dental growth in elephants would be accepted as an odontoma and hence per definition as tumorous, this would amount to interpreting a biological phenomenon in terms of a metaphor. As a result, the presence of well-formed roots in tumorous anomalies, for instance, would then be considered possible, whereas this may well be a false conclusion where elephants are concerned. A survey of relevant cases therefore appears necessary.

A preliminary survey of anomalies published as odontomas

– GUENTHER (1955: 28/29, pl. 6, fig.2) described a tumorous growth in a *M. primigenius* tooth from the valley of the river Emscher near Gelsenkirchen (GFR) as an odontoma. The swelling measures 50 mm across and completely fills the pulp cavity of the posterior root of a tooth he considered to be a right M^2, but whose features – especially those of the root complex – rather tally with M^3 in advanced wear. The substance of the tumour is reported to be slightly granular and believed to have been soft to a certain degree, because it apparently shrank post mortem. It is partly covered by cement.

Since no other details were mentioned, the possibility exists that the growth represents a complex odontoma in a comparatively early stage of development. Its location, however, is suggestive of a calcified pulpal abscess, so that a microscopic examination of the fossilized tissue would be required to determine whether this is an odontogenic tumour or not.

– HUNTER & LANGSTON (1965) published a complex odontoma from the Klondike District, Yukon Territory, Canada. The specimen is attributed to a woolly mammoth and is a single independent nodular and lobular mass. It measures 31x27.5x17.5 cm and weighs 10.19 kg. Once cut and polished, it revealed the presence of histologically normal enamel, dentine, and cementum, the first of which is quantitatively underrepresented (5%). Dentine and cement are present in about equal quantities. Calcified matter was "interspersed with narrow spaces originally occupied by pulp and fibrous connective tissues". The entire specimen was characterized as "a conglomeration of islands of enamel and dentine together with masses of cellular cementum" (ibid.: 676).

Although there is a minimal degree of differentiation, determination as a complex odontoma is not objectionable. Its totally disorderly build, cauliflower shape and apparent potential of prolonged growth testify to its tumorous character. The authors do not consider this specimen as unique, but probably meant that it is not the only odontoma; no other elephantid complex odontoma is known to the present author, unless the German specimen mentioned above should prove to belong to this category.

– MAKIYAMA (1938: 45-46, fig. 25) published a find referable to a straight-tusked elephant from the Japanese Inland Sea. It consists of a right M_3 that is anteriorly fused with an anomalous element the author believed to represent the M_2. If this is correct, its lingual posterior part is fused with the lingual anterior part of the M_3, while its anterior end points away from the M_3 at square angles. The anomalous element is reported to have eleven plates, which number falls within the range of *Palaeoloxodon* M_2 (e.g., POHLIG 1888: 251; MAGLIO 1973: 43). They are compressed within a length of 125 mm. Some plates are laterally shared with the M_3, and wear has produced a concave occlusal surface on the combined crowns. There is at least one thick root, as can be gathered from Fig. 25. TAKAI (1939) apparently followed MAKIYAMA in his identification of this anomaly as an M_2, which he described as "regularly formed" and "compressed longitudinally". Yet he applied the term "composite odontoma", by which he implicitly characterized the specimen as a "heterogeneous mass of dentine, enamel, and cement [which] is formed attached to some part of the normal tooth" (ibid.: 101). The mutual exclusiveness of the words "regularly formed" and "heterogeneous mass" was apparently not felt.

The same specimen is also among the four elephantid odontomas that HUNTER & LANGSTON (1965: 677-78) regarded as confirmed. Basing themselves on GORLIN et al. (1961), these authors explain that "composite odontomas are composite in the sense that they contain mature enamel, dentine, and cementum and are further subdivided on the basis that in one, the complex form, the specimen is a single mass, while the compound form occurs as an aggregation of discrete, calcified particles numbering, at times, into the hundreds" (HUNTER & LANGSTON 1965: 674). By this definition their above-mentioned gigantic specimen from the Yukon Territory, Canada, is certainly a complex odontoma, but the undoubted compound ones in elephants are not exactly analogous to the human form. The Dutch example described below, for instance, cannot be said to be an aggregation of *discrete* particles. It is the degree of differentiation therefore that causes human and elephantid compound odontomas to differ: PINDBORG (1970: 402) remarks upon the human form that it prefers the incisor-canine region and "shows the presence of several small, rather well-defined, malformed teeth", with a recorded maximum of 2000 dispersed in mandible and maxilla. The particles and the teeth in these definitions may be taken to be synonymous, because in humans these elements are small, not quite perfect teeth and therefore like particles. An example from an archaeological context was figured by BROTHWELL (1972: pl. 16a) and shows some "hard dental particles" (ibid.: 154) packed within a buccally fenestrated cavity at the root level of the mandibular teeth, and indeed in the incisor-canine region. Even though this highly differentiated form is considered an odontogenic tumour, it does not look tumorous because there is no calcified matrix of unorganized dental matter, as observed in the case of the mammoth. In fact it is difficult to envisage an elephantid compound odontoma that would be strictly analogous to the human form described in that it merely showed an aggregation of tiny and slightly malformed teeth, unless some of the comparatively small anomalies listed above as Category II supernumerary teeth are in fact former cluster members, once situated in a cavity near the roots of a mandibular tooth. However, no examples of such groupings have so far been found in elephant jaws. On the other hand, the supernumerary teeth in the *L. africana* cow at the Basel Zoo (LANG et al. 2000) are single specimens, situated in the dental canal behind the M_3s, not in a separate cavity in the incisor-canine region. Given the presence of cover cement layers and multiple roots that match the outlines of the crowns, they strongly suggest completed teeth, random and definitive results of malformation that apparently lacked the potential for prolonged growth – in this case: the addition of many more similar specimens – that is typical of an odontogenic tumour. It is therefore highly unlikely that a single 'imperfect tooth' of this nature might ultimately be the analogue of the aggregations in humans. This corroborates the equation with the supernumerary teeth mentioned by LAWS (1966).

The question whether the roots themselves in category II specimens are often 'malformed' needs further study: Because the maximum root diameter in the specimen shown in Fig. 17 is 67. mm, it may well be that the Sheath of Hertwig in elements as these does not always function as one might expect, in the sense that no subdivision into several smaller roots takes place. With two to four roots basally bent in posterior direction, the supernumerary specimens in the cow from the Basel Zoo for the time being form an exception (LANG et al. 2000). It would therefore be interesting to know if monolithic roots would be capable of further size increase without at some stage turning into a root complex.

In the elephantid compound odontomas preserved, one indeed observes calcified particles, i.e., haphazardly distributed digitations and little clusters of digitations at most, but certainly not little teeth, however imperfectly built. Not even a single complete lamella is formed here (see TOKUNAGA & TAKAI 1937, RAUBENHEIMER et al. 1989, and the description below). It seems illogical then, that the specimen from the Japanese Inland Sea should still be called an odontoma: It is neither a single tumorous mass, nor a tumorous anomaly including calcified particles, nor a cluster of little teeth, but consists of a number of partly deformed and poorly aligned plates. These are partly fused with the M_3 in a very peculiar way, and borne by at least one firm root (MAKIYAMA 1938: fig. 25). At the occlusal surface, the plates are even recognizable as belonging to a straight-tusked elephant. The specimen is therefore differentiated and organized beyond the level of 'particles' and looks like a malformed single tooth, possibly a supernumerary element. Because of the anterior position of this element, the configuration might be explained by a fusion in an uncalcified state during the earliest stage of formation of the M_3 and a further joint development. Fusion as a category of abnormal tooth morphologies in humans is defined as "a union between the dentin and/or enamel of two or more separate developing teeth" (PINDBORG 1970: 51), but the regular teeth of elephants can hardly be argued to develop together, as in humans. The uncalcified stages of M_2 and M_3 do not overlap, so that MAKIYAMA (1938) may have been wrong in supposing that the anomalous element is in fact the M_2. If he should be right after all, the cause of the strange dislocation of the M_2 germ and the bad timing of its development are probably beyond reconstruction. Classification of the specimen as a non-isolated, malformed supernumerary tooth with lamellar build – provisionally named Category III – seems to be the least problematic alternative, even though it developed approximately at the same time as the M_3, not after it. In fact this timing is rather close to wear stage XXV, at which point LAWS (1966) observed the first appearance of supernumerary teeth in *L. africana* mandibles (see Introduction).

– KULCZYCKI (1955: 43, pl. IV, figs. 3a-d) published a right M^3 of *M. primigenius* with an anteriorly attached anomaly that is very reminiscent of the above-mentioned *Palaeoloxodon* specimen as figured by MAKIYAMA (1938). The find, although probably from Poland, is of unknown provenance. Its whereabouts in Poland are also unclear ("no. 108" may be a serial number given by the author). KULCZYCKI (1955: 43) characterized the anomaly as an odontoma that developed from the germ of the second lamella.

The plate formula of the M^3 is "x 24 x" in 250. mm, and Fig. 3a shows that the anterior talon and 13 lamellae are in wear. Against the anterior lingual side of the M^3 crown, and at square angles to its lamellae, "6 x" rooted plates of the *M. primigenius* type have developed. As a result, the anomalous plates present their sides when the M^3 is looked at from the front (KULCZYCKI 1955: fig. 3b). Their widths are variable and all are in wear. The anomaly caused a narrowing of the anterior part of the M^3 and deformation of the lamellae 1 and 2, whose lingual ends now point in anterior and posterior direction respectively. The lingual ends of the lamellae 3 and 4 are similarly deflected to the rear, but to a lesser extent (KULCZYCKI 1955: fig. 3a).

The first root of the M^3 is situated buccally, as usual, but because of the development of the anomaly its position has shifted in buccal direction and the root has grown in a direction off the vertical axis. The root portion of the anomaly seems to be a single large unit with vague vertical furrows. The anomalous root and the first root of the M^3 merge at a level not far from the crown base (KULCZYCKI 1955: fig. 3b).

In occlusal view this configuration differs from that of the analogous Japanese elements in that no plates can be said to belong to the M^3 and the anomaly at the same time: Lingually a rather thick layer of cement is seen to separate both elements, and the lingual cover cement of the M^3 originally extended onto the anomaly, so that an in horizontal section Y-shaped cement junction exists next to the lamellae 5 and 6 (KULCZYCKI 1955: fig. 3a). As KULCZYCKI already pointed out, the innermost anomalous plate and the lingual extreme of lamella 2 touch, and so mark the anterior end of the stretch of cement between the two elements. Fig. 3a suggests that both plates retained their enamel, so that their dentine cores probably do not merge.

The above details indeed suggest that the anterior part of the M^3 and the anomaly developed at approximately the same time. Since the latter was wedged into the body of the still incompletely calcified M^3, it was probably slightly ahead in its development. At that stage the alveolar bone was apparently significantly harder than the M^3 and could largely withstand the mounting pressure, albeit probably with a little loss through resorption. The layer of cover cement shared by the two elements might be the result of a local fusion of two thinner layers belonging to the M^3 on one side and to the anomaly on the other. With only seven plates, the anomalous element does not support the idea that it could be a malformed M2, and hence also corroborates the interpretation of the analogous Japanese specimen as a supernumerary tooth. Again there is a differentiation that goes well beyond anything observed in undoubted odontomas. There is a greater likeness to normal teeth, including an extensive root portion, which is presumably undivided: Apart from what the Figs. 3b and d (KULCZYCKI 1955) show, KULCZYCKI (1955: 43) uses the singular form. Thus one is reminded of the large roots that may be encountered in Category II supernumerary specimens (see the present Fig. 17). The Polish specimen is therefore most likely a non-isolated, malformed supernumerary tooth with lamellar build (Category III). It may first have appeared during the early forties of the individual.

– TAKAI (1939) also described a "simple odontoma" from China. The accompanying faunal remains indicate that this element belongs to a Late Pleistocene mammoth. HUNTER & LANGSTON (1965: 677), referring to the published plate as much as to TAKAI's short text, reported that the specimen is "…irregularly pyramidal in form and about 1.5 times as wide as a normal mammoth molar. … Arrangement of dentine, enamel, and cementum is said to be normal, but the cut section reveals an almost complete absence of organized cheirolites [lamellae]; numerous elongate, vertical tubules of dentine surrounded by thick plicated enamel were present instead. Ridges and grooves seen in lateral aspect suggest normal cheirolites, but these merely reflect serial arrangement of some of the tubules. The entire specimen seems to be enclosed in cementum and there is no indication of wear".

In many aspects of its 'crown' this specimen is reminiscent of the compound odontoma in *L. africana* published by RAUBENHEIMER et al. (1989: fig. 3), which shows digitation-like structures that are very coarse with respect to the M_3 with which it is laterally fused. The African specimen does not seem to have roots of its own, because roots are not mentioned in the description. Rootlessness and fusion with the accompanying tooth might well be (regular) distinctive features of compound odontomas in elephants (see also the description of the Dutch specimen below). Fusion with the accompanying tooth may only be a matter of the degree of calcification it had reached as the odontoma started to develop. In addition, the above-mentioned complex odontoma from Canada is an independent growth, so that rootlessness for the time being remains as a shared characteristic of the truly tumorous forms.

The Chinese specimen is not fused with another element, a feature shared with the rooted anomalies shown in the present Figs. 16 & 17. These were provisionally grouped among the supernumerary teeth (category II), but have the random arrangement of separate digitations or lamellar fragments in common with the unfused Chinese as well as with the fused African specimen.

TAKAI (1939) did not mention anything about the presence of a root or pulp cavity, but gave 126 mm as the crown height of the Chinese specimen. To judge by the accompanying plate (ibid.: fig. 1), this is the total height. It is therefore not clear whether or not this value includes a few centimetres contributed by a single conical root, even though the lateral view suggests the loss of relief towards the tip of the pyramidal shape and possibly a small central cavity there. Especially this detail seems important, because well-formed roots with pulp cavities distract from the notion of tumorous malformations with prolonged growth potential (odontomas). Because of the uncertainties that remain, no definitive classification of the Chinese specimen is possible yet, although its seemingly fixed size suggests that it is a malformed supernumerary tooth.

– Another find from the Japanese Inland Sea was published by TOKUNAGA & TAKAI (1937) and briefly touched again by TAKAI (1939). The specimen consists of a fragmentary right mandibular corpus which is reported to contain M_1, M_2, and the antero-medial portion of M_3. It is referred to a straight-tusked elephant. M_1 and M_2 are said to have formed a compound odontoma of the "second type". The definition of this type (subtype 'c') was later given as "the result of adhesion between permanent teeth in which case the teeth diminish in number" (TAKAI 1939: 101). The plate in TOKUNAGA & TAKAI (1937: 96) shows that the situation in front of the normal M_3 fragment is highly irregular and more than just a concrescence of two teeth:

The M_1 and M_2 referred to by the authors are not recognizable as such. There is a large lump of nearly unorganized dental matter that merely takes the place of these teeth. It is at least twice as wide as the M_3 and therefore its volume seems to be bigger than that of a normal M_1 and M_2 combined, especially since part of the original total was already lost by wear. A considerable hypertrophy of the buccal (and presumably also the lingual) mandibular bone is concomitant with this anomaly (ibid.: plate 19, fig. 1). In the occlusal surface of the worn part (which the authors attribute to M_2) some meandering strings of enamel are visible, as well as some deformed, isolated lamellar pillars. With a dotted line the authors indicated where they observed signs of a division between the 'M_1' and the 'M_2' and between the latter and the M_3 fragment (ibid.: fig. 3). The part ascribed to M_2 is indeed bigger than that of the 'M_1'. Generally, however, these parts are fused. The crack between the anomaly and the front of the M_3 (ibid.: fig. 2) suggests that the fusion here is superficial and perhaps rather an invasion of the cover cement of the M_3 than a fusion that started when both elements were incompletely calcified. The odontoma in *L. africana* (RAUBENHEIMER et al. 1989) is reported to be fused with the cover cement. The buccal mandible wall and the anomaly of the Japanese specimen are generally well separated, but local fusion seems present in the 'M_1' part. The sagittal axis of the M_3 fragment is in an oblique position, so that the apex of its frontal part is at a much lower level than the occlusal surface of the anomaly, and therefore not in wear. The photo does not allow a definitive statement about the presence of roots, although the impression exists that either an irregular lump of the anomaly or the edge of the fracture of the basal mandibular bone is seen instead of a root.

Because this appears to be a rootless tumorous mass of dental matter with a former potential for prolonged growth and a somewhat higher degree of differentiation than a complex odontoma, it is likely to be an almost independent compound one and perhaps constitutes a category all of its own. HUNTER & LANGSTON (1965: 677) considered it as "a little more mature in terms of morpho-differentiation" than the complex odontoma and therefore closely related to it. If M_1 and M_2 should indeed be represented by this large anomaly, as is suggested by its place in the jaw and its subdivision, this would also be an odontoma that cannot be simultaneously characterized as supernumerary. Because of the fusion of two elements, it could even be argued that it formally reduces the original number of six elements to five. This was in fact the bearing of the definition of the 'second type' of odontoma given by TAKAI (1939).

Four out of the six cases listed above are considered confirmed by HUNTER & LANGSTON (1965). Other elephantid anomalies published (Pales 1930 [tusk-like growth at tusk base], PONTIER 1930; STOVALL & JOHNSTON 1934) were queried by them because the original publications were not detailed enough. Their acceptance of the other four suggests a rather wide concept of 'odontoma', and implicitly of the word 'tumorous'. A stricter application of the requirement that odontomas should have a clearly tumorous nature leaves the complex specimen from Canada (HUNTER & LANGSTON 1965), perhaps the specimen from Germany (GUENTHER 1955), and the compound one published by TOKUNAGA and TAKAI (1937), in which the normal components of elephantid teeth are barely at all or very poorly expressed macroscopically. The specimen discussed below belongs to this category as well.

The compound odontoma from the Rhederlaag concession

M_3 – The left M_3 around which the odontoma developed is a tooth of about normal size and shape in a rather advanced stage of wear (Table 3). The shallow remains of some frontal lamellae were broken off, presumably by the dredging machinery. Since 19 lamellae are still countable, the lost portion may have comprised three to five lamellae, to which part of the odontoma adhered. At the very front of the tooth a dentine platform had probably started to develop, because wear proceeded to a level that intersects the anteriormost preserved lamellae just above their bases. The median dentine bridges between them (Fig. 18a) are a typical feature of this wear level. As further wear would have shortened it, the occlusal surface had reached its optimal length (wear stage XXVI according to LAWS 1966). The age that corresponds with this stage is 50 AEY (LAWS 1966; CRAIG in HAYNES 1991: 339).

In occlusal view (Fig. 18a) some buccally and/or lingually deformed lamellae are visible, particularly within the series VI-XIII. The insertion of the half lamella is presumably responsible for the shape of lamella VI.

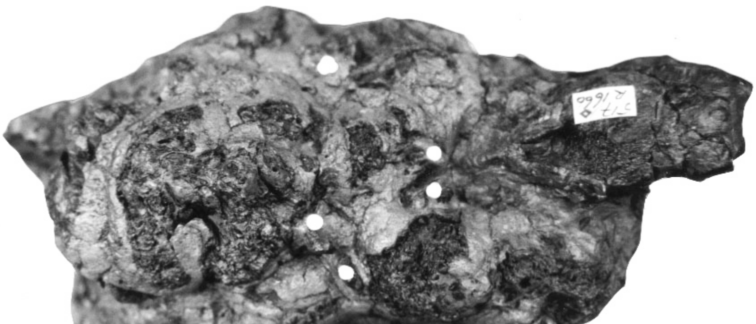
The front of the tooth broke off irregularly; the lamellae XVIII and XIX are represented by their buccal parts only. It is remarkable that at least the buccal part of lamella XX was replaced by part of the odontoma.

The lateral borders of the occlusal surface of the M_3 are not sharply defined. Single digitations that belong to the odontoma have fused with the lateral ends of some lamellae or extend well into interlamellar cement, whether in an oblique or in an upright position. At the level of the occlusal surface, fusions between the lateral parts of the lamellae and digitations of the odontoma do not occur buccally, but six cement intervals here were invaded by digitations (up to ± 10 mm inward from the buccal ends of the lamellae). At the lingual edge of the occlusal surface, fusions are abundant. The dentine of the lamellae XVII and XVI, XIV through XII, and IX through VII is (mostly even bilaterally) confluent with that of clusters of digitations that belong to the odontoma. The enamel of these clusters completely cuts off the lingual ends of some cement intervals.

a

10 cm

b



c

10 cm

d

e

Fig. 18. *M. primigenius*. M_3 sin. with compound odontoma; a – occlusal view, b – lingual view, c – basal view; white dots indicate root tips of M_3, d – buccal view, e – posterior view. Rhederlaag concession, Giesbeek, Gelderland, The Netherlands (ac, no. 517/R1660).

Some of the cement intervals have a peculiar surface structure, with little round or irregular holes (up to ± 1 mm in diameter).

In basal view (Fig. 18c), some root tips (marked • in white) can be seen to emerge from the irregular mass of the odontoma. They are partly encrusted by cement. Because they are all underneath the crown and point away from the occlusal surface in the same direction, they are interpreted as belonging to the M_3. This state of affairs suggests that the normal further development of the root portion into a keel-shaped unit was largely blocked by the enveloping odontoma. Quite interestingly this development did in the end commence in the hindmost part of the M_3, which remained uncovered. The V-shaped anterior dentine ridge on the median line can still be discerned there (between the hindmost toot tips and the label). Behind it is the roof of the elongate pulp cavity, in part bordered by remains of the outer dentine walls. The total length of this complex is about 90. mm.

Odontoma – The odontoma is composed of wildly contorted, bulging and radiant masses of the dental tissues enamel and dentine. The anterior fracture surface shows that there may be empty spaces up to a few cm^3 between the intumescences. Enamel tends to enclose dentine in the form of shorter or taller digitations, and cement is largely seen as a covering layer, as usual in normal teeth. Because of this differentiation and because it meets the above-mentioned definition by SCOTT & SYMONS (1961) as well as that by HUNTER & LANGSTON (1965; after GORLIN et al. 1961), it may be classified as a "compound odontoma" (see above under Terminology).

The crown of the M_3 and the odontoma are worn down to the same level. Just as in the occlusal surface of the M_3, the dentine in the odontoma has slightly darker colours than the cement (shades of brown and brownish beige). The structures that are nearest to a normal lamella in shape – though they are still far removed from it – are leaf-like clusters of incurvate and diverging digitations. The greatest cluster height found is 82 mm. Other amassments are about spherical, with digitations more or less radiating from the centre. Partly because of the patchy cement cover, the odontoma gives the impression that enamel is concentrated in certain areas.

Digitations are often irregular and have various diameters; 6 to 7 mm is about the average of single specimens. The enamel thickness roughly varies with the size of the digitations, but its average value lies below that of the M_3; the lowest values correspond to lengths below 30 mm (table 3). A peculiarity of many (slightly worn) digitations is that their dentine shows concentric rings. Some of these stand out as if they were the result of some form of selective weathering, and there is a tiny central hole in each of these digitations. The greatest remaining depth, sounded with a single hair, is about 15 mm.

The developing odontoma is likely to have caused resorption of the alveolar walls (VAN AALDEREN, pers. comm.). In humans, fusion with the healthy bone tissue of the mandible sometimes occurs (EULER 1929: 442), but the specimen in a *L. africana* mandible published by RAUBENHEIMER et al. (1989) is reported to have remained separate from the surrounding bone (in which features of osteomyelitis were detected), and to have caused lingual and buccal swelling of the mandible. It is also considered to have halted the progression of the M_3 it is fused with. Because the mandible of the Rhederlaag specimen is missing, it cannot be confirmed that all these effects came about here, although it at least seems likely that the complex had become more or less immobile. A macroscopic feature of the odontoma is that the large majority of the digitations lies open laterally and/or apically. Especially the lingual face is fairly smooth. It is not clear whether this should be interpreted as a symptom of former fusion with the mandibular bone – which then would incorporate the outside of these digitations – or as damage through some external factor, because the specimen was embedded in a fluvial environment.

To judge by the extent and volume of the fossilized odontoma at the inferred age of 50, there is no analogy with the earliest occurrence of supernumerary teeth in the sample of *L. africana* as observed by LAWS (1966). If odontomas in elephants grow slowly, as in humans, the present one is for that reason alone likely to have manifested itself before the age of ± 47 AEY (group XXV) that was found to be the minimum age in connection with supernumerary teeth of *L. africana*. The above-mentioned lateral fusion of the M_3 crown and the odontoma suggests that both developed at about the same time, so that the first (uncalcified) intumescences of the odontoma could fuse with the uncalcified or incompletely calcified crown sides. The difference in the degree of lamellar fusion between the buccal and lingual crown sides (see above under M_3) indicates that the odontoma initially developed mainly against the lingual side and there fused with the still uncalcified lamellae. Buccally only the cement intervals were invaded, which probably means that the more apical regions of the lamellae behind no. XX were already too much calcified by the time that part of the odontoma had reached the buccal side of the M_3. The cement intervals of a tooth are filled after the completion of the adjacent lamellae and would still have been accessible. With its initial growth coinciding with that of the anterior part of the M_3 germ, the odontoma would approximately date back to wear stage XVI, i.e., to the early twenties of the individual (CRAIG in HAYNES 1991: 339), although its true origin is probably embryonic.

Table III

Measurements (in mm) of M3 with compound odontoma (ac 517/R1660)

Lam. formula M_3		- 14 ½ 5 (p)	½ lingually
In wear		- 14 ½ 3	about 60% of the tooth volume worn away
L		270.+	anteriormost portion broken off
L occlusal surface		235.+	,,
L odontoma ling.		255.+	,,
W		92.	± true maximum; at occlusal surface lamella XIV
W incl. odontoma		150.	maximum at lamella IX
H odontoma		134. / 136.	maxima at lam. XIV/half lamella (occl. surface)
LF		8.19	antero-medially; at occlusal surface
ET	**minimum**	1.4	
	mode	1.5	
	maximum	1.6	
ET in digitations of odontoma		0.4-1.8;	mean and midrange 1.1
Weight of M3 + odontoma		4.85 kg;	weight before fracture 5 kg

IV. SUMMARY AND CONCLUSIONS

A *M. primigenius* mandible with a unilateral supernumerary tooth behind M_3 was described and compared with a similar mandible from Germany that contains two supernumerary teeth formerly interpreted as M_3s (ADAM 1994). These are the first European examples of fossil post-M_3 supernumerary teeth still contained within mandibles. A preliminary set of characteristics of such elements was based on these examples and on the maxillary specimen from Villeneuve, Alberta, Canada (BURNS et al. 2003).

Supernumerary teeth in the post-M3 category I are M3-like in appearance and their formation apparently takes place at different times relative to the formation and completion of M3. Although they appear late in the elephant's life, category I teeth, too, may reach completion and sometimes even early wear. Their plate number is variable but tends to be lower than that of a true M3, perhaps because it is predetermined and not dependent on any circumstance during tooth formation, looking apart from the death of the animal. At least some of these specimens are likely to develop too fast with respect to the slow progression and wear of the preceding M3s. The M3s occupy the jaw for many years and thus hamper the progression of supernumerary teeth. Especially the larger ones then forcibly remain contained largely within the narrow space afforded by the ascending ramus of the mandible or the hindmost part of the maxilla, so that deformations are usually the result.

Category II specimens are rooted clusters of digitations, plates, or a mixture of these, and therefore much further removed from the normal tooth model than category I specimens. They are of limited size and likely to be analogous with the specimens published by LAWS (1966) and LANG et al. (2000) as supernumerary teeth.

In two cases so far, rooted specimens laterally attached to an M3 were at some time identified as odontomas. This appears to be based mainly on a wider interpretation of that term, because the hard tissues seem to be non-tumorous and show a spatial organization that is too much organized for these specimens to be called odontomas. They are therefore provisionally labeled as category III specimens.

A number of European collections include one or more possible representatives of these categories. The preliminary survey of isolated specimens that belong to Category I and II suggests that several more may exist in other collections but have hitherto not been recognized. An active search for such anomalies in museum collections could therefore be fruitful.

A macroscopic description of the first compound odontoma referable to a European woolly mammoth was given in relation to data from the literature. Because textbooks of oral pathology describe – often microscopic – characteristics of human odontomas, their application to elephantid ones sometimes appears problematic. It may be useful to make a preliminary macroscopic distinction between odontomas as rootless, clearly tumorous and sometimes fused forms at a comparatively low level of differentiation and spatial organization on the one hand, and rooted, more tooth-like supernumerary specimens at a higher level of spatial organization on the other.

Variable degrees of differentiation form the basis of the subdivision of odontomas. In a similar way, various morphological types could lead to a further subdivision of supernumerary teeth, although strongly-expressed individual traits could complicate this. At a later stage, when more material will have been recovered, a complete revision and microscopic study are advisable and would very probably lead to a refinement of statements about tumorous lesions and supernumerary anomalies in elephantid dentitions.

REFERENCES

ADAM K. D. 1994. Anomalien des Zahnwechsels bei *Elephas primigenius* aus dem Quartär des Oberrheins. *Stuttgarter Beiträge zur Naturkunde*, Stuttgart. Ser. B, **211**: 1-36.

BEDEN M. 1983. Family Elephantidae. [In:] HARRIS (ed.) – Koobi Fora Research Project: Vol. 2. The fossil Ungulates: Proboscidea, Perissodactyla, and Suidae, (Clarendon Press, Oxford): 40-129.

BROTHWELL D. R. 1972. Digging up Bones. The Excavation, Treatment and Study of Human Skeletal Remains. London (Trustees of the British Museum) 196 pp., 17 pl.

BURNS J., BAKER C. G., MOL D. 2003. An extraordinary woolly mammoth molar from Alberta, Canada. [In: REUMER, DE VOS, MOL (eds) – Advances in Mammoth Research (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16-20 1999). Rotterdam (Natuurmuseum Rotterdam) *Deinsea*, **9**: 77-85.

BUSS I. O. 1990. Elephant Life. Fifteen years of high population density. 191 pp.; Ames (Iowa State University Press).

EULER H. (ed.) 1929. Lehrbuch der Zahnheilkunde. 727 pp.; München (J. F. BERGMANN).

GORLIN R. J., CHAUDRY A. P., PINDBORG J. J. 1961. Odontogenic tumors – classification, histopathology and clinical behavior in man and domesticated animals. New York. *Cancer*, **14**: 73-181.

GUENTHER E. W. (1955. Mißbildungen an den Backenzähnen diluvialer Elefanten., pl. 1-7. Kiel. *Meyniana*, **4**: 12-36.

HAYNES G. 1991. Mammoths, Mastodonts, and Elephants. Biology, Behavior, and the Fossil Record; Cambridge (Cambridge University Press) 413 pp.

HEINRICH A. 1982. Ein Mammutschädel aus Valburg, Niederlande. *Der Aufschluss*, **33**: 35-39. Heidelberg.

HUNTER H. A., LANGSTON W. Jr. 1965. Odontoma in a northern mammoth. London. *Palaeontology*, **7**(4): 674-681.

KULCZYCKI J. 1955. Les ossements des mammouths. *Palaeontologica Polonica*, **7**, I-VI, 1-65, pl. I-X. Warszawa

LANG E. M., MEIER D., OPPLIGER D. 2000. Siebente Backenzähne (4. Molaren) im Unterkiefer eines Afrikanischen Elefanten (*Loxodonta africana*). Jena. *Der Zoologische Garten*, N.F. **70**(5): 295-303.

LAWS R. M. 1966. Age criteria for the African elephant *Loxodonta a. africana*. Nairobi. *East African Wildlife Journal*, **4**: 1-37.

LISTER A. M. 1996. Evolution and taxonomy of Eurasian mammoths. [In:] SHOSHANI, TASSY (eds) – The Proboscidea. Evolution and Palaeoecology of Elephants and Their Relatives, Oxford/New York/Tokyo (Oxford University Press): 203-213.

LISTER A. M., JOYSEY K. A. 1992. Scaling effects in elephant dental evolution – the example of Eurasian *Mammuthus*. [In:] SMITH, TCHERNOV (eds) – Structure, function and evolution of teeth: 185-213. Tel Aviv (Freund).

MAGLIO V. J. 1973. Origin and Evolution of the Elephantidae. Transactions of the American Philosophical Society held at Philadelphia for promoting Useful Knowledge, N. S., **63**(3): 1-149. Philadelphia (The American Philosophical Society).

MAKIYAMA J. 1938. Japonic Proboscidea. Memoirs of the College of Science, Kyoto Imperial University, Kyoto, Ser. B, **14**(1): 1-59.

OSBORN H. F. 1942. Proboscidea: A monograph of the Discovery,Evolution, Migraton and Extinction of the Mastodonts and Elephants of the World. Vol. II: Stegodontoidea, Elephantoidea. New York: American Museum of Natural History.

PALES L. 1930. Paléopathologie et Pathologie Comparative. 480 pp.; Paris (Masson).

PINDBORG J. J. 1970. Pathology of the dental hard tissues. Copenhagen (Munksgaard)/ Philadelphia (W.B. Saunders) 442 pp.

POHLIG H. 1888-1891. Dentition und Kranologie des *Elephas antiquus* Falc., mit Beiträgen über *Elephas primigenius* Blum. und *Elephas meridionalis* Nesti. Halle, *Nova Acta Leop. et Carol*., **53**(1): 1-279; **57**(5): 267-466.

PONTIER G. 1930. À propos d'anomalies dentaires observées chez les Proboscidiens. Lille. *Annales de la Societé géolique du Nord*, **55**: 2-10.

RAUBENHEIMER E. J., VAN HEERDEN W. F., TURNER M. L., MARÉ L. K. 1989. Odontoma in an African elephant (*Loxodonta africana*). Pretoria. *Journal of the South African Veterinary Association*, **60**(3): 149-150.

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

SCOTT J. H., SYMONS N. B. B. 1961. Introduction to Dental Anatomy. 388 pp.; Edinburgh and London (E. & S. Livingstone).

STOVALL J. W., JOHNSTON C. S. 1934. Hypertrophy in the jaw of an Oklahoma proboscidean. Notre Dame. *The American Midland Naturalist*, **15**: 622-624.

TAKAI F. 1939. Three different kinds of odontoma found in the molars of Asiatic fossil elephants. Tokyo. *Journal of the Geological Society of Japan*, **46**: 581-582.

TOEPFER V. 1957. Die Mammutfunde von Pfännerhall im Geiseltal. Halle (Saale). *Veröffentlichungen des Landesmuseums für Vorgeschichte in Halle*, **16**: 1-58, Taf. I-XXIV.

TOKUNAGA S., TAKAI F. 1937. Odontoma in a fossil elephant from the Inland Sea of Japan. Tokyo. *Journal of the Geological Society of Japan*, **44**: 445-446.

VAN ESSEN H. 2003. Tooth morphology of *Mammuthus meridionalis* from the southern bight of the North Sea and from several localities in the Netherlands. [In:] REUMER, DE VOS, MOL (eds) – Advances in Mammoth Research (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16-20 1999). 13 figs., 16 tables; Rotterdam (Natuurmuseum Rotterdam). *Deinsea*, **9**: 453-511.