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Fossil proboscideans from The Netherlands, the North Sea and the Oosterschelde Estuary

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This paper reviews the most important findings of proboscidean fossils from The Netherlands, both from the mainland as well as those dredged by fisherman from the estuaries and the Southern Bight of the North Sea. The oldest, Pliocene, proboscidean remains from The Netherlands are a few isolated molars of *Mammut borsoni* from Liessel. Also *Anancus arvernensis* occurs at this locality. An Early Pleistocene fauna with *A. arvernensis* and *M. meridionalis* has been dredged from the Oosterschelde Estuary. The Oosterschelde fauna, with an estimated age of 1.9 myr, is slightly older than the vertebrate fauna from the clay pits at Tegelen. The postcranial fossils of *Anancus* and *Mammuthus meridionalis*, both heavily mineralized, can be easily distinguished based on size differences, but also on morphological grounds. Whereas *Anancus* has its latest occurrence in the Oosterschelde assemblage, *M. meridionalis* continues well into the Middle Pleistocene and is known from Dutch mainland localities as well as from the North Sea. From the North Sea also a few molars of *M. trogontherii* have been dredged. Fossils of the straight-tusked elephant, *E. antiquus*, are rare. Some of the earlier remains of this species occur in mainland sites and have a late Middle Pleistocene age. Late Pleistocene proboscideans are restricted to *M. primigenius* and *E. antiquus*, both showing a light degree of fossilization. While the woolly mammoth is known from a wealth of shallow localities in The Netherlands, it is especially common amongst fossils dredged from the North Sea. Late Pleistocene *E. antiquus* remains are rare.

Fossiele olifantachtigen uit Nederland, de Noordzee en het Oosterschelde bekken – In dit artikel worden de belangrijkste vondsten van olifantachtigen uit Nederland beschreven, zowel van het vasteland als het opgeviste materiaal uit de zeearmen en de Noordzee. Het oudste, Pliocene olifantmateriaal zijn enkele losse molaren van *Mammut borsoni* uit Liessel. Uit deze vindplaats is ook *Anancus arvernensis* bekend. Een vroeg-Pleistocene fauna met *A. arvernensis* en *M. meridionalis* is opgevist uit de Oosterschelde. De Oosterschelde fauna is met een leeftijd van ca. 1,9 miljoen jaar iets ouder dan de fauna van Tegelen. Het postcraniale materiaal van *Anancus* en *Mammuthus meridionalis*, beide zwaar gemineraliseerd, kan worden onderscheiden op basis van maatverschillen en morfologie. Terwijl *Anancus* in de Oosterschelde zijn jongste voorkomen heeft, komt *M. meridionalis* voor tot in het Midden Pleistoceen, zowel op het vasteland als in de Noordzee. Uit de Noordzee is ook een aantal kiezen van *M. trogontherii* bekend. Fossielen van de bosolifant, *E. antiquus*, zijn zeldzaam. Enkele vroege vondsten van deze soort komen van het vasteland en dateren uit het late Midden Pleistoceen. Laat Pleistocene olifanten bepreken zich tot *M. primigenius* en *E. antiquus*, beide slechts licht gefossiliseerd. Terwijl de wolharige mammoet bekend is uit veel ondiepe vindplaatsen in Nederland, is deze soort bijzonder veelvuldig aangetroffen tussen fossielen die uit de Noordzee zijn opgevist. Laat Pleistocene overblijfselen van *E. antiquus* zijn zeldzaam.

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INTRODUCTION

Fossil teeth and bones of Quaternary mammals are commonly preserved in the unconsolidated sediments underlying the Dutch delta. The fossils can usually not be found at the exposed landsurface, but are dredged up as a result of sand- and gravel dredging operations in the alluvial plains of the rivers Rhine, Waal, Meuse and IJssel. In the North Sea however, fossil-bearing strata crop out on the seabottom at several places, and an important source of fossil terrestrial mammals in The Netherlands are fishing boats. The trawlers use beamtrawls that are towed over the sea bottom. During these operations large debris, including mammalian fossils, is collected inside the nets. The trawlers that operate in the southern bight of the North Sea between England and The Netherlands and also in the Schelde Estuary, have over the years brought in an enormous amount of mammalian fossils in this way. Because the mesh diameter of the nets is about 5 cm, mostly larger fossils are brought in by the fishing boats. Many well-preserved dredged mammalian fossils have ended up in private collections, several of which are well documented. Also, a considerable amount of this dredged material is stored in Naturalis, the National Museum of Natural History (NNM) at Leiden (formerly the National Museum of Geology and Mineralogy), which institution contains one of the largest collections in the world of fossils of the woolly mammoth, *Mammuthus primigenius*. Also, dredged fossils are being sold in many countries, and The Netherlands have become the top country in the world in the export of mammoth teeth. During the last 45 years the museum in Leiden has also been actively involved in the search for fossil remains from the sea bottom, by employing a fishing boat once every year to bring up fossils from the Oosterschelde. Finally, many important fossil remains from the North Sea can be found in a wide scala of smaller natural history musea throughout The Netherlands. A third source of mammalian fossils in The Netherlands are the clay pits near Tegelen. A well-documented terrestrial fauna of ca. 1.7 My old has become known from this type locality of the Tiglian stage.

Proboscidean remains constitute an important element from these various sources, ranging in age from Pliocene to Late Pleistocene. The majority of the fossils originate from Late Pleistocene layers. Though the latter are usually not mineralized, they are often well preserved, especially those dredged from the North Sea bottom. *Mammuthus primigenius* is one of the most common elements in the Late Pleistocene faunas. Less well known from The Netherlands are the rarer occurrences of Pliocene and Early Pleistocene proboscideans, such as *Anancus arvernensis*, and *Mammut borsoni*. In addition, various collections comprise a fair amount of fossils of *Mammuthus meridionalis* and *Elephas antiquus*, whereas *Mammuthus trogontherii* remains are very rare in The Netherlands. The scientific significance of the dredged fossils is often considered as less important, because the exact stratigraphic level of origin is not known. On the other hand, the fossils often have an excellent state of preservation, and also the large amount of fossil specimens makes them an important source of information. Besides, the mapping of the North Sea Quaternary (Cameron *et al*. 1984) in combination with information on the dredging locations has made it possible to reconstruct the age of many fossil findings from the North Sea (Van Kolfschoten & Laban 1995). Also the subsurface geology of the Dutch delta has become increasingly well known, so that fossil specimens from sand and gravel dredging operations can now often be placed within their stratigraphical context with reasonable certainty. Also the fossil assemblages themselves from certain locations provide clues concerning the age of these faunas. The Early and Middle Pleistocene fossils can be distinguished from Late Pleistocene fossils because of their state of preservation. It is not so much the color of the fossils, which is of

importance to make this distinction (Drees 1986), but the degree of mineralization: the fossils originating from older formations are heavily mineralized and have a relatively high density. They produce a high-pitched sound when tapped on with a hard object. The Late Pleistocene bones on the other hand, such as the remains of *M. primigenius*, have a relatively low density and produce a dull sound.

In this paper we will give a brief overview of the various proboscidean remains from The Netherlands. The geological context of the various Plio-Pleistocene fossil-bearing deposits in the North Sea and a description of the proboscidean molar remains from the North Sea have already been dealt with in other papers (Van Kolfschoten & Laban 1995, Van Essen & Mol 1996). Here we will give a review of the proboscidean remains from The Netherlands, including the North Sea and Oosterschelde estuary. Postcranials of *Anancus arvernensis* and *Mammuthus meridionalis* from the North Sea and Oosterschelde have not yet been described before and they will be compared and described in this paper. Also attention will be put on the accompanying faunas in which the various proboscideans occur.

PROBOSCIDEANS FROM THE NETHERLANDS

Mammut borsoni

The rarest proboscidean from The Netherlands, *Mammut borsoni*, was first reported by von Koenigswald in 1950, who described a lower M3 of unknown provenance. The specimen is nowadays in the collection of the Natuurmuseum Rotterdam. More recently, two lower M3 were discovered at Liessel (Mol & Van Essen 1990, Peters *et al.* 1991). From this locality also *Anancus arvernensis* has been reported. Whereas *M. borsoni* disappears from Europe during the Pliocene, *A. arvernensis* continues into the Pleistocene. The latter is present amongst the dredged material from the Oosterschelde, from where so far no *M. borsoni* material has been reported with certainty. This suggests that the Liessel locality has yielded the oldest proboscidean remains in The Netherlands, with a Pliocene age.

Anancus arvernensis

This taxon has its oldest occurrence in various Late Miocene (Late Turolian) localities in Spain and had a wide Eurasian distribution during the Pliocene, but became extinct during the Early Pleistocene. The various *Anancus* remains from The Netherlands are thought to represent the latest populations before this species became extinct. Most material originates from the Oosterschelde (Schreuder 1944, 1945, Hooijer 1953), where *Anancus* seems to be associated with remains of *Mammuthus meridionalis* and other terrestrial mammals, broadly indicative of an Early to Middle Pleistocene age. The fossils originate from part of the Oosterschelde where the Tegelen Formation crops out (Drees 1986). However, from the beginning it was realised that the fauna from the Oosterschelde was older than the famous fauna from the clay pits near Tegelen (Province of Limburg). The Oosterschelde fauna has been indicated as Pre-Tiglian (Hooijer 1950, 1953, 1957, Van der Vlerk 1951, Van der Feen 1968, Dumon Tak 1973). Because the pollen spectra from the Tegelen clays have shown that the sequence represents a longer period with a succession of colder and warmer phases (Zagwijn 1963), it is better to speak of the Tiglian Complex. The Tegelen vertebrate fauna is now placed in the TC5 zone of the Tiglian (Van Kolfschoten & Van der Meulen 1986), which represents a warm period and has an age of approximately 1.7 My. *Anancus* is often included in this fauna. However, the one molar fragment attributed to *Anancus* was not found at the same locality as most of the other vertebrate remains, but in the clay pit Van Cleef near Maalbeek, 3 km south of Tegelen (Van Essen & Mol 1996). The associated pollen spectrum

of the *Anancus* molar indicates a cold period, according to Zagwijn (1960, 1963) representing the Eburonian, which followed the warm-temperate Tiglian stage during which the famous Tegelen fauna lived. However, based on recent studies of the clay pit Maalbeek, Westerhof (personal communication to van Kolfschoten & Laban, 1995) concluded that the *Anancus* molar predates the famous Tegelen fauna. This suggests that the Oosterschelde fauna is older than the TC5 stage and there is good additional evidence for this. The Oosterschelde fauna shows great resemblance with the fauna from Chilhac (Haute-Loire, France; Mol & De Vos 1996). The Chilhac fauna has been dated at 1.9 My (Bout 1979) and contains the following taxa according to Boeuf (1983, 1993):

- *Ursus etruscus*, the Etruscan bear
- *Megantereon megantereon*, a sabre-toothed cat
- *Pachycrocuta* (=*Hyaena*) *perrieri*, the hyaena of Perrier
- *Nyctereutes megamastoides*, a fox-like animal
- *Anancus arvernensis chilhiacensis*, a mastodont
- *Mammuthus meridionalis*, the southern mammoth
- *Equus stenonis guthi*, a large horse
- *Dicerorhinus* (=*Stephanorhinus*) *etruscus*, the Etruscan rhino
- *Eucladoceros senezensis*, a large deer
- *Cervus philisi*, a middle-sized deer
- *Croizetoceros ramosus*, a small deer
- *Gazellospira torticornis*, a gazelle

The Oosterschelde assemblage contains the following taxa according to the review given by Mol & De Vos (1996):

- a sabre-toothed cat (Hooijer 1962, 1991)
- cf. *Hyaena perrieri* (Mol & De Vos, 1995a,b)
- *Mammuthus meridionalis* (Hooijer 1953, 1962, 1981, Van Essen & Mol 1996)
- *Anancus arvernensis* (e.g. Hooijer 1953, 1991)
- a large, heavily built horse (see among others: Hooijer 1953; Kortenbout van der Sluijs 1985)
- *Stephanorhinus cf. etruscus* (Mol & De Vos 1995a)
- *Eucladoceros ctenoides*, the large cervid of Tegelen (De Vos *et al*. 1995)
- *Cervus rhenanus*, the middle sized deer of Tegelen (De Vos *et al*. 1995)
- a large boar (Mol & De Vos 1996)

There is general agreement nowadays that the large cervid of Senèze and Chilhac, referred to as *Eucladoceros senezensis*, is the same species as the large cervid from Tegelen, usually referred to as *Eucladoceros tegulensis* (Germonpré 1983, Azzaroli *et al*. 1988, Azzaroli & Mazza 1992, Spaan 1992). In a review of the Early Pleistocene cervids from Europe (De Vos *et al*. 1995) it was concluded that the name *Eucladoceros ctenoides* (NESTI, 1841) has priority and should be used for this large cervid. The antler of the middle-sized deer from the Oosterschelde consists of a beam, one brow tine and at the end one side tine, similar to the middle-sized deer of Tegelen, which is known under the name *Cervus rhenanus* DUBOIS, 1904. Spaan (1992) made a detailed study of the Tegelen deer and concluded that *Cervus philisi* SCHAUB, 1941 and *Cervus perolensis* (AZZAROLI, 1952), see Bout & Azzaroli (1952) are synonyms of *Cervus rhenanus* from Tegelen. As follows from the species lists given above, the faunas from Chilhac and the Oosterschelde show great resemblance to each other, and an age of 1.9 myr for the Oosterschelde fauna, somewhat older than the Tegelen Fauna, which lacks *Anancus arvernensis*, seems well funded.

In addition to the Oosterschelde, *Anancus* material has also been dredged from the Thornton Bank approximately 12 nautic miles off the coast of the province of Zeeland (51° 35' 49" N, 03° 01'39" E). Also here *Anancus* occurs in association with *M. meridionalis* and the close proximity to the Oosterschelde suggests that they originate from the same Tegelen Formation. Two *Anancus* molar frag-

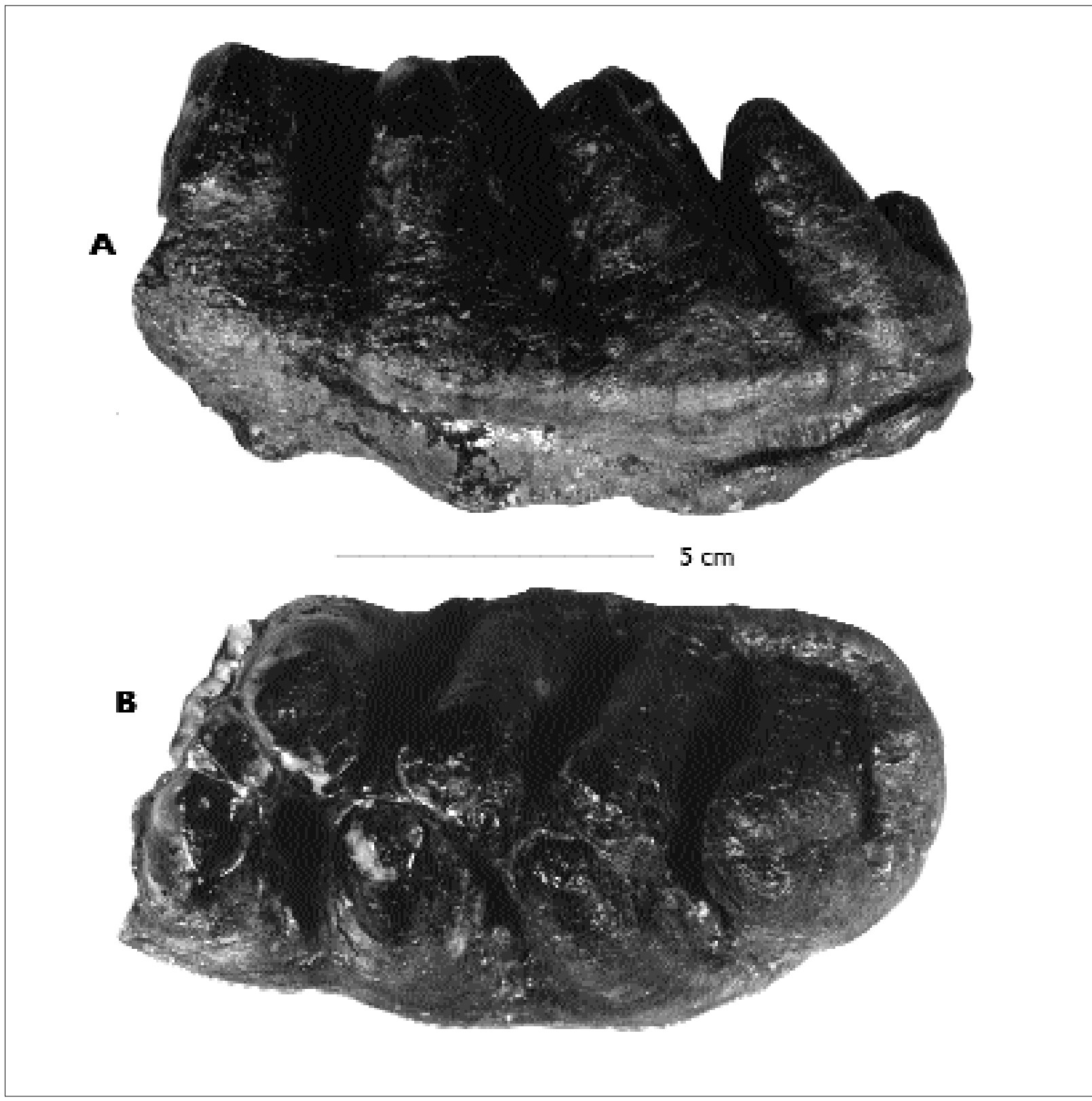

Figure 1 Posterior fragment of a left M1 of *Anancus arvernensis* (Coll. NNM no. St-401326). This specimen was dredged up from the Oosterschelde Estuary near Wisseke rke, Province of Zeeland, The Netherlands. **A** lingual view, **B** occlusal view.

ments are known from the Thornton Bank (Coll. Mol No. 1752 and one specimen in the Collection Jager at Goes). The specimen in the Mol collection is a lower left M2 fragment, it was figured in Van Essen & Mol (1996: fig. 20.3). The *Anancus* material dredged from the Oosterschelde consists of 39 nicely preserved molars (Fig. 1), including elements of the milk dentition (Fig. 2), and tusk fragments. In addition, about a hundred postcranial elements originate from the same locality, the larger part fragmentary, except for bones of the manus and pes. Most of this material is stored in the collections of the NNM. Some of the carpal and tarsal bones, typical for *Anancus*, will be described and compared with *M. meridionalis* and *M. primigenius* in the last section of this paper.

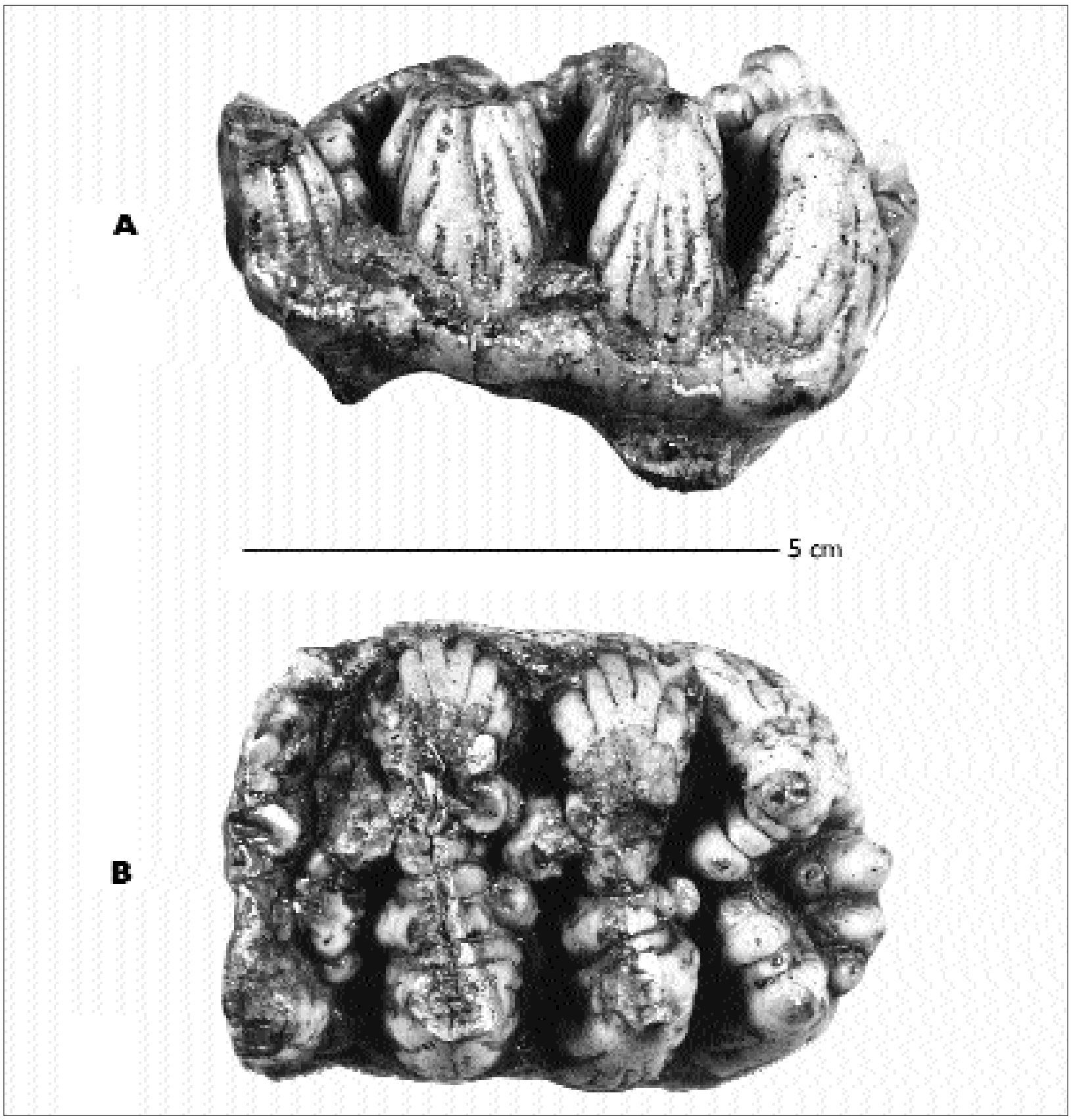

Figure 2 Posterior fragment of a right DP4 of *Anancus arvernensis* (Coll. NNM no. St-118934), dredged up from the Oosterschelde Estuary near the Flauwerspolder, Province of Zeeland, The Netherlands. **A** lingual view, **B** occlusal view.

Mammuthus meridionalis and *Mammuthus trogontherii*

Mammuthus meridionalis was much larger than *Anancus arvernensis*, with which it co-occurs in the Oosterschelde fauna (De Vos *et al.* 1996). Besides from the Oosterschelde (Fig. 3), remains of *M. meridionalis* have also been found in the North Sea, mainly from the Deep Water Channel. Hooijer (1984) was the first one who described in detail dental elements of *Mammuthus meridionalis* from the North Sea. Based on molar measurements, Van Essen & Mol (1996) intended to ascribe the North Sea and Oosterschelde material to one or more of the evolutionary stages of *M. meridionalis* (Van Essen & Mol 1996). These stages, recognised by Maglio (1973) and other authors before, have been

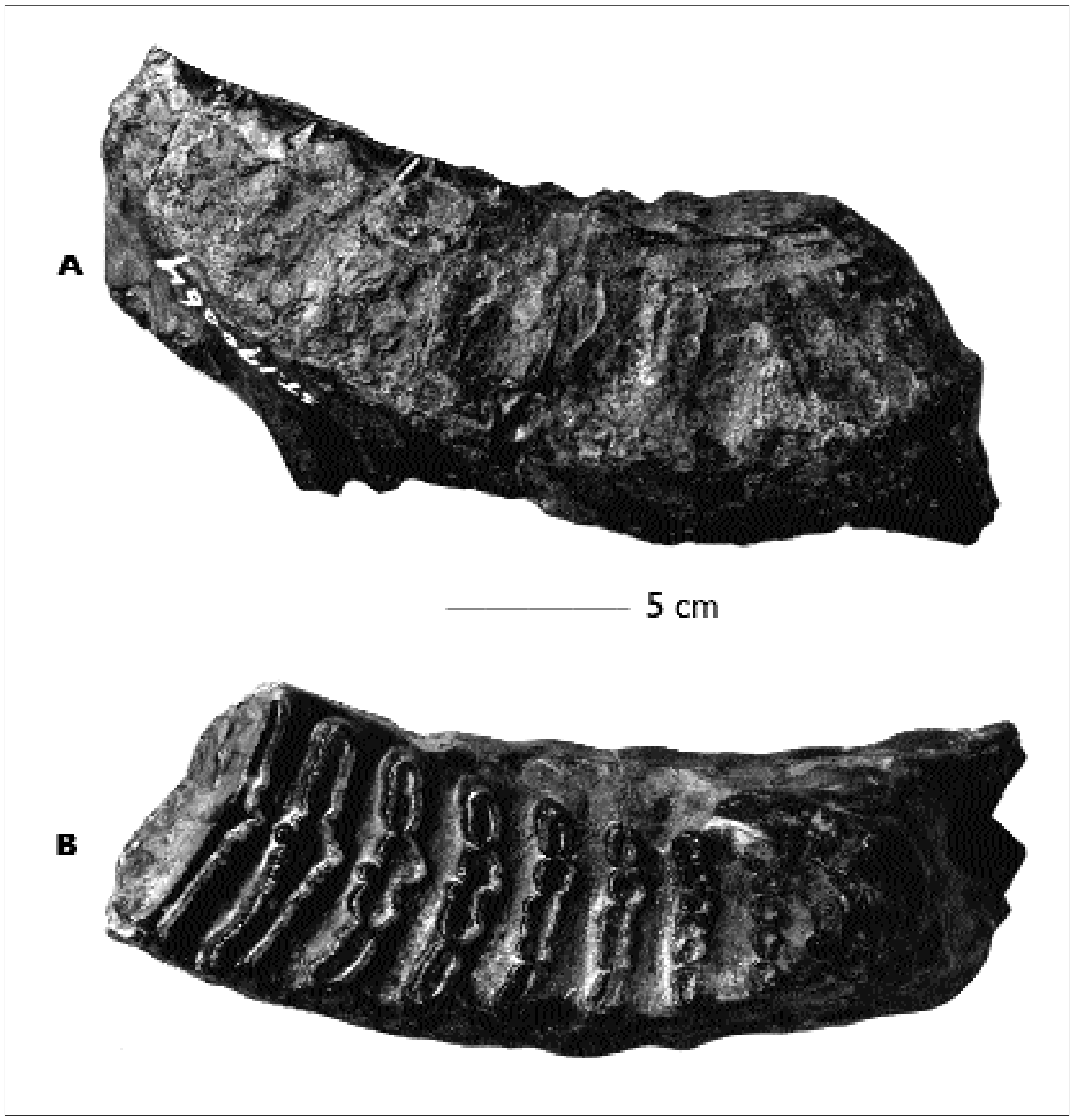

Figure 3 Posterior fragment of a right m3 of *Mammuthus meridionalis* (Coll. NNM no. St-170064), dredged up from the Oosterschelde Estuary. **A** lingual view, **B** occlusal view.

labelled 'Laiatico stage', 'Montevarchi stage' and 'Bacton stage' ('primitive', 'typical' and 'advanced' stage respectively). These successive stages are characterised by increasing plate numbers, hypsodonty index and lamellar frequency, and decreasing enamel thickness as defined by Maglio (1973). The upper M3's from the North Sea have 13 lamellae (Van Essen & Mol 1996). This corresponds with the material from Chilhac, which has an age of approximately 1.9 myr (Bout 1970). Three of the Chilhac skulls have M3 with 13 lamellae and one has 12 lamellae. According to Maglio (1973) the Laiatico stage is characterised by 11 or 12 lamellae in the upper M3. Thus, the North Sea material tends to be slightly more advanced than the Laiatico stage.

From the Deep Water Channel, a deep gully in the Southern Bight of the North Sea, Early to early Middle Pleistocene terrestrial mammal remains have been trawled. The only proboscideans known from this site are: *M. meridionalis* and *M. trogontherii* (Hooijer 1984, Mol & Van Essen 1992). *A. arvernensis* is not known from this site. In the Oosterschelde and the Thornton Bank *M. meridionalis* and *A. arvernensis* occur in the same fauna (Mol & De Vos 1996). As argued above, the Oosterschelde Fauna is probably equivalent to the 1.9 myr old Chilhac Fauna. Based on the absence of *A. arvernensis* amongst the North Sea material it is considered likely that this material is slightly younger than the Oosterschelde/Thornton Bank material. This assumption is strengthened by the fact that amongst the North Sea material there are various molar fragments referable to *Mammuthus trogontherii* (Van Essen & Mol 1996), which species is believed to have gradually evolved from *M. meridionalis*.

In addition to molars there are numerous heavily mineralized postcranial remains from the North Sea and the Oosterschelde that must belong to *M. meridionalis*. Below we will describe some carpals and tarsals from the North Sea, Thornton Bank and the Oosterschelde. These can be easily distinguished from homologues of *A. arvernensis* from the Oosterschelde and Thornton Bank, based on morphological characters and size measurements (the possibility remains that some of the early Middle Pleistocene postcranial remains actually belong to *M. trogontherii* instead of *M. meridionalis*). From *M. primigenius* they are distinguished by their usually larger size and consistently heavier mineralization. A well preserved complete but anomalous m3 with 15 plates of an advanced *M. meridionalis* was dredged from the floodplain of the river Meuse near Alphen aan de Maas (Province of Gelderland). The stratigraphical position is unknown but could be late Early to early Middle Pleistocene based on the evolutionary stage ('Bacton Stage') of this m3.

In a paper reviewing the Pleistocene Proboscideans originating from the Early Pleistocene deposits from The Netherlands the next three onshore sites should be mentioned. First of all the famous Tegelen site, with an age of 1.7 My, has yielded in total 11 fragmentary molar remains of *M. meridionalis*, which have been thoroughly studied by Guenther (1986). Rutten (1909) figured and described in detail a set of molars of a single individual (m1 sin. and dex. and M1 sin. and dex.) of *M. meridionalis*, which were found in 1842 in a clay pit near Oosterhout (Province of Noord-Brabant). These molars were found together with, according to Rutten (1909) remains of M2's and some postcranial material, probably belonging to the same individual. Unfortunately it is only known where the four M/m1's are kept, which is the Brabants Museum at 's-Hertogenbosch (Bois-le-Duc). According to Rutten (1909), the finds from Oosterhout were collected *in situ* and have an Early Pleistocene age. However, their exact stratigraphical position is unknown. *Mammuthus meridionalis* molars were collected in a clay-pit called 'Surae', situated east of the village of Dorst (Province of Noord-Brabant). The Dorst-Surae material was described by Van Kolfschoten (1990), and its geological age was discussed. The clay layer from which the fossils originated was deposited during the end phase of the Leerdam Interstadial and the Dorst Stadial (the last interstadial and stadial of the Bavelian; Zagwijn & De Jong 1984). They would have an age slightly younger than the Jaramillo Subzone (0.97-0.90 My), the latter which correlates with the Bavel Interstadial (the first interstadial of the Bavelian) according to Zagwijn & De Jong (1984). This age would be in accordance with the advanced evolutionary stage of the *M. meridionalis* molars from Dorst-Surae.

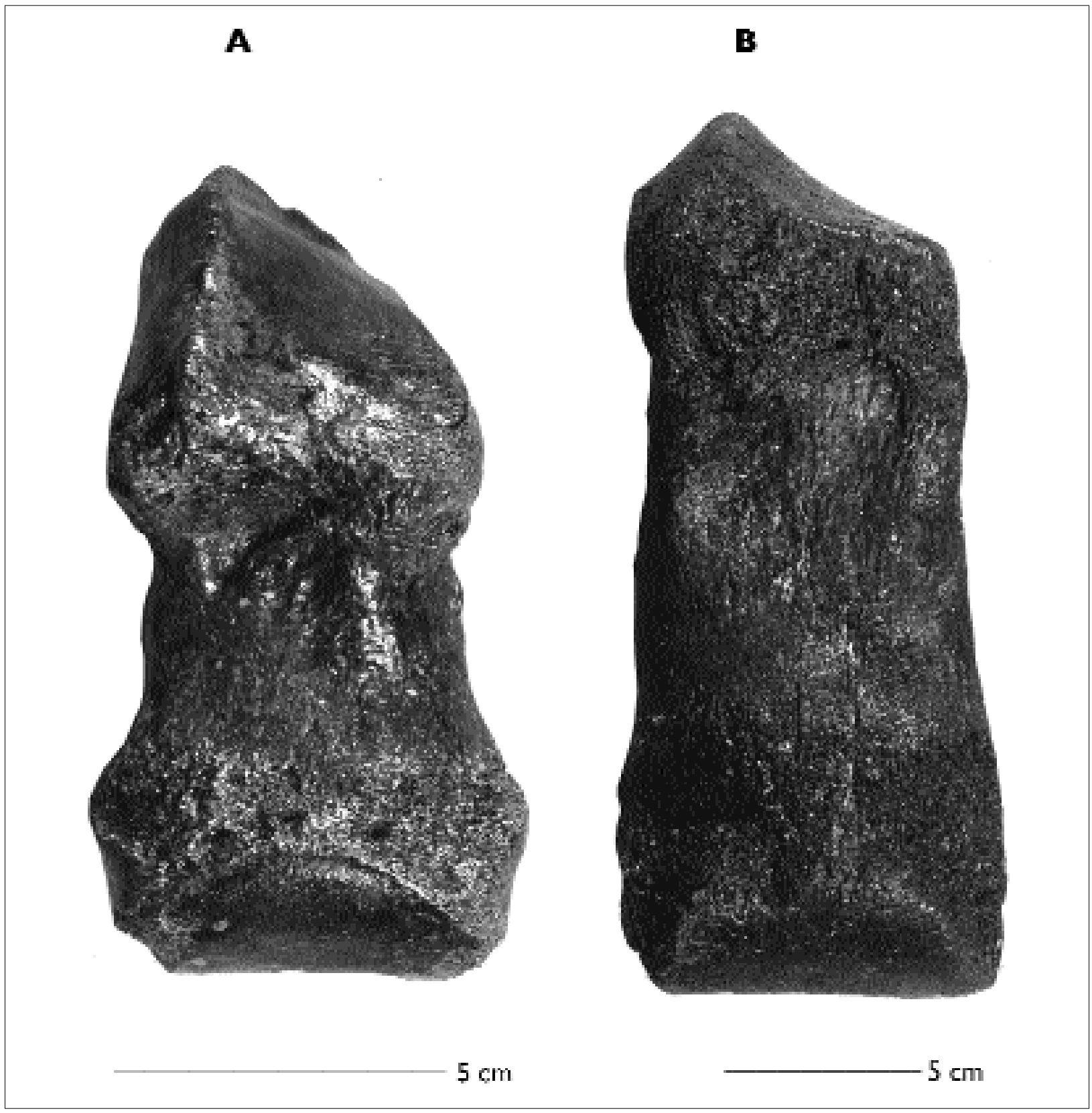

Figure 4 Metacarpus III dex. of *A. arvernensis* (**A** Coll. NNM no. St-119327) and *M. meridionalis* (**B** Coll. NNM no. St-145585), both dredged up from the Oosterschelde Estuary and both shown in anterior view. Note the steeper inclination of the facets for articulation with the magnum and uncinatum and the wider protrusion of the distal and proximal epiphyses in *Anancus*.

From the same pit at Dorst, Van Kolfschoten (1990) described one m3 (Coll. NNM, St-85531) and attributed this to *Elephas antiquus*. Our examination of St-85531 revealed that Van Kolfschoten misidentified the molar: it is not an m3 but a very worn-down remnant of a left m1 or m2. The maximum width (7.2 cm), the lamellar frequency of 5.1, and the enamel thickness (1.9-3.1 mm) all fall within the range of a m2 of *M. meridionalis* according to Maglio (1973).

Lister (1993) places the *M. meridionalis/M. trogontherii* boundary at 0.7-0.6 My. The

Dorst-Surae *M. meridionalis* are probably the youngest dated fossils of this species in The Netherlands, though some of the North Sea material may be younger or equivalent in age with the Dorst-Surae mammoths.

Elephas antiquus

The straight-tusked elephant, *Elephas antiquus*, is well known from temperate European interglacials, especially from the late Middle and Late Pleistocene. Several finds are recorded from The Netherlands and the North Sea. Their geological age is not always clear. Most of the finds are from below the water level of the sea or from dredging operations alongside the great rivers, e.g. the rivers Rhine and IJssel. Roding (1953) described some molar fragments of *E. antiquus* from the Needse Berg (Neede, Province of Gelderland). The scarce remains, which have been found *in situ*, originate from Middle Pleistocene sediments, which are placed in the Holstein Interglacial. According to Van Kolfschoten (1988) it is not clear if the elephant remains from the Neede site belong to *E. antiquus* or *M. meridionalis*. One of the fragments is rather brachyodont. Van Kolfschoten (1981) mentioned some molar fragments of *E. antiquus* from the Middle Pleistocene ice-pushed ridge near Rhenen (Prov. of Gelderland). From the *in situ* site Belvédère near Maastricht (Province of Limburg), Van Kolfschoten (1988) mentioned the straight-tusked elephant of Maastricht-Belvédère-2 and -4, which are placed in the early Saalian (late Middle Pleistocene).
A molar of *E. antiquus* is known from dredging operations in the floodplain of the river IJssel near Giesbeek (Province of Gelderland). It originates probably from the same sediments in which the Late Pleistocene *Hippopotamus incognitus* was recovered (Mol 1993). From the Maasvlakte, an artificial peninsula on the coast of the Province of Zuid-Holland, *E. antiquus* is mentioned by Mol (1994). Mol (1994) suggests a Late Pleistocene (Eemian) age for *E. antiquus*.

Some superb *E. antiquus* remains are found in the collections of the Koninklijk Zeeuwsch Genootschap der Wetenschappen, stored in the Zeeuws Museum at Middelburg. One large hemi-mandible with the m3, and some extremely large, heavily built postcranial remains, which were trawled by fisherman from the mouth of the Westerschelde, are stored in the collections. From the same Schelde Estuary a very large humerus, also heavily built, attributed to *E. antiquus*, is stored in the NNM at Leiden. Again from the Westerschelde, the Late Pleistocene *Hippopotamus incognitus* is known. A Late Pleistocene age is inferred, based on the occurrence of the latter species and on the state of fossilization of the Westerschelde material. The material is characterised by a low density and weak mineralisation.

The Eemian fauna of Haerst (Province of Overijssel) includes, amongst others, *E. antiquus* and *H. incognitus*. Again from this site, sampled by a dredging operation, only proboscidean molars are known of the straight-tusked elephant. It is the northernmost occurrence of *E. antiquus* in The Netherlands.

Hooijer (1984) described a fragment of *E. antiquus* (then called *E. namadicus*) that was trawled from the bottom of the North Sea. Since then more material has been collected. This material is stored in private collections. So far one mandible with an m3 and four isolated molars of *E. antiquus* have been recognised from the Southern Bight of the North Sea. The state of preservation is the same as usual in the Late Pleistocene terrestrial mammal remains from the North Sea and the Westerschelde, that is, low density and weak mineralisation. The geological age is unknown. However, we suggest a late Middle or Late Pleistocene age. If the remains of *E. antiquus* from the North Sea originate from Eemian deposits, they might indicate a land connection of the British Isles with the continent. *E. antiquus* is well known from various sites in the British Isles and the

Figure 5 The same specimens as in Figure 4, here shown in lateral view. Note the relatively more proximally extending distal joints, the steeper proximal articulation facet and the more anteroposteriorly protruding epiphyses in *Anancus* (**A**) as compared to *Mammuthus* (**B**).

continent with an Eemian age (Sutcliffe 1985). As already noted above, the molar from Dorst-Surae, described by Van Kolfschoten (1990: fig. 6) as *E. antiquus*, with an Early Pleistocene age (Bavelian), should be attributed to *M. meridionalis*. Therefore, *E. antiquus* should be removed from the fauna list of Dorst-Surae. There is no evidence that *E. antiquus* was already present in The Netherlands during the Early Pleistocene.

Mammuthus primigenius

Proboscidean remains most frequently recovered from the North Sea bottom are those of

the woolly mammoth (Mol 1989, 1991). Thousands of fossils have been collected so far. Van Essen & Mol (1996) give measurements of some dental elements of *M. primigenius* for comparison with the *M. meridionalis* teeth. *M. primigenius* is amongst the most abundant species of the Weichselian Mammoth Fauna from the North Sea. This fauna includes: *Homo sapiens*, *Castor fiber*, *Canis lupus*, *Vulpes vulpes*, *Ursus spelaeus*, *Ursus arctos*, *Crocuta crocuta spelaea*, *Panthera leo spelaea*, *Mammuthus primigenius*, *Equus caballus*, *Equus hydruntinus*, *Coelodonta antiquitatis*, *Sus scrofa*, *Megaloceros giganteus*, *Alces alces*, *Cervus elaphus*, *Capreolus capreolus*, *Rangifer tarandus*, *Ovibos moschatus*, *Bison priscus* and *Bos primigenius*.

Mammal remains attributable to these taxa originate from the Brown Bank or Brown Ridge, and are characterized by a low density and weak mineralisation. The state of preservation is in most cases excellent. Most of the material is winnowed from the seabed by marine currents, and depending on the time they were lying on the sea bottom the fossils are overgrown to various degrees with bryozoans and barnacles. Unfortunately, to date, there are no ^{14}C datings available of the Late Pleistocene terrestrial mammal material from the North Sea. Some of the above listed species therefore could have an Early Holocene age (Van Kolfschoten & Laban 1995). The extensive collection of *M. primigenius* material (the largest collection is to be found in the NNM) shows that all ontogenetic stages are represented and also that the size variability is considerable. Some of these remains are very small and may represent the latest populations before this species became extinct in Western Europe.

M. primigenius remains have also been recovered from many sites onshore, though large bone accumulations like those occurring in Siberia are not known from The Netherlands. One of the earliest finds of *M. primigenius* in The Netherlands is that of a male skull of an adult individual. Age assessment according to the dental criteria set up by Laws (1966) gives an estimated age of 43 ± 2 AEY for this individual. ^{14}C dating carried out at Utrecht University gave an absolute age of 31,000 ± 400 yBP (UtC-4551). This skull was found after a flooding of the River Linge near Heukelum (Province of Zuid-Holland) in 1820. The skull was described by Van Marum (1824) and by Cuvier (1834). The history of this early find, which is now in the Teylers Museum at Haarlem, was described by Mol *et al*. (1995, 1996). In the same paper most of the skulls of woolly mammoth stored in Dutch museums are listed. Two are well preserved and have been ^{14}C dated.

The first one is a superb skull with tusks and mandible with complete dentition. It was dredged from a depth of 12 m below the water level in the floodplain of the River IJssel near Olburgen (Province of Gelderland). The skull belonged to a 40 AEY old and very small female individual. Its estimated shoulder height is less than 250 cm. A ^{14}C age of 22,160 ± 260 yBP (UtC-4550) was obtained for this specimen.

The second specimen is a nice, slightly damaged cranium, the mandible missing, of an old bull, which was brought to daylight by divers in the artificial lake 'De Groene Heuvels' near Borgharen (Province of Gelderland) in 1994. The ^{14}C dating results for this specimen are 38,900 ± 900 yBP (UtC-3621, Thijs van Kolfschoten, personal communication 1996). An accumulation of many hundreds of Weichselian woolly mammoth bones was recovered in the 1960's in the floodplain of the River Meuse near Gewande, north of 's-Hertogenbosch (Province of Noord-Brabant). The Gewande collection, which belongs to one of the best in The Netherlands, was stored in the Institute of Earth Sciences of Utrecht University, and was recently moved to the NNM (Naturalis). Unfortunately, the collection was never studied in detail. A partial ske-

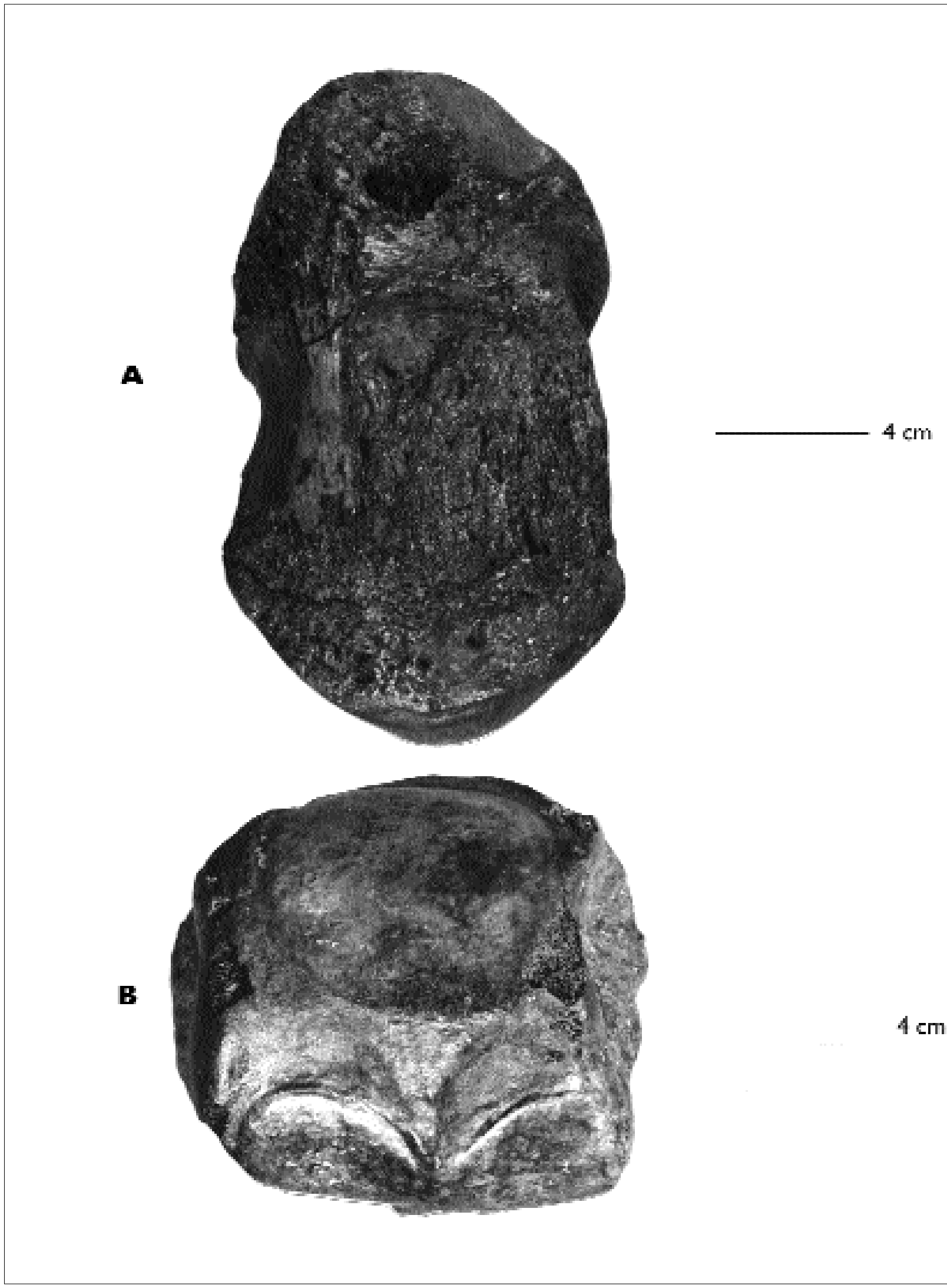

Figure 6 **A** Metacarpus V sin. of *Mammuthus meridionalis* (Coll. NNM no. St-119044), lateral view. **B** Metacarpus II sin. of *Mammuthus meridionalis* (Coll. NNM no. St-145901), distal view. Anterior side is up. Note the pointed profile of the distal articulation surface (**A**) and the presence of distinct fovea on this surface (**B**) .

leton is known from Gewande. About 27 remains, mainly large bones and some footbones, were attributed by Mol (1984) to one and the same individual, a relatively young female. A well preserved skull of a large old male from Gewande was published and figured by Mol (1992) when he compared it with another interesting, pathological skull of a woolly mammoth. This latter skull, including the mandible, was dredged from a gravelpit at Valburg(Province of Gelderland). The molars in the upper and lower jaw (M3 sin. and dex. and the m3 dex.) show that we are dealing with a skull of an old individual with an estimated age of 53 ± 2 AEY. The dentition is anomalous: the m3 in the left lower jaw is missing. As its alveole is worn and the crown of the M3 sin. is considerably higher than that of the M3 dex. (the difference is 110 mm) it can be deduced that the left m3 was lost *in vivo*.

In situ sites of *M. primigenius* are very rare in The Netherlands. Van der Meulen (1991) described remains that were found in a construction pit near Grou (Province of Friesland) in the northeastern part of The Netherlands. Remains of Pleistocene mammals are very rare in the northern provinces. According to Boekschoten (1965) they are almost completely absent in the Saalian and Weichselian deposits of the northern Netherlands. The *in situ* finds of Grou were situated in Early Weichselian sediments, deposited in shallow fresh water.

Remains of woolly mammoths were excavated at Orvelte (Province of Drenthe) during a rescue excavation covering 80 square metres. The remains represent at least three, and perhaps four individuals. Most of the excavated material, amongst others the mandible with both m3's and many cranium fragments, was attributed to one single individual: a bull approximately 46 AEY old and with an estimated shoulder height of 280 cm (Mol & Van Kolfschoten 1993, Van Kolfschoten & Mol 1993). The tip of a tusk, broken off before fossilization, as well as a lower m1 and a fragmentary m2, is assigned to a female individual. The molars indicate an age of about 15 AEY. A fragmentary humerus was attributed to a juvenile individual with a shoulder height of approximately 90 cm. To date, the Orvelte fossils are the only *in situ* mammoth remains from The Netherlands that have been ^{14}C dated. The dating results are 46,800 +1500/-1250 yBP (GrN-18780, Van der Sanden 1993).

The oldest *M. primigenius* remains in The Netherlands are known from a sand pit called 'De Fransche Kamp' at Wageningen (Province of Gelderland). According to Van Kolfschoten (1988) the mammoths from this site should be placed in the Early Saalian and might have an age of approximately 250,000 year.

At Maastricht-Belvédère-2, *M. primigenius* is found together with *Equus* sp., *Coelodonta antiquitatis* and *Cervus elaphus* (Van Kolfschoten 1988). A nearly complete curved and spirally twisted tusk with a length of three metres and some molars from the same specimen were collected in situ. According to Van Kolfschoten (1988), Maastricht-Belvédère-2 is of an Early Saalian age, probably the same as that of Wageningen-'Fransche Kamp'. The Maastricht-Belvédère-2 mammoths lived in a tundra-steppe environment with cool climatic conditions (Van Kolfschoten 1988). Maastricht-Belvédère-5, of an Early Weichselian age, also has *M. primigenius* together with woolly rhino in its fauna. According to Van Kolfschoten (1988) the Maastricht-Belvédère-5 fauna composition points to a tundra-steppe environment and a cold and rather dry climate during the period in which the fauna lived.

COMPARISON OF MANUS AND PES BONES OF *ANANCUS* AND *MAMMUTHUS*

Postcranial parts attributed to *A. arvernensis* are considerably smaller than those of most other Pleistocene and recent proboscideans

Table 1 Size measurements (in mm) of metacarpalia of *A. arvernensis* and *M. meridionalis* from the Oosterschelde Estuary and the North Sea, present in the NNM collection and the Collection Mol. The measurements are defined in Appendix 1(1).

1a) Metacarpus II						1b) Metacarpus III		
M. meridionalis					*A. arvernensis*	*M. meridionalis*		*A. arvernensis*
NNM St 145341 dex.		NNM St 145501 sin.	Coll. Mol 1644 sin. (juv., dist. epiph. gone) (North Sea)	Coll. Mol 1537 dex. (North Sea)	NNM St. 118412 Mc. II dex. (juv., dist. epiph. lacking)	NNM St 145585 Mc. III dex.		NNM St 119927 Mc. III dex.
MC1	208 (mm)	201	208	187+	91+	MC1	243	139
MC2	79	97	96	97	59	MC2	87	60
MC4	110	-	128	127	64	MC4	110+ (damaged)	80
MC5	77	85	81	82	53	MC5	85	51
MC6	59	81	73	75	37	MC6	70	40
MC7	97	113	ca. 99	ca. 98	ca. 61	MC7	106	72
MC8	88	101	104	106	-	MC8	105	63
MC9	56	50	55	-	-	MC9	58	52
Ratio						Ratio		
MC1/MC2	2.63	2.07	2.17	-		MC1/MC2	2.79	2.32
MC1/MC6	3.53	2.48	2.85	-		MC1/MC6	3.47	3.48
MC1/MC8	2.36	1.99	2.00	-		MC1/MC8	2.31	2.21
MC1/MC9	3.71	4.02	3.78	-		MC1/MC9	4.19	2.67
MC8/MC9	1.57	2.02	1.89	-		MC8/MC9	1.81	1.21

1c) Metacarpus IV			1d) Metacarpus V				
M. meridionalis			*M. meridionalis*				*A. arvernensis*
NNM St.118853 Mc. IV sin.		Coll.Mol 1066 Mc. IV dex. (juv., dist. epiph. lacking) (North Sea)		NNM St 119041 Mc.V sin.	NNM St 118876 Mc V dex.	Coll.Mol 2020 Mc.V sin. (North Sea)	NNM St 118902 Mc V sin.
MC1	223	147+	MC1	201	182	189	129
MC2	95	92	MC2	156	153	150	102
MC4	119	107	MC3	94	88	ca. 96	75
MC5	80	84	MC4	113	103	114	85
MC6	66	63	MC5	84	65	91	65
MC7	109	ca. 94	MC6	104	81	109	70
MC8	104	93	MC7	97	84	101	71
MC9	69	-	MC8	115	95	111	83
Ratio			MC9	53	56	72	43
MC1/MC2	2.35	-	Ratio				
MC1/MC6	3.38	-	MC1/MC3	2.14	2.07	ca. 1.97	1.72
MC1/MC8	2.14	-	MC1/MC6	1.93	2.25	1.73	1.84
MC1/MC9	3.23	-	MC1/MC8	1.75	1.92	1.70	1.55
MC8/MC9	1.51	-	MC1/MC9	3.79	3.25	2.62	3.00
			MC8/MC9	2.17	1.70	1.54	1.93

(excluding the pygmy elephants from the Mediterranean islands). A complete *A. arvernensis* skeleton was found in 1826 by Filipo Nesti near Montecarlo (Val d'Arno, Tuscany, Italy) and is now exhibited in the Geological and Paleontological Museum in Florence. Osborn (1936: fig. 595) presented a 1:100 scaled reconstruction of *A. arvernensis*. He gave a shoulder height of 2550 mm and a total body length (excluding tusks) of 4.2 m. The *A. arvernensis* molar remains from the Oosterschelde seem particularly small when compared with specimens cited by Tobien (1973). Schreuder (1944) also reached this conclusion after comparison with data from the older literature. The elements of manus and pes are particularly suited to demonstrate the relatively small size, as they are often

Table 2 Size measurements (in mm) of carpalia of *A. arvernensis* and *M. meridionalis* from the Oosterschelde Estuary and the North Sea, present in the NNM collection and the Collection Mol. The measurements are defined in Appendix 1 (2-7).

(Ia) Lunatum				(IIb) Uncinatum		(Ia) Magnum			
	M. meridionalis				*M. meridionalis*		*M. meridionalis*		*A. arvernensis*
	NNM St 401383 lunatum dex.	NNM St 401539 sin.	Coll Mol 2021 sin. (very old individual) (North Sea)		NNM St 401326 Uncinatum sin.		NNM St. 145709 Magnum dex.	Coll Mol 1674 dex (North Sea)	Coll Mol 2006 Magnum sin (Thornton Bank)
L1)	141	141	ca. 151	U1)	129	M1	188	163	107
L2)	132	151	136	U2)	113	M2	138	160	84
L3)	129	ca. 141	119	U3)	110	M3	ca. 137	ca. 132	73
L4)	140	158	ca. 168	U4)	132	M4	90	98	57
L5)	93	98	114	U5)	112	M5	129	115	82
L6)	179	162	196	U6)	113	M6	149	159	97
L7)	157	164	173	U7)	116	M7	135	124	79

(Id) Trapezium		(IIe) Trapezoideum			(If) Pisiforme		
	A. arvernensis	*M. meridionalis*		*A. arvernensis*		*M. meridionalis*	
	NNM St 401477 Trapezium dex	Coll. Mol 1940 Trapezoideum dex. (North Sea)		NNM St 401409 Trapezoideum sin.		NNM St 145698 pisiforme dex.	Coll Mo 1910 dex. (North Sea)
T1)	69	Td1)	102	84	P1)	179	145
T2)	51	Td2)	59	56	P2)	113	76
T3)	29	Td3)	139	96	P3)	96	80
T4)	56	Td4)	70	57	P4)	ca. 69	ca. 41
T5)	53	Td5)	80	39	P5)	60	72
T6)	37	Td6)	105	77	P6)	88	82
T7)	55	Td7)	68	53	P7)	63	44

found intact. The collection of the NNM contains the following elements from the Oosterschelde that could be attributed to *A. arvernensis*: a juvenile right metacarpus II lacking the distal epiphysis (no. St-118412); a right metacarpus III (no. St-119327); a left metacarpus V (no. St-118902); a right trapezium (no. St-401477); a left trapezoideum (no. St-401409), and a right astragalus (no. St-140740). Furthermore, there is a left magnum of *A. arvernensis* originating from the Thornton Bank in the collection Mol (no. 2006).

M. meridionalis hand and foot bones are more frequently dredged from the Oosterschelde and the North Sea. *M. meridionalis* equivalents of the available *A. arvernensis* elements are in the NNM and Mol collections, except for the trapezium. In addition, there are one or more *M. meridionalis* specimens of the following elements in the same collections: metacarpus IV, lunatum, uncinatum, pisiforme, calcaneus and naviculare.

M. meridionalis was one of the largest proboscideans from the Eurasian Pleistocene with a shoulder height of about 4 m. The Nogaisk skeleton in the St. Petersburg Zoological Museum stood 420 cm at the shoulder, that of Georgyevsk in the Stavropol Museum 396 cm. The maximum lengths of the femora are 146 and 143.5 cm respectively (Garutt 1964). Diverse large-sized skeletal parts from East Anglia (Britain) were described by Adams (1877-1881). A complete femur from Mundesley has a maximum length of 150 cm (Adams 1881). An excep-

Table 3 Size measurements (in mm) of tarsalia of *A. arvernensis* and *M. meridionalis* from the Oosterschelde Estuary and the North Sea, present in the NNM collection and the Collection Mol. The measurements are defined in Appendix 1 (8-10).

IIIa) Calcaneus			IIIb) Navicular		
M. meridionalis			*M. meridionalis*		
	NNM Sr 118350 Calcaneus sin.	Coll. Mol 1998 Calcaneus sin. (North Sea)		NNM Sr 401527 Navicular sin.	Coll. Mol 1999 Navic. dex. (North Sea)
C1)	177	176	N1)	86	79
C2)	158	143	N2)	140	ca 175
C3)	146	149	N3)	116	117
C4)	118	110	N4)	176	162
C5)	274	278	N5)	171	ca.155
C6)	151	167	N6)	ca 80	ca. 86
C7)	92	84	N7)	69	63
C8)	143	147	N7a)	56	72
C9)	192	218	N7b)	50	50
			N7c)	46	42

IIIc) Astragalus		
M. meridionalis		*A. arvernensis*
	NNM Sr 104799 Astragalus sin. (North Sea)	Coll. Mol 1999 dex. (North Sea)	NNM Sr 140740 dex
A1)	131	164	90
A2)	145	159	79
A3)	164	198	99
A4)	175	223	122
A5)	132	125	69
A6)	167	ca.208	106
A7)	170	159	74
A8)	104	129	65

tionally complete skeleton from Scoppito, l'Aquila (Italy) was described by Maccagno (1962) and stood 400 cm at the shoulder. The likewise very complete skeleton from Borro al Quercio, Arezzo (Valdarno, Italy) measures 380 cm at the shoulder. It must be noted that it is doubtful whether skeletal parts of *M. trogontherii* can be distinguished from those of *M. meridionalis*. The basis for comparison is relatively small. The nearly complete *M. trogontherii* skeleton from Edersleben in the Spengler Museum at Sangerhausen (Germany) stands about 250 cm at the shoulder (Krutsch 1953; Garutt & Nikolskaja 1988). A male skeleton in the Azov Museum reaches 450 cm at the shoulder according to Garutt & Nikolskaja (1988). This height may be slightly overestimated because the vertebrae have been mounted between the tips of the shoulderblades and therefore the dorsal spines protrude too much above the shoulderblades. A humerus from Mosbach Sande near Wiesbaden (Germany) is 144 cm long, 15 cm longer than the hume-

rus in the Azov skeleton. Since the presence of *M. trogontherii* in the Southern Bight of the North Sea was demonstrated by several teeth, there is a possibility that some postcranial parts from the North Sea referred to here as *M. meridionalis*, were misinterpreted. Also sporadic *E. antiquus* molars have been dredged from the Southern Bight of the North Sea, but their weak degree of fossilization differs from the heavily mineralized bones here attributed to *M. meridionalis*.
Tables 1-3 give the size measurements of the various *A. arvernensis* and *M. meridionalis* metacarpals, carpals and tarsals studied. Unless otherwise stated, the specimens have been dredged from the Oosterschelde. The definitions of the measurements taken are indicated in Appendix 1 (1-10). Not included in the tables are specimens of *Mammuthus primigenius* from the North Sea. These lightly mineralized fossils are usually intermediate in size. Material of the woolly mammoth from the North Sea is much more numerous and will be dealt with in another paper.

Intraspecific variation in the shape of proboscidean (meta)carpals and (meta)tarsals is rather large. Especially the morphological outline of the articulation facets is quite variable. Considering the metapodials, the ratio between length and transverse or anteroposterior diameter seems subject to considerable variation. Compare, for example, the ratios between various measurements of the three metacarpals-II attributed to *M. meridionalis* in Table 1a: especially NNM St-145341 is quite slenderly built as expressed by the relatively high MC1/MC3 and MC1/MC6 ratios. A similar wide range in the length/width ratios is observed in the three metacarpals-V attributed to *M. meridionalis* (Table 1d). The relatively large morphological variation is probably due to the fact that ontogenic development is much constrained by the space left available by the surrounding bones. The large intraspecific morphological variation often hampers the determination of isolated elements to species and even to genus level. In our case the large size difference between the *Anancus* and *Mammuthus* elements facilitates their distinction. As follows from the measurements given in Tables 1-3, the *A. arvernensis* bones in the studied sample are on average between 60 and 70 percent smaller than their equivalents in *M. meridionalis*. Apart from their small size, the metacarpals, carpals and tarsals of *A. arvernensis* are generally speaking characterised by their well delineated and more concave/convex or more inclined proximal and distal articulation facets, when compared to *M. meridionalis* (Fig. 4). Carpals and tarsals of the latter species have overall flatter articulation facets on the proximal and distal surfaces, better suited for the transfer of force but allowing only limited movement. Furthermore, the metacarpals of *Anancus* have comparatively widely protruding distal and proximal terminations, as follows from the relatively low MC1/MC3 ratios, but similar MC1/MC6 ratios as compared to *M. meridionalis* (Tables 1b and 1d).

Of course, the material available to us, especially that of *A. arvernensis*, is too limited to assess intraspecific variation and overlapping morphologies, so that at the moment these remarks cannot be more than general statements. However, there are a few characteristic differences that should be noted. First of all, the distal articulation surface of the *A. arvernensis* metacarpals continue more proximally on the anterior and posterior sides. In sagittal cross section these articulation surfaces describe an almost perfect halfcircle, whereas in *M. meridionalis* metacarpals the cross-sectional outline corresponds with a segment less than twofifth of a circle (Fig. 5). This difference is clearly expressed by the small to very small ratio in *Anancus* between total metacarpal length and the vertical height of the articulation facet (ratio MC1/MC9, Tables 1b, 1d). Also, the articulation facet is not perfectly round but rather pointed in most *Mammuthus* metapodials (Fig. 6). Obviously, *Anancus* metacarpals stood more closely to the ancestral condition where the hinging

movement between metapodials and digits could take place freely, whereas in graviportal limbs of *M. meridionalis* hinging movement had been largely reduced. Another distinction can be made at the proximal articulation surfaces of the metacarpals II and III. The anteroposterior crest dividing the proximal articulation surfaces into two facets (for the trapezoideum and magnum in the Metacarpus II and for the magnum and uncinatum in the Metacarpus III) is clearly sharper in *A. arvernensis* (Fig. 4). Especially the narrow lateral facets for articulation with the magnum and uncinatum, respectively, are more inclined in the latter species. The same holds true for the corresponding medial facet on the distal articulation surface of the magnum, which articulates with the metacarpus II (no uncinatum of *A. arvernensis* is present in the collections). The foot construction of *Anancus arvernensis* seems to have allowed more internal movement, and was probably better adapted to walk over soft soils than the graviportal limbs of *M. meridionalis*.

CONCLUSIONS

Large numbers of proboscidean and other terrestrial mammals have been brought to light as a by-product of trawling in the Southern Bight of the North Sea and the Oosterschelde Estuary. The oldest fauna association from The Netherlands, with *Anancus arvernensis* and *Mammuthus meridionalis* originates from the Oosterschelde Estuary and has an estimated age of around 1.9 My, slightly older than the 1.7 My old Tegelen fauna. A few molars of *Mammut borsoni* from Liessel may be older in age than the Oosterschelde assemblage. A heavily fossilized Early to Middle Pleistocene fauna association originates from the North Sea, mainly from the Deep Water Channel. This material includes the proboscideans *M. meridionalis* and rare *M. trogontherii* fossils. A Late Pleistocene fauna association including abundant remains of *M. primigenius* originates from the Brown Bank and has a light degree of fossilization. Also a few lightly fossilized *E. antiquus* fossils originate from the Southern Bight of the North Sea and the Westerschelde Estuary. Proboscidean material dredged or excavated from sand and gravel pits located on the Dutch alluvial plains are less frequently encountered, though the stratigraphic context is usually better documented. A few mainland localities have yielded *M. primigenius* remains from single individuals. Commonly dredged elements of fossil proboscideans which are complete are the (meta)carpals and tarsals. These elements can be well distinguished in the case of *A. arvernensis* and *M. meridionalis*, due the size difference but also on the basis of morphological grounds.

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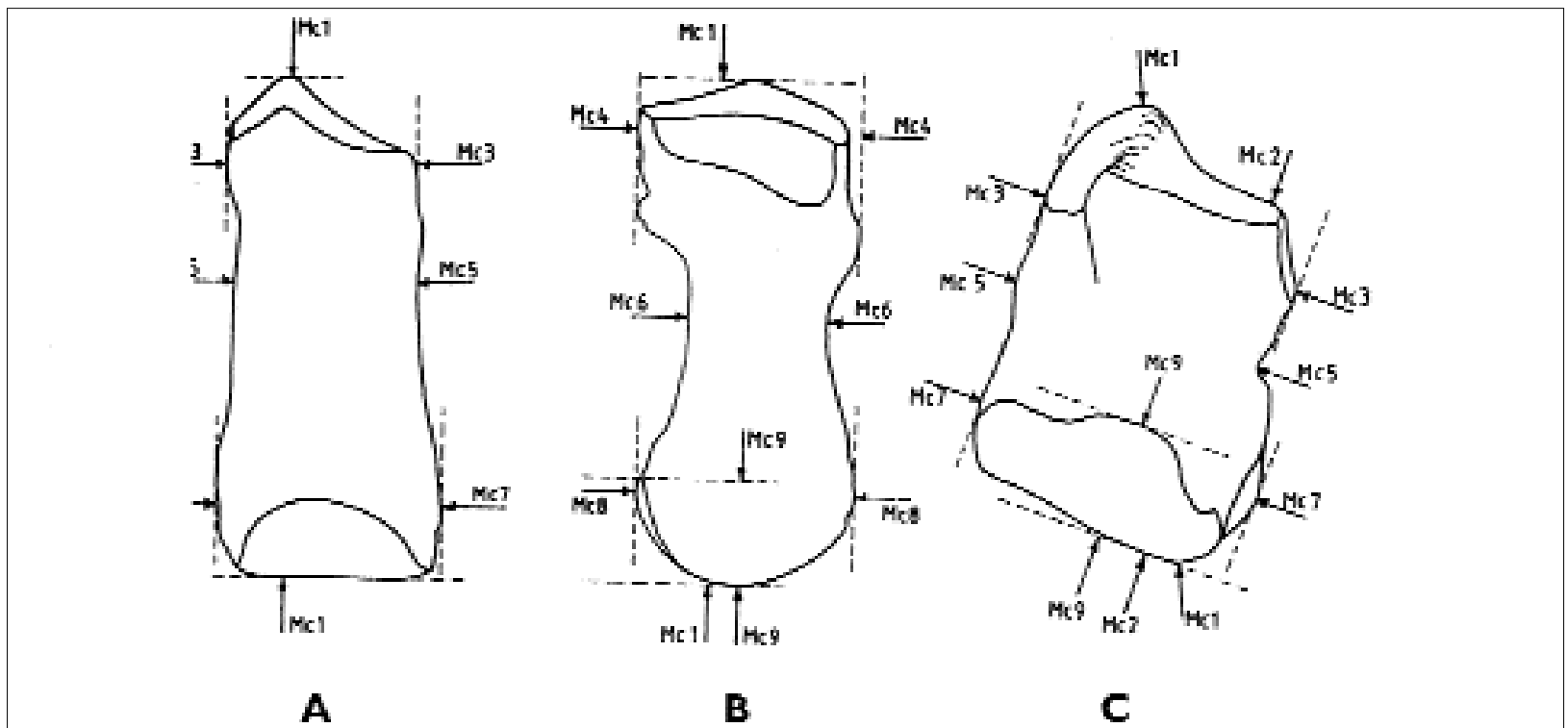
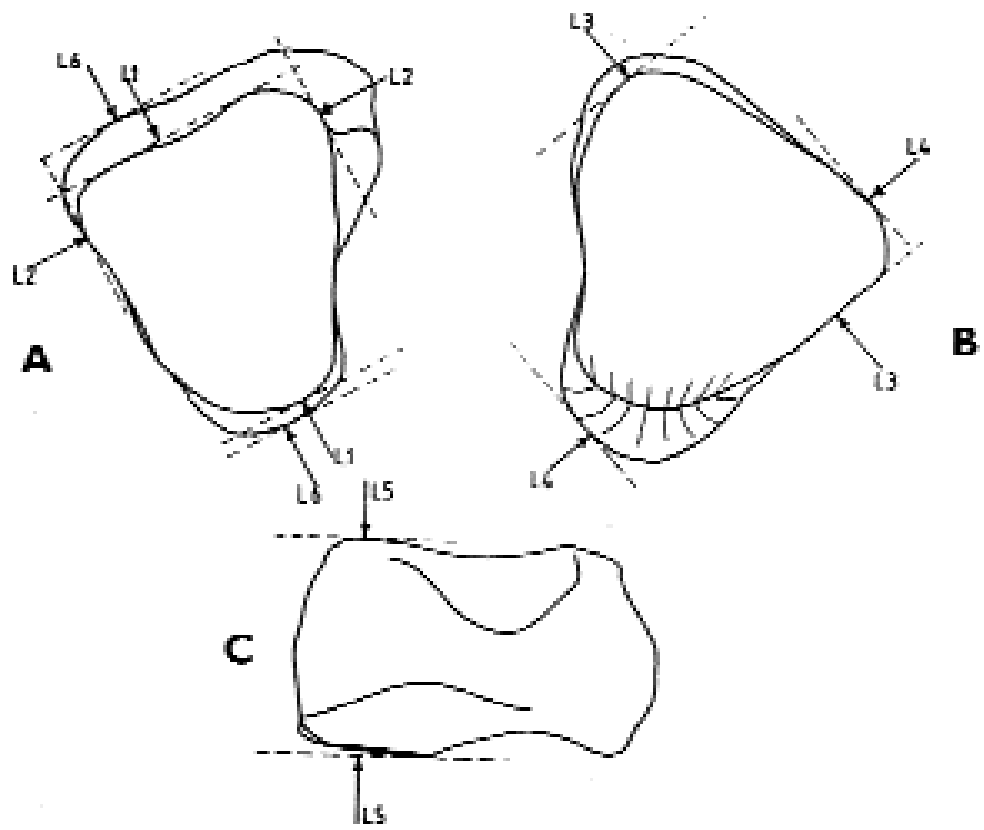
APPENDIX 1 Definition of the size measurements taken on the metacarpalia, carpalia and tarsalia of Tables 1-3. DT = transverse diameter, DAP = anteroposterior diameter.

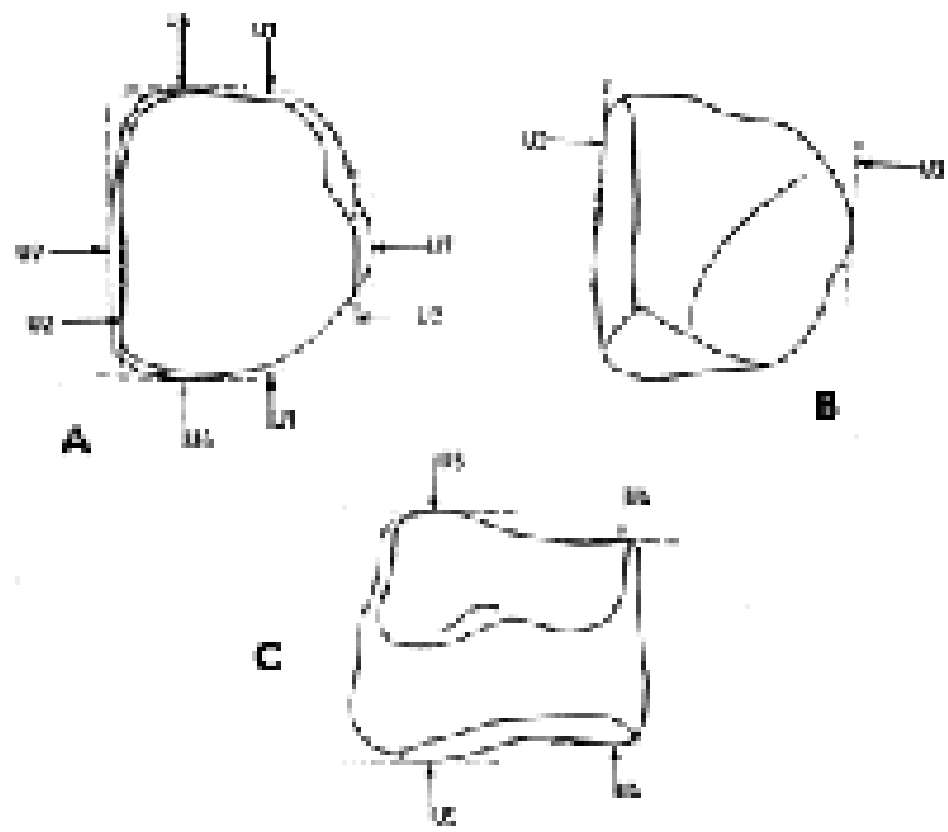


1 Metacarpals. **A** = anterior view of metacarpus III dex.; **B** = lateral view of metacarpus III dex.; **C** = posterior view of metacarpus V sin. MC1 = Maximum length; MC2 = Length between the articulation surfaces (= MC1 except for the metacarpus V); MC3 = DT proximal; MC4 = DAP proximal; MC5 = Minimum DT diaphysis; MC6 = Minimum DAP diaphysis; MC7 = Maximum distal DT; MC8 = Maximum distal DAP; MC9 = Height distal articulation surface (posteriorly).

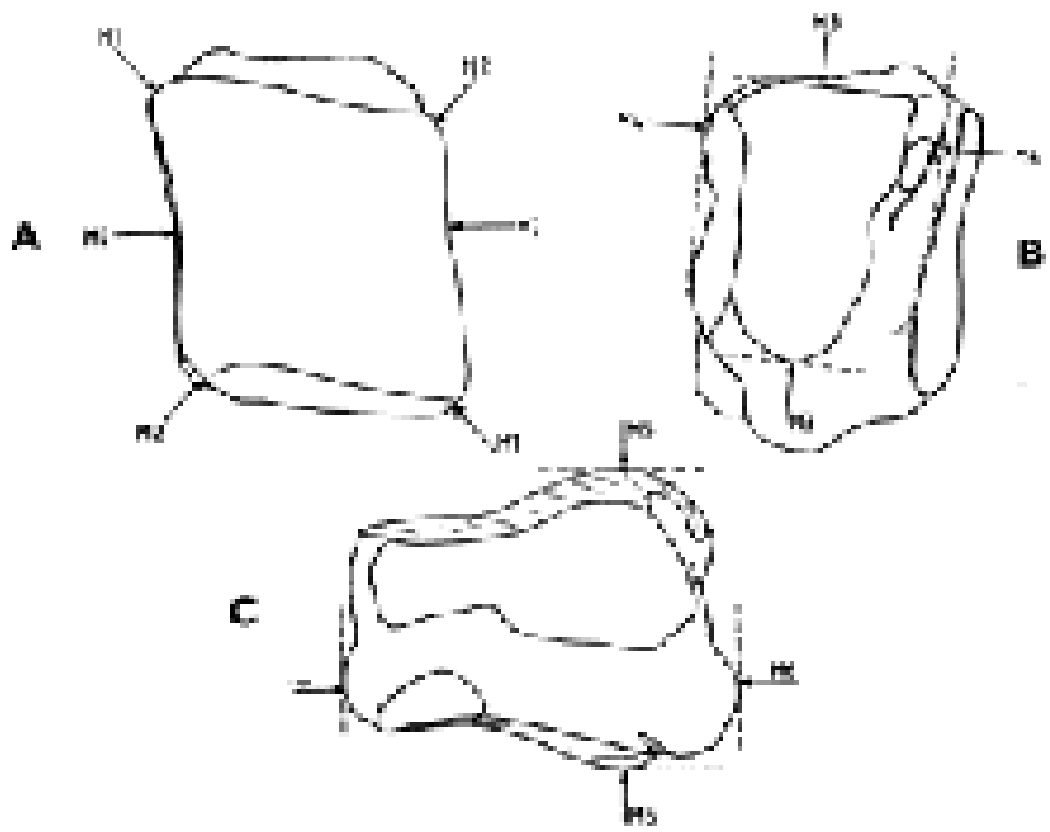


2 Lunatum dex. (= Lunare = Os carpi intermedium). **A** = proximal view (anterior side up); **B** = distal view (anterior side up); **C** = lateral view (anterior side to the right). L1 = DAP proximal articulation facet; L2 = DT proximal articulation facet along anterior border; L3 = DT distal articulation facet; L4 = DAP distal articulation facet; L5 = Maximum height (medially); L6 = Maximum DAP; L7 = Maximum DT.

APPENDIX I (continued)

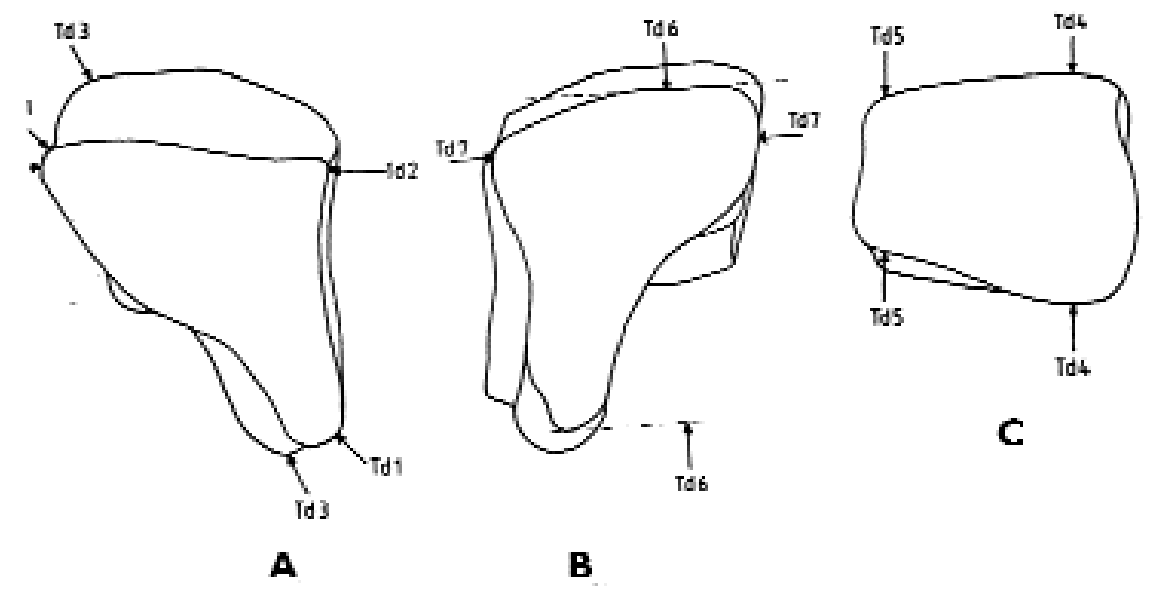


3 Uncinatum sin. (= Uncifo rme = Hamatum = Os carpale quartum). **A** = proximal view (posterior side up); **B** = distal view (anterior side up); **C** = medial view (anterior side to the right). U1 = DAP maximum proximal articulation facet; U2 = DT maximum proximal articulation facet; U3 = Maximum DT distal articulation facets (anteri o rly); U4 = Maximum height anteri o rly; U5 = Maximum height posteri o rly; U6 = Maximum DAP; U7 = Maximum DT.

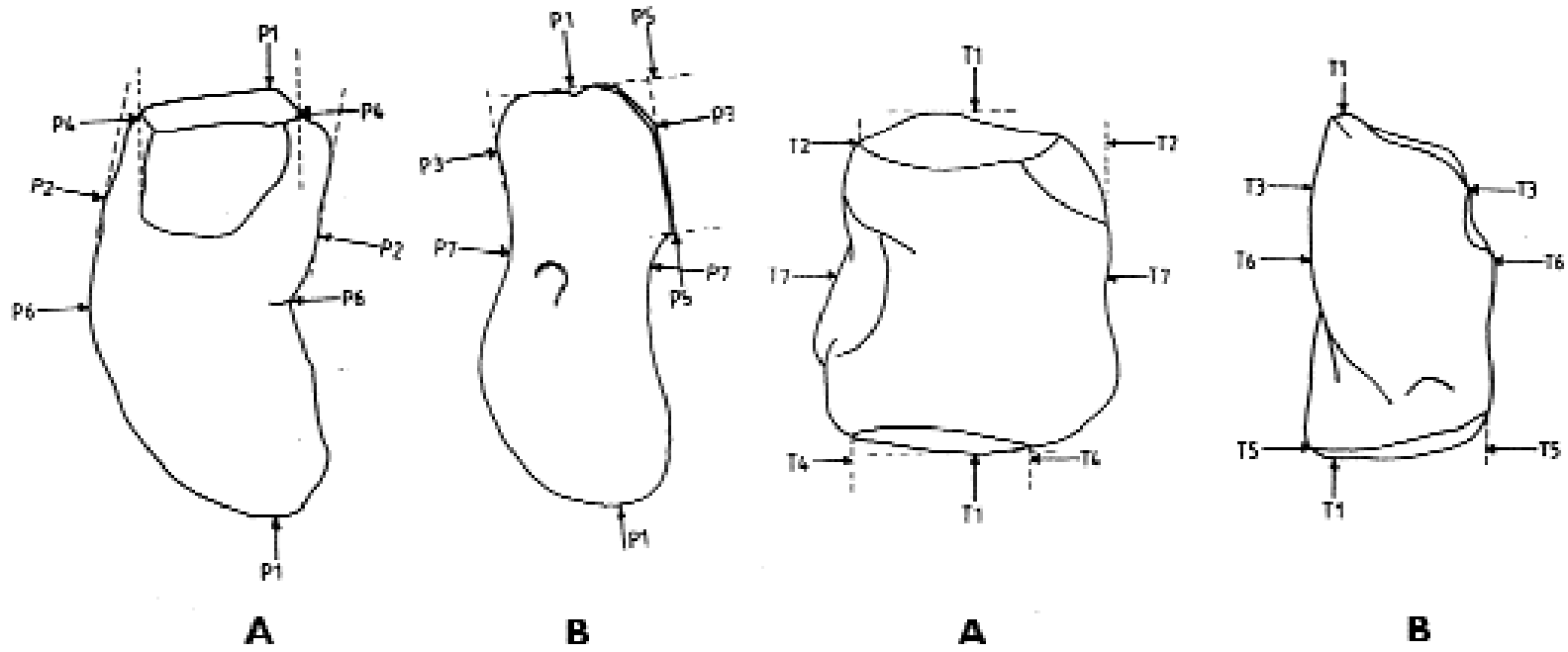


4 Magnum sin. (= Capitatum = Os carpale tertium). **A** = proximal view (anterior side up); **B** = distal view (anterior side up); **C** = lateral view (anterior side to the left). M1 = Greatest diagonal diameter at proximal articulation facet; M2 = Smallest diagonal diameter at proximal articulation facet; M3 = Maximum DAP of distal articulation facet; M4 = Maximum DT of distal articulation facet; M5 = Maximum height; M6 = DAP maximum; M7 = DT.

APPENDIX I (continued)



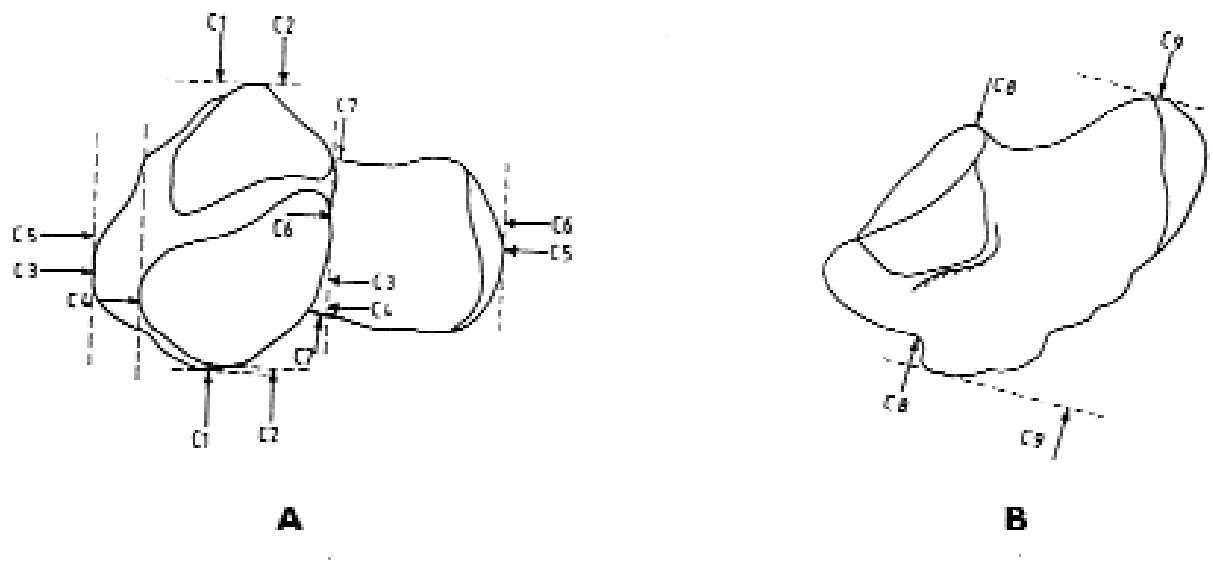
5 Trapezoideum sin. (= Os carpale secundum).
A = proximal view (anterior side up); **B** = distal view (anterior side up); **C** = anterior view. Td1 = Maximum DAP proximal articulation facet; Td2 = DT proximal articulation facet anteriorly; Td3 = Maximum DAP; Td4 = Height anterior surface medially; Td5 = Height anterior surface laterally; Td6 = DAP distal articulation facet for Mc II; Td7 = DT distal articulation facet for Mc II.



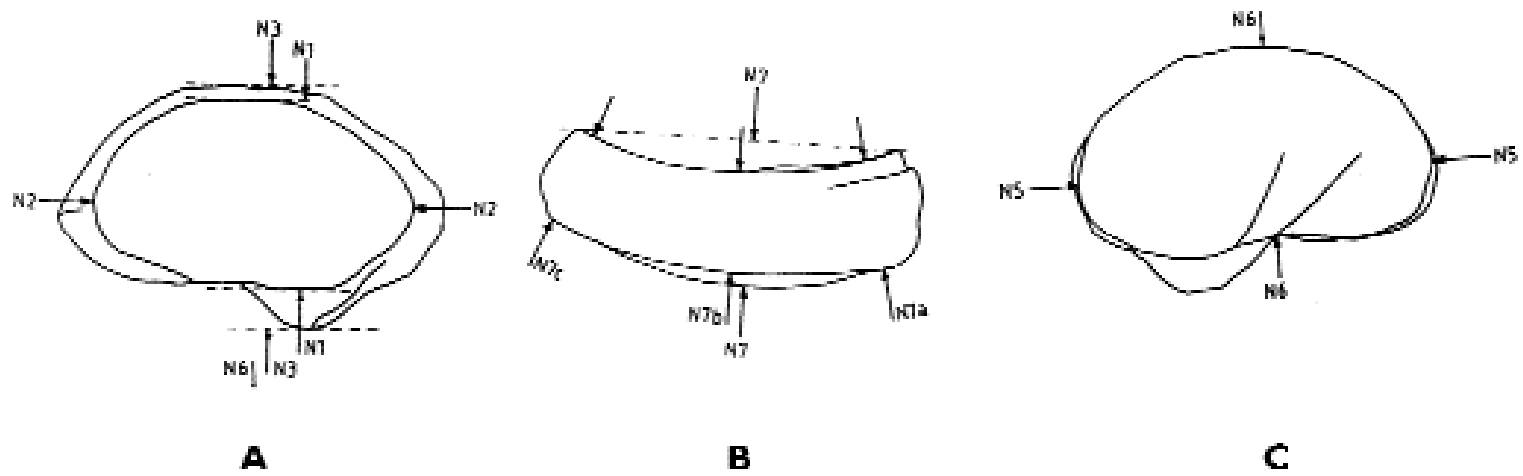
6 Trapezium dex. (= Os carpale primum).
A = lateral view; **B** = posterior view. T1 = Maximum Length; T2 = DAP maximum proximal articulation facets; T3 = DT maximum proximal articulation facets (posteriorly); T4 = DAP maximum distal articulation facet (Mc I); T5 = DT maximum distal articulation facet; T6 = DT maximum midshaft (over tuberosity); T7 = DAP midshaft.

7 Pisiforme dex. (= Os carpi accessorium).
A = medial view; **B** = posterior view. P1 = Maximum length; P2 = DAP maximum proximal; P3 = DT maximum proximal; P4 = Maximum DT proximal articulation facet; P5 = Maximum DAP proximal articulation facet; P6 = Minimum DAP midshaft; P7 = Minimum DT midshaft.

APPENDIX I (continued)

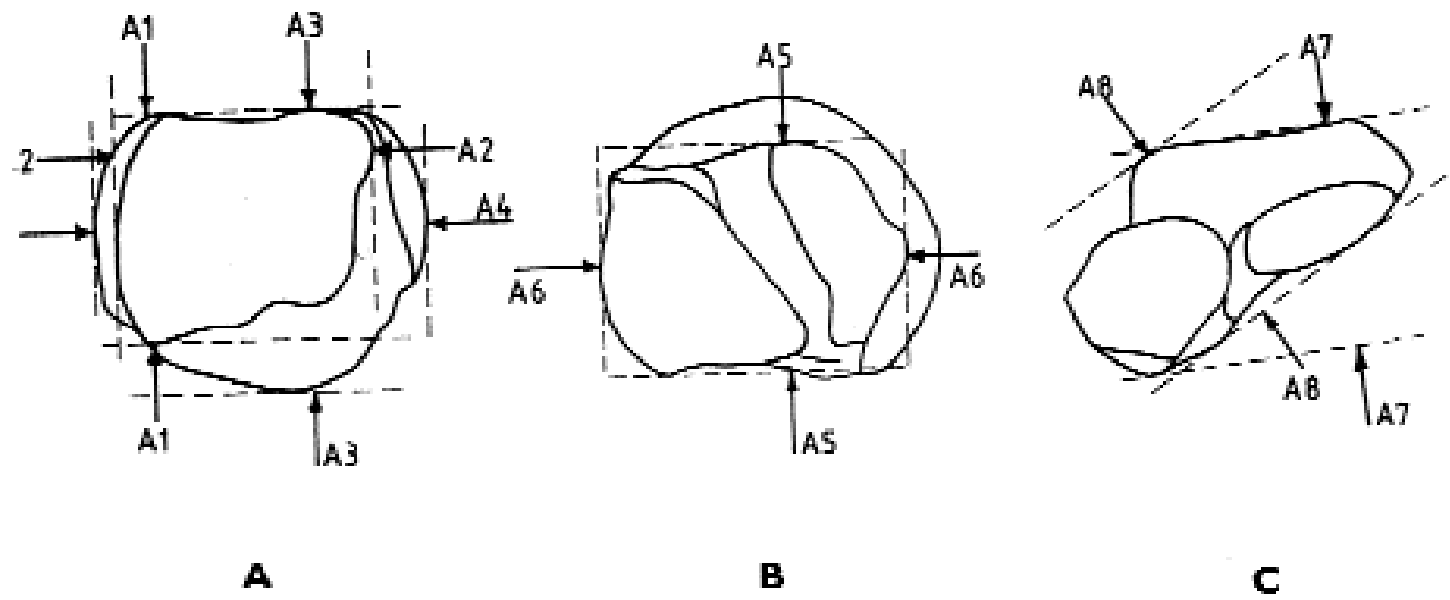


8 Calcaneus sin. (= Os tarsi fibulare). **A** = proximal view; **B** = lateral view. C1 = Maximum DT proximal epiphysis; C2 = Maximum DT proximal articulation facets; C3 = DAP proximal epiphysis; C4 = DAP proximal articulation facet; C5 = Greatest DAP calcaneum; C6 = DAP tuber calcanei; C7 = Minimum DT tuber calcanei; C8 = Maximum height articulation facets (in life position); C9 = Maximum height calcaneum (in life position).



9 Naviculare sin. (= Os tarsi centrale). **A** = proximal view (anterior side up); **B** = anterior view; **C** = distal view (anterior side up). N1 = DAP proximal articulation facet of astragalus; N2 = DT proximal articulation facet of astragalus; N3 = DAP maximum proximal articulation facets; N4 = DT maximum; N5 = DT maximum distal articulation facets; N6 = DAP distal articulation facets along the centre of the naviculare; N7 = Maximum height naviculare; N7a = Height navicular (anteriorly) medially; N7b = Height navicular (anteriorly) centre; N7c = Height navicular (anteriorly) laterally.

APPENDIX 1 (continued)



10 Astragalus dex. **A** = proximal view; **B** = distal view; **C** = posterior view. A1 = DAP maximum proximal articulation facet (caput tali); A2 = DT maximum proximal articulation facet; A3 = DAP maximum; A4 = DT maximum; A5 = DAP maximum distal articulation facets (with calcaneus); A6 = DT maximum distal articulation facets (with calcaneus); A7 = Maximum height (life position); A8 = Maximum height (with distal articulation facets in horizontal position).

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