Tracing transitions : an overview of the evolution and migrations of the genus Mammuthus BROOKES, 1828 (Mammalia, Proboscidea)

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Part III

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Tooth morphology of *Mammuthus meridionalis* from the southern bight of the North Sea and from several localities in the Netherlands

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Dental remains of *M. meridionalis* (Nesti, 1825) from the southern bight of the North Sea and from the continental part of The Netherlands are morphologically compared with a sample from the fluvio-lacustrine beds of the Valdarno Superiore (Italy), from which the lectotype of the species was collected. In part, the samples from Italy and northwestern Europe have different ages, yet there is a large amount of morphological overlap. This leads to the conclusion that *M. meridionalis* was conservative in its dental evolution. The reliability of dating based on morphological characteristics of smaller samples is therefore reduced. Bavelian *in situ* material from Oosterhout and Dorst shows typical morphological characteristics in the ontogenetically earlier teeth (M1/m1), and somewhat advanced traits in the later teeth (M2-M3/m3). With reference to similar material from Germany and Italy this is interpreted as indicative of a minor shift in mean dental morphology.

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Introduction

This paper deals with the largely unstratified dental remains of Plio-Pleistocene to late Early Pleistocene mammoths - *Mammuthus meridionalis* (Nesti, 1825) - from The Netherlands and the southern bight of the North Sea. Most specimens from this area were trawled or dredged from marine, brackish marine or deltaic / fluviatile deposits of Early Pleistocene age that occur within the geographical limits of approximately 51°- 53° N and 2° - 6° E (Figs. 1 and 2). The subdivision of the area is chosen as follows:

I Southern bight of the North Sea;
II The Netherlands,
a Oosterschelde,
b Maasvlakte,
c Oosterhout, Dorst and other inland sites, including Tegelen.

The Red Crag, Norwich Crag, and Cromer Forest-bed Formations are adjacent to the western limit of the study area and in part have lateral equivalents among the now submarine strata in the southern North Sea basin. The morphology of their mammoth remains, however, is beyond the scope of this paper.

The taxon *M. meridionalis* spans more than a million years, and morphology-based subdivisions (e.g., Depéret & Mayet, 1923; Maglio, 1973) discern between 'primitive', 'typical', and 'advanced' forms. Various regional populations have under a (sub-)specific name been referred to one of these, especially those that are believed to show some level of advancement, such as *Elephas meridionalis cromerensis* DEPÉRET & MAYET, 1923, *Archidiskodon meridionalis jockgrimensis* DIETRICH, 1958, *A. meridionalis voigtstedtensis* DIETRICH, 1958, *A. meridionalis tamanensis* DUBROVO, 1964, *A. meridionalis vestinus* AZZAROLI, 1972, and *Mammuthus meridionalis depereti* COPPENS & BEDEN, 1982.

In the present text a morphological analysis of the extant material from The Netherlands and the North Sea is undertaken in order to define its evolutionary position with respect to the typical sample from Italy. Really primitive specimens, in all respects equivalent to, e.g., the small British Red Crag sample, have so far not been found within the study area, so that this group is not treated here. Some of the 'advanced' forms are quoted from the literature, whereas the small sample of *M. m. voigtstedtensis* (DIETRICH, 1958) is discussed on the basis of the author's own measurements. This late Early / early Middle Pleistocene subspecies is of special interest because it represents the last population commonly referred to *M. meridionalis*. It existed at a time the species was about to be finally replaced by a more advanced form. Although a general scenario of this replacement was suggested by Lister & Sher (2001), much of the regional detail of the process remains unsolved for lack of sufficient quantities of relevant material or stratigraphical data. From the early Middle Pleistocene onward, it is the advanced *M. trogontherii* (POHLIG, 1885) that firmly establishes itself in Europe. Within this context, the morphological distance that existed between the two species at the time their geographical ranges overlapped is important, and an attempt is therefore made to outline some morphological characteristics of advanced dental elements of *M. meridionalis* from various parts of Europe, including the study area and Voigtstedt. The possible presence of two morphological types within the Voigtstedt sample is discussed.

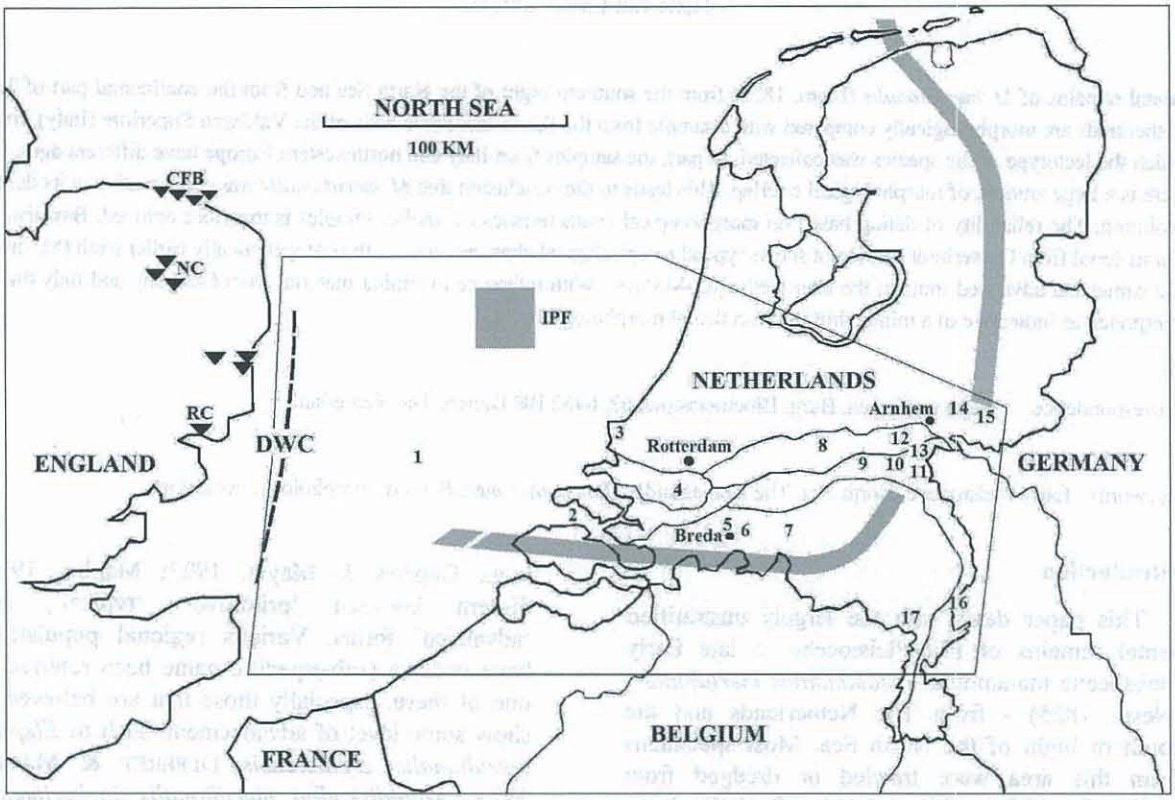

Fig. 1. Areas and localities where the majority of dentition remains of *M. meridionalis* (Nesti, 1825) from the study area have been found. **1** - North Sea : **DWC** - area of Deep Water Channel, **IPF** - area of ice-pushed formations; **2** - Oosterschelde; **3** - Maasvlakte; **4** - Mijnsheerenland; **5** - Oosterhout; **6** - Dorst; **7** - Goirle; **8** - Zoelen; **9** - Alphen a.d. Maas; **10** - Wychen; **11** - Groot Linden; **12** - river Waal near Nijmegen; **13** - Bemmel; **14** - Giesbeek; **15** - Braamt; **16** - Tegelen; **17** - Wessem. Outside the delineation of the study area: Red Crag (**RC**), Norwich Crag (**NC**) and Cromer Forest-bed (**CFB**) localities, East Anglia. Thick grey line - approximate configurations of the paleocoastlines during the Pliocene to Praetiglian (southern limit after Kasse 1988) and the Middle Tiglian (southern and eastern limits after Zagwijn 1979).

Abbreviations

An - Alphen a.d. Maas; Bl - Bemmel; BRH - Brunhes; Bt - Braamt; ac - author's collection; CFB - Cromer Forest Bed; Dt - Dorst; DWC - Deep Water Channel; e (after measurements) - estimate(d); OS - Oosterschelde; Fm - Formation; FU - Faunal Unit; GSS - Gauss; Ge - Goirle; Gk - Giesbeek; IGF - Institute of Geology, University of Florence; IPF - ice-pushed formations; FSFQ - Forschungsinstitut Senckenberg, Forschungsstation für Quartärpaläontologie, Weimar; JAR - Jaramillo; Ln - Groot Linden; MAT - Matuyama; MCI - Musei Civici di Imola, Imola; MV - Maasvlakte; NAT - Naturalis, Leiden; NBM - Noordbrabants Museum, 's-Hertogenbosch; NC - Norwich Crag; n.m. - nautical miles; NHMB - Naturhistorisches Museum, Basel; NNHM - National Natural History Museum, London; NS - North Sea; OIS - Other Inland Sites; OLD - Olduvai; O(t) - Oosterhout; PM - Paleomagnetism; RC - Red Crag; SMC - Sedgwick Museum, Cambridge; SMS - Spengler-Museum, Sangerhausen; Tn - Tegelen; Wm - Wessem; Wn - Wychen; Zn - Zoelen

Morphological symbols

x - talon(id); p - posteriormost platelet; ∞ (in plate formulas) - dentine platform (featureless anterior dentine area in many occlusal surfaces, where the basal parts of lamellae were worn away and abrasion continued on the root dentine).

Notation of dental elements

M3- upper teeth; m3 - lower teeth, etc.

Short survey of relevant research in The Netherlands

Within the study area, the scarce remains of *Mammuthus meridionalis* have been collected for about 150 years. In the 19th century the fossils referable to this species were not recognized in The Netherlands, but probably taken to represent the woolly mammoth. In his dissertation, Rutten (1909a) could list only two sites: He pointed out that finds made already in 1842 in a clay pit near Oosterhout were referable to "*Elephas meridionalis*" and also identified a molar fragment from the river Waal near Nijmegen (Fig. 1: 12). This first report on *M. meridionalis* from The Netherlands earned Rutten an offhand and undeserved refutation by Pohlig, who had not seen the material (Pohlig 1909: 249, footnote 3; reply: Rutten 1909b, 396-398). Twelve years later, the first molar fragment from Tegelen was reported on the authority of Schlosser (Richarz 1921).

Finds of relatively primitive morphology were to be temporarily labelled *Elephas, Archidiskodon*, or *Mammuthus (A.) planifrons* (e.g., Schreuder 1944; Hooijer 1953; Kortenbout van der Sluijs 1955) in the wake of Schlesinger (1911, 1912, 1913) and others, e.g., Mayet & Roman (1923), who held the theory that *Elephas planifrons* Falconer & Cautley, 1845 was the ancestral form of *M. meridionalis*.

Early Pleistocene material from the study area is comparatively rare, and publications that include morphological data on dental remains of *M. meridionalis* are therefore still few in number (e.g., Schreuder 1944; Hooijer 1953, 1984, 1985; Guenther 1986; Van Kolfschoten 1990; Van Essen & Mol 1996). Mol *et al.* (1999) gave measurements of (meta-)carpal and tarsal bones of *M. meridionalis* in comparison with those of *Anancus arvernensis* (Croizet & Jobert, 1828).

Find circumstances

North Sea - Among vast quantities of Late Pleistocene fossils, a number of *M. meridionalis* teeth and postcranial bones have been serendipitously brought to light as a result of commercial fishing fot flatfish in the shallow southern bight of the North Sea. Van Kolfschoten & Laban (1995) described particulars of the fishing method. Water depths in the southern bight of the North Sea now range from about 20 to 50 m. They are less than 20 m in near-coastal areas and over ridges and banks.

Oosterschelde -Trawling for mussels (*Mytilus edulis*) has produced teeth and bone fragments of the Early Pleistocene mammoth and other faunal elements from the bottom of the Oosterschelde. From 1951 until this day, 'bone fishing' - for the benefit of science and the collections in Leiden and Zierikzee - has been a yearly event (Hooijer 1991; De Vos *et al.* 1998; Kahlke 2001). The most-frequented fossiliferous deposit in the Oosterschelde is at ± 35-40 m below the water surface.

Maasvlakte - The Maasvlakte is an industrial building terrain raised by pumping up a sand-in-water slurry from local deposits within a range of approximately 10 km and from various depths. It therefore contains a mixture of faunal remains of different ages, divided into four faunal assemblages (0-III) on the basis of palaeoecological and stratigraphical implications of the species identified, and the degree of mineralization of the fossils (Vervoort-Kerkhoff & van Kolfschoten 1988; Van Kolfschoten & Vervoort-Kerkhoff, 1999b). These authors place the *M. meridionalis* material in Fauna I.

Inland sites - The Oosterhout, Dorst and Tegelen specimens are *in situ* finds from clay pits. The rest of the inland material has been found as a result of dredging operations in riverbeds or the surrounding flatlands and is therefore without detailed stratigraphical context. In addition, the formations that contain the fossils vary widely in age. Late Middle to Late Pleistocene deposits yield reworked material.

Characteristics of preservation

All specimens here referred to *M. meridionalis* are moderately to heavily mineralized. The latter qualification mostly applies to specimens from the North Sea and the Oosterschelde, the former to the inland finds from fluviatile deposits. A number of North Sea and Oosterschelde specimens were at some time subject to weathering, probably prior to their mineralization. The dentition remains of *M. trogontherii* (Pohlig, 1885) and *M. meridionalis* from the North Sea show no significant difference in the degree to which they are mineralized.

Mineralization therefore offers no clue with regard to their identification or relative geological ages; it can only be interpreted as a general indication that specimens are of Early or early Middle Pleistocene age. The same is true of the bronzy metallic shine that characterizes fractured dentine surfaces of many specimens from inland fluviatile deposits.

Analysis of the mostly sandy sediment that adheres to some of the teeth used for this study has not been attempted. It is apparent, however, that the colour ranges of the North Sea, Oosterschelde, and inland material to some extent allow grouping according to former sedimentary and chemical environment. The groups formed may reflect differences with regard to facies or stratigraphic levels and suggest the geographic extent of the fossiliferous strata involved. Some of the North Sea specimens, for instance, are indistinguishable from (Pre-) Pastonian material from the British coast and likely to have been trawled from near-coastal waters in the British sector. Some specimens within the dredged inland group are intensely waterworn fragments, washed from Early Pleistocene deposits upstream. They were largely disregarded for lack of morphological detail. Most teeth mentioned in the text are considered to be of local provenance.

General stratigraphical background

North Sea - During the Early Pleistocene, the North Sea was a wide bay of the Atlantic Ocean, not connected with the Channel by the Straits of Dover. In the Praetiglian its southern bight still covered most of the area of the present-day Netherlands as far south as the Belgian border (Kasse 1988) (Fig. 1). The rivers of northwestern Europe made the coastline shift to the West, Northwest, and North by extending their deltas into the shallow margins of the shelf sea (IJmuiden Ground / Smith's Knoll Fm.; Winterton Shoal Fm.; Yarmouth Roads Fm.) (Cameron *et al.* 1984). Zagwijn (1975, 1979) reconstructed the configurations of palaeocoastlines related to interglacials (Middle Tiglian and later; see also Funnell 1991, 1996). During cold stages, the sea in all probability retreated from the continental shelf over considerable distances because of eustatic lowering of the sea level. Early Pleistocene strata in the southern North Sea basin generally dip to the Northeast or North due to basinal subsidence centered north of the study area (Heybroek 1974; Ziegler & Louwerens 1979; Cameron *et al.* 1984; Kasse 1988). They mostly outcrop along the basinal margin in the Southwest, near the British coast, where formations of similar age - the Crags and the older beds of the Cromer Forest-bed Fm. - continue inshore. In northeasterly direction the Early Pleistocene formations increase in thickness and are covered by Middle to Late Pleistocene and Holocene strata. In the northeastern part of the Flemish Bight sheet (± 52° 50' N / 03° 55' E), sediments of the Yarmouth Roads Fm. down to the IJmuiden Ground Fm. locally underwent ice-pushing during the Elsterian glacial and now subcrop beneath Holocene deposits (Laban, pers. comm.; Cameron *et al.* 1984; Laban 1995: 43 ff.).

Oosterschelde - In the Oosterschelde area the fluviatile Tegelen Fm. filled an erosional valley (the so-called 'Zealand Valley') that had been formed in the underlying marine strata, presumably during the Tiglian C4c, a cold phase that caused a minor regression of the North Sea (Kasse 1988: 168). The local Tegelen Fm. is followed by a very extensive erosional and non-depositional hiatus that extends until the Eemian Schouwen Fm. Post-Tiglian erosion removed part of the Tegelen Fm., so that its thickness now varies between 0.8 and 22 m. Its present top is locally at ca. 20-25 m below sea level, and partly denuded by tidal scouring. The fossils of marine mammals now and then encountered probably originated from denuded parts of the marine Maassluis Fm. or from the fluviatile Tegelen Fm., in which they signal Late Tiglian erosion (Van Rummelen 1970). The exact stratigraphical horizon of the terrestrial fossils from the Oosterschelde presents a problem: they are generally held to be of TC3 age, for instance because *A. arvernensis* is well represented in the assemblage. However, the first non-marine formation in the area is the fluviatile Tegelen Fm. that was most likely deposited after the TC4c. This suggests that the TC3 assemblage remained in the area after erosion of deposits of that age, which have also become very patchy in the adjacent part of the North Sea.

Maasvlakte / Inland sites - During the Pleistocene, the rivers Rhine and Meuse took various courses through the Netherlands and were the main contributors to the accumulation and subsequent erosion of several formations that overlie the older marine deposits in the area (Fig. 2). A series of faults that strike SE-NW divide the southeastern border area of The Netherlands (about 51°10' N) into three major tectonic units: the Peel Horst flanked by the Central Graben to the Southwest and the Venlo Graben to the Northeast. As a result, Early Pleistocene deposits will be found at different levels throughout this area or may be absent because of subsequent fluviatile erosion. Further north (about 51°50' N), Early Pleistocene deposits were locally ice-pushed during the Saalian Glacial and later became subject to fluviatile erosion. In general the stratigraphic context of inland finds is therefore not uniform.

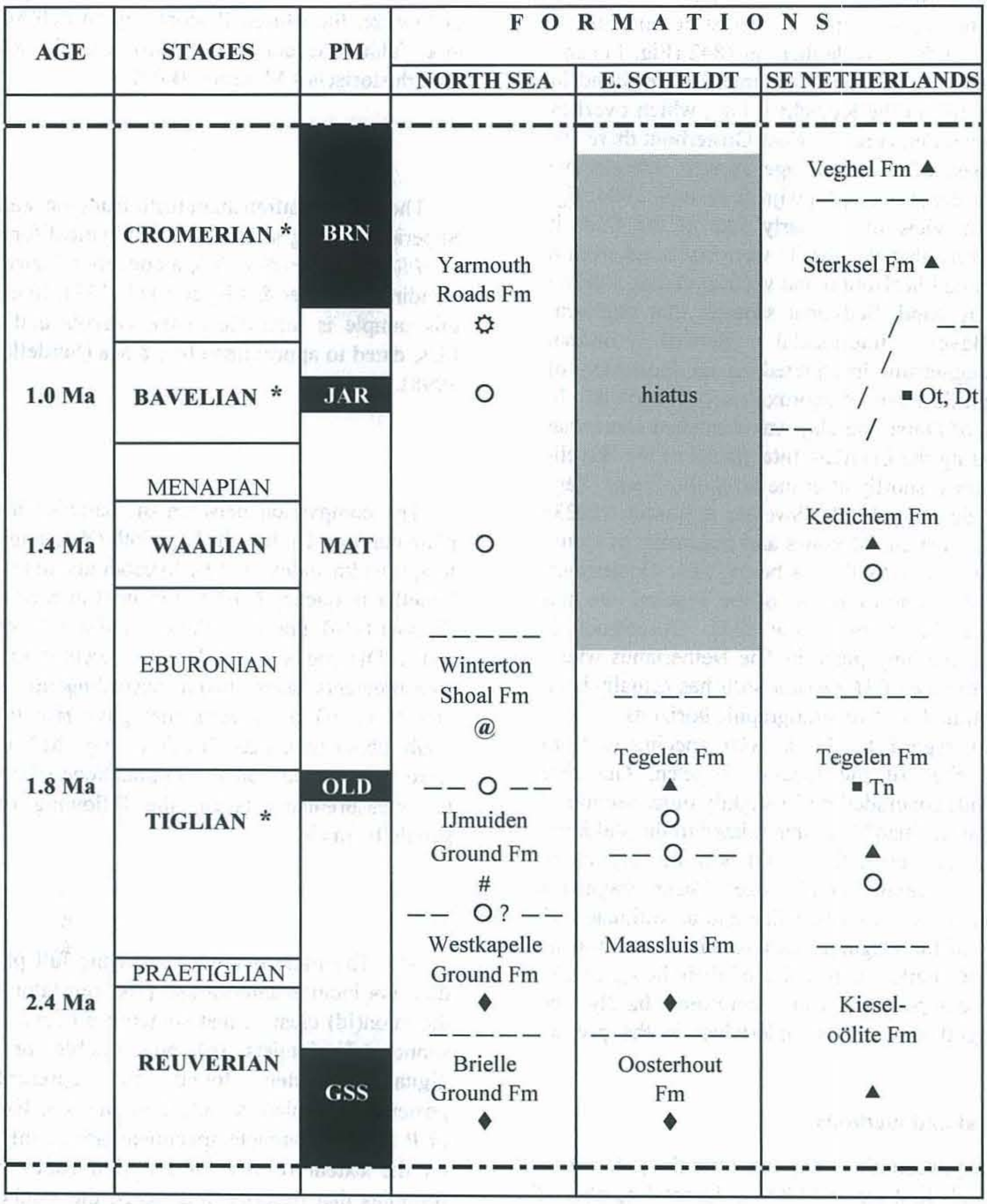

Fig. 2. Survey of Pliocene and Early to Middle Pleistocene chrono- and lithostratigraphy (modified after Cameron *et al.* 1984; Van Rummelen 1970; Zagwijn 1985). * - complex stages; stage names in **bold** indicate (the inclusion of) warm-temperate intervals; **formation types:** ◆ - marine; # - prodelta; @ prodelta, delta, & fluviatile; ✿ - mainly fluviatile; ▲ - fluviatile; ■ - *M. meridionalis in situ* [Tegelen (Tn), Oosterhout (Ot), Dorst (Dt)]; O - possible origin of *M. meridionalis* fossils.

The sites of Oosterhout and Dorst (Fig. 1: 5 and 6) near Bavel are of special interest because of the *Mammuthus* finds made there in 1842 (Fig. 11) and 1955 respectively. These specimens were found in clay pits dug in the Kedichem Fm., which overlies the Tegelen Fm. (Fig. 2). Near Oosterhout there are clay lenses of Bavelian age (Bavel Interglacial) very near the surface (Zagwijn & de Jong 1984: fig. 3), and in view of the early date of the finds it seems likely that the fossils were collected from a pit of limited horizontal and vertical extent, worked largely by hand. Sediment samples that represent the Bavel Interglacial showed normal palaeomagnetism, interpreted as an indication of the Jaramillo Event at approximately 1.0 Ma BP. In the case of Dorst, the clay was deposited somewhat later, during the Leerdam Interglacial of the Bavelian Complex, shortly after the Jaramillo Event (Zagwijn & de Jong 1984). Swemle & Rutten (1923) reported "remains of bones and fragments of teeth" of *M. meridionalis* from a boring near Oosterhout. The fossils came from clay of the Tegelen Fm. at a depth of 34.75 m below O.D. Oosterhout is therefore the only place in The Netherlands where the occurrence of *M. meridionalis* has actually been demonstrated for two stratigraphic horizons.

With regard to 11 *in situ* specimens from various sites of the locality Tegelen, Guenther (1986: 60) concluded on "a slightly older section of the Villafranchian" than that related to the Valdarno material. However, this result may be seen as an artefact of small sample size: These fragments comprise only 1 to 4 lamellae and an estimated 50 to 90% of the original tooth volume is worn away (*ibid.*: 56, table 2). In spite of their being *in situ* finds, comparison can therefore hardly be meaningful and is not undertaken in the present study.

Material and methods

Today, more than 90 years after the publication of Rutten's first report (1909a), the total number of (mostly fragmentary) *M. meridionalis* teeth from the study area has risen to at least 230. Many of these have come from the North Sea (85 or more) and the Oosterschelde (65 or more). The large majority could be used for the present study. Postcranial material, apart from (meta-)carpal and (meta-)tarsal bones, is also mostly fragmentary and has reached a similar quantity. Because stratigraphical detail is absent in the large majority of cases, a morphological approach is chosen for the interpretation of the extant material.

A number of the (milk) molars dP4/dp4 through M3/m3 from the study area were compared with an undivided sample from the Figline Clays and Tasso Sands of the Valdarno Superiore deposits, Italy. The analysed material is kept in the Museo di Geologia e Paleontologia dell'Università degli Studi di Firenze, the Museo Paleontologico dell'Accademia Valdarnese del Poggio, Montevarchi, and the Naturhistorisches Museum, Basel.

The Late Villafranchian teeth from the Valdarno Superiore belong to the so-called 'typical form' (*M. meridionalis meridionalis*), a concept of fairly long standing (Depéret & Mayet 1923: 139). In essence this sample is referable to the Olivola and Tasso FUs, dated to approximately 1.8 Ma (Sardella *et al.* 1998).

The comparison between the samples includes plate number (P), length (L), width (W), height (H), length-width index (LWI), hypsodonty index (HI), lamellar frequency (LF) and enamel thickness (ET) (Tables 1-16). For an explanation of the Divergence Index (DI), see below under LF. Except those of W, measurements were taken according to Maglio (1973: 11 ff). Fragments that gave rise to some doubt about their classification - e.g., M2 or M3 - were disregarded. On the implications of some of the measurements taken, the following remarks should be made:

P - The plate number represents full plates. It does not include anterior and posterior talon(id)s or the talon(id) clusters that sometimes occur, nor the subnormal platelets (p) and double or single digitations often found to represent the posteriormost plate structure in M3/m3. Estimates of P in near-complete specimens are mainly based on the extent of loss of the first root. In plate formulas that describe fragments, the symbol '$-\frac{1}{2}$' or '$\frac{1}{2}-$' indicates lamellae that were vertically split through their dentine core, e.g., $-\frac{1}{2}$ 6 $\frac{1}{2}-$. It distinguishes these fractures from those that went through a cement valley and are indicated by, e.g., - 6 - .

L - Forward-leaning anteriormost plates and their slightly bulging talon(id)s normally cause the anterior part of the crown to project beyond the frontal border of the first root. Because of this, specimens are soon worn to a level below the point where their length is maximal. Many measurements of length are therefore tabulated as estimates of the original maximum (Tables 1-8).

W - Contrary to usage, width is measured without cover cement to avoid bias. In *M. meridionalis* the thickness of the cover cement ranges from normal to extreme values, but in most cases it is not (fully) present through erosion or damage. Natural presence and thickness of the enamel cover relate to the stage of wear of a tooth, so that in this sense, too, cement thickness is accidental. Since H is taken from the extent of the enamel sheath only, the HI will be more accurate when W measurements are treated in the same manner, especially because the maximum thickness of a cement cover that was never formed cannot be estimated, but may at best be subsituted by the mean of the observed range. If the lateral extent of the enamel sheath is measured only, indexes will become slightly higher. For want of complete specimens, W may function as a parameter of absolute size (Lister & Joysey 1992) (Figs. 4AB). However, volume compensations may be caused by a greater crown height, more or thicker plates, and longer cement intervals, so that not every comparatively narrow fragment indicates a tooth that was to the same extent small.

H - Height is measured to the basal extreme of the enamel sheaths, where they merge with those of the neighbouring lamellae. The alternative approach - down to the cingulum - would normally have resulted in lesser values. Both methods influence the value of the HI.

HI - Since the HI varies almost per lamella, the values used are crown values, i.e., computed from the highest and the widest lamella (without cover cement), which may or may not be the same one. The value of a single plate in an incomplete tooth is substituted for the crown value only if it is likely to almost coincide with it.

LF - The formula through which the LF is calculated (N of lam. x 100 / L in mm) is not explicit with regard to the cement intervals included in the count. Because one lamella corresponds to one interval half on either side, i.e., to one complete interval, the L measurement should include as many intervals as lamellae instead of one interval less. The latter variant unduly augments the LF value. On complete crowns, the measurement was repeated four times: along the top and the base, buccally and lingually. The mean value of these was listed. Values for well-worn specimens are based on one buccal and one lingual measurement only. In such complete remains as well as in fragments the LF is likely to differ slightly from the original value, and was in some cases reconstructed.

DI - In order to test if the absence or presence of basal divergence of lamellae in m3 can be correlated with evolutionary stages, especially within *M. meridionalis*, LF values were used to compute the Divergence Index (DI), i.e., the mean apical LF divided by the mean basal value (x 100). Exactly parallel lamellae have a DI of 100. Values above 100 indicate basal fanning in various degrees, and below 100 the divergence is at the apical side (M2, M1).

ET - According to the stage of wear or the degree of fragmentation of specimens, the number of ET measurements that can be performed on each of them is rather variable. Values considered not representative - e.g., those at extremely basal crown levels or in zones of strong plication - were disregarded. Ideally, ET measurements result in the range of representative values and the mode, which is the value found most often in a single specimen, e.g., 2.9 (min.) / 3.4 (mode) / 4.0 (max.). Because the modal ET was not known for all specimens represented in this study, the individual midrange points calculated from both extremes were used instead to avoid loss of data. Differences in the mean values resulting from the use of these two methods appear to be small; for the set of teeth with known modal ET they amount to 0.01 - 0.34 mm, with an average of 0.085 mm. The ET of dP4/dp4 - M3/m3 is summarised in Tables 9-16, and in scatter diagrams Figs. 6AB.

Tooth shape

In order to represent the three-dimensional shape of the teeth compared, a ternary diagram was prepared in which the maximum L, W and H are shown as percentages of their sum (Figs. 8AB). The perpendicular A-B represents all objects in which W=H, in this case teeth whose HI amounts to 100. This line was supplemented with a - necessarily warped - grid indicating regular intervals in the ranges of HI and LWI. Point B, in which the share of L, W and H in their sum is 33.3333 % (i.e., HI=LWI=100.), represents all cubic shapes. Point A represents bar shapes with a square cross section and a L of 4.6666 x W. The diagram visualizes subtle shifts in overall shape, but the use of L causes the restriction that the teeth have to be complete.

Observations from morphological data and discussion

1 - Plate number (Tables 1-8)

(1) All complete specimens from the study area fall within the respective ranges of the Valdarno Superiore sample and the means are very close to one another. (2) The average P in lower molars from the Valdarno Superiore is slightly higher than in the analogous upper ones. (3) Averaged differences between representatives of the two regions amount to less than one lamella per element of the dentition.

Increase in P is one of the most important parameters of the evolution of the *Mammuthus* lineage. Because one is dealing with a gradual shift of range values, the overlap of consecutive ranges hampers the interpretation of unstratified samples and especially single specimens. The P of M3 found in four skulls from Chilhac (Haute-Loire, France), which are dated to ± 1.9 Ma, is 12 once and 13 thrice (mean: 12.8) (Boeuf 1983: 194). For the 20 complete Valdarno Superiore M3 in Table 1 the distribution is: 12: 6 (30%); 13: 11 (55%); 14: 3 (15%) (mean: 12.8). It is therefore probable that 13 was the modal value around 1.9-1.8 Ma.

North Sea - Specimens with 12 lamellae are lacking in the North Sea M3 sample, but this is probably due to the small number of complete specimens it includes. The present range, modal and mean value (13-14e, 13, and 13.3 resp.; Fig. 3) are very close to the values of the Chilhac and Valdarno specimens. It is not known for how long 13 remained the predominant P value in M3, nor can its last occurrence be pinpointed, but it is likely to have persisted into the late Early or even the early Middle Pleistocene (see the section 'Inland sites'). Additional arguments are therefore required to make plausible that at least part of the North Sea sample is of Tiglian age. Firstly, there is the occurrence of *Anancus arvernensis* in the Thornton Bank area (51° 34' N / 03° 00' E) (Van Essen & Mol 1996), accompanied by *M. meridionalis* dental remains, *Eucladoceros*, and a horse (Post, pers. comm.). Secondly, some m3 have a HI below the range of the Valdarno Superiore sample (see under 3). Thirdly, the morphology as well as the type of sediment-related preservation of part of the sample are indistinguishable from those observed in specimens of Pre-Pastonian to Pastonian age from the British coast (Lister & van Essen, unpublished data), and there are good reasons for correlating these stages with the Tiglian C4c and C5-6 respectively (summarized by Lister 1998: 275ff). Until now, *Anancus arvernensis* has not been recorded from the Pre-Pastonian - Pastonian sequence, nor from the Tegelen type locality (Westerhoff *et al.* 1998: 61-62) so that its occurrence near the Thornton Bank suggests an age greater than that corresponding to the Tiglian C4c. The presence of (a) lateral equivalent(s) of the fossiliferous Oosterschelde deposit(s) that contain(ed) *A. arvernensis* (at ± 24 n.m. ENE) seems plausible and would imply the Tiglian C3. This is consistent with the geology of the Thornton Bank area, where prodeltaic/deltaic strata of Praetiglian and Tiglian age (Westkapelle Ground Fm., IJmuiden Ground Fm.) are present but have largely been eroded (Ebbing *et al.* 1992).

Oosterschelde - The Oosterschelde terrestrial fauna, which includes *Anancus arvernensis*, is considered to be of Tiglian C3 age (Van Kolfschoten & van der Meulen 1986; De Vos *et al.* 1998; Reumer *et al.* 1998). Of the only complete m3 in the *M. meridionalis* sample (NAT RGM 401853; P=12) can only be said that it is within the expected range. The plate formula of an anteriorly damaged specimen (NAT RGM 20033) was reconstructed as "x 9 x" by Schreuder (1944: 51) on the basis of its root pattern (*ibid.*, pl. IV, fig. 1b), but according to the present author she mistook the second root for the first. The reconstruction x 3 $\frac{1}{2}$- or x 4 $\frac{1}{2}$- plus the remaining -$\frac{1}{2}$ 7 p (i.e., x 11 p or x 12 p) seems more realistic. These two Oosterschelde m3 apparently happen to belong to the subgroup with presumably the lowest P value within a distribution pattern similar to that of the Chilhac and Valdarno Superiore material. The combination with the occurrence of an individual ET maximum of 5.0 mm (see under 5) could be interpreted as an indication that some comparatively primitive features appear in the *M. meridionalis* m3 sample and might relate to the inferred age of the assemblage (TC3, ± 1.9 Ma), which may be composed of fossils that remained in the area after erosion. This would be consistent with the signs of weathering mentioned above (see: Characteristics of preservation). The morphological proximity to the Valdarno Superiore sample remains clear, however, and could indicate virtual stasis during the Tiglian. On the other hand it might mean that a number of specimens were trawled from the Tegelen Fm. and are therefore of late Tiglian age (TC5-6). In this case stasis would still be possible (the sample is too fragmentary for this matter to be decided), but *A. arvernensis* would then have been contemporaneous with the older part of the sample only.

Maasvlakte - The *M. meridionalis* material from the Maasvlakte is placed in Fauna I of Bavelian to early Cromerian age according to a reinterpretation by Van Kolfschoten & Vervoort-Kerkhoff (1999b). This attribution is motivated by the complete absence of the rodent *Allophaiomys* from the early Maasvlakte faunas. So far there is only one near-complete *M. meridionalis* M2 from the Maasvlakte (Van de Weg coll. 72). It had an estimated 10 lamellae, possibly 9, and is therefore indistinguishable from the Valdarno specimens. With some uncertainty, the P of a large m3 with ∞ 11 p in 245 mm, a W of 102.5 mm, and a LF of 4.85 (Kerkhoff coll. RM 3746/3846/3912) may be reconstructed as ± 14-15 in about 310-335 mm (LWI ± 302-327). This value is at the upper extreme of the Valdarno range but could well represent a later stage because of overlapping ranges (see the section 'Inland sites'). The Bavelian specimens from Oosterhout and Dorst (see under 3) suggest that only M3/m3 and possibly M2/m2 could be advanced enough to be noticed as such.

Inland sites - The complete m3 from Alphen a.d. Maas (Stolzenbach coll.) is not reworked and has 14 lamellae. Although the last five plates in this remarkable specimen were expressed twice because of a genetic defect and the two collateral rows form a 'swallow-tailed' tooth, this count is beyond doubt. The stratigraphy of the Alphen region (Fig. 1: 9) suggests that the specimens from this area were dredged from the Kedichem Fm., which overlies the Tegelen Fm. This would make a Waalian age most likely, because Bavelian deposits are not often incorporated in the Kedichem Fm. in this area (Verbraeck 1984), and the Tegelen Fm. is at greater depth. The LF of the specimen confirms its somewhat advanced character (see under 4). The near-complete M3 from Wessem (ac 550; lam. form.: - 11 p) probably originated from the Sterksel Fm., which is locally at normal dredging depths (Fig. 2). The Sterksel Fm. is of Bavelian to Cromerian age. The top of the Kedichem Fm. in this part of the Central Graben is virtually out of reach at about 55 m below the water level of the Meuse. The top of the Tegelen Fm. lies another 70 m deeper (Zagwijn 1960: 44, profile III; the locality Wessem is very close to the boring Herten 746/75). The specimen is not reworked but in the dredging process has lost the portion of the crown that corresponds to the first root. The estimate of its P is 13, perhaps 14, so that it might belong to the category of 'last occurrences'. Its LF is slightly advanced, but it was definitely low-crowned and has very weakly folded enamel with a thickness indicative of *M. m. meridionalis*, so that it is not as advanced as the Dorst specimen below, whereas it could well be younger.

The Dorst M3 (NAT RGM 85541), a Bavelian *in situ* find (Van Kolfschoten 1990), is the only M3 in the sample and unfortunately only a fragment. The reconstruction of the specimen by the present author (Fig. 12) is based on the observation of the falling apical outline after lamella 7, the incipient posterior fanning around lamella 9, and the antero-medial LF of 5.74. The reconstructed specimen may be characterised as follows: P : 14 - 15e; L : 270.e; W : 87. (true max. at plate 5); H : 145.e (± true max. at plate 5); LWI : 310.e; HI : ≥ 165.e; LF : 5.5e; ET 2.0 - 2.5.

Edersleben, Rio Pradella, Voigtstedt - The P of the four more or less advanced molars last mentioned - 14/15, 14 (m3) and 13/14, 14/15 (M3) - is similar to that of the M3 in the palato-alveolar skull fragments of the mammoth from the early Middle Pleistocene 'lower' or 'red' gravels at Edersleben (SMS, GFR). The left M3 has 15 lamellae. Its L is an estimated 270 mm, its HI ± 176, its LF ± 6.00, and its modal ET 2.3 mm. Lister (1996) considers the specific identity of this female skeleton (*ibid.*: 208, table 19.1) to be uncertain, whereas it is usually referred to *M. trogontherii* because of its advanced traits, e.g., by Garutt & Nikolskaja (1988). These authors regarded it as a representative of an early form of the steppe mammoth, which they expressed by naming it *Archidiskodon trogontherii.* The degree of similarity between the M3 from Edersleben and the reconstructed Dorst specimen - which is of late Early Pleistocene age - explains the doubt about the identification of the former, but also questions that of the latter. The low reconstructed P, the measured cleft depths (up to 51 mm in the collateral Dorst specimen NAT RGM 85536; lam form.: x 4 ½ -), as well as the morphology of the specimens by which it is accompanied speak for *M. meridionalis*. (Clefts are the two main apical incisions of the lamellar body. Their spacing determines the character of the enamel figures in early wear).

Very similar teeth from the early Middle Pleistocene Rio Pradella site (Imola Sands, Imola, northern Italy) were referred to *M.* cf. *meridionalis* (Azzaroli & Berzi, 1970) or *M.* aff. *meridionalis* (evolved form) (Masini *et al.* 1995; Ferretti 1999). The P in M3 (MCI 7644) is reported as 16 including talons (Ferretti 1999), which implies x 14 p or x 15 for the present paper. H=145./158., W=85./90, LF=6./6.6, ET= - /2.4 (Azzaroli 1977: 163/ Ferretti 1999: 508, table 3).

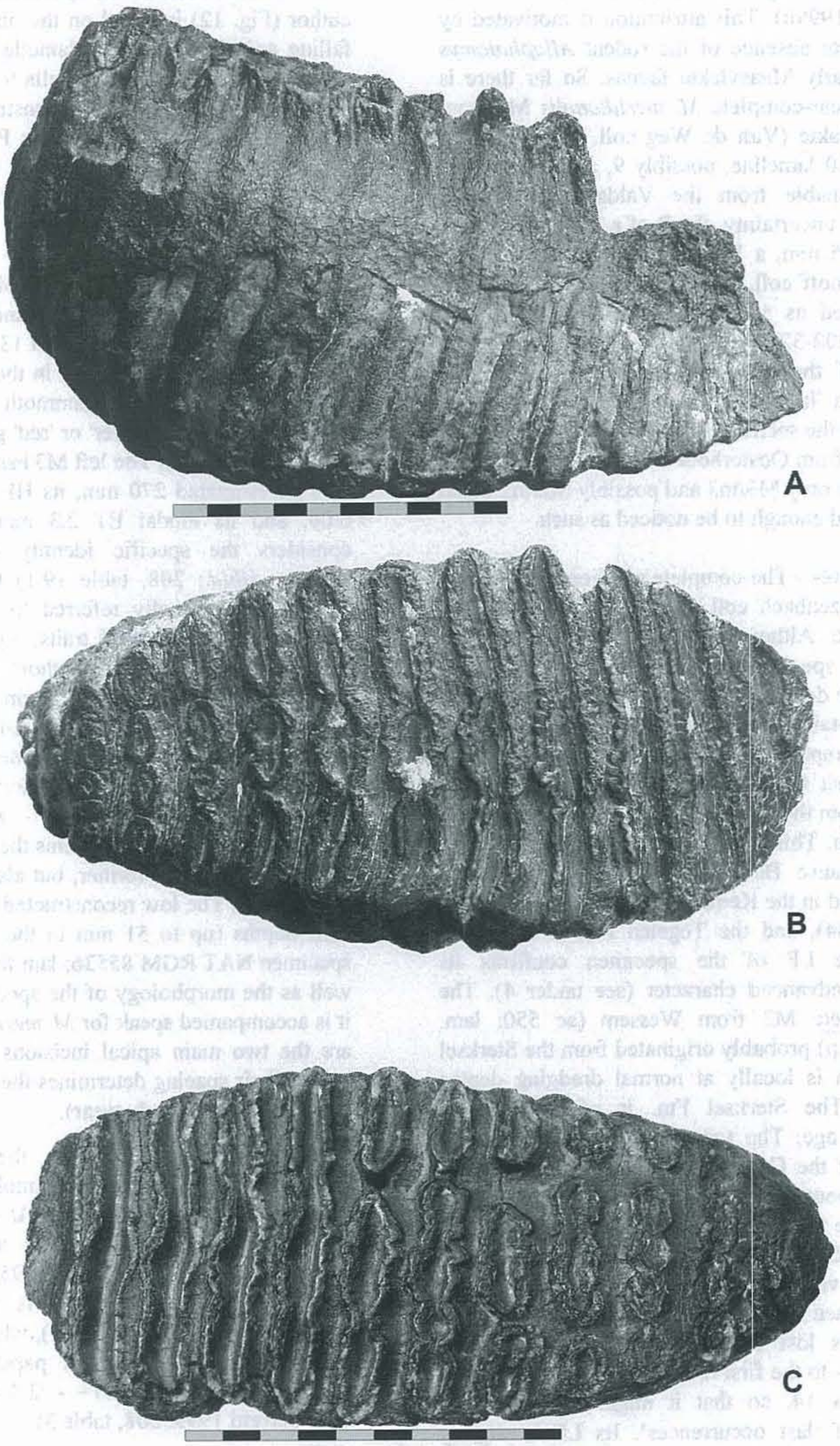

Fig. 3. *M. meridionalis* from the North Sea. Left M3; **A** - ac424, lingual view; **B** - ac324, occlusal view; **C** - ac464, occlusal view. Bar is 10 cm.

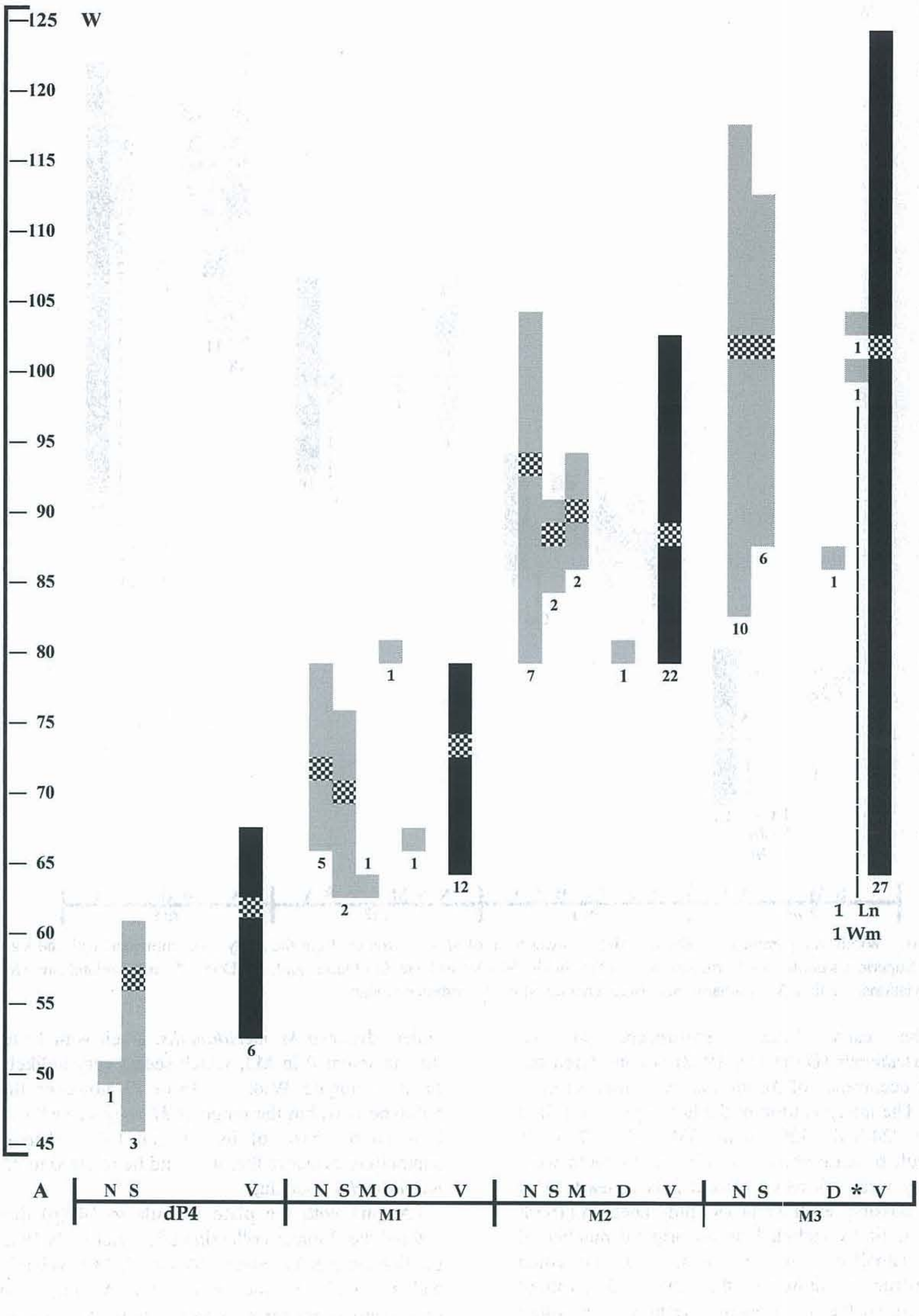

Fig. 4A. Width as a parameter of absolute size in upper teeth of *M. meridionalis* from the study area, compared with the Valdarno Superiore sample. **N** - North Sea; **S** - Oosterschelde; **M** - Maasvlakte; **O** - Oosterhout; **D** - Dorst; ***** - other inland sites (for abbreviations, see list); **V** - Valdarno Superiore; chequered field - arithmetic mean.

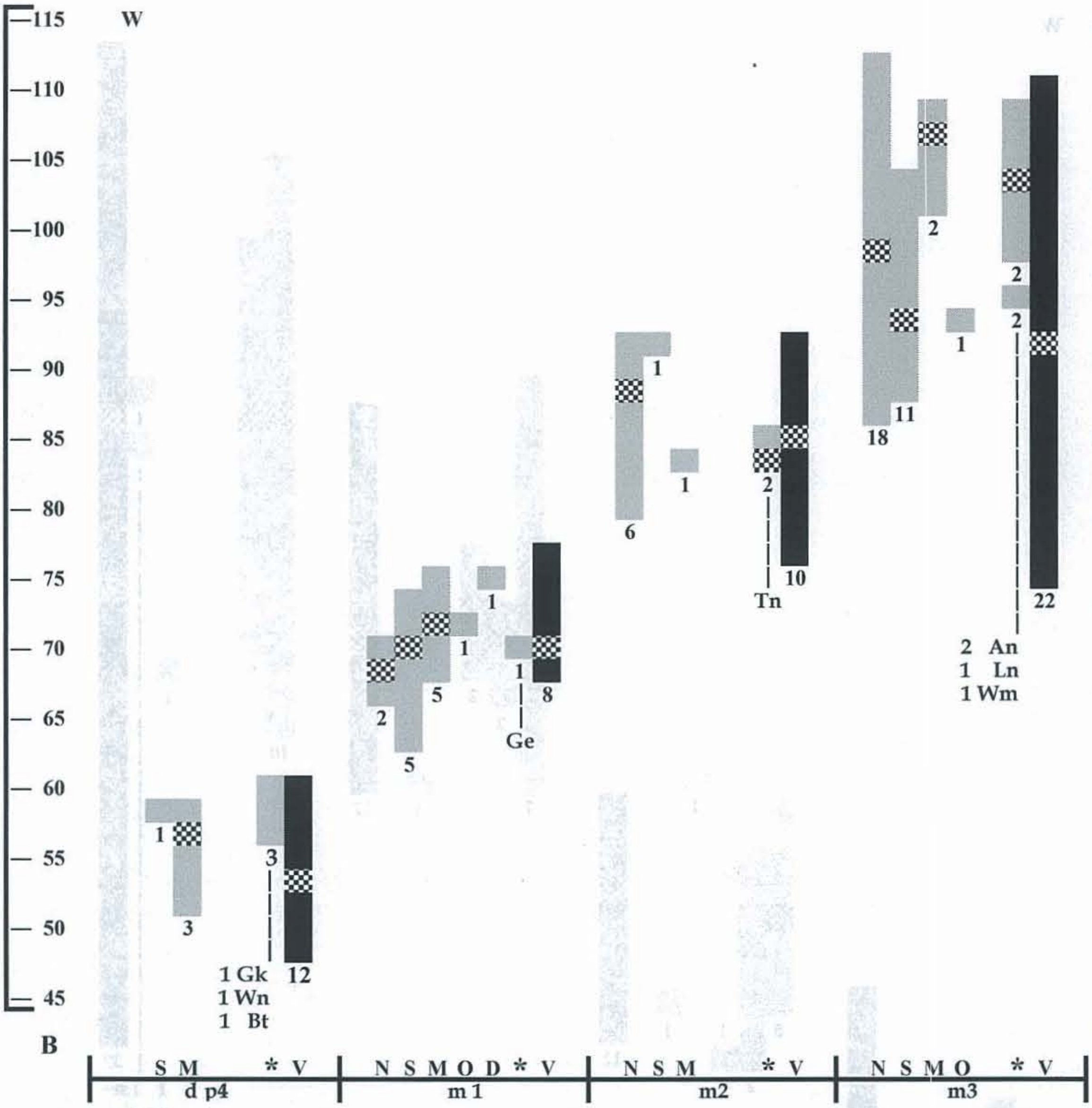

Fig. 4B. Width as a parameter of absolute size in lower teeth of *M. meridionalis* from the study area, compared with the Valdarno Superiore sample. **N** - North Sea; **S** - Oosterschelde; **M** - Maasvlakte; **O** - Oosterhout; **D** - Dorst; ***** - other inland sites (for abbreviations, see list); **V** - Valdarno Superiore; chequered field - arithmetic mean.

The early Middle Pleistocene *M. m. voigtstedtensis* (DIETRICH, 1958) is considered the latest occurrence of *M. meridionalis* discovered to date. The interpretation of the holotype (M3, FSFQ 1965/2924/Voi. 320, olim SMS Voi. 796) is difficult because about 65 vol% of the tooth were lost by wear. Its reconstructed P is at least 15 in 265., possibly even 17 in 295 mm. Dietrich (1958: 797) at first concluded on an original number of "15 lamellae" in his text, but presented reconstruction drawings that show 13 (without talon/p), so that he probably meant x 13 p within his estimated tooth length of 220 mm. On p. 799 he is willing to allow for "17x in 250" mm in case he should have been too conservative in his earlier estimate. Maglio (1973, 56) deems it "not unjustified" to subsume the Voigtstedt material under advanced *M. meridionalis*, albeit with 14 as the maximum P in M3, which seems very unlikely for the holotype. With P = 16 or 17, however, the holotype is within the range of *M. trogontherii* - as it is on the basis of its ET and LF - whereas compelling evidence that it should be referred to *M. meridionalis* is lacking.

An m3 with the plate formula ∞ 14 (p) that entered the Weimar collection after Dietrich's 1965 publication (FSFQ 1966/6764/Voi. 3558.) probably had ± 16 (17?) lamellae in total. Although the uncertainty is greater with respect to the fragmented large M3 SMS Voi. 2403 (lam. form. $-\frac{1}{2}$ 10 p; figured by Dietrich 1965: 532, Taf. XXXIV), its P was probably very similar.

The scanty evidence listed above seems to indicate that the P 14 had been on the increase and possibly reached modal status during the Waalian (± 1.4 Ma), with 15 following in its trail and becoming common ultimately during the Bavelian Stage (± 1.0-0.8 Ma.). During the early Middle Pleistocene, 16 and possibly 17 may ultimately have been reached, so that the average increase in modal M3/m3 values would have amounted to 2, possibly 3 lamellae in 1 Myr., provided the Voigtstedt material is retained as *M. meridionalis*.

M1 - Teeth that are ontogenetically earlier than M3 have fewer lamellae and therefore show proportionally less absolute change. They corroborate the evidence for a slow evolution in the sense that already M1 evokes a picture of complete stasis: All but one of the nine complete M1 from the study area have 8 lamellae, and since specimens from Oosterhout and Dorst are among these, some are separated by about 800 Kyr. Instead of indicating an absence of change, the unaltered P value could by chance represent specimens from successive ranges that were largely repetitive with respect to the Valdarno distribution (7-9), but with a gradual shift in emphasis.

An advanced M1 (FSFQ 1965/3776/Voi. 1820) from Voigtstedt referred to *M. m. voigtstedtensis* by Dietrich has 10 lamellae, the highest value recorded for *M. meridionalis*, but also the lowest observed in *M. trogontherii* M1 by Guenther (1969: 717) and Maglio (1973: 59). In all morphological detail this specimen and also the very worn M2 FSFQ 1965/3828/Voi 2245 seem indistinguishable from *M. trogontherii*. Hence the question arises whether the Voigtstedt sample as a whole should be regarded as belonging to *M. meridionalis* - as Dietrich saw it - or as providing evidence of the presence of *M. trogontherii* as well (see under 'Mammoths in a Time of Transition').

2 - Size (L, W, and H in Tables 1-8; Figs. 4AB, 5AB, 6AB)

(**1**) The size ranges of the subsamples, as indicated by bar diagrams of W (Figs. 4AB), in each case show a considerable overlap and minor differences in their extremes.

(**2**) Arithmetic means of larger subsamples of W are comparatively close to one another, even identical in M3.

(**3**) W range extremes in Valdarno Superiore m3 and M3 are 35 and 43 mm apart respectively, further than those of the m3/M3 subsamples from the study area.

(**4**) Very small specimens are found among dP4 from the North Sea and the Oosterschelde, m1 from the Oosterschelde and m3 from the Valdarno Superiore. The latter form a nearly separate lobe on m3 clusters (Figs. 5B, 6B).

(**5**) The M1 from Oosterhout is the largest of all M1 from the study area and also slightly larger than the largest specimen from the Valdarno Superiore. The M1 from Dorst is very small.

In comparison with *M. m. meridionalis* (Olivola and Tasso FUs), size increase is indicated for remains of *M. meridionalis vestinus* (AZZAROLI, 1972) that belong to the Farneta FU (e.g., Azzaroli 1977; Ferretti 1999). The Farneta FU is currently dated to about 1.45 Ma (Sardella *et al.* 1998). It is size increase and skull morphology rather than differences in dental morphology that determine the attributions to the subspecies *M. m. vestinus* (see also under 3).

M. meridionalis molars from two discrete horizons within the Cromer Forest-bed Fm. in Norfolk, England, show an appreciable average size increase, albeit with a fair amount of range overlap (Lister & van Essen, unpublished data).

Because the notion of size increase is based on *in situ* sample averages, it obviously cannot be used in order to define relative age levels within unstratified samples, which requires other data as well. Size (W) in combination with the HI is therefore used in an attempt to analyse the samples with respect to their relative ages (see under 3). Large size is indicated for some comparatively high-crowned specimens that have low LFs (see under 4, I). Where the *in situ* finds are concerned, some specimens appear to confirm the expected trend, although these subsamples are very small. On the whole, it seems defendable to assume size increase mainly by analogy with the Pre-Pastonian to Pastonian specimens from the nearby British coast and the later material from Italy (Farneta FU).

Small teeth form the other extreme of the range, as shown in, e.g., Figs. 5B and 6B. Although a number of small specimens in the samples measured very likely belonged to relatively early populations with on average smaller-sized teeth, a marked size differentiation within a tooth sample - apart from the possibility of stratigraphical mixing - does not preclude contemporaneity, as can be gathered from the existence of so-called diminutive specimens. The size of these sometimes extremely small teeth has effects on their LF and also stands in a vague relation to their ET (see under 4 and 5). Their nature as well as the reasons for including them in samples deserve some attention, because they are encountered among remains of the mammoth species from the European mainland and elsewhere, as well as among those of the straight-tusked elephant.

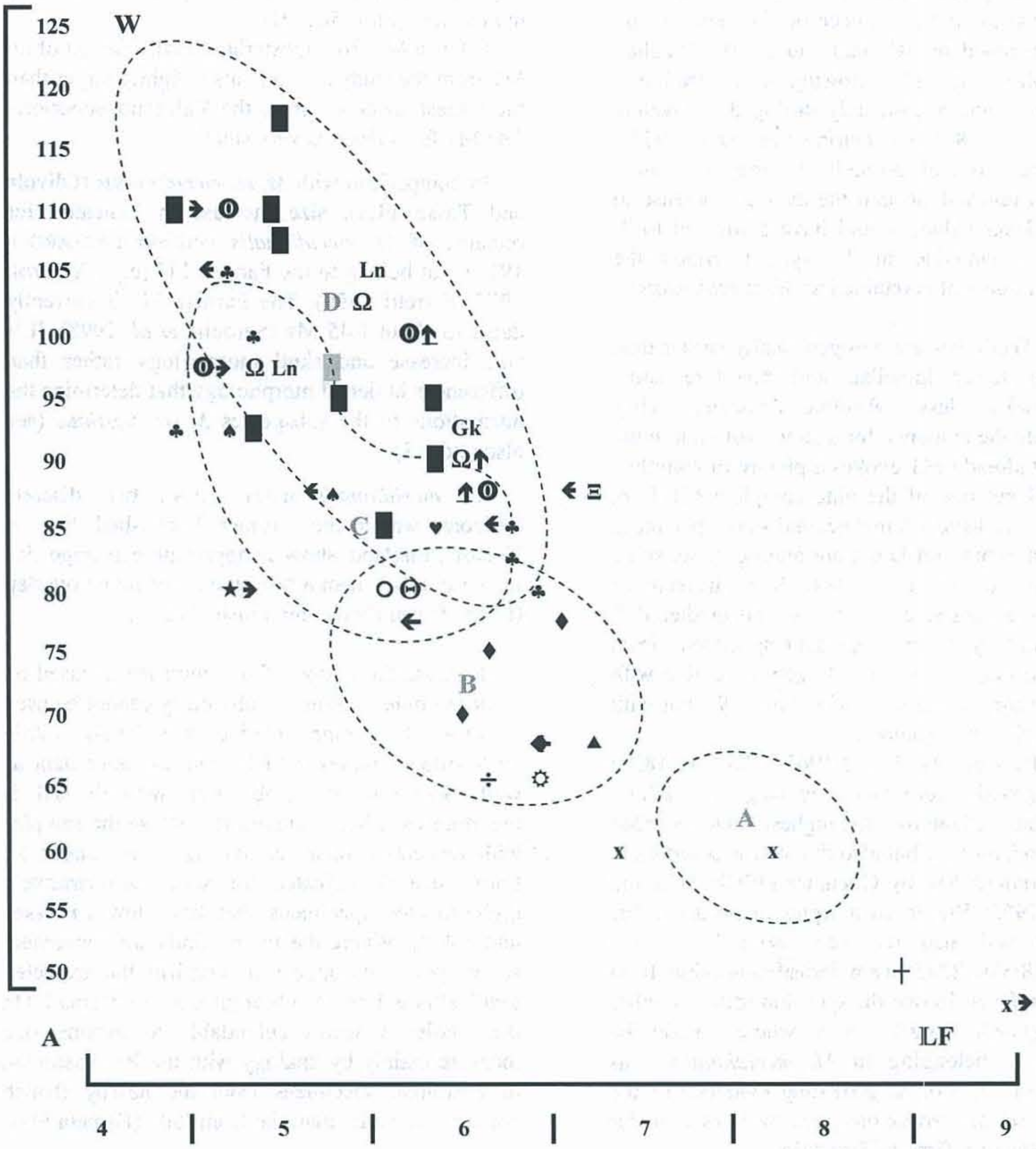

Fig. 5A. Scatter diagram of W vs. LF for dP4 - M3 of *M. meridionalis* from the study area. Dashed lines delineate Valdarno Superiore clusters. **A**-dP4, **B**-M1, **C**-M2, **D**-M3; →/← - original LF value of specimen somewhat higher/lower than plotted (measured) value; ↥ - measured maximum W ≤ true maximum.

Key to symbols in Fig. 5AB and other figures:

	NS	ES	MV	Ot	Dt	OIS	VS
dP4/dp4	+	x	@			δ	A
M1/m1	♦	☼	÷	○	▲	ε	B
M2/m2	♣	Ξ	♠		★	Θ	C
M3/m3	█	⓿	▒	□	♥	Ω	D

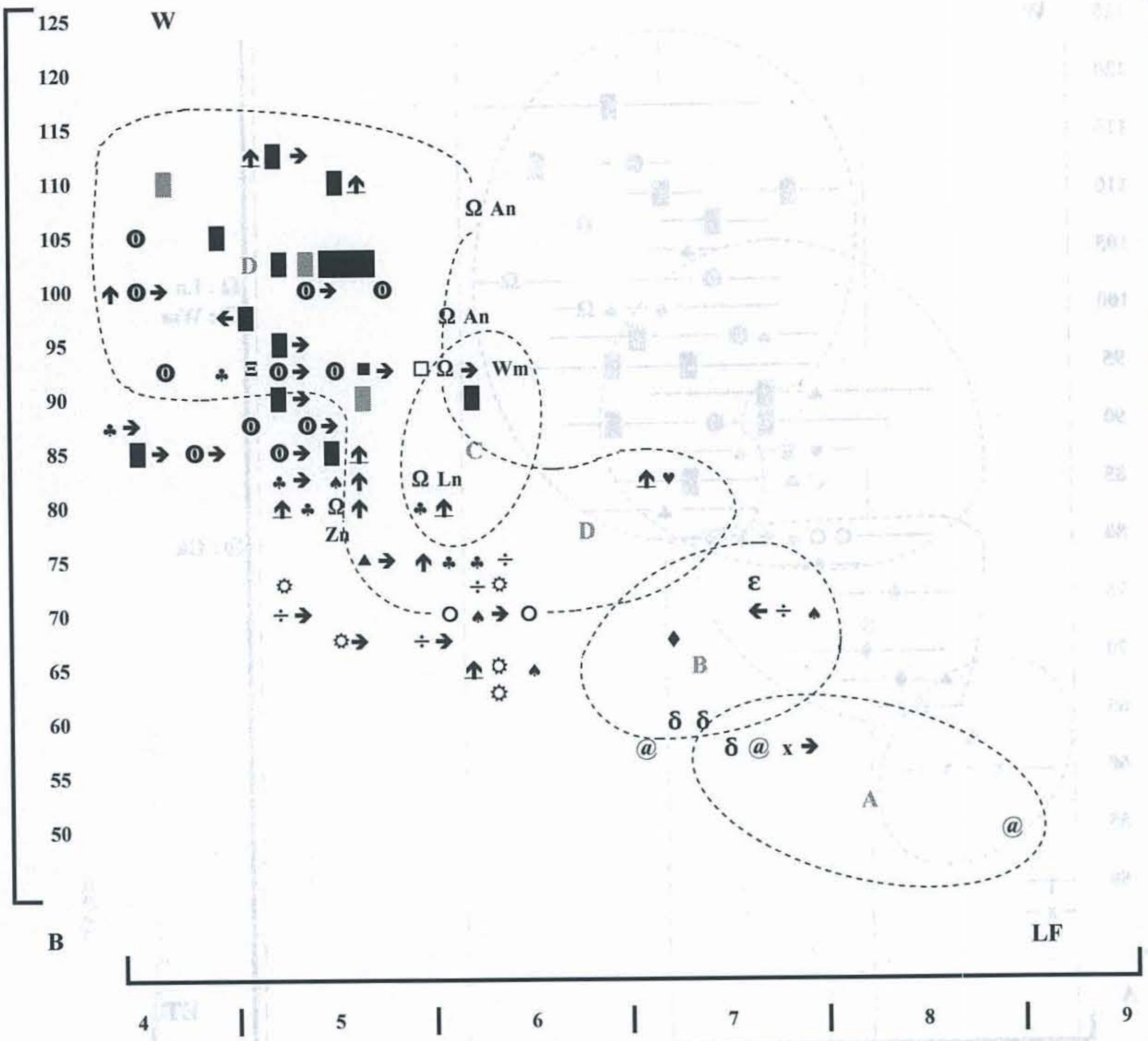

Fig. 5B. Scatter diagram of W vs. LF for dp4 - m3 of *M. meridionalis* from the study area. Dashed lines delineate Valdarno Superiore clusters. **A**-dp4, **B**-m1, **C**-m2, **D**-m3; →/← - original LF value of specimen somewhat higher/lower than plotted (measured) value; ↥ - measured maximum W ≤ true maximum. For key to symbols, see Fig. 5A.

The status of diminutive specimens - The status of diminutives has not been the subject of very much recent debate, nor is there a viable morphological definition that could focus the application of the term. The next smaller size category is that of the endemic dwarfs, another rather loosely applicable term. Extensive morphological comparisons between these two groups of very small teeth have so far not been made.

Among diminutive mammoth teeth in general, M3 lengths below 200 mm occur (e.g., in western Europe and Wrangel Island) and in the present author's view need not always indicate female individuals, although sexual dimorphism probably plays a role. Guenther (e.g., 1955: 34) commented on the phenomenon of diminutives in various samples from Germany, pointing out that the observed ranges show no hiatuses and render any attempt at subdivision of the samples arbitrary. In suggesting that the sizes of skeleton, skull, and teeth may have been incongruent in their evolution, he already questioned the tight correlation between tooth size and body size that is often assumed, and later (e.g., Guenther 1988) stated that these were inherited independently. According to the present author, the correlation between jaw and tooth size seems somewhat weak, but is probably not the result of random combinations. Unfortunately, the very small *M. primigenius* skeleton from Rottweil, SW Germany, does not comprise elements of its dentition (Ziegler 2001).

Guenther found a similar size distribution in tooth samples of *Palaeoloxodon antiquus* (FALCONER & CAUTLEY, 1847) and *M. trogontherii*, and hence suspected that in each

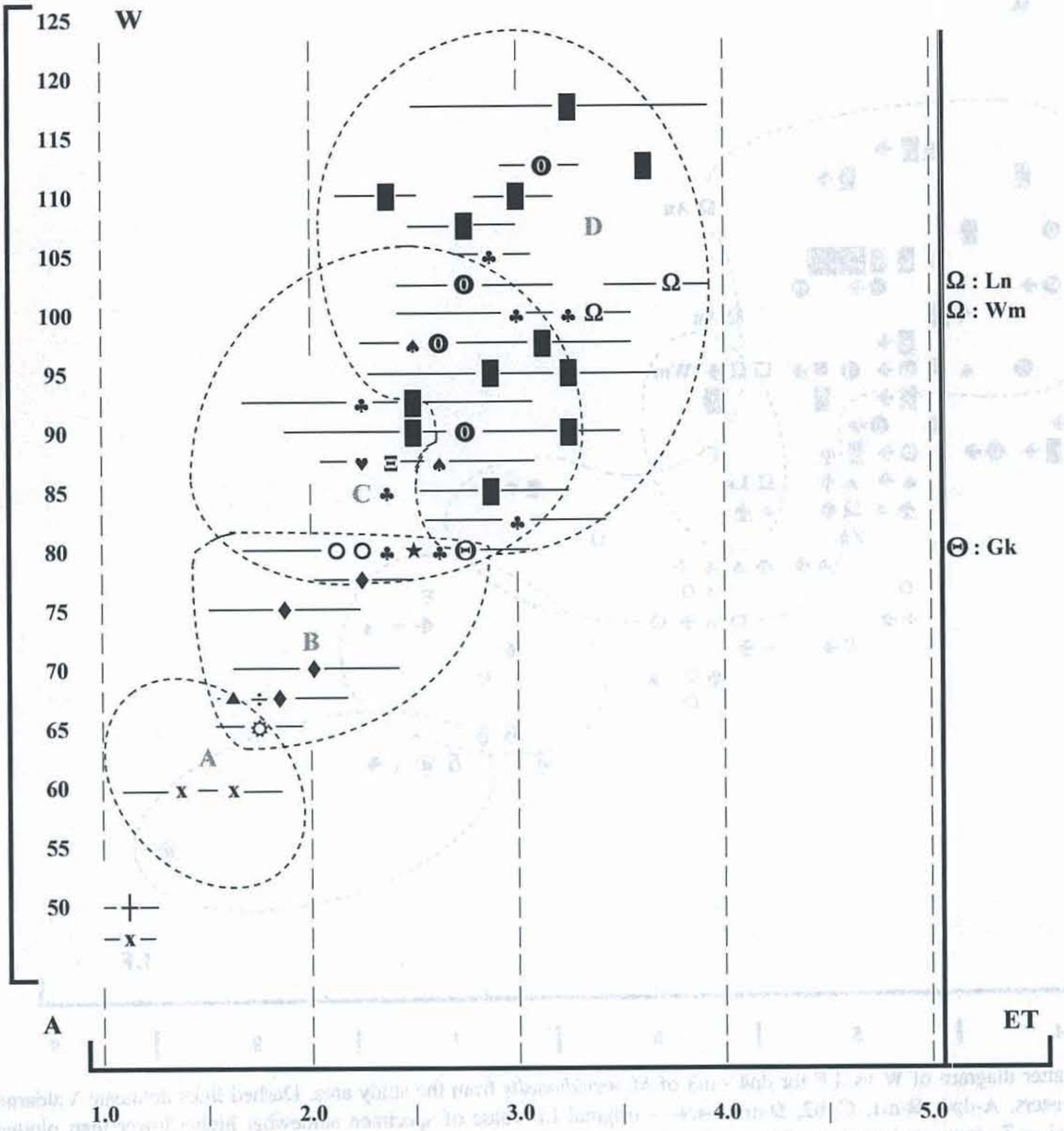

Fig. 6A. Distribution of Enamel Thickness vs. Width in upper teeth of *M. meridionalis* from the study area. Plots represent midrange points. Overlap of individual ranges is not indicated. Valdarno Superiore clusters are shown in outline. **A** - dP4, **B** - M1, **C** - M2, **D** - M3. For key to symbols, see fig. 5A.

species the bearers of small and large molars belonged to the same herds and produced offspring. Some researchers have opposed this view and advocated the existence of a subspecific branch of the mammoth lineage that emerged from (early) *M. trogontherii*, evolved towards ever smaller size, different skeletal proportions, smaller average P, and fewer phalanges to become extinct at the same time as the typical form of *M. primigenius* (discussion in Musil 1968: 164-167). The name *M. primigenius minor* (GROMOW, 1929) applies to the later part of this supposed lineage. However, diminutive specimens that belong to *M. meridionalis* do exist, and for this reason the hypothetical emergence of the separate branch of small mammoths should have taken place during the Early Pleistocene, if not earlier. Examples are provided by M3 specimens from the Cromer Forest-bed Formation at Bacton in the NNHM collection (pers. obs.); for other specimens see Falconer 1868: 138-140 and references therein, as well as the length minimum of the Valdarno Superiore sample in Table 1. At least one posterior m3 fragment from the North Sea (Mol coll., not measured) belongs to a diminutive specimen.

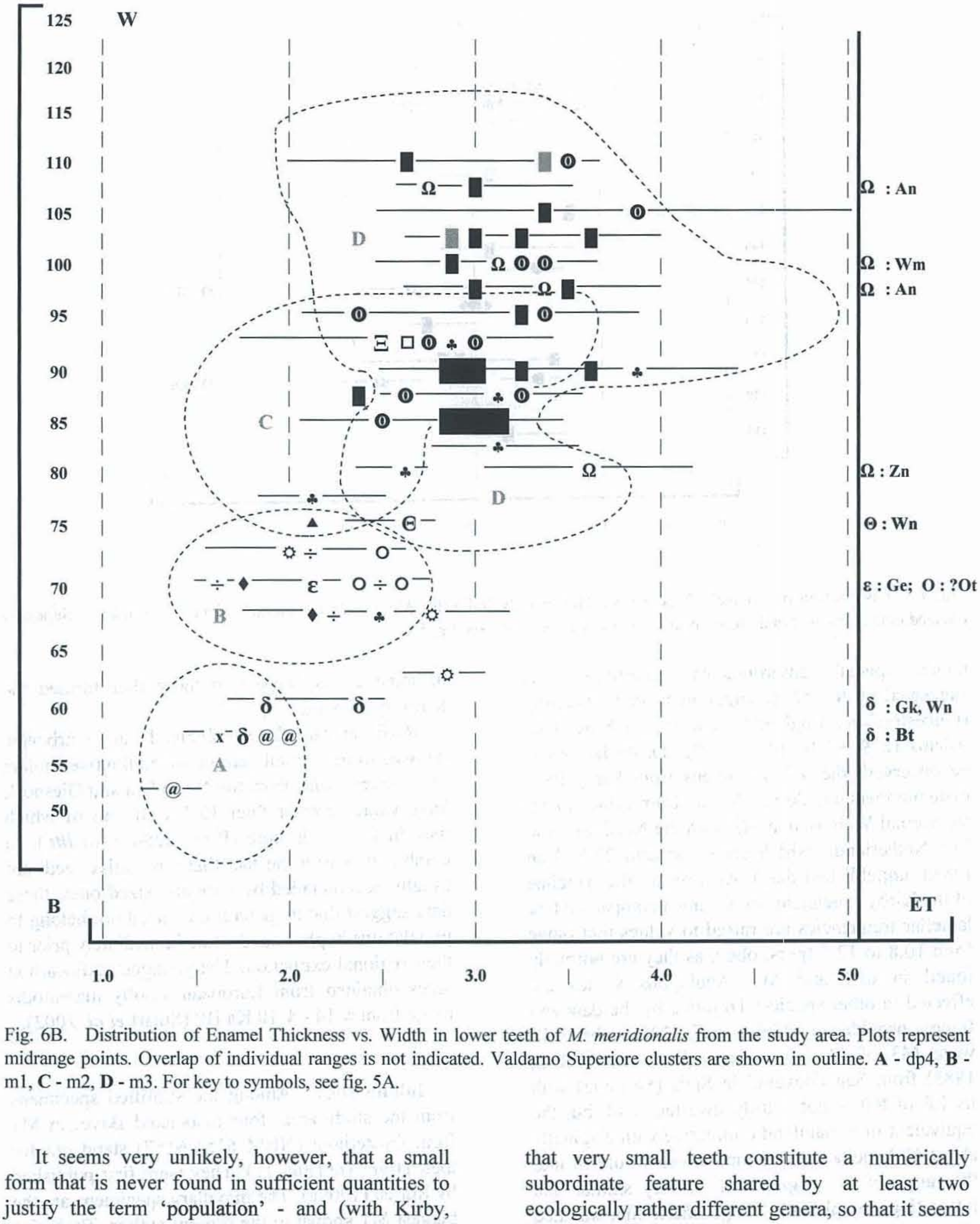

Fig. 6B. Distribution of Enamel Thickness vs. Width in lower teeth of *M. meridionalis* from the study area. Plots represent midrange points. Overlap of individual ranges is not indicated. Valdarno Superiore clusters are shown in outline. **A** - dp4, **B** - m1, **C** - m2, **D** - m3. For key to symbols, see fig. 5A.

It seems very unlikely, however, that a small form that is never found in sufficient quantities to justify the term 'population' - and (with Kirby, England, as the one exception: see below) always among normal to large specimens - should have accompanied the parent form through the entire Pleistocene and all its climatic vicissitudes to become extinct at the same time. By implication it would also have copied the transition between *M. meridionalis* and *M. trogontherii*, which is even more improbable.

On the other hand, the presence of diminutives in samples of the straight-tusked elephant shows that very small teeth constitute a numerically subordinate feature shared by at least two ecologically rather different genera, so that it seems likely that diminutives as a rule represent the lower end of the size range in any elephantid population. Apart from the lack of a definition that could separate them from the main stock, those are the reasons for including extremely small specimens in the observed ranges. The extremes are probably the result of genetic as well as nongenetic (e.g., ecophenotypical) variability. As such, the diminutive component of populations could have gained local and temporary numerical dominance

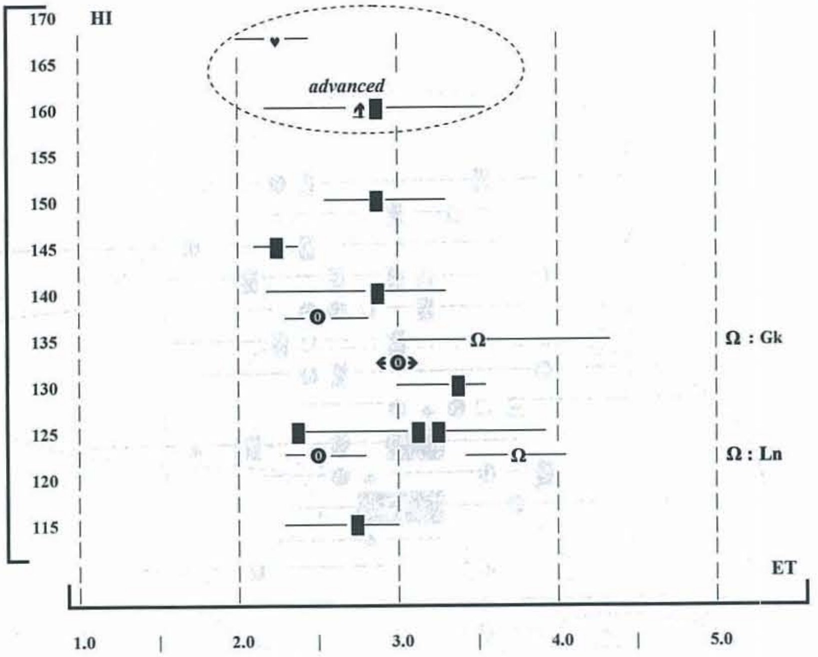

Fig. 7. Distribution of Enamel Thickness vs. Hypsodonty Index for M3 of *M. meridionalis* from the Valdarno Superiore (dashed cluster outline) and the study area. For key to symbols, see fig. 5A.

under special environmental conditions, as suggested by the *M. primigenius* teeth from Kirby (Leicestershire, England), kept in the SMC (see Adams 1879: 95 ff., pl. XIII, fig. 1). As far as can be observed, the M3 specimens from Kirby have plate numbers that do not deviate from values found for normal Weichselian M3 from the North Sea and The Netherlands, which cluster around 22.5 (Van Essen, unpublished data). As a result, the lamellae of the Kirby specimens are so much compacted that lamellar frequencies are raised to values that range from 10.8 to 12.5 (pers. obs.), as they are normally found in dP4 and M1. Analogous values are effected in other species: To judge by the data and figures provided by Melis *et al.* (2001), the well-worn M3 of *M. lamarmorae* (FORSYTH MAJOR, 1883) from San Giovanni in Sinis (Sardinia) with its LF of 8.0 is not a truly dwarfed tooth but the equivalent of a mainland diminutive with originally about 17 lamellae in 210 mm, which would fit into the range of *M. trogontherii*. A very similar and interesting complete *M. trogontherii* m3, situated abnormally high in a rather juvenile-looking mandible ramus from Ipswich (Suffolk, England) is in the Ipswich Natural History Museum (pers. obs.). Values around 6.5 are to be expected in diminutive *M. m. meridionalis* M3 (see also under 4). The small mammoths from Wrangel Island, which have been named *M. primigenius vrangeliensis* GARUTT, AVERIANOV et VARTANYAN, 1993, may represent individuals that lived under conditions comparable in some critical aspect to those that formed the Kirby specimens.

Radiocarbon dates obtained at Fairbanks, Alaska, from a small sample of diminutive molars of *M. primigenius* from the North Sea and Giesbeek have values greater than 30 Ka BP, all of which may in fact be infinite (R.D. Guthrie, *in litt.*). In combination with the fact that diminutive teeth are usually accompanied by normally-sized ones, these data suggest that in general they need not belong to populations in physical decline immediately prior to their regional extinction. The youngest radiocarbon dates obtained from European woolly mammoths range from ± 14 - ± 10 Ka BP (Stuart *et al.* 2002).

Inland sites - Among the stratified specimens from the study area, four associated Bavelian M1 from Oosterhout (NBM 6154-6157) stand out for their large size (Fig. 11). They were first published by Rutten (1909a). The maxillary specimens are the biggest M1 known to the present author. Their size (Table 5) is reflected by their low LF of 5.6. The lower jaw fragment with the corresponding m1 had an apparently well-developed rostrum that was broken off at its base. The individual was probably a robust young male, but since it was about the largest and certainly the latest of all robust young males within the compared samples, the teeth perhaps afford a glimpse of general size increase beyond sexual dimorphism.

The left M1 from Dorst (NAT RGM 85530), on the other hand, is strikingly small. It was recovered from sediments deposited during the Leerdam Interglacial, the second interglacial within the Bavelian Complex. The size of the tooth is equivalent to that of the smallest Valdarno M1. Its shape is that of the typical form, without a hint of an increased HI. Because of its length of at least 140 mm it is considered too big for even a large dP4. There is also an incomplete left m1 (NAT RGM 85531) from the same clay pit, and it is equally indistinguishable from the typical form. The data behind this observation are discussed under 3 (M1).

3 - Shape
(LWI, and HI in Tables 1-8; Figs. 8AB, 9, 10AB)

(1) All complete specimens from the study area fall within the Valdarno Superiore clusters. **(2)** Generally speaking there is little difference between upper and lower molars in HI values. **(3)** The fragmentary M3 from Dorst (Bavelian Complex) is outside the Valdarno Superiore cluster of M3 on the basis of its HI, which is ≥ 165 (its LWI position is an estimate). **(4)** The HI (176e) of the complete M3 of the early Middle Pleistocene *Mammuthus* sp. from Edersleben, Germany (Fig. 8A: 'En'), is of the same category as that of the Dorst specimen. **(5)** The HI of some m3 from the North Sea is below the lower range extreme of the Valdarno Superiore m3, whereas that of other specimens, including those from Oosterhout, is above it.

Length-Width Index - At the level of individuals, the LWI shows the relative lengthening of teeth from dP4/dp4 to M3/m3. Averages are somewhat lower in maxillary teeth (up to 40 index points in Valdarno M3) because differences in L between upper and lower elements are usually rather insignificant, whereas W in maxillary teeth tends to be greater than in mandibular ones. Ranges are so wide that for comparative purposes the LWI should preferably be represented by sample averages and standard deviations.

Hypsodonty Index - Along the tooth row, the HI averages of the available specimens of *M. meridionalis* show a distribution pattern that, at higher levels in the scale, is essentially repeated by Weichselian *M. primigenius* from the study area, especially with respect to lower teeth (Fig. 9). The *M. primigenius* M2 and M3 values are further removed from M1 and the upper milk molars than their *M. meridionalis* counterparts. A remarkable recurrent feature of the distribution is the high average HI of m1, which is probably a basic characteristic of the dentition of mammoths, or of all elephants. A similar overall distribution pattern for any evolutionary stage between *M. m. meridionalis* and *M. primigenius* is inferred. HI values from the study area plot outside the Valdarno Superiore range in M3 and m3 only and suggest the inclusion of some older and some younger specimens.

m3 (Fig. 10B) - Evolution of HI in *Mammuthus* m3 is rather slow and results in much overlap of ranges: The lower end of the range of Weichselian *M. primigenius* m3 from the study area even falls within that of *M. meridionalis* from the North Sea. The ranges are 130-200 (N: 30, mean : 161) and 134-190 (N: 15, mean : 163) respectively for the Giesbeek and North Sea *M. primigenius* samples (Van Essen, unpublished data). Within the cluster of Fig. 10, the about contemporaneous Valdarno Superiore and Oosterschelde ranges virtually coincide and correspond to a mere 11 points on the HI scale. The verticality of these clusters shows that the specimens are different in size, but hardly so in shape (HI).

North Sea - A much wider HI range, some 50 index points, and a generally inverse relation between W and HI is found for *M. meridionalis* teeth from the North Sea, which presumably indicates several overlapping ranges: The overall diagonality of the cluster signifies a clear decrease of W and variability or some increase of H. The Late Villafranchian teeth represent but a slice of this cluster. Where the HI is distinctly lower than in the Valdarno Superiore sample (e.g., < 120), the North Sea specimens have a 'primitive' appearance (e.g., Fig. 13). It is doubtful, however, whether such teeth have a somewhat greater age (on the assumption of some increase in HI during the Tiglian); they could just show a variability that by chance is lacking in the Italian sample.

The Valdarno Superiore and Oosterschelde HI ranges end between 130 and 135. The wide North Sea specimens in the top of that section may be considered as marginally advanced because they plot beyond the Valdarno Superiore and Oosterschelde samples in spite of their comparatively great width (which tends to lower the HI). The narrower specimens along the right cluster border occur in an area where a slightly advanced Bavelian m3 from Oosterhout is found, but no Italian or Oosterschelde specimen. They can be interpreted as a continuation of the cluster of large-sized advanced specimens. Their HI is higher mainly because they are narrower. Their H is variable. The narrowest specimens have cleft depths up to 57 mm (which provides an argument against referring these fragments to *M. trogontherii*) and may well correspond to advanced

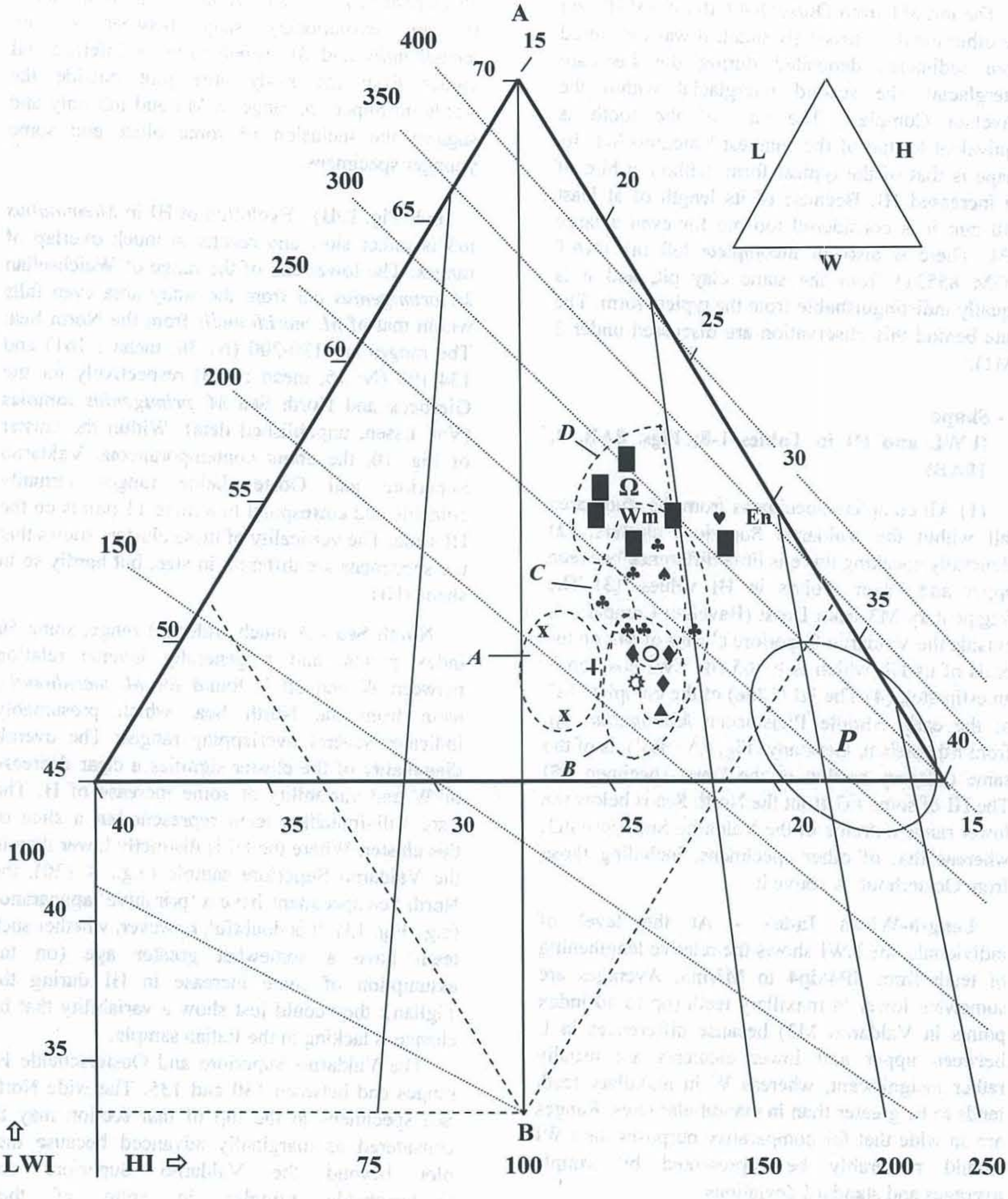

Fig. 8A. Bakhuis Roozeboom diagram for samples of (near-) complete dP4 - M3 of *M. meridionalis* from the Valdarno Superiore (dashed cluster outlines) and the study area (plots). The cluster outline of M3 of *M. primigenius* from Giesbeek (Fig. 1, 14) is added for comparison (*P*). **A** - dP4, **B** - M1, **C** - M2, **D** - M3. En - M3 of *Mammuthus* sp., skeleton from Edersleben, Spengler-Museum, Sangerhausen, GFR. For key to symbols, see fig. 5A.

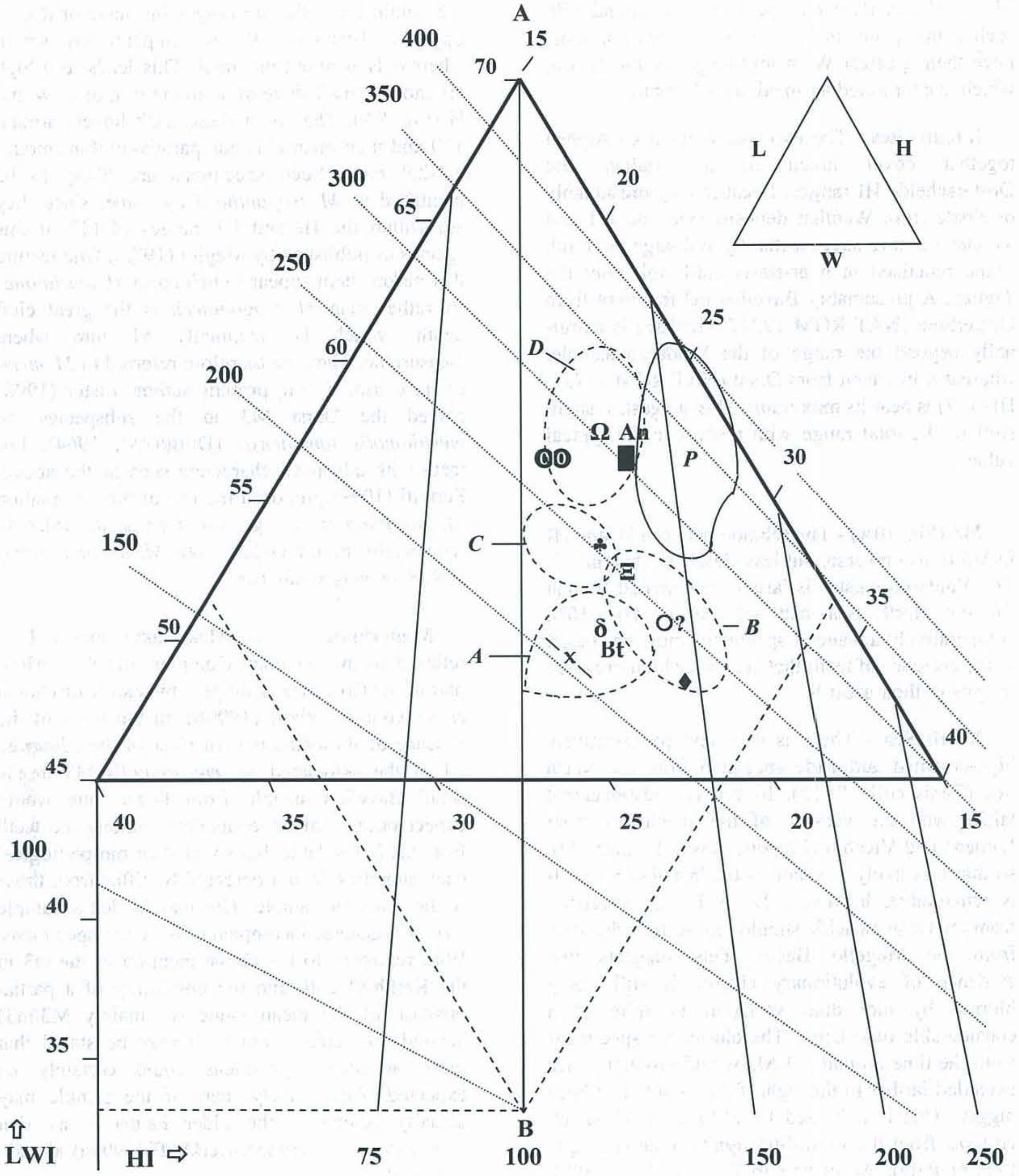

Fig. 8B. Bakhuis Roozeboom diagram for samples of (near-) complete dp4 - m3 of *M. meridionalis* from the Valdarno Superiore (dashed cluster outlines) and the study area (plots). The cluster outline of m3 of *M. primigenius* from Giesbeek (Fig. 1, 14) is added for comparison (p). **A** - dp4, **B** - m1, **C** - m2, **D** - m3. For key to symbols, see fig. 5A.

M3 of *M. meridionalis* ssp. with a HI around 170, such as the specimen from Dorst (see below). Some have their greatest W in mid-height of the crown, which is interpreted as an advanced feature.

Inland sites - The two specimens from Alphen together cover much of the Italian and Oosterschelde HI ranges. Because they presumably originate from Waalian deposits (see under 1 and 4), they seem to suggest that by and large the tooth shape remained in near-stasis until well after the Tiglian. A presumably Bavelian m3 fragment from Oosterhout (NAT RGM 12297; HI=136) is marginally beyond the range of the Valdarno sample, whereas a fragment from Dorst (NAT RGM 85794; HI=127) is near its maximum. This suggests a slight shift of the total range with respect to the typical values.

M3 (Fig. 10A) - The relation between W and HI in M3 is also inverse, but less clearly so than in m3. The Valdarno cluster is largely overlapped by that for the North Sea material. As in Fig. 10B, comparatively advanced specimens must be sought in the category of teeth that are rather high-crowned in spite of their great W.

North Sea - There is only one comparatively high-crowned and wide specimen from the North Sea (Tanis coll.; P=13). Its relative advancement tallies with the vicinity of the specimens from Lumena and Vícchio (Mugello Basin, Farneta FU), so that it is likely to relate to the Waalian Stage. It is remarkable, however, that a Tiglian specimen from the Oosterschelde should plot so near the teeth from the Mugello Basin. This suggests that evidence of evolutionary change is still easily blurred by individual variation in spite of a considerable time lapse. The cluster for specimens from the time around 1.4 Ma would probably have extended farther to the right if the sample had been bigger. This is indicated by M3/m3 of *M. m.* cf. *vestinus* from the Pietrafitta lignite mine (Perugia, Central Italy). According to Ferretti (1999: 507), the average W in M3/m3 is slightly smaller than in the Valdarno Superiore specimens, which influences the HI. An M3 from Pietrafitta measured by the present author has a HI of 159.

Inland sites/North Sea - The only specimens from the study area which are clearly beyond the range of the Italian sample occupy this position on the basis of their HI. A few fragmentary M3 are available: a pair from Dorst, an *in situ* find of Bavelian age (Van Kolfschoten 1990; Fig. 12), and three specimens from the North Sea (Mol coll., Mulder coll.). Both H and W of these specimens are within the Valdarno ranges but have drifted in opposite directions: W is comparatively small, whereas H is about maximal. This leads to a high HI and the small share of W in the sum of L, W and H (Fig. 8A). The HI of these teeth hovers around 170 and their enamel is comparatively thin (modes 2.4-2.9 mm). Such specimens are likely to be identified as *M. trogontherii* by some, since they are within the HI and ET ranges of M3 of this species as published by Maglio (1973). One feature that makes them appear to belong to *M. meridionalis* rather than *M. trogontherii* is the great cleft depth, which is maximally 51 mm where measurable. They are therefore referred to *M. meridionalis* ssp. by the present author. Lister (1998) placed the Dorst M3 in the subspecies *M. meridionalis tamanensis* (DUBROVO, 1964). For teeth with advanced characters such as the above, Ferretti (1999) proposed the use of the designation *M. meridionalis* ex gr. *tamanensis* in order to temporarily accommodate both *M. m. tamanensis* and *M. m. voigtstedtensis*.

Maasvlakte - The Maasvlakte Fauna I is referred to the Bavelian Complex and the earliest part of the Cromerian Complex by Van Kolfschoten & Vervoort-Kerkhoff (1999b) on the basis of the absence of *Allophaiomys*. In view of the advanced HI of the associated *M. meridionalis* M3 in the small Bavelian sample from Dorst, one would expect occasional HI equivalents among the teeth from the Maasvlakte, but so far their morphological characteristics do not perceptibly differ from those of the Valdarno sample. This may be due to sample size and general incompleteness of the specimens. With reference to the above mention of the m3 in the Kerkhoff coll. and the possibility of a partial increase of the mean value (of mainly M3/m3) beyond the Italian sample, it may be stated that more advanced specimens could certainly be expected. Alternatively, part of the sample may actually belong to the older Fauna 0, as Van Kolfschoten & Vervoort-Kerkhoff (1999a) already surmised.

Other European sites - An M3 (MCI 7644) from the early Middle Pleistocene Rio Pradella site (mentioned under 1) has a HI of 171/176 (inferred from Azzaroli 1977: 163/ Ferretti 1999: 508, table 3) and represents the same level of HI development. The material is interpreted as the first occurrence of *M. m.* ex gr. *tamanensis* in Italy (Slivia FU, 0.8 Ma)(Ferretti 1999: 513). The holotype of *M. m. voigtstedtensis* (M3, FSFQ 1965 / 3924/ Voi. 320) has an estimated HI of 171 (based on the hindmost lamella preserved) and therefore seems to be in the same category as the Dorst and Rio Pradella M3.

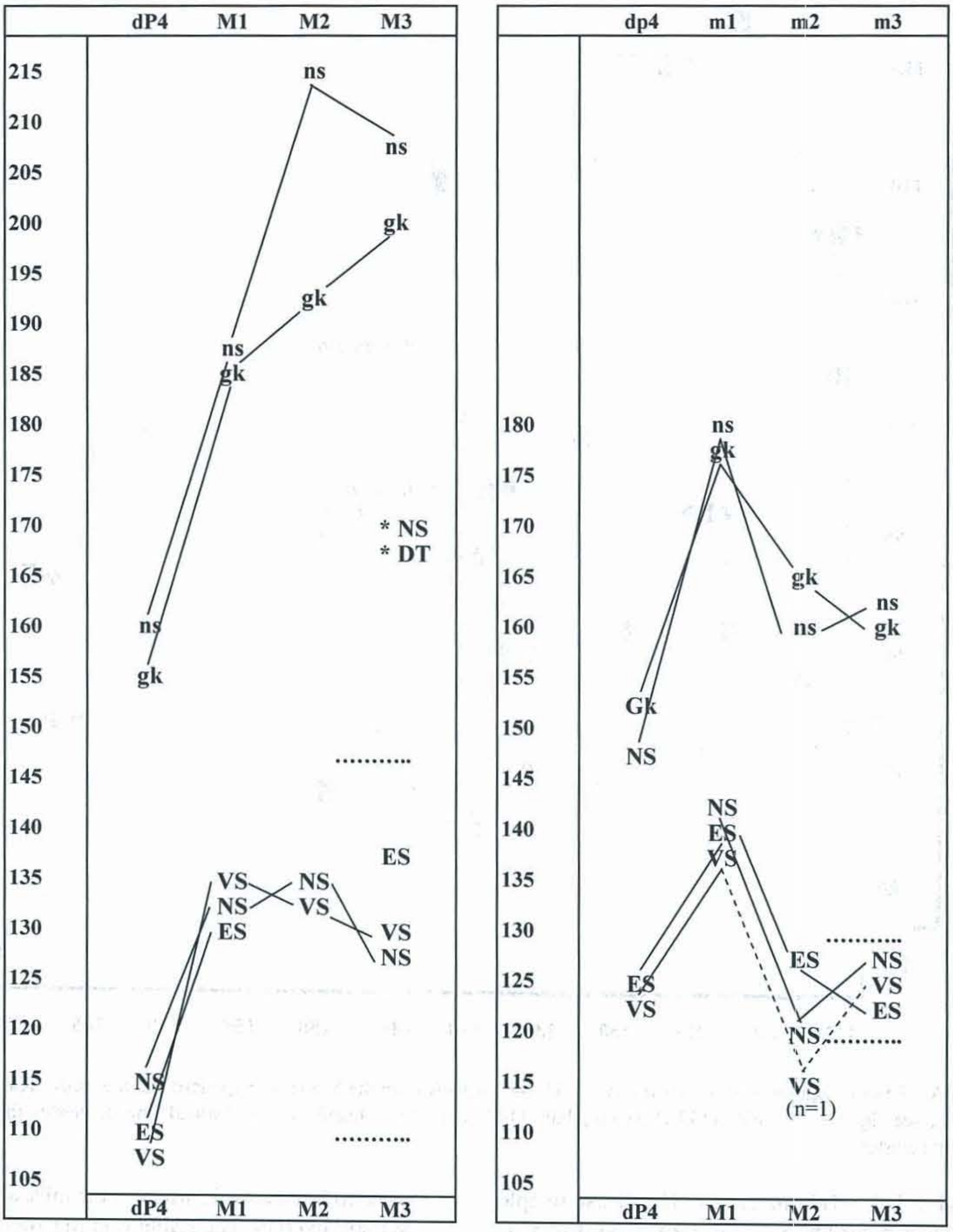

Fig. 9. Mean values of Hypsodonty Indexes of upper and lower teeth of *M. meridionalis* (upper case abbreviations) and *M. primigenius* (lower case abbreviations). **VS** - Valdarno Superiore, **NS/ns** - North Sea, **OS** - Oosterschelde, **gk** - Giesbeek, ***NS/*DT** - advanced M3 from the North Sea and Dorst. Dotted lines indicate observed ranges of Valdarno Superiore M3. Solid lines connect averages of one population; n *M. meridionalis* = 130, n *M. primigenius* = 235.

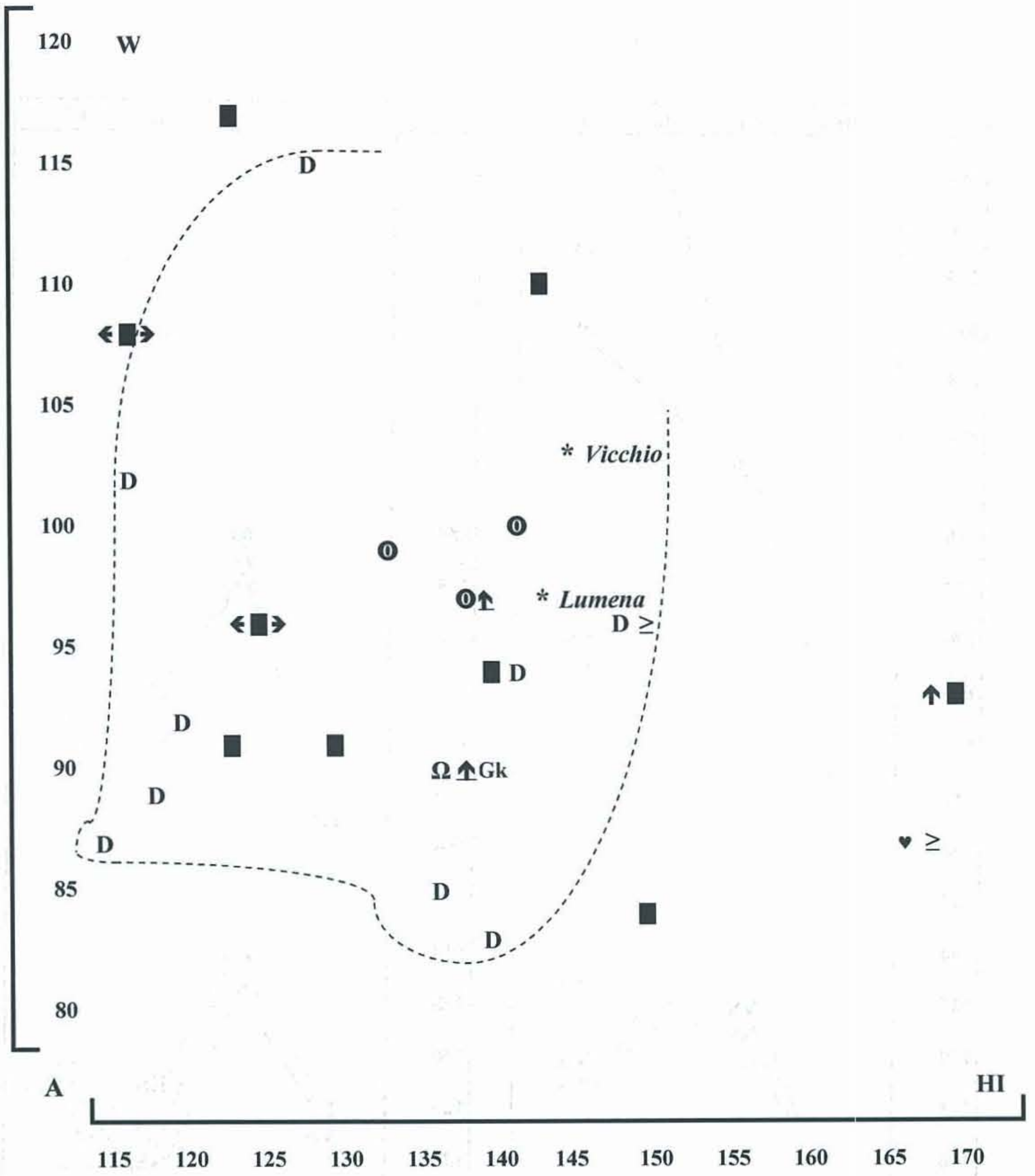

Fig. 10A. Scatter diagram of W vs. HI for M3 of *M. meridionalis* from the Valdarno Superiore and the study area. For key to symbols, see fig. 5A. * - IGF 1149 (Vícchio), IGF 1142 (Lumena), Mugello Basin. Dashed line delineates the Valdarno Superiore cluster.

M2 / M1 - Inland sites - The Dorst sample contains a fragmentary M2 d. (NAT RGM 85534) whose reconstructed HI is ≥ 150, i.e., equivalent to or beyond the upper extreme of the Valdarno sample and for this reason probably a morphological equivalent of the advanced Dorst M3. It bears no posterior pressure scar and therefore does not match the M3 d. NAT RGM 85536, which has a very pronounced anterior one. The specimen suggests that the Dorst sample as a whole is morphologically coherent and about centered on the edge of the Valdarno range in the sense that M3 and perhaps M2 at least in part have come to lie beyond it, whereas the milk dention and M1 still overlap. The stable P in M1 was explained in this way under 1. The Dorst sample could then be interpreted as near-equivalent to the HI level of *M. m. vestinus*. The somewhat older Oosterhout population, with its slightly advanced m3 mentioned above, did probably not experience the Linge Glacial, and in morphology may have remained virtually indistinguishable from the typical form. The small sample size of the Dorst and Oosterhout material precludes a definitive opinion on the degree of advancement in these groups.

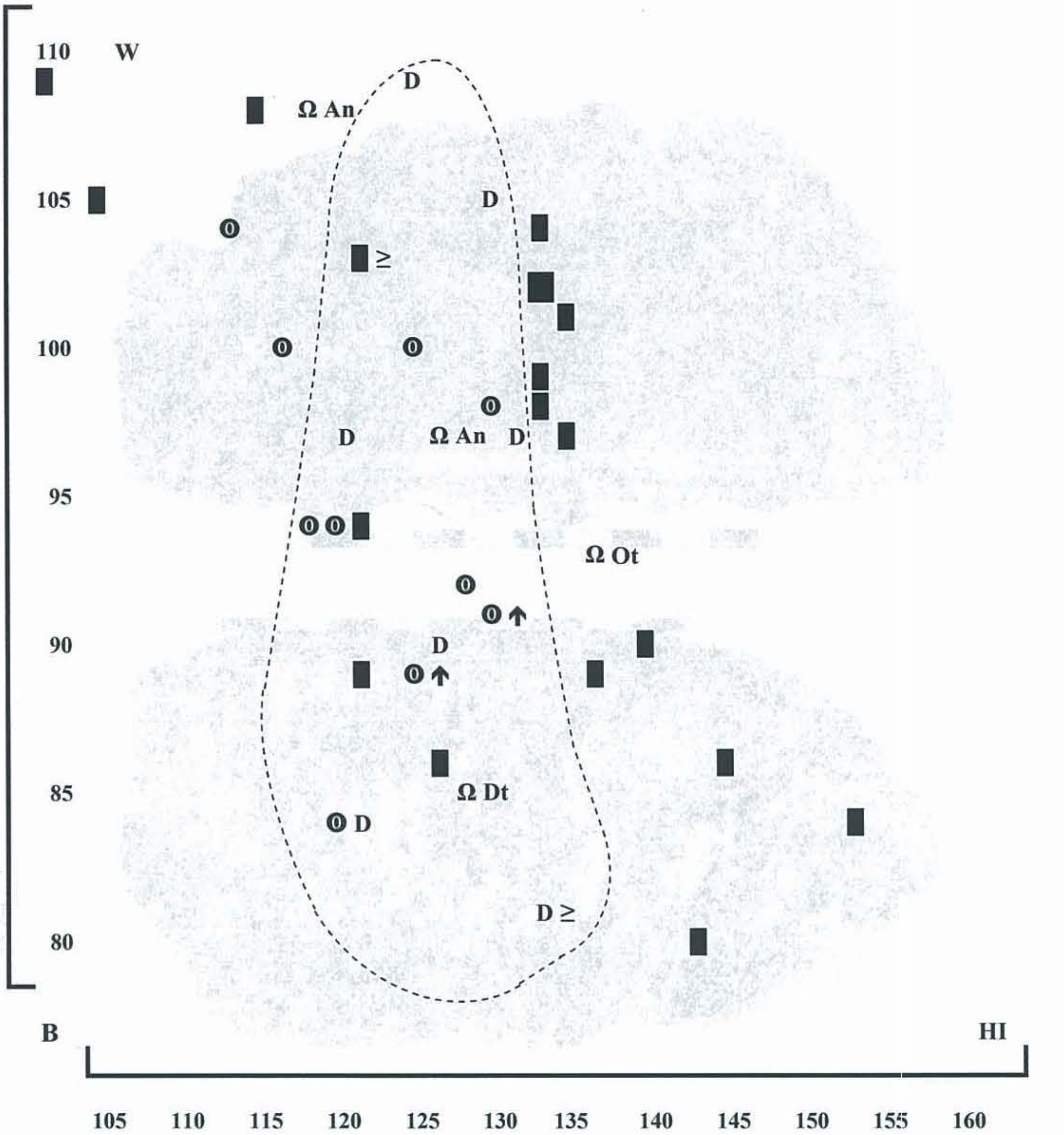

Fig. 10B. Scatter diagram of W vs. HI for m3 of *M. meridionalis* from the Valdarno Superiore and the study area. For key to Symbols, see fig. 5A. Dashed line delineates the Valdarno Superiore cluster.

4 - Lamellar frequency (LF in Tables 1-8; Figs. 5A & 5B)

(**1**) Upper teeth in general show an inverse relation between W (size) and LF. Within the M3 cluster, however, sections may be found where three to four specimens of different W have about the same LF. (**2**) Lower teeth also show a generally inverse relation, but the cluster of m3 as a whole is nearly circular, so that series may be found where LF has a normal relation to W. (**3**) The right border of the m3 cluster is lined by specimens from inland sites (An, Ot, Wm, Ln). The LF conveys information on different levels. With respect to populations it reflects adaptive changes over long periods of time, but it also relates to the individual size of specimens (Lister & Joysey 1992). The correlation between LF and size has already been touched upon, but there is more to it than a simple inverse relation, because the LF is ultimately defined by two factors. These are the available space in the jaw and the number of plates it is going to be filled with (relative to the evolutionary stage of the individual and the element in question). This is the cause of the rather weak correlation between size and LF. Combinations of P and space maxima result in various degrees of compaction of the plates, to which these - as well as the cement intervals -may respond by flattening. There will be combinations of small, normal, and large teeth with

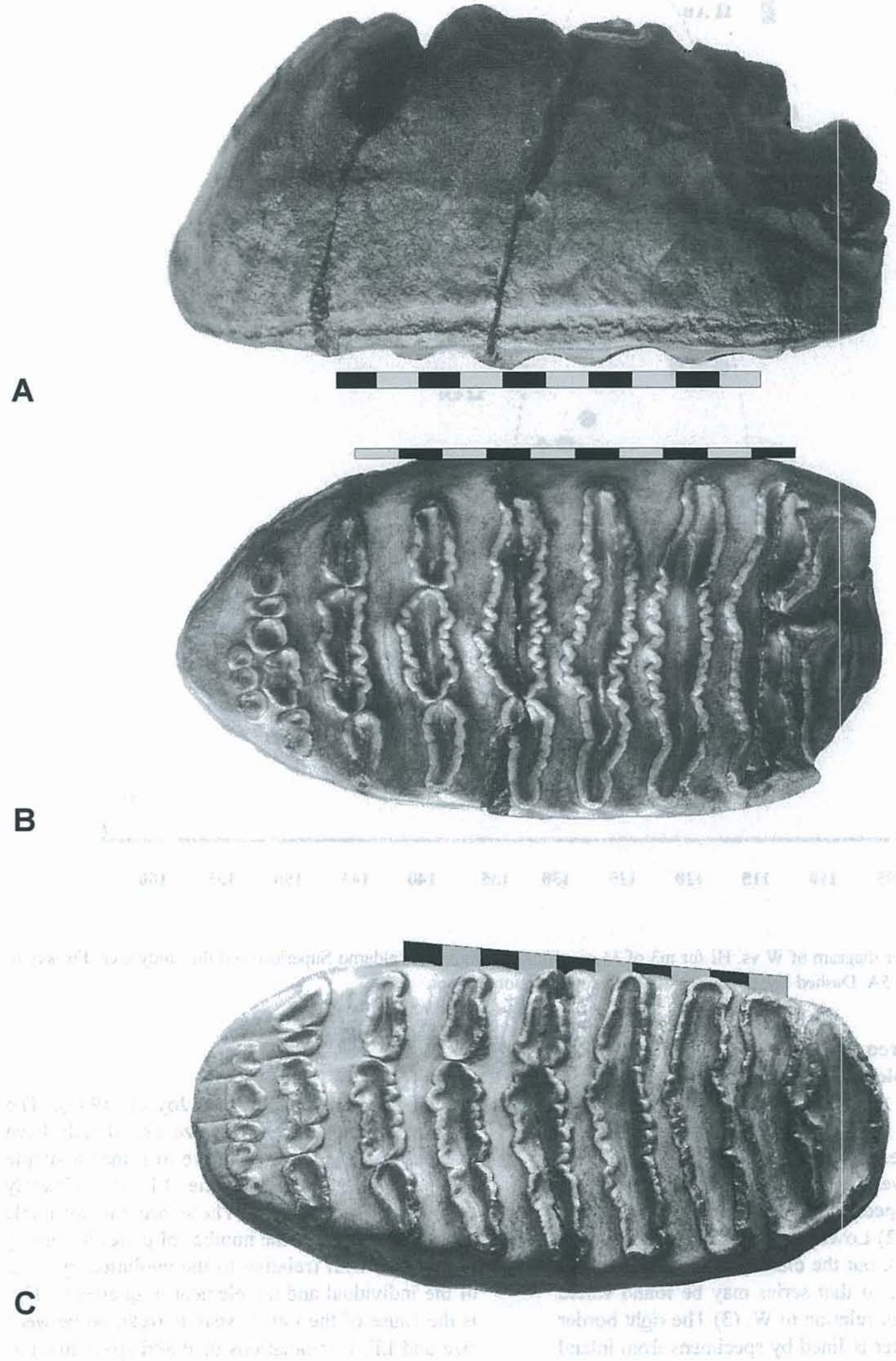

Fig. 11. *M. meridionalis* from Oosterhout (Bavelian Stage). Left M1 and m1 from a set of four belonging to one individual. Found in 1842. NBM nos. 6157 and 6154 respectively. A - M1, lingual view, B - M1, occlusal view, C - m1, occlusal view. Bar is 10 cm.

a relatively low, normal, or high P. Extremes are caused by [1] many plates in small teeth (that lead to a high LF, e.g., in diminutives of *M. primigenius*), and [2] few plates in large teeth (that lead to a low LF, e.g., in archaic forms of *Mammuthus*). [3] Few plates in small teeth (e.g., in diminutives of *M. meridionalis*), and [4] many plates in large teeth (e.g., in large M3/m3 of *M. primigenius*) are combinations that result in LF values that are respectively lower and higher than in [1] and [2]. An important deduction from these observations is that a certain degree of compaction may be caused by different Ps in different space maxima. If teeth are incomplete, the LF in itself therefore offers no direct clue with regard to the way in which it was influenced by P on the one hand and by the available space (size) on the other. The question whether fragments with the same LF are directly comparable with each other will have to be solved with the help of a reconstruction of P and size classification, in which W and morphological detail play a role.

In the more or less complete M3 from the Valdarno Superiore, pseudo-advanced LF values up to ± 6.5 occur because of small size (type [3]), whereas in large specimens they may drop to about 4.0 (type [2]). In m3 the lower range extreme is ± 3.8. Because of these effects, the ranges of all smaller samples tend to fall within these extremes in spite of the probable inclusion of some material that is younger than 1.8 Ma. A number of relatively advanced teeth become visible where comparatively high LF values are recorded in combination with indications of large size (a moderate version of type [4]).

Inland sites - Such large specimens with comparatively high LFs are found among M3/m3 from inland sites such as Alphen, Wessem, Giesbeek, and in part Groot Linden (Figs. 5AB, Tables 1 and 2), which tallies with what is known of their stratigraphical setting. Where measurable, their HI falls within the Valdarno range because of the great W involved. The LF value in the reconstructed Bavelian M3 fragment from Dorst (Figs. 5A and 12) is of an intermediate type ('slightly increased P in average space maximum') and probably would have passed for a minor P/size effect if the high HI of the specimen had not been known.

North Sea - Certain North Sea m3 specimens are large and also have a HI between 130 and 135 (the upper extreme of the Valdarno range). Because of this marginality and the increased tooth size, this group is strongly reminiscent of specimens from the Farneta FU in Italy and may belong to a Waalian (or even later?) group linked with the Yarmouth Roads Fm. The large majority of these more or less advanced specimens have their greatest W near the base of the crown, which betokens a partial morphological conservatism. In exceptional cases (Van der Steen coll. GL32A), the level of greatest W appears to have become less basal, as in a near-complete m3 of *M. m. voigtstedtensis* (FSFQ 1966/6764/Voi. 3558). Furthermore, this characteristic is common in the morphologically advanced species *M. trogontherii* and *M. primigenius* and it is therefore interpreted as a general indication of - presumably post-Waalian - advancement. In all of these cases, and sometimes probably due to a size effect, the LF falls within the range 4.5-5.5, i.e., around the Valdarno mean for m3. The LF by itself therefore does not allow distinction between the evolutionary stages of *M. meridionalis*. Even for the marginal specimens in the diagrams, the vicinity of Oosterschelde molars underscores that the evolution of dental characteristics between the Tiglian and the Waalian Stages was slow. Otherwise contamination of the supposedly Tiglian C3 Oosterschelde sample with TC5-6 or even post-Tiglian material would have to be assumed. In M3 the situation is similar, but the size of the small number of comparatively high-crowned specimens (HI > 140) is large enough to make the average LF value drop below the Valdarno mean (5.3). This could be regarded as circumstantial evidence for size increase after the Tiglian.

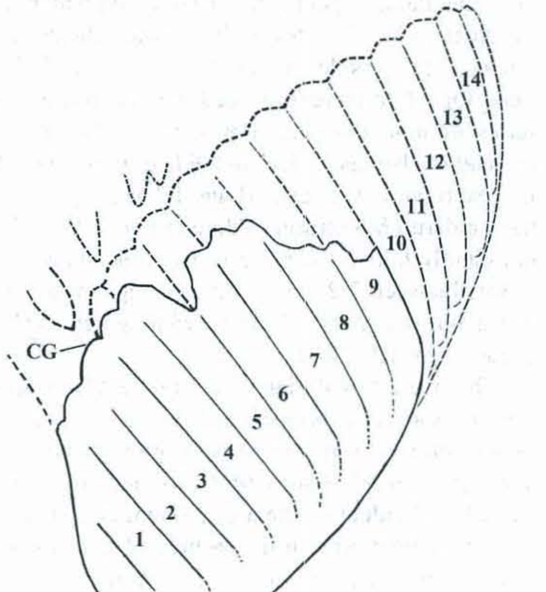

Fig. 12. *M. meridionalis* ssp., left M3 from Dorst (Bavelian Stage); NAT RGM 85541. Antero-medial portion and reconstruction of posterior part; **os** - occlusal surface; **cg** - cingulum.

Divergence Index - On the basis of LF values the Divergence Index (DI) was determined for *M. meridionalis* m3 samples from the Valdarno Superiore and the North Sea. The *M. primigenius* m3 sample from the study area was added for comparison. The averages are:

M. meridionalis (Valdarno Superiore) **120.1**
(N: 10; range:113-130; σ: 6.8; V: 0.057)
M. meridionalis (North Sea) **123.1**
(N: 9; range:103-150; σ: 13.6; V: 0.111)
M. primigenius (study area) **129.1**
(N: 26; range:108-152; σ: 12.1; V: 0.094)

The result seems to confirm the general increase of basal divergence in m3 and the presence of some relatively advanced specimens in the rather variable North Sea *M. meridionalis* sample, which also has a wider range than the Valdarno sample. Because of the almost total overlap of species ranges (103-150 for all *M. meridionalis*, 108-152 for all *M. primigenius*) it is evident that the interpretation of single specimens with regard to any level of advancement is precluded. However, the DI may still be useful for descriptive purposes.

5 - Enamel thickness
(Tables 9-16; Figs. 6AB & 7)

(**1**) Virtually all measurements of ET on specimens from the study area fall within the analogous Valdarno Superiore clusters. A dp4 from Wychen, two m1 from the Oosterschelde, as well as two m2 from the North Sea have thicker enamel than the Italian specimens. Two individual range extremes of m3 - from the Oosterschelde and Zoelen - lie outside the Valdarno cluster. (**2**) The trend for ET to increase throughout the entire tooth series of individuals is shown. (**3**) In M3/m3 the correlation between size and ET is weak. (**4**) An inverse relation between HI and ET is suggested by the Valdarno M3 cluster outline in Fig. 7, but this is not clearly borne out by teeth from the study area, values between 2.2 and 3.0 mm being spread over just about the entire HI range, while greater values occur below HI ± 140.

The overall evolution of ET in the *Mammuthus* lineage shows a decrease of values and in *M. primigenius* M3/m3 reaches a point where the average *M. meridionalis* M3/m3 values have been halved. Individual maxima of 5.0 mm or just below seem to appear only in the earliest *M. meridionalis* M3/m3 samples, e.g., in an M3 from Le Strette (near Péccioli, Valdarno Inferiore, IGF 13093), in the Chilhac skulls (Boeuf 1983: 194) as well as in Oosterschelde and Valdarno Superiore specimens, and in a recently found m3 fragment from Giesbeek (ac 586; Fig. 1: 14). With its HI of ± 103 and a LF of 4.49 the latter suggests that some of the reworked inland specimens from Middle to Late Pleistocene formations originated from Tiglian deposits within the ice-pushed ridges later levelled by the river Rhine. A general decrease, however, is hard to trace among intraspecific ET values of *M. meridionalis*. Moreover, there is a slight trend towards increase with individual size: The M3/m3 clusters present themselves as a continuation of the trend for ET to increase throughout the entire tooth series, whereas the relatively oldest specimens (from the Oosterschelde) are to be found in any part of the ET range (see especially Fig. 6B). On the other hand, per element of the dentition the overall trend is more often broken by groups that show an inverse relation, e.g., in the top of the Valdarno m3 cluster, where one of the widest specimens has the lowest ET value, and the highest ET value is reached by a specimen of average W. The relation between ET and size is therefore of an unpredictable nature.

ET was plotted against the HI of M3 (Fig. 7) in order to test for the inverse relation that becomes apparent on the wider generic scale. The Tiglian Oosterschelde material is scattered through the lower HI / thinner ET section of the diagram, so that there seems to be no gradual development towards, but merely a more or less sudden and possibly selective confinement to the lower ET values, which is then maintained into the phase of the advanced North Sea and Dorst specimens. Modal values higher than 3.0 seemingly disappear above HI=135, i.e., in a narrowing type of tooth, but are known to occur in advanced teeth from outside the study area (in *M. m. voigtstedtensis*; see below). Sample size and a more or less stable ET within a range of about 30 HI points do not allow the underpinning of supposed Waalian and Bavelian subgroups in terms of ET.

The occurrence of Late Villafranchian (Valdarno and Oosterschelde) specimens with - for *M. meridionalis* - sometimes downright thin enamel is in itself interesting, e.g.:

tooth	loc.	P	HI	ET min.-max.	collection
M3	VS	13	147	2.2-2.9	NHMB V.A. 796
M3	VS	13	141	1.5, talon	NHMB V.A. 2277
m3	VS	12	-	1.9-2.5	NHMB V.A. 2277 (from different indiv.)
M3	OS	-	-	2.4-2.8	NAT RGM 401346
M2	OS	-	136	1.9-2.3	NAT RGM 172062

The thin enamel of such specimens does not automatically mean that they are small, and analogous finds from the North Sea and elsewhere are fairly common. They may be the result of plain variability that could have become the subject of later selection.

Inland sites - Bavelian specimens that have already been mentioned because they are characterized by unaltered P and HI, add an about typical ET to this feature list with the midrange values 2.95 (in m3 NAT RGM 85794 from Dorst), 1.75 (in M1 NAT RGM 85530 from Dorst), 2.05/2.2 (in M1 NBM 6157/6155 from Oosterhout), and 2.3 (in m1 NAT RGM 85531 from Dorst). The modal value 2.5 characterizes the M2 NAT RGM 85534 from Dorst, which has a slightly increased HI. In comparison, the 2.25/2.3 mm measured in the advanced M3 (NAT RGM 85541/85536) from Dorst seems a rather low figure, but in view of the low Tiglian values listed above it is acceptable for a tooth that belongs to the same population.

In the majority of advanced M3 of about 1.0-0.7 Ma, modal ET values range from 2.3 to 2.6 mm (Dorst, Rio Pradella (Ferretti 1999), Edersleben, Voigtstedt holotype). The modal ET in the Voigtstedt m3 FSFQ 1966/6764 /Voi. 3558 is 2.6, its range 2.3-3.2 mm. The M3 range, however, is appreciably widened by a large specimen from Voigtstedt (SMS Voi. 2403: min. 2.2, mod. 3.3, max. 3.7 mm; figured by Dietrich 1965: 532, Taf. XXXIV). This value possibly relates to its position in the upper section of the size range (W ≥ 105), but still the specimen testifies to the persistence of typical ET values in at least *M. m. voigtstedtensis*, probably with a shift in emphasis to the area around 2.5 mm.

On the whole, evolutionary changes in ET of *M. meridionalis* barely suffice to separate the typical form from advanced subspecies, to which end a combination with the HI is needed. The general impression is that ET is weakly correlated with tooth size, but the link between tooth size and body size is again too vague for sexual dimorphism to become evident in ET.

Foronova & Zudin (1999) discuss the Eurasian mammoth lineage in terms of adaptive peaks in ET, which they consider as nuclei of autochthonous speciation. Thin- and thick-enamelled phenotypes are discerned and interpreted as adaptations to periglacial and interglacial environments respectively. This phenotypical dichotomy is also attributed to *M. meridionalis* (*ibid.*: 113). The species lived through at least four cold stages - Tiglian TC4c, Eburonian, Menapian, and intra-Bavelian - and, if populations remained within their sphere of influence even in more southern regions, may at every occasion have begun to develop adaptive traits. Characteristics of 'cold' phenotypes (relatively high HI, long cement intervals, narrow plates, and weakly folded, thin enamel) and their 'warm' counterparts (relatively low HI, wide plates, strongly folded, thick enamel, and more median sinuses) are, of course, recognizable within the samples compared, but never combined in single specimens that could be grouped accordingly. In smaller samples as well as in cases of mixed character combinations, it will be hard to distinguish between individual / sexual variability and variability that was favoured by selection, so that for the time being ET seems to be among the least distinctive characters in individual teeth.

Mammoths in a time of transition

In the HI of M3/m3, and possibly also in that of M2/m2, the small Oosterhout and Dorst samples as well as some specimens from the North Sea apparently hardly evolved beyond *M. m. vestinus* and its equivalents, if at all, whereas M1/m1 - and presumably the milk dentition - retained values that render them indistinguishable from the Valdarno specimens in the analogous ranges. Contemporaneous and early Middle Pleistocene samples in most cases are regrettably hardly bigger, but interesting because they encompass the transition from *M. meridionalis* to *M. trogontherii*. Within the study area, no *in situ* finds of *M. trogontherii* have so far been made, and indeed the dental remains of this species are the rarest here even among the unstratified material. As indicated under "Characteristics of preservation" above, *M. trogontherii* and *M. meridionalis* from the North Sea do not differ in the degree to which they are mineralized. Since this circumstance in itself cannot prove that the two species overlapped in time, or whether they at one time lived in a shared biotope or not, the situation in the rest of Europe becomes important.

A late Early Pleistocene migration into Europe of a mammoth form that by 1.2-0.8 Ma had developed a *M. trogontherii*-like dental morphology under permafrost conditions in NE Siberia was substantiated by Lister & Sher (2001). They interpret the morphological variability (including mosaic specimens) and sometimes bimodality of European samples between 1.0 and 0.5 Ma as indicative of incomplete reproductive isolation of the resident and incoming populations. Their European sample group with an age of ± 1.0 Ma includes the eastern European locality Taman', where P and HI are clearly bimodal and signal the arrival of the immigrants, whereas contemporaneous western European samples such as that from St.-Prest (*M. m. depereti*) are said to have remained "at a primitive *M. meridionalis* level" (*ibid.*: 1096). Within this frame of reference, the contemporaneous Oosterhout sample clearly constitutes an analogue of the St.-Prest population in the sense that it appears as a minor extension of the *M. m. meridionalis* - *M. m. vestinus* line at most, apparently neither geographically nor genetically reached by *M. trogontherii*-like immigrants from the East.

A dP4 from Untermassfeld (Thuringia, GFR; ± 1.0 Ma) was described by Dubrovo (2001). According to Dr. Dubrovo, the specimen (FSFQ 1984 / 20052 / Mei. 19572) belongs to *M. trogontherii* and is a dp4. This, however, does not tally with the buccal position of the first root, which is partly outlined by a dentine ridge: In a lower molar it would have been centered on the median line. The relative shortness of the crown (LWI=174) also speaks for dP4. Instead of 9 x (Dubrovo 2001), the present author recorded x 8 (x) as the plate formula, because at the basal level there are eight main extensions of the pulpal cavity into the crown, the first and the last of which branch at a more apical level to form the talons. When compared with the Valdarno Superiore *M. m. meridionalis* sample, the specimen falls within the range extremes of W and H, but is equivalent to the upper end of the range in P (8) and HI (115). Its L (108.5) is slightly below the Valdarno range and has its effect on the LF (8.54), which is slightly beyond it. (The measurements given in the text are by the present author). The specimen probably represents a *M. meridionalis* subspecies with a level of advancement hardly at all beyond that of the typical form, just as the about contemporaneous material from Oosterhout.

A second group, with an age of ± 0.8 Ma, comprises the samples of Dorst, Rio Pradella, Dorn-Dürkheim 3 (southern Mainz Basin, GFR), and possibly Kärlich (Unit Ba; Neuwied Basin, GFR). The first two of these contain *M. meridionalis*, apparently a form interpretable along the same lines as the Oosterhout sample, but the German sites at this level are reported to contain teeth of *M. trogontherii* only (Van Kolfschoten & Turner 1996; Franzen *et al.* 2000). The provisionally reported occurrence of *M. meridionalis* within the Kärlich Unit F (Van Kolfschoten & Turner 1996) is not borne out by the morphological data. In stark contrast with the single tooth fragment attributed to the Kärlich Unit Ba, 250 specimens were recovered at Dorn-Dürkheim. The Kärlich specimen was collected by the late Mr. Konrad Würges, who insisted that the unit it originated from was Ba. It is now uncertain whether this was reported fact or interpretation of a loose find (E. Turner, pers. comm.), so that this site regrettably does not provide hard evidence and is kept out of the discussion. The Dorn-Dürkheim specimens are in a bad state of preservation, and only 10% of them have so far been prepared. According to the present author, the data published by Franzen *et al.* (2000) corroborate their interpretation.

Although the correlation of Dorn-Dürkheim 3 with the subdivision of the Pleistocene is not fully understood, palaeomagnetism indicates a level below the Matuyama-Brunhes boundary (Franzen *et al.* 2000). The cryoturbation that occurs at Dorn-Dürkheim 3 could be consistent with some phase of the Dorst Glacial (latest Bavelian), that followed the Leerdam Interglacial. The *M. meridionalis* subspecies at Rio Pradella (northern Italy), dated to the same time level (Ferretti 1999), is morphologically indistinguishable from the Dorst material.

The three sites mentioned above seem to suggest contemporaneity, but also - presumably environment-related - mutual exclusiveness of the two mammoth species in Europe around ± 0.8 Ma. However, more material is needed for this matter to be decided.

A third group, with an age of ± 0.7 Ma, relates to various stages within the Cromerian Complex. It is constituted by the Thuringian samples of Edersleben and Voigtstedt. As indicated above, the specific identity of the skeleton from Edersleben is subject to debate. In P, HI, and ET its M3 is very similar to that from Dorst and therefore might represent *M. meridionalis*. There are two other M3 specimens (SMS III/57/2752a+b). Both are much worn but probably do not belong to the same maxilla, since their modal ET varies from 2.3 to 2.8. In preservation and morphological detail these specimens are reminiscent of the holotype of *M. m. voigtstedtensis*. Within the small sample of mammoth teeth from nearby Voigtstedt there are two groups that clearly differ in their sediment-related preservation: The reddish subsample includes the holotype of *M. m. voigtstedtensis*. A complete M1 (FSFQ 1965/3776/Voi. 1820; Dietrich 1965: 529, pl. XXXII, fig. 7) and a much worn M2 (FSFQ 1965 /3823 / Voi. 2245; Dietrich 1965: 531, pl. XXXII, figs. 5, 6) are pale to dark grey brown and grey. These two plus an extremely worn specimen (Voi. 2230) constitute the second group. According to Dietrich (1965: 528), who referred all specimens to his new subspecies, this difference has no chronological meaning for finds from the 'Hauptfundschicht', but merely relates to the circumstance that the strata were disturbed (possibly through cryoturbation), and to the length of the period the specimens were still covered by bone tissue. In arguing thus, he seemingly ignored the effects of cryoturbation on fossiliferous strata and overlooked the fact that occlusal surfaces are not covered by bone tissue. He also made contradictory statements with regard to the M1, which was counted among the finds from the 'Hauptfundschicht' (*ibid.*: 524), but was later described as being bare of sediment, so that the layer it originated from was uncertain (*ibid.*: 529).

From the morphological point of view there are some difficulties: The rather high-crowned M1 (HI=167.) is indistinguishable from specimens that belong to *M. trogontherii*, but on the other hand might match the holotype of *M. m. voigtstedtensis* (HI≈170.) because an approximate equality in HI between M1 and M3 is found in the typical form (Fig. 9). In the more advanced taxa *M. trogontherii* (Maglio 1973: 59) and *M. primigenius* (Fig. 9) the average M1 value stays behind that of M3. The relation between the individual M1 and M3 from Dorst and Voigtstedt is clearly not identical (136e - ≥ 165e / 167-170e respectively), so that the Voigtstedt M1 appears as a considerable leap forward, but since neither the M1 nor the M3 HI ranges at these particular levels are known, not much can be said about the mutual (in-) compatibility of the difference. Although a referral of the M1 to *M. trogontherii* cannot be proved, it is likely with regard to the M2, which in spite of the basally convergent plates must have had a LF of nearly 10 when complete. Its P would have amounted to ± 16 in ± 180 mm. In these features it is even primigenioid, so that there is a clear symmetry break with respect to the holotype of *M. m. voigtstedtensis* (M3; LF ± 6.50, P ± 15-17).

All in all, there are reasons for severe doubt about the homogeneity of the group of teeth that alledgedly originated from the 'Hauptfundschicht'. If all specimens should indeed have formed a coherent sample, the morphological variability could be due to some genetic input from more advanced Siberian immigrants as suggested by Lister & Sher (2001). Alternatively, an *in situ* mix of faunal remains could have occurred in a similar way as at Dorn-Dürkheim 3, where *M. trogontherii* molars sank into the Upper Miocene Dorn-Dürkheim Fm. (Franzen *et al.* 2000). The fact that the two morphologically more or less aberrant specimens also differ in their preservational characteristics speaks for the latter possibility. In addition, the exquisite state of preservation of the M1 and M2 suggests that they were embedded in clay rather than in sand or gravel. Several strata of such description are found directly above the 'Hauptfundschicht', in the lower part of section IV (the so-called 'Lehmschichten'; Krutzsch 1965). The 'Tonbank 1' (t_1) and part of the banded clays on top, within which a change from interglacial to boreal and lastly subarctic conditions within 2 m is indicated by pollen (Erd 1965: 266), are the lowermost deposits of this group. Large molars from t_3 that belong to '*Elephas*' were mentioned by Krutzsch (1965: 242). Gravels above the 'Hauptfundschicht' yielded a mandible fragment with a partial m3 referred to *M. trogontherii* (Dietrich 1965: 533). It seems possible therefore that the Voigtstedt sample documents the alternating presence of two taxa that preferred different environments, i.e., climatic conditions, however short the interval(s) between them may have been.

Both advanced *M. meridionalis* and *M. trogontherii* are known from the North Sea, so that stratigraphical proximity of these species may be possible there in view of the situation at Voigtstedt, but at present this is beyond proof. Because sample sizes in most cases are very small, interpretations are necessarily tentative and in need of more material from unambiguously dated sites. The preliminary concept based on the data discussed is as follows: During cold stages, *M. trogontherii* probably made incursions into all parts of Europe that suited its needs, perhaps meeting *M. meridionalis* in climatically transitional times until the latter became extinct. Bimodality in samples is therefore likely to have been caused mainly by small differences between the taxa with regard to the time of occupation of a certain region.

Fig. 13. *M. meridionalis* from the North Sea. Fragment of right m3, ac163. Posterior view of fractured lamella in mid-crown area. Bar is 5 cm.

Summary and conclusions

Morphological traits

Plate number - The evolution of the plate number in western European *M. m. meridionalis* was slow. In combination with European evidence from outside the study area, the samples studied suggest a slow shift in emphasis between the Middle/Late Tiglian and the Bavelian (1.9-1.0 Ma; P=12-14 to 13-15 in M3). During the early Middle Pleistocene, one or two lamellae more were possibly achieved (*M. m. voigtstedtensis*). The plate number of comparatively high-crowned, so-called 'advanced' specimens of Bavelian and later age appears to be the result of a continuation of the development within *M. m. meridionalis*. Because of the slow range shift, a relation between plate number and geological age cannot be established within smaller unstratified samples. Early Pleistocene cold stages in Europe apparently had a limited effect on the number of plates, presumably because they were intermittent and not very severe, and their onset could have been followed by migrations to the South, where some interbreeding with populations under less selective pressure may have taken place.

Size - There is evidence for average dental size increase within Late Villafranchian stocks of *M. m. meridionalis* in Italy and England (Lister & van Essen, unpublished data). By analogy, the same shift is expected to have taken place in the study area, where some specimens known to be of post-Tiglian age are particularly large, such as the Bavelian associated M1 from Oosterhout. Recognizable candidates for a post-Tiglian (Waalian/Bavelian/Cromerian) subgroup display large size in combination with an increased lamellar frequency and a comparatively high hypsodonty index. Small to diminutive specimens constitute the lower end of the size range of elephantid populations all through the Pleistocene. Small size alone provides no argument for interpreting them as either the first or the last representatives of their species, or as a separate branch of mammoths.

Shape - A post-Tiglian rise in hypsodonty index is indicated by M3/m3 from the study area. It is mainly based on a decrease of width, but somewhat blurred by variable height values. An M3 from a Bavelian site at Dorst is advanced because of its hypsodonty index (± 170.), which it shares with several other M3 of late Early and early Middle Pleistocene age in Germany and Italy, as well as with some North Sea specimens. At this evolutionary level the hypsodonty index of M3 provides a better contrast with earlier stages than its number of plates. Bavelian M1 from Oosterhout and Dorst are in no way morphologically advanced beyond the Valdarno sample and in combination with the M3 value suggest a partial increase of the mean in this population, mainly borne by M3. In this interpretation the advanced M3 hypsodonty indexes around 170./175. appear as continuations of the development within *M. m. meridionalis*, intermediate populations in Italy having reached values of at least 160. (Pietrafitta; Farneta FU). A comparatively high average hypsodonty index of m1 is shared by *M. m. meridionalis* and *M. primigenius* and may be regarded as an inherent characteristic of presumably all mammoths and possibly all elephants, rather than as an indication of advancement.

Lamellar frequency - Because of the generally inverse relation between size and lamellar frequency, teeth with a comparatively high lamellar frequency in spite of their large size signal relative advancement. On this basis a number of large specimens from the study area are considered as post-Tiglian.

Enamel thickness - Individual maxima of 5.0 mm in M3/m3 samples from the study area are considered as indications of Tiglian age, but the large number of intermediate values found for Late Villafranchian *M. m. meridionalis* in general are not suitable as a means to distinguish between earlier and later forms, the pattern of extremes and mean values generally being too uniform. A weak correlation between tooth size and enamel thickness is suggested by the samples studied. The range extremes of enamel thickness in the early Middle Pleistocene *M. m. voigtstedtensis* appear to be not much different from those in the Late Villafranchian form, but an adaptive lowering of the average value in the German sample is likely. As distinctive morphological features are mixed in individual teeth from the northwestern European samples studied, possible adaptive thinning and thickening of the enamel under the influence of periglacial and interglacial conditions respectively (Foronova & Zudin 1999) does not become apparent here.

Geographical distribution

North Sea (southern bight) - This material forms the largest subsample from the study area. The presence of *M. meridionalis* during at least the Tiglian C3, the Tiglian C5-6, the Waalian, and the Bavelian (Middle/Late Villafranchian to Early Galerian) is suggested. Sample size and distribution of characters do not allow the unambiguous identification of cold-stage phenotypes. A few rather high-crowned M3/m3 equivalent to the subspecific M3 from Dorst (Bavelian Complex, Leerdam Interglacial) occur. They could indicate an initiated autochthonous response to cold-stage conditions, although sample size does not allow a check on all characters supposed to relate to periglacial conditions.

Oosterschelde - The terrestrial Oosterschelde assemblage may or may not be composite (TC3 + TC5-6). The presence of *A. arvernensis* tallies with a TC3 age, whereas some comparatively primitive features (plate number and enamel thickness) in m3 of *M. meridionalis* are likewise found in the Valdarno Superiore sample and could therefore also imply a later Tiglian age (TC5-6), which is that of the local Tegelen Fm. Signs of weathering may link some specimens with an erosional phase (TC4c?) that removed the deposits of TC3 age likely to have originally contained them.

Maasvlakte - The Maasvlakte specimens are morphologically indistinguishable from *M. m. meridionalis* from the Valdarno Superiore. Only one m3 merely hints at the possibility that it could be of post-Tiglian age. The absence of truly advanced traits may be largely due to the fragmentary state of most finds, but could also imply that the teeth at least in part relate to the stratigraphical hiatus between the Tiglian and the Bavelian to which Van Kolfschoten & Vervoort-Kerkhoff (1999) refer their Fauna 0.

Inland sites - The four associated Bavelian M1 from Oosterhout are of very large size but in morphological detail do not differ from Valdarno M1. In hypsodonty index, an m3 fragment is marginally advanced beyond the corresponding Valdarno range. The sample is interpreted as coherent and presumably not advanced beyond the level of subspecies such as *M. m. vestinus*.

The Dorst sample includes somewhat advanced M2 and M3, whereas all other specimens of the sample and particularly M1 are indistinguishable from the Valdarno material. This ambiguity is likewise interpreted as a partial increase of mean values with respect to previous forms, in the sense that ontogenetically earlier elements of the dentition - especially the milk molars - have a lesser potential for absolute change than the teeth that come after them.

Most morphological characters of dredged specimens from inland sites (Early to Late Pleistocene fluviatile formations) fall within the Valdarno clusters, which in itself is not a sufficient indication of their geological age. These fossils are often, but not always, reworked. Among the reworked Giesbeek sample, a Tiglian m3 was recognized. The material from Alphen a.d. Maas was probably dredged from the Kedichem Fm. and is likely to be of Waalian age also for morphological reasons. The M3 from Wessem is presumably younger (Sterksel Fm.; ?Bavelian / ?Cromerian), but more reminiscent of *M. m. meridionalis* than of relatively advanced contemporaries, whereas an m3 fragment from this locality is advanced in its LF.

The present study shows that the dental evolution of *M. meridionalis* was slow but about continuous. The various morphological characteristics of the typical form and its descendants therefore grade into each other and at the same time some may be influenced by individual tooth size, so that the interpretation of unstratified samples with the explicit aim of subdivision presents difficulties not normally met with. Especially the remaining morphological characteristics of well-worn fragments are often anything but distinctive, so that any conclusions with regard to relative advancement are based on a smaller number of specimens than is suggested by the sample as a whole. In spite of these limitations, it has proved possible to discern between morphologically typical specimens and those that represent two levels of advancement, supposed to relate to the Waalian (and Bavel?) Interglacial on the one hand and the Leerdam Interglacial on the other. Small sample size does not allow an opinion on whether the material from the Bavel Interglacial was as advanced as that from the later Leerdam Interglacial or not. The first level of advancement is situated in the outer margin of the hypsodonty index range of the typical form M3/m3 and shows size increase and increased lamellar frequency in spite of individual large size. The second level, although it does not comprise large teeth, maintains the somewhat higher lamellar frequency and is further characterized by a perceptible increase in the hypsodonty index of M3 and M2. Individual variation probably obscures much of the slowly evolving characters, but the hypsodonty index emerges as the clearest indicator of progress. It may be considered a lucky coincidence that the type from the Leerdam Interglacial is represented by some *in situ* finds from Dorst and the about contemporaneous Rio Pradella specimens, so that the level of advancement that leads up to *M. m. voigtstedtensis* has a face, even if it is mainly visible in M3 and M2 and in very small samples. For lack of sufficient material it is not clear whether the plate number 16 (without talon(s) / p) in M3 already occurred at Dorst or Rio Pradella. Neither can it be proved that any early Cromerian specimens - morphologically about equivalent to *M. m. voigtstedtensis* - are among the most advanced group within the study area. A preliminary comparison of sites of about 0.8 Ma BP suggests that the replacement of *M. meridionalis* by a more advanced form was most likely a matter of alternating presence in certain areas until the extinction of the former. A morphological dichotomy within the Voigtstedt sample may therefore be the result of cryoturbation rather than genetic mixing.

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Legend for Tables 1 - 16:

A - area or locality of origin of the specimens;
M - arithmetic mean;
N - number of specimens;
Ne - number of estimates included in calculation;
OR - observed range;
Rind - range of values in individual tooth;
Rmax - range of maximum values;
Rmin - range of minimum values;
SD - standard deviation;
V - coefficient of variation.

Summary measurements of M3 from the Valdarno Superiore (**VS**), the North Sea (**NS**/1), the Oosterschelde (**OS**/2), Dorst (**Dt**/6), Groot Linden (**Ln**/11), Giesbeek (**Gk**/14), and Wessem (**Wm**/17); numbers refer to map (Fig. 1); advanced specimens from the North Sea are listed separately.

M3 SUP.	**N**	**Ne**	**OR**	**M**	**SD**	**V**	**A**
P	**20**	**0**	**12 - 14**	**12.8**	**0.6**	**4.8**	**VS**
	6	4	13 - 14	13.3	0.5	3.9	NS
	1	1	14 / 15				Dt
	1	1	13 / 14				Wm
L	**20**	**9**	**220.0 - 335.0**	**265.8**	**35.1**	**13.2**	**VS**
	6	6	240.0 - 310.0	279.2	25.8	9.2	NS
	1	1	270.0				Dt
	1	1	270.0 / 290.0				Wm
W	**27**	**2**	**80.0 - 123.5**	**100.8**	**12.0**	**12.0**	**VS**
	10	0	84.0 - 117.5	101.2	11.3	11.1	NS
	6	3	90.0 - 111.5	101.4	6.1	6.0	ES
	1	0	87.0				Dt
	1	0	102.5				Ln
	1	0	99.0				Wm
H	**16**	**1**	**104.0 - 147.0**	**120.8**	**13.0**	**10.8**	**VS**
	6	2	112.0 - 145.0	130.3	17.6	13.5	NS
	3	3	135.0 - 155.0	143.3			ES
	1	1	144.0				Dt
	1	1	125.0				Wm
LWI	**18**	7	**215.0 - 301.0**	**265.5**	**22.0**	**8.3**	**VS**
	6	6	255.0 - 291.0	273.7	13.3	4.9	NS
	1	1	310.0				Dt
	1	1	≥275.0				Wm
HI	**15**	**1**	**113.0 - 147.0**	**127.7**	**9.9**	**7.8**	**VS**
	6	3	123.0 - 149.0	130.7	13.0	10.0	NS
	3	3	>160.0-≥180.0				NS
	3	1	133.0 - 143.0	137.7			ES
	1	1	≥165.0				Dt
	1	1	136.0				Gk
	1	1	126.0				Wm
LF	**29**	**0**	**4.18 - 6.41**	**5.3**	**0.6**	**11.5**	**VS**
	8	0	4.93 - 5.83	5.4	0.4	6.8	NS
	4	0	4.59 - 5.69	5.0	0.5	10.4	ES
	1	1	5.50				Dt
	1	0	5.38				Ln
	2	0	5.53 - 5.93	5.7			Gk
	1	0	5.45				Wm

Summary measurements of m3 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), Oosterhout (Ot/5), Dorst (Dt/6), Alphen a.d. Maas (An/9), Groot Linden (Ln/11), Giesbeek (Gk/14), and Wessem (Wm/17); numbers refer to map (fig. 1).

M3 INF.	N	Ne	OR	M	SD	V	A
P	**13**	**0**	**12 - 15**	**13.2**	**1.0**	**7.8**	**VS**
	1	0	13 - 14	13.5			NS
	1	0	12				ES
	1	0	14				An
L	**13**	**8**	**250.0 - 330.0**	**265.4**	**30.2**	**11.4**	**VS**
	2	2	290.0 - 310.0	300.0			NS
	1	1	250.0				ES
	1	0	310.0				An
W	**22**	**3**	**75.0 - 110.0**	**91.5**	**10.9**	**11.9**	**VS**
	22	8	86.0 - 112.0	95.3	8.4	8.9	NS
	11	1	84.0 - 104.0	92.9	6.8	7.4	ES
	2	0	102.5 - 109.0	105.7			MV
	1	0	92.5				Ot
	2	0	97.0 - 108.0	102.5			An
	1	1	95.0				Ln
	1	1	95.0				Wm
H	**6**	**3**	**101.0 - 135.0**	**120.6**	**12.7**	**10.5**	**VS**
	17	10	104.0 - 140.0	121.1	10.8	8.9	NS
	7	3	105.0 - 128.0	118.4	8.1	6.9	ES
	1	1	125.0				MV
	1	0	125.5				Ot
	2	0	122.0 - 129.0				An
	1	0	109.0				Ln
	1	1	120.0				Wm
LWI	**14**	**10**	**257.0 - 356.0**	**305.2**	**28.2**	**9.3**	**VS**
	2	2	315.0 - 326.0	320.5			NS
	1	1	260.0				ES
	1	0	320.0				An
HI	**6**	**3**	**120.0 - 130.0**	**125.3**	**4.3**	**3.4**	**VS**
	19	12	101.0 - 144.0	127.8	11.9	9.3	NS
	9	3	119.0 - 129.0	121.0	7.4	6.1	ES
	1	1	122.0				MV
	2	1	136.0 - 142.0	139.0			Ot
	1	1	127.0				Dt
	2	0	119.0 - 126.0	122.5			An
	1	1	103.0				Gk
	1	1	115.0				Ln
	1	1	126.0				Wm
LF	**18**	**0**	**3.83 - 6.55**	**5.0**	**0.7**	**14.6**	**VS**
	14	1	4.02 - 6.21	5,0	0.6	11.4	NS
	6	1	3.90 - 5.69	4.5	0.5	11.2	ES
	1	0	4.85				MV
	1	0	5.03+				Ot
	2	0	5.65 - 5.69	5.7			An
	1	1	4.49				Gk

Summary measurements of M2 from the **Valdarno Superiore** (VS), the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), and Dorst (Dt/6); numbers refer to map (fig. 1).

M2 SUP.	N	Ne	OR	M	SD	V	A
P	**15**	**1**	**8 - 10**	**9.3**	**0.6**	**6.6**	**VS**
	3	0	9 - 10	9.7			NS
	1	1	10				MV
L	**16**	**5**	**174.0 - 248.0**	**210.9**	**20.1**	**9.5**	**VS**
	3	3	195.0 - 242.0	212.3			NS
	1	1	245.0				MV
W	**22**	**3**	**80.5 - 103.0**	**87.7**	**5.9**	**6.8**	**VS**
	7	1	79.0 - 104.5	92.2	10.0	10.9	NS
	2	0	87.0 - 90.5	88.8			ES
	2	0	88.0 - 93.0	90.5			MV
	1	0	80.0				Dt
H	**13**	**0**	**102.0 - 143.0**	**117.5**	**12.8**	**10.9**	**VS**
	4	3	105.0 - 135.0	119.7	12.3	10.2	NS
	1	0	123.0				ES
	2	1	106.0 - 129.0	117.5			MV
LWI	**16**	**5**	**205.0 - 270.0**	**241.9**	**21.2**	**8.8**	**VS**
	4	4	234.0 - 260.0	243.7	12.4	5.1	NS
	1	1	237.0				MV
HI	**13**	**2**	**121.0 - 151.0**	**133.5**	**8.6**	**6.4**	**VS**
	5	4	129.0 - 151.0	135.0	9.2	6.8	NS
	1	0	136.0				ES
	2	1	120.0 - 139.0	129.5			MV
	1	1	>150.0				Dt
LF	**16**	**0**	**4.66 - 6.12**	**5.4**	**0.4**	**7.8**	**VS**
	5	0	4.49 - 6.29	5.5	0.8	14.9	NS
	1	0	5.64				ES
	2	0	4.90				MV

Summary measurements of m2 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), and Tegelen (Tn/16); numbers refer to map (fig. 1); * after Guenther 1986.

M2 INF.	**N**	**Ne**	**OR**	**M**	**SD**	**V**	**A**
P	**9**	**2**	**9 - 10**	**9.6**	**0.5**	**5.5**	**VS**
	1	1	9 / 10				NS
L	**8**	**4**	**181.0 - 220.0**	**204.9**	**13.8**	**6.7**	**VS**
	1	1	200.0				NS
W	**10**	**0**	**76.5 - 92.5**	**85.0**	**5.1**	**6.0**	**VS**
	6	1	80.5 - 92.5	87.6	4.9	5.6	NS
	1	0	92.0				ES
	1	0	83.0				MV
	2	0	83.0 - 85.0*	84.0			Tn
H	**1**	**0**	**94.0**				**VS**
	1	0	96.0				NS
	1	0	117.0				ES
LWI	**6**	**5**	**242.0 - 288.0**	**257.5**	**16.8**	**6.5**	**VS**
	1	1	248.0				NS
HI	**1**	**0**	**114.0**				**VS**
	1	0	119.0				NS
	1	0	127.0				ES
LF	**8**	**0**	**5.24 - 7.05**	**5.4**	**0.4**	**7.8**	**VS**
	1	0	5.33	5.5	0.8	14.9	NS
	1	0	4.41+				ES
	1	0	4.70+				MV

Summary measurements of M1 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), Oosterhout (Ot/5), and Dorst (Dt/6); numbers refer to map (fig. 1).

M1 SUP.	N	Ne	OR	M	SD	V	A
P	**11**	**0**	**7 - 9**	**7.8**	**0.6**	**7.7**	**VS**
	5	0	8	8			NS
	3	1	7 - 8	7.7			ES
	1	0	8				Ot
	1	0	8				Dt
L	**11**	**3**	**141.0 - 170.0**	**153.8**	**35.1**	**13.2**	**VS**
	5	3	140.0 - 170.0	153.0	13.11	8.6	NS
	3	2	142.0 - 148.0	145.0			ES
	1	1	180.0				Ot
	1	1	140.0				Dt
W	**12**	**1**	**66.5 - 79.0**	**73.0**	**5.6**	**7.6**	**VS**
	6	1	67.0 - 78.2	72.1	4.3	5.9	NS
	4	0	65.0 - 75.0	71.0	4.4	6.2	ES
	1	0	65.5				MV
	1	0	81.2				Ot
	1	0	67.0				Dt
H	**9**	**1**	**91.0 - 107.0**	**95.1**	**6.4**	**6.8**	**VS**
	4	1	85.5 - 105.0	96.9	8.3	8.5	NS
	3	0	82.5 - 99.0	88.5			ES
	1	1	95.0				MV
	1	1	105.0				Ot
	1	1	91.0				Dt
LWI	**11**	**3**	**178.0 - 256.0**	**210.8**	**24.6**	**11.7**	**VS**
	5	4	193.0 - 230.0	214.0	14.8	6.9	NS
	3	2	193.0 - 223.0	208.7			ES
	1	1	217.0				Ot
	1	1	209.0				Dt
HI	**9**	**1**	**126.0 - 137.0**	**134.4**	**5.4**	**4.0**	**VS**
	4	2	128.0 - 137.0	133.8	4.0	3.0	NS
	3	0	117.0 - 135.0	127.0			ES
	1	1	130.0				Ot
	1	1	136.0				Dt
LF	**12**	**0**	**5.49 - 6.86**	**6.3**	**0.4**	**6.4**	**VS**
	4	0	5.99 - 7.87	6.7	0.8	12.2	NS
	3	0	5.80 - 6.39	6.1			ES
	1	0	6.25				MV
	1	0	5.61				Ot
	1	0	6.64	5.7			Dt

Summary measurements of m1 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), Oosterhout (Ot/5), Dorst (Dt/6), Goirle (Ge/7), and Groot Linden (Ln/11); numbers refer to map (fig. 1); * after Hooijer 1985.

M1 INF.	**N**	**Ne**	**OR**	**M**	**SD**	**V**	**A**
P	**7**	**0**	**8 - 9**	**8.7**	**0.5**	**5.6**	**VS**
	1	0	9				NS
	1	0	8				Ot
	1	1	8				Dt
	1	1	8*				Ln
L	**7**	**1**	**150.0 - 173.0**	**161.0**	**7.8**	**4.8**	**VS**
	1	0	150.				NS
	1	1	170.				Ot
W	**8**	**1**	**67.0 - 76.0**	**70.5**	**3.8**	**5.4**	**VS**
	2	1	67.0 - 70.0	68.5			NS
	5	0	63.5 - 73.5	69.2	4.0	5.8	ES
	5	0	68.0 - 75.0	71.0	2.6	3.7	MV
	1	0	72.0				Ot
	1	0	70.5				?Ot
	1	0	75.2				Dt
	1	0	70.5				Ge
	2	1	65.0* - 70.0	67.5			Ln
H	**5**	**0**	**90.0 - 102.0**	**94.4**	**6.1**	**6.5**	**VS**
	2	2	95.0 - 100.0	97.5			NS
	3	2	93.0 - 103.0	98.7			ES
	2	1	100.0 - 105.0	102.5			MV
	1	1	100.0				Ot
	1	0	99.0				Ge
	1	0	97.0				Ln
LWI	**6**	**1**	**222.0 - 254.0**	**233.5**	**12.5**	**5.4**	**VS**
	1	1	224.0				NS
	1	1	236.0				Ot
HI	**5**	**1**	**127.0 - 150.0**	**136.6**	**8.4**	**6.2**	**VS**
	2	2	142.0 - 143.0	142.5			NS
	3	2	129.0 - 143.0	137.3			ES
	2	2	140.0 - 143.0	141.5			MV
	1	1	135.0				Ot
	1	0	140.0				Ge
	1	0	149.0				Ln
LF	**6**	**3**	**6.20 - 7.19**	**6.7**	**0.4**	**5.6**	**VS**
	2	0	6.71 - 6.81	6.8	0.2	3.8	NS
	1	0	5.74				Ot
	1	0	7.16				Ge
	2	0	5.85 - 7.50*	6.7			Ln

Summary measurements of dP4 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), and the Oosterschelde (OS/2); numbers refer to map (fig. 1).

dP4 SUP.	N	Ne	OR	M	SD	V	A
P	**5**	**0**	**7 - 8**	**7.2**	**0.4**	**6.2**	**VS**
	3	1	7	7			ES
L	**5**	**4**	**110.0 - 120.0**	**117.4**	**4.3**	**3.7**	**VS**
	3	2	100.5 - 115.0	108.5			ES
W	**6**	**1**	**57.0 - 68.0**	**61.4**	**4.8**	**7.8**	**VS**
	1	0	50.5				NS
	3	0	48.0 - 60.8	56.3			ES
H	**4**	**1**	**58.0 - 78.0**	**65.0**	**9.2**	**14.2**	**VS**
	1	1	58.0				NS
	2	2	52.0 - 68.0	60.0			ES
LWI	**5**	**4**	**186.0 - 211.0**	**195.8**	**13.0**	**6.7**	**VS**
	3	2	183.0 - 209.0	193.7			ES
HI	**4**	**2**	**98.0 - 115.0**	**106.8**	**7.4**	**6.9**	**VS**
	1	1	115.0				NS
	2	2	108.0 - 112.0	110.0			ES
LF	**6**	**0**	**6.44 - 7.91**	**7.4**	**0.5**	**7.3**	**VS**
	1	0	8.35				NS
	3	0	6.89 - 9.16	7.9			ES

Summary measurements of dp4 from the **Valdarno Superiore (VS)**, the Oosterschelde (OS/2), the Maasvlakte (MV/3), Wychen (Wn/12), Giesbeek (Gk/14), and Braamt (Bt/15); numbers refer to map (fig. 1).

dP4 INF.	**N**	**Ne**	**OR**	**M**	**SD**	**V**	**A**
P	**10**	**0**	**6 - 9**	**7.9**	**1.0**	**12.6**	**VS**
	1	1	7				ES
	1	1	8				Bt
L	**10**	**4**	**105.0 - 128.0**	**118.2**	**6.5**	**5.5**	**VS**
	1	1	118.0				ES
	1	1	120.0				Bt
W	**11**	**1**	**49.0 - 60.0**	**54.2**	**4.1**	**7.5**	**VS**
	1	0	58.0				ES
	3	0	52.5 - 58.0	56.3			MV
	1	0	59.0				Wn
	1	0	60.0				Gk
	1	0	57.4				Bt
H	**3**	**1**	**55.0 - 72.0**	**62.3**	**8.7**	**14.0**	**VS**
	1	1	73.0				ES
	1	0	68.0				MV
	1	1	70.0				Wn
	1	0	74.0				Gk
	1	1	65.0				Bt
LWI	**9**	**5**	**188.0 - 233.0**	**217.1**	**17.9**	**8.2**	**VS**
	1	1	203.0				ES
	1	1	209.0				Bt
HI	**4**	**3**	**100.0 - 131.0**	**116.5**	**12.9**	**11.0**	**VS**
	1	1	126.0				ES
	1	0	130.0				MV
	1	1	119.0				Wn
	1	0	123.0				Gk
	1	1	113.0				Bt
LF	**8**	**0**	**6.92 - 8.90**	**7.9**	**0.7**	**9.2**	**VS**
	1	1	7.5				ES
	3	0	6.52 - 8.41	7.3			MV
	1	0	6.83				Wn
	1	0	6.79				Gk
	1	0	6.99				Bt

Summary measurements of Enamel Thickness in M3 from the **Valdarno Superiore (VS)**, the North Sea (NS/1; NS* - specimen is advanced in Hypsodonty Index), the Oosterschelde (OS/2), Dorst (Dt/6), Groot Linden (Ln/11), Giesbeek (Gk/14), and Wessem (Wm/17); numbers refer to map (fig. 1); extremes of total range underlined (N ≥ 2).

M3 SUP.	N	SUBRANGES	MIDRANGE MEAN	SD	V	A
Rmin.	23	2.0 - 3.5				
Rmid.	**24**	**2.5 - 3.8**	**3.10**	**0.39**	**12.5**	**VS**
Rmax.	23	2.9 - 4.3				
Rmin.	10	2.0 - 3.0				
Rmid.	12	2.5 - 3.5	2.92	0.36	12.3	NS
Rmax.	10	2.5 - 3.9				
Rind.	1	2.3 - 3.5	2.90			NS*
Rmin.	4	1.9 - 3.0				
Rmid.	4	2.6 - 3.1	2.76	0.23	8.3	ES
Rmax.	4	2.8 - 3.5				
Rind.	1	2.0 - 2.5	2.25			Dt
Rmin.	2	2.5 - 3.5				
Rmid.	2	3.0 - 3.7	3.38			Ln
Rmax.	2	3.5 - 4.0				
Rind.	1	3.1 - 4.0	3.55			Gk
Rind.	1	2.5 - 3.9	3.20			Wm

Summary measurements of Enamel Thickness in m3 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), Oosterhout (Ot/5; Ot T - Tiglian specimen from boring; Ot?B - ?Bavelian specimen), Dorst (Dt/6), Zoelen (Zn/8), Alphen a.d. Maas (An/9), Wychen (Wn/10), Groot Linden (Ln/11), Bemmel (Bl/13), and Wessem (Wm/17); numbers refer to map (fig. 1); extremes of total range underlined (N ≥ 2).

M3 INF.	N	SUBRANGES	MIDRANGE MEAN	SD	V	A
Rmin.	20	1.9 - 3.9				
Rmid.	**23**	**2.2 - 4.2**	**3.09**	**0.47**	**15.1**	**VS**
Rmax.	20	2.5 - 4.8				
Rmin.	18	2.0 - 3.5				
Rmid.	20	2.3 - 3.8	**3.06**	0.31	10.3	NS
Rmax.	18	3.2 - 4.3				
Rmin.	13	2.1 - 3.2				
Rmid.	13	2.5 - 3.9	**3.04**	0.42	13.7	ES
Rmax.	13	2.7 - 5.0				
Rmin.	2	2.8 - 3.0				
Rmid.	2	2.9 - 3.3	**3.10**			MV
Rmax.	2	3.1 - 3.5				
Rind.	1	3.0	3.00			Ot T
Rind.	1	2.5 - 2.8	2.65			Ot ?B
Rind.	1	2.7 - 3.2	2.95			Dt
Rind.	1	3.0 - 4.2	3.60			Zn
Rmin.	2	2.5 - 2.6				
Rmid.	2	2.7 - 3.3	3.00			An
Rmax.	2	2.9 - 4.0				
Rind.	1	3.0 - 3.7	3.35			Wn
Rind.	1	3.5	3.50			Ln
Rind.	1	3.5 - 4.1	3.80			Bl
Rind.	1	3.0 - 4.2	3.60			Wm
Rind.	1	3.2 - 5.0	4.10			Gk

Table 11 - Summary measurements of Enamel Thickness in M2 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), Dorst (Dt/6), and Giesbeek (Gk/14); numbers refer to map (fig. 1); extremes of total range underlined (N ≥ 2).

M2 SUP.	N	SUBRANGES	MIDRANGE	MEAN	SD	V	A
Rmin.	12	1.5 - 2.6					
Rmid.	**13**	**1.9 - 2.8**	**2.33**		**0.34**	**14.7**	**VS**
Rmax.	12	2.1 - 3.5					
Rmin.	7	1.7 - 3.0					
Rmid.	8	2.2 - 3.3	2.72		0.37	13.6	NS
Rmax.	7	2.7 - 3.5					
Rind.	1	2.1 - 2.5	2.30				ES
Rmin.	2	2.4 - 2.5					
Rmid.	2	2.5 - 2.7	2.60				MV
Rmax.	2	2.5 - 3.0					
Rind.	1	2.5	2.50				Dt
Rind.	1	2.5 - 2.6	3.55				Gk

Table 12 - Summary measurements of Enamel Thickness in m2 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), and Wychen (Wn/10); numbers refer to map (fig. 1); extremes of total range underlined (N ≥ 2).

M2 INF.	N	SUBRANGES	MIDRANGE	MEAN	SD	V	A
Rmin.	10	1.5 - 3.3					
Rmid.	**10**	**1.7 - 3.5**	**2.44**		**0.58**	**23.6**	**VS**
Rmax.	10	2.0 - 3.7					
Rmin.	7	1.9 - 3.7					
Rmid.	7	2.1 - 3.8	2.84		0.60	21.1	NS
Rmax.	7	2.4 - 4.0					
Rind.	1	1.8 - 3.2	3.00				ES
Rind.	1	3.2 - 3.4	3.30				MV
Rind.	1	2.3 - 2.8	2.55				Wn

Table 13 - Summary measurements of Enamel Thickness in M1 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), Oosterhout (Ot/5), and Dorst (Dt/6); numbers refer to map (fig. 1); extremes of total range underlined (N ≥ 2).

M1 SUP.	N	SUBRANGES	MIDRANGE	MEAN	SD	V	A
Rmin.	7	1.5 - 2.0					
Rmid.	**7**	**1.7 - 2.5**	**1.99**		**0.31**	**15.5**	**VS**
Rmax.	7	1.8 - 2.9					
Rmin.	4	1.6 - 2.4					
Rmid.	4	1.8 - 2.5	2.15		0.32	15.0	NS
Rmax.	4	2.1 - 2.7					
Rind.	1	1.5 - 1.9	1.70				ES
Rind.	1	1.5 - 1.8	1.65				MV
Rind.	1	1.7 - 2.4	2.05				Ot sin.
Rind.	1	1.9 - 2.5	2.20				Ot dex.
Rind.	1	1.6 - 1.9	1.75				Dt

Table 14 Summary measurements of Enamel Thickness in m1 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), the Oosterschelde (OS/2), the Maasvlakte (MV/3), Oosterhout (Ot/5), ?Oosterhout (?Ot/5; left and right), Dorst (Dt/6), Goirle (Ge/7), and Groot Linden (Ln/11); numbers refer to map (fig. 1); extremes of total range underlined (N ≥ 2).

M1 INF.	N	SUBRANGES	MIDRANGE	MEAN	SD	V	A
Rmin.	5	1.3 - 1.7					
Rmid.	**7**	**1.5 - 2.1**	**1.99**		**0.22**	**11.4**	**VS**
Rmax.	5	1.7 - 2.6					
Rmin.	2	1.5 - 2.0					
Rmid.	2	1.8 - 2.2	1.98				NS
Rmax.	2	2.1 - 2.3					
Rmin.	4	1.6 - 2.5					
Rmid.	4	2.0 - 2.9	2.54		0.37	14.6	ES
Rmax.	4	2.5 - 3.1					
Rmin.	4	1.5 - 2.1					
Rmid.	4	1.6 - 2.4	2.04		0.36	17.8	MV
Rmax.	4	1.6 - 2.7					
Rind.	1	2.0 - 2.7	2.35				Ot
Rind.	1	2.1 - 2.8	2.45				?Ot sin.
Rind.	1	1.9 - 2.8	2.35				?Ot dex.
Rind.	1	1.9 - 2.9	2.30				Dt
Rind.	1	1.6 - 2.5	2.05				Ge
Rind.	1	1.5 - 2.3	1.90				Ln

Table 15 - Summary measurements of Enamel Thickness in dP4 from the **Valdarno Superiore (VS)**, the North Sea (NS/1), and the Oosterschelde (OS/2); numbers refer to map (fig. 1); extremes of total range underlined (N ≥ 2).

dP4 SUP.	N	SUBRANGES	MIDRANGE MEAN	SD	V	A
Rmin.	6	1.0 - 1.5				
Rmid.	**6**	**1.2 - 2.0**	**1.58**	**0.27**	**17.0**	**VS**
Rmax.	6	1.4 - 2.5				
Rind.	1	1.0 - 1.3	1.15			NS
Rmin.	3	1.0 - 1.2				
Rmid.	3	1.1 - 1.5	1.32	0.20	15.3	ES
Rmax.	3	1.2 - 1.8				

Table 16 - Summary measurements of Enamel Thickness in dp4 from the **Valdarno Superiore (VS)**, the Oosterschelde (OS/2), the Maasvlakte (MV/3), Wychen (Wn/10), Giesbeek (Gk/14), and Braamt (Bt/15); numbers refer to map (fig. 1); extremes of total range underlined (N ≥ 2).

dP4 INF.	N	SUBRANGES	MIDRANGE MEAN	SD	V	A
Rmin.	9	1.2 - 1.6				
Rmid.	**11**	**1.3 - 1.9**	**1.59**	**0.18**	**11.2**	**VS**
Rmax.	6	1.4 - 2.0				
Rind.	1	1.4 - 1.7	1.55			ES
Rmin.	3	1.0 -				
Rmid.	3	1.3 -	1.50e			MV
Rmax.	3	1.4 - 2.0				
Rind.	1	1.3 - 1.8	1.55			Bt
Rind.	1	1.7 - 2.1	1.90			Gk
Rind.	1	2.1 - 2.5	2.30			Wn