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FOSSIL ODOBENIDAE IN SOME DUTCH COLLECTIONS (MAMMALIA, CARNIVORA)

D. P. BOSSCHA ERDBRINK & P. J. H. VAN BREE

Prinses Marielaan 27, 3743 JA Baarn, the Netherlands

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Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam, P.O. Box 20125, 1000 HC Amsterdam, the Netherlands

ABSTRACT

Eight cranial and five postcranial fossil specimens are described and identified as remains of Odobenidae. Two of these (one, from Rhenen, certainly, and the other tentatively) are ascribed to the fossil, Early Pleistocene *Odobenus huxleyi* (Lankester, 1865); the others to the recent form, *O. rosmarus* (L.), while it appears possible to ascribe two of these even to the Atlantic subspecies *rosmarus*. Some critical remarks are made regarding the systematic value of the genera *Trichecodon* and *Alachtherium* and the species *antverpiensis* (Rutten, 1907). The latter may eventually prove to be identical with *huxleyi*.

INTRODUCTION

In the course of the last years a large and varied assortment of fossil terrestrial mammals from the bottom sediments of the southern part of the North Sea has become known. Descriptions appeared in papers by several authors (Bosscha Erdbrink, 1967, 1981, 1982, 1983a, b, c, 1985; Hooijer, 1960, 1984a, b, 1985; Louwe Kooymans, 1972; Kortenbout van der Sluys, 1971, 1972; Martin, 1941; Mulder, 1973; and others). Few records exist of fossil remains of marine mammals such as seals and walruses from the same area. One of us (Erdbrink, 1972) shortly described a walrus skull recovered somewhere West of the Brown Ridge, now in the Flonk collection (Museum Flehite, Amersfoort). This particular region, part of the bottom of the North Sea between Smith's Knoll and the Brown Ridge (fig. 1), consists of a number of longitudinal gullies and deeps running in a general South to North direction. There evidently occur a number of outcrops in the sides or slopes of these channels from which, now and again, fossil bones are washed or worked out through different causes. These are sometimes caught in the nets dragged along the bottom by trawlers fishing for flat-fish. Given the variation in depth of the several gullies (inset, fig. 1b), it is not unreasonable to expect mixtures of fossil bones of varied age to come up from the deeper channels.

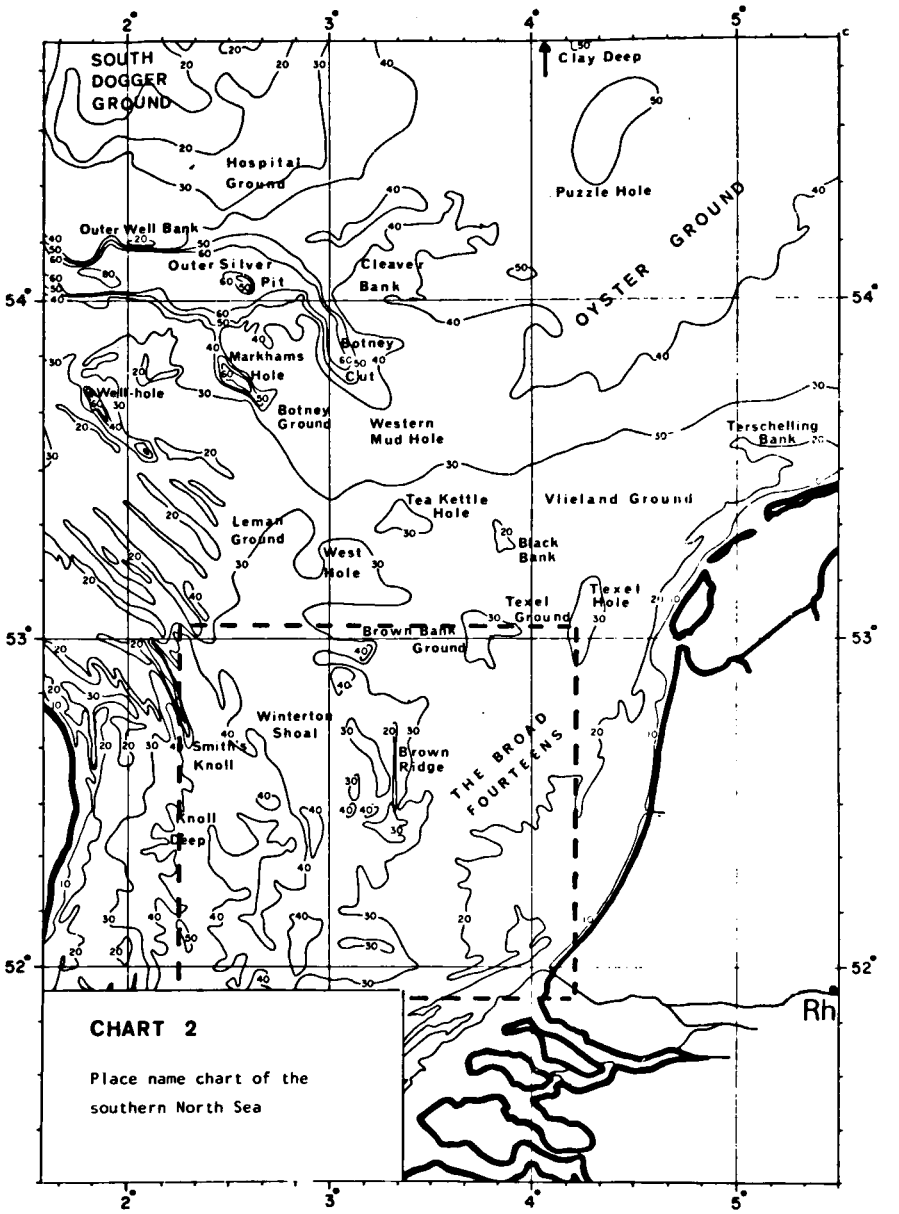

Fig. 1a (after Creutzberg). General area in which the described fossils were found. Rh = the Grebbeberg near Rhenen on the Rhine. Depths in meters.

According to Mulder (op. cit.), some of the more accurately-minded fishermen ventured the information that, especially around four locations (marked with black stars on fig. 1b) within the already mentioned area, namely at 52°29′N/ 3°25′E, 52°25′N/ 2°50′E, 52°8′N/3°8′-10′E and 51°56′N/2°45′E, there exist abundancies of fossil bones. It appears from a paper by Zagwijn (1983) that a schematic profile, using the results of a number of borings, can be reconstructed from South to North and approximately in the area under consideration, that to the West of the Brown Ridge. An abbreviated edition of this profile, in which only the results of borings 1 to 5 have been reproduced, is given here in fig. 2. It can be seen there that, especially near the locations of borings 1 and 2, nearest to the Brown Ridge, continental Weichselian

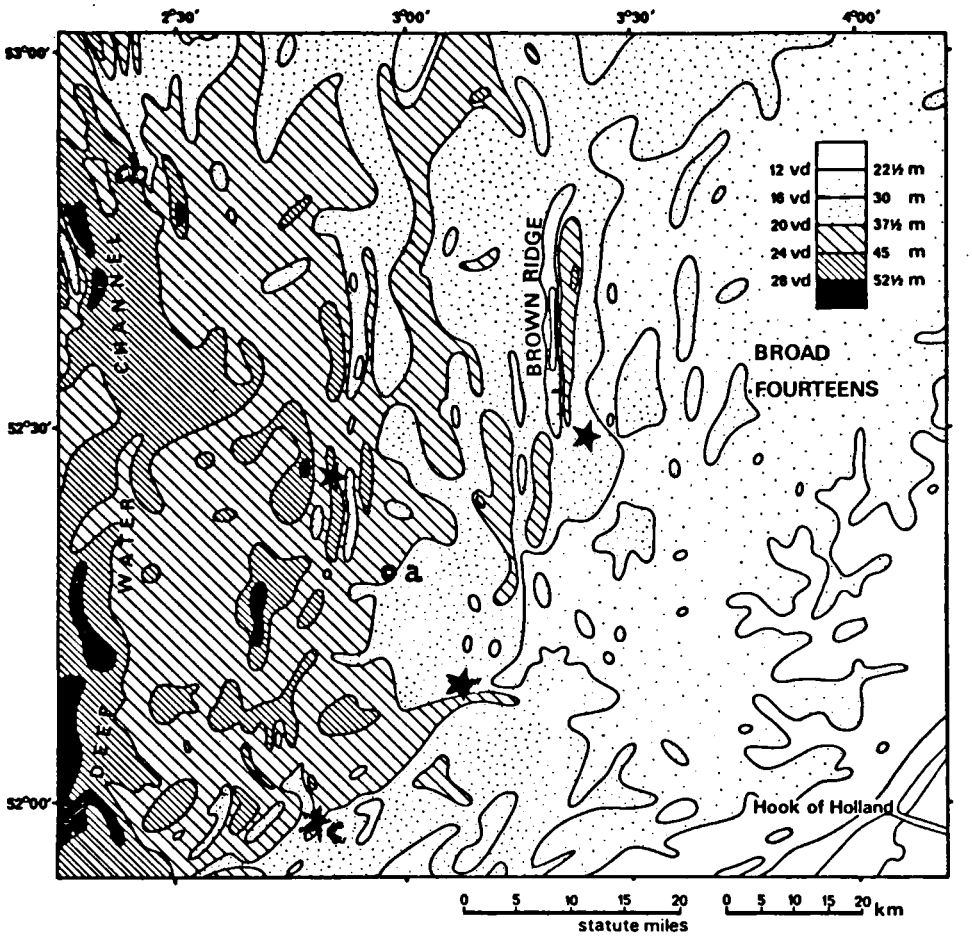

Fig. 1b (after Louwe Kooijmans, 1972). Part of the area of fig. 1a (inset, edges marked in broken line) with depths in meters and in fathoms (vd = vadem). The four principal fossil locations according to Mulder are marked with black stars. Open circle with a = site of no. 1075; id., with b = site of no. 1076, both coll. Mol. The Van Tuyll specimen was possibly found at point c, one of the Mulder locations.

sediments occur at depths between 35 and 40 metres below sea level. These contain bones of terrestrial animals. Most are thought to occur in freshwater clays, the so-called Brown Bank Beds, dating to the beginning of the Weichselian (= Würm-)glaciation, when a single, or perhaps several large lakes existed there. The Brown Bank Beds are underlain (from 38 to 48 m below sea level) by marine sandy shell-bearing deposits of Eemian (interglacial) age. As was already suggested in the 1972 description of the walrus skull in the Flonk collection, such sediments can of course be expected to contain fossil remains of marine mammals; although the equally marine, sandy sediments of the older and much deeper situated Holsteinian interglacial near boring 2 (between 50 and 60 m below present sea level) may, theoretically, also be considered to hold such fossils.

Many of the bones described in the following part of the present paper exhibit a fairly heavy degree of mineralization, combined with a frequently light-brown, rusty or buff colour, as is displayed also by the Flonk walrus skull. This may as well point to a sandy, perhaps Eemian sediment of origin. It is a point of observation in our experience of several decades, that fossils from sandy media quite often display a light-

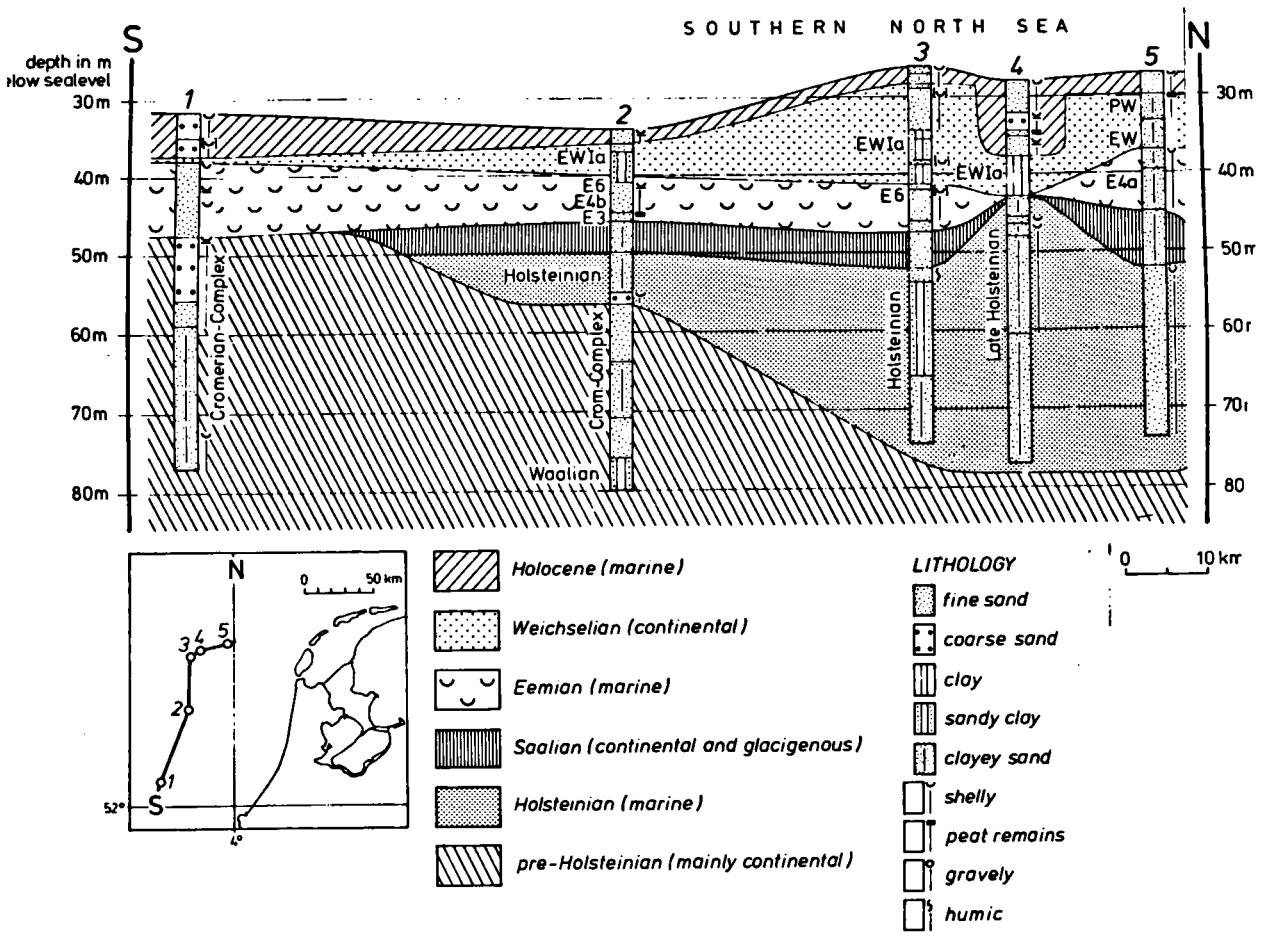

Fig. 2 (after Zagwijn, 1983). Abbreviated profile along the line 1-5 in the inset maplet showing the position and depth of a number of Pleistocene stratigraphic units.

brown or rusty colour. Those from clays are usually dark-brown to grey or even blue-black (when the clays contain appreciable amounts of humic components). Those from peaty surroundings customarily exhibit very dark, black or almost black hues.

We have thought it expedient to note the colours of all individual specimens in the following description. To obtain a certain degree of exactitude we have used the notation of the Revised Standard Soil Color Charts (Oyama, Takehara & Ooi, 1967). A recent description of dredged fossils from a single locality along the Meuse by Ligtermoet (1985) has shown that arrangement according to colour gradations may possibly be a useful method to distinguish between faunal components of various ages, when these are found together.

The material forming the substance of the present paper concerns fossil cranial and postcranial specimens ascribable to the family Odobenidae. The various fossils form part of the collections of the Zoological Museum of Amsterdam University (ZMA) and of a number of amateur collectors, in alphabetical order: Messrs D. J. Mol (De Tuger 141, 's-Heerenberg); Drs. J. Mulder (Merellaan 17, Nieuwleusen); H. Sekeres (Boekweitkamp 8, Hattem); Mr S. Boersen (den Oever) & Mr S. Smit (Amsterdam); L. and O. Stolzenbach (Regent Smitsstraat 24, Sint

Michielsgestel); and the Reverend C. F. H. van Tuyll van Serooskerken (Molenweg 36, Oostkapelle).

DESCRIPTIONS

Thirteen specimens are ascribable to Odobenidae; five are postcranial, and the rest cranial remains. In four cases tusks or parts of tusks are involved.

1. The first of these fossils is number 919R in the Sekeres collection. It is a 65 mm long fragment of a nearly straight tusk (fig. 3, B, D, E), having lost an appreciable amount of its outermost covering at one side. It thereby becomes possible to measure the thickness of dentine and cementum at a number of places. A maximum value of some 2.5 mm was recorded by us. Furthermore one immediately observes a mass of globular osteodentine filling the pulp cavity of the tooth. This feature is considered typical for walrus-like mammals (Ray, 1960: 132). All planes of fracture make the impression of having originated fairly long ago. The transverse fracture through its lower end shows concentrical oval growth rings of dentine (amongst which is an inner annular growth of 9 by 11 mm and a more external one of 21 by 18 mm). As the walrus appears to be the sole mammal with fairly large tusks that are oval in cross-section (Ray, loc. cit.), this forms an unmistakable indication for the determination of this particular fossil. We think it is impossible to determine whether the tusk was of the left or of the right side. The specimen was collected from material sucked up by a sucking dredger in the sand-and-gravel pit of the firm of Leccius de Ridder at the southern base of the Grebbeberg near Rhenen. It is presumably a section not too far distant from the tusk's extremity, as comparison with an artificial section of a recent walrus-tusk (fig. 3, F) shows. In the present series it is the only fossil not recovered from sediments of the bottom of the North Sea. The colour of the external ivory surface is light grey, 7.5Y 7/1. It thus conforms with the colour of most other fossil bones from this site, which also display light grey or light yellow to whitish hues. The majority of the sediments in the Leccius de Ridder pit containing these fossils are considered to be of Holsteinian (interglacial) age. They belong to the preglacial core of an ice-pushed ridge of Saalian (= Riss-) glacial times; the Grebbeberg forms part of that ridge. In view of recorded cases of individual wanderings by walruses it does not seem unreasonable to suppose that this tooth fragment belonged to an individual that ventured upstream along a Pleistocene Rhine.

2. A second, unnumbered, tusk forms part of the Mulder collection (fig. 3, C). It was collected in the general area West of the Brown Ridge. The specimen represents a complete tusk of the left side of what is, perhaps, a female individual (see, however, the remarks further on), as might be indicated by its relatively slender appearance and modest size. The tooth is gently curved backwards and outwards. A number of shallow fluted channels is present along the medial as well as the distal and posterior sides, running from root to tip of the tusk. The somewhat adze-like tip ends in a sharp mesiodistally oriented, 11 mm long cutting edge, which displays two minor flake scars on its posterior side. At its root the tusk possesses an oval cone-like cavity (presumably the entrance to the pulp cavity) with a maximum depth of 5 mm in its centre. Here the tooth measures 29 mm (in an anteroposterior direction) by 16 mm (transversally). Seen from behind there exists a slight counter-clockwise torsion of the tusk's axis from above downwards. Almost halfway, where it measures 34 by 21 mm in transverse section, the specimen seems to have been broken through recently, but it has satisfactorily been glued together again. Some recent external damage has resulted from a partial flaking-off of the outermost ivory layers, mainly in the upper half of the tusk. The inner globular osteodentine, visible as a result of this, has a light grey colour, near to 5Y 8/1. Elsewhere the external layer of ivory displays a colour which changes from 7.5YR 4/6 to 5/8 (brown to bright brown). It has a thickness of only 2 mm. The specimen has been impregnated with a colourless artificial resin to arrest further flaking. Its entire

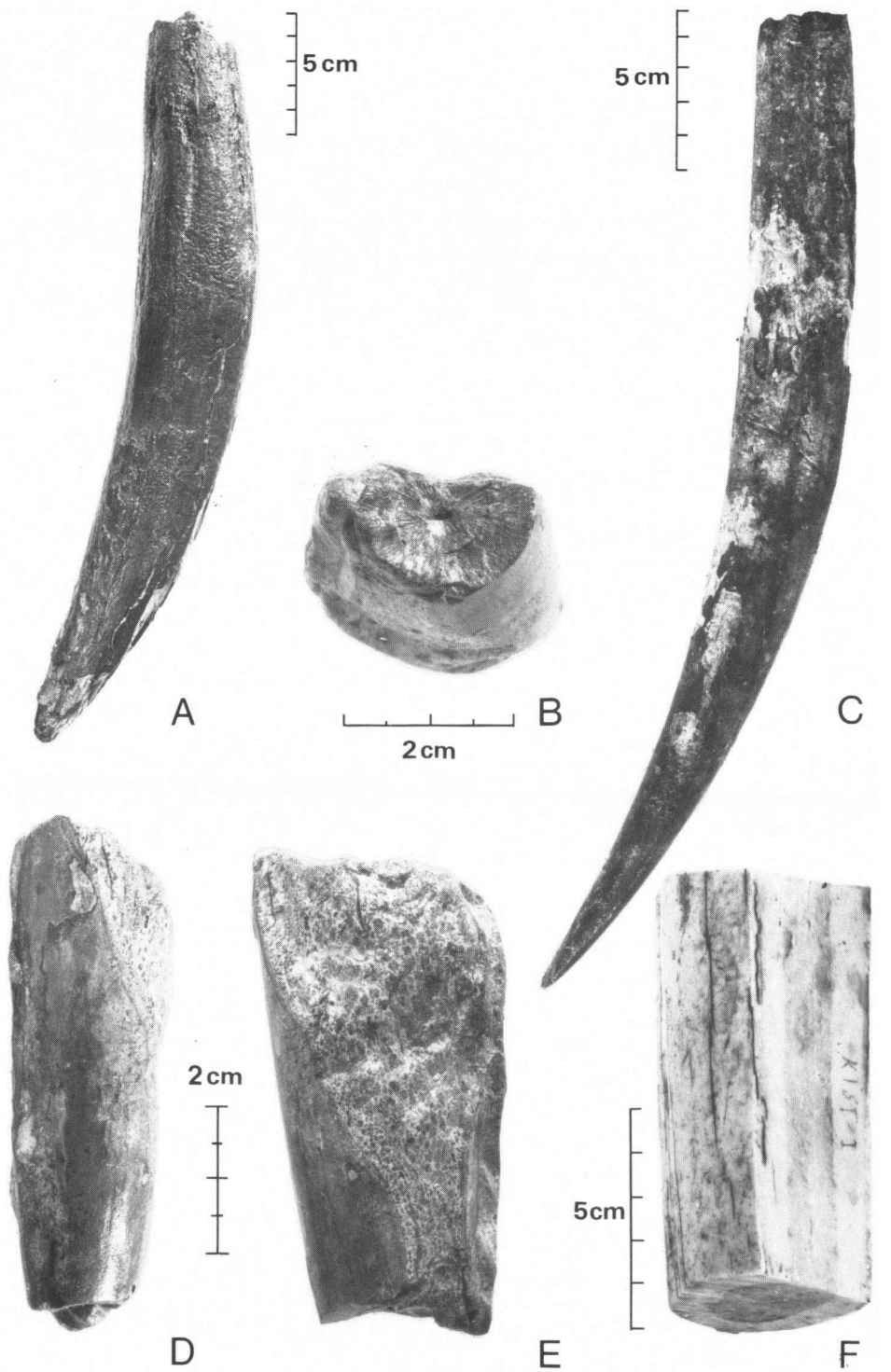

Fig. 3. A, external side aspect of right tusk, Coll. Mol no. 1075. B, D, E, tusk fragment no. 919R, Coll. Sekeres, from the Grebbeberg near Rhenen. B, seen head-on at the tip, to show oval cross-section; D, side view from back to front; E, external or internal side view displaying core of globular osteodentine. F, section of tusk fragment of recent walrus, also with core of globular osteodentine but with much thicker outer cover. C, internal side of left tusk, Coll. Mulder.

length along the anterior (outer) side measures 341 mm. Along the posterior, inner side this length is 323 mm. A few small Bryozoan colonies are present on the posterior and anterior sides of the last 70 mm of the tusk near its extremity.

3. A third specimen, a large fragment of a tusk, number 1075 in the Mol collection (fig. 3, A), was recovered in January or February 1983 by Mr P. van Es of Stellendam, owner and skipper of the fishing vessel GO 27, approximately (a on fig. 1b) at 52°20′N/2°60′E. It is much thicker and also straighter (i.e. with less torsion along its longitudinal axis when seen from behind) than the previous tusk. It is slightly curved in an anteroposterior sense and at the same time somewhat inclined to the right at its tip, again when seen from behind. Together with the circumstance that here also a series of shallow fluted channels can be observed in a lengthwise direction (developed more conspicuously at the left or supposedly internal side, seen from behind, than at the right side), this indicates that the tusk is one of the right side. Its considerable size and thickness may perhaps be considered typical for a male tooth, although this is emphatically denied to be a sexual character by Mohr (1942: 74). Some comparatively recent flaking of the external 8 mm thick ivory has occurred at the inside of the tip, and in a single oval spot halfway along the inner side. The internal osteodentine visible here has a colour describable as 10YR 8/1 (light grey), while the external part of the tooth can be called dark-brown, 10YR 3/3.

The length of the tusk fragment along the anterior side is 320 mm. Along the posterior side it is 300 mm. The anteroposterior diameter at the upper end is 42 mm, while the transverse diameter there measures 27 mm. Approximately in the centre of the tooth these diameters are, respectively, 52 and 38 mm.

4. The fourth fossil, number 1076 in the Mol collection, recovered by Mr Van Es in January 1983 approximately (b on fig. 1b) at 52°50′N/2°20′E, consists of a left maxillary fragment of a possibly female specimen, containing the tusk, the peg-like I^3 and the foremost premolar at that side (fig. 4, A, B, C). In addition the alveoli of I^2 and of the two posterior (of three) premolars are still observable. A shallow pit in front may represent the alveolus of I^1.

The anterior part of the left half nasal cavity, together with exactly half of the nasal aperture at that side, are also preserved. Half of a narrow 43 mm long furrow running obliquely upwards and backwards from the palate to the bottom of the nasal cavity in the vertical sagittal plane of fracture at a level opposite the foremost premolar, represents the left half of the incisive fossa and incisive channel. It is possible to look into half the nasal aperture when viewing the cranial fragment from in front; a feature considered characteristic for the Atlantic subspecies of the recent walrus. The fluted channels along the tusk described in the previous two specimens are also visible in this one. Here again the more intensely fluted part runs along the inner side of the tooth down to its tip.

The fossil has been impregnated with a colourless artificial resin to arrest further flaking. The remaining parts of maxillary bone are heavily encrusted with Bryozoan colonies and fragments of *Balanus*. External surfaces of bone and tusk ivory display colours running from 10YR 3/4 (dark brown) to 5B 2/1 (blue-black). At places where flaking has revealed deeper situated parts of ivory and bone the colours vary from 7.5YR 8/4 (light yellow-orange) to 2.5Y 8/1 (light grey). Several measurements can be taken from this specimen. Those pertaining to the dentition (alveolar as well as dental data) have been combined with similar measurements taken from the fifth item in our description, thus forming table I. The thickness of the dentine-cum-cement cover of the osteodentine in the tusk varies from six to ten mm.

The length of the tusk in this, the fourth, specimen, when measured from the edge of its alveolus to the tip, is 220 mm in front and 212 mm along the posterior side. At the alveolar edge the anteroposterior diameter of the tusk is 60 mm and the transverse diameter 43 mm. The height of the nasal aperture has a maximum value of 41 mm. Near its base half of the width of this aperture has a greatest dimension of 19 mm. The distance between the tusk's inner alveolar edge

Table I. Dental and alveolar measurements of the specimina Coll. Mol. no. 1076 and Coll. Stolzenbach no. N.Z. 63.

I^2sin., Mol 1076,	ant.- post. diam. of alv.	5	mm
	transv. diam. of alv.	6.5	mm
I^3sin., Mol 1076,	ant. post. diam.	16	mm
	transv. diam.	14	mm
P^1sin., Mol 1076,	ant. post. diam.	17.5	mm
	transv. diam.	17	mm
P^1sin., N.Z. 63,	ant.- post. diam. of alv.	24	mm
	transv. diam. of alv.	16	mm
P^1dext., N.Z. 63,	ant.- post. diam. of alv.	21	mm
	transv. diam. of alv.	15	mm
P^2sin., Mol 1076,	ant.- post. diam. of alv.	18	mm
	transv. diam. of alv.	18	mm
P^2sin., N.Z. 63,	ant.- post. diam. of alv.	16	mm
	transv. diam. of alv.	11	mm
P^2dext., N.Z. 63,	ant.- post. diam. of alv.	16	mm
	transv. diam. of alv.	12	mm
P^3sin., Mol 1076,	ant.- post. diam. of alv.	14.5	mm
	transv. diam. of alv.	16	mm
P^3sin., N.Z. 63,	ant.- post. diam. of alv.	—	
	transv. diam. of alv.	—	
P^3dext., N.Z. 63,	ant.- post. diam. of alv.	12	mm
	transv. diam. of alv.	11	mm

and the projected sagittal central plane of fracture through the palate has a minimum value of 37 mm. Thus the two tusks may have stood at a distance of 74 mm from each other, a value considered by Mohr (op. cit., table , p. 75) to indicate that an individual is female.

The plane of fracture through the midline of the palate has a sagittal length of about 120 mm, while the distance between the lower edge of the nasal aperture and the alveolar edge near I^2 approaches 60 mm.

5. A fifth specimen, numbered N.Z. 63 in the Stolzenbach collection, was found between Smith's Knoll and the Brown Ridge. It consists (fig. 5, D, E) of a heavy cranial fragment containing almost the entire praemaxillae, parts of the maxillae and of the floor of the nasal cavity, and the complete margin of the nasal aperture including fragments of the nasalia. The fossil appears to have been broken and rolled anciently, perhaps even prior to its fossilization. Almost every edge and fracture is rounded and no longer sharp to the touch. Only a small peg-like remnant of P^2 dexter makes the impression of having broken recently. The colour of the fossil varies between 10YR 3/3 (dark-brown) and 8/8 (yellow-orange), mostly a dull yellowish brown. The still present weakly concave part of the palatum is bordered by the alveoli of the two P^1, that of P^2sinister, of P^3dexter and that of the lingual half of P^3sinister. The alveolus of P^2dexter, as observed above, still contains part of the original tooth. Next to the alveoli for each of the P^1 one sees partial remnants of the lingual sides of the alveoli for each tusk. The minimum distance between the inner alveolar edges of the two tusks is 82 mm, a value within the range of male specimens according to the table (p. 75) by Mohr cited above. No traces of alveoli for any of the incisors or of the two M^1 remain, nor are there any vestigial remnants of sutures between the separate skull bones. In a central sagittal position, at a level halfway between the two P^1 and the two P^2, a 30 mm deep orifice is present in the palate. This incisive channel is directed backward towards the floor of the nasal cavity, where it has its other opening. More to the back, approximately at the height where the two M^1 must have been situated, one sees a pair of small foramina palatina, each at one side of the mid-sagittal plane through the fossil. The maximum depth (or rather height) of the concave palate, measured along the transversal line right across these foramina, is 14 mm. Alveolar measurements are given in table I. What is left of the canine alveoli in an antero-posterior direction measures approximately 50 mm at left and at right. The tusks must have been nearly straight, with a sagittal diameter in excess of this measurement.

The height of the nasal aperture has a maximum value of 44 mm and a maximum breadth (slightly below half the height; the aperture is nearly cordiform) of 37.5 mm. This agrees quite well with the size of a recent specimen (ZMU 4, a male) in the collection of the Zoological Museum of Utrecht University (Erdbrink, 1972, table I, p. 29). The distance between the lower edge of the aperture and the central point of the edge of the upper jaw is approximately 55 mm.

As in the previous specimen, here also the

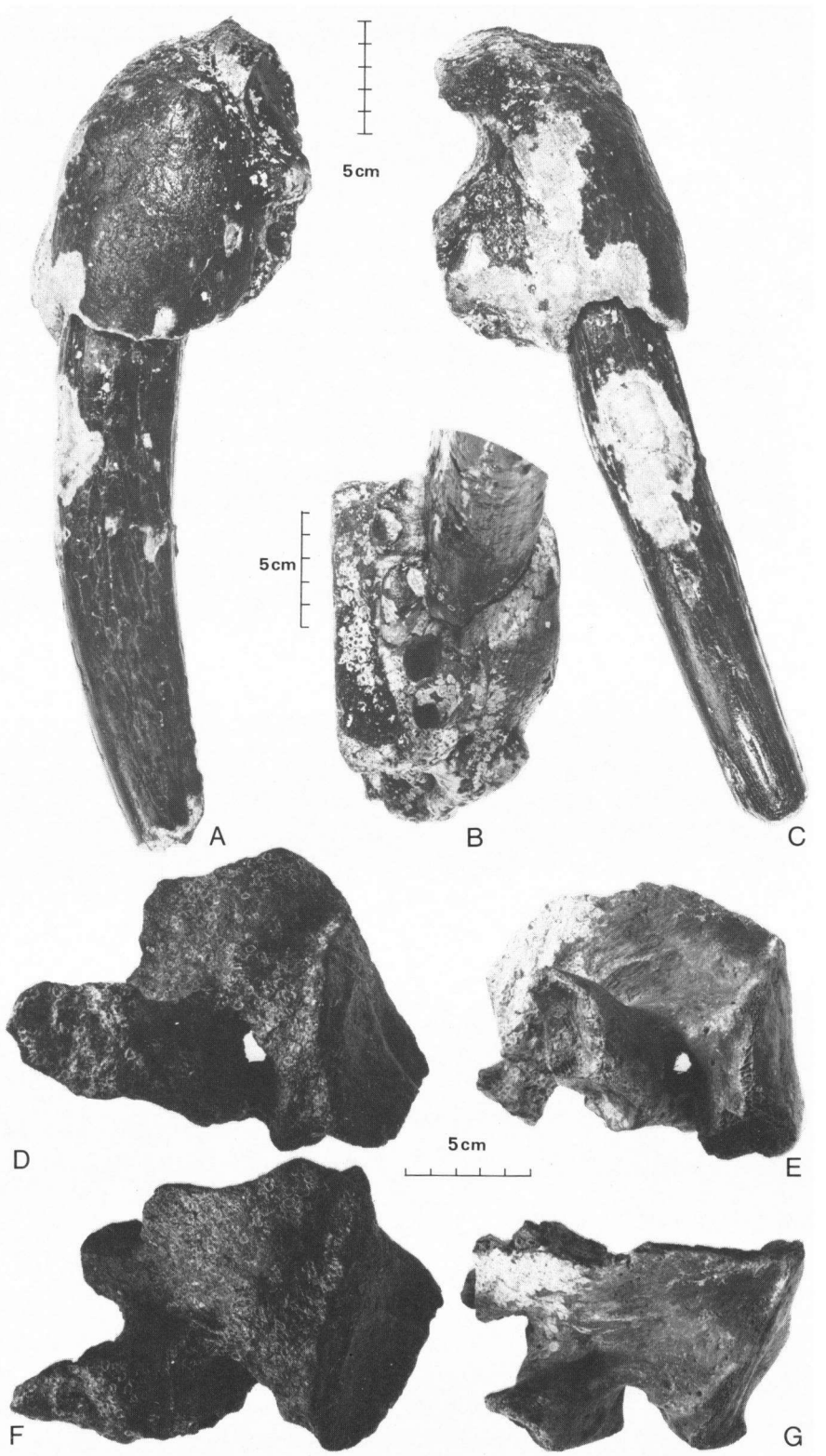

Fig. 4. A, B, C, maxillary fragment with tusk, Coll. Mol no. 1076. A, external side view; B, occlusal aspect (part of tusk cut away in photograph); C, frontal aspect, displaying haf of nasal opening. D, F, the purplish red, and E, G, the brown left periotic/zygomatic fragments in the Stolzenbach Collection. D, E, external views into the auditory meatus; F, G, oblique aspects from above.

situation of the nasal aperture is characteristical for the Atlantic subspecies; and as there, the individual must have been male. In view of the loss of the incisors and because of the synstosis of the cranial bones the conclusion can be drawn that it has reached a considerable age.

6-7. Two further cranial specimens in the Stolzenbach collection come from the same region, where they were found in 1984. Curiously enough, each item (fig. 4, D-F, E-G) consists of roughly the same region of the skull: the posterior or squamous part of the left zygomatic arch, the outer part of the left periotic bone, the left squamosal with some of the adjoining parietal bone, and the left central part of the occipital (without the supraoccipital and exoccipital bones, which have broken off long ago). On the inner side of each cranial fragment part of the braincase can be observed, while the auditory meatus ending at what remains of the tympanic bulla can be looked right through. One specimen displays a purplish-brown colour, to be defined as 7.5R 2/2 to 3/2 (dark to very dark reddish brown). The other fossil's colour is 7.5YR 4/4 to 4/6, uniformly brown. No other measurement than that of the external auditory meatus can be taken from either specimen: that of the brown fossil has an external height of 17 and a width of 14 mm, and that of the dark red-brown one an external height of 27 and a width of 20 mm.

8. The last cranial specimen described here (fig. 5, A, B, C) is a complete mandibula without any of its dental elements. It belongs to Mr S. Boersen at Den Oever, province of North Holland; it was brought to our attention by Mr S. Smit of Amsterdam and it was collected in the Brown Ridge area. The colour of the specimen varies from 10YR 8/4 to 7/4 (light yellow orange to dull yellow orange) on its external sides, while near the empty alveoli and at the posterior inner sides of the mandible the dominant colours are 10YR 4/4 (brown) to 6/1 (brownish grey). The fossil has been considerably eroded, resulting in a rounding of all originally acute edges and ridges. The locations of incisors and canines can no longer be established for the same reason. The angle between the left and right horizontal mandibular rami, seen from above (fig. 5, B), is 76° and therefore the specimen agrees with the morphology of the female walrus lower jaw as postulated by Mohr (op. cit.). There is a short distance between the two tusks, a narrow palate in front and, consequently, it is a narrow triangular mandible. The empty alveoli of P_1, P_2, P_3 and M_1 are observable left and right. A very small and shallow concavity lies some 25 mm behind the relatively small alveolus of M_1 sinister. It is impossible to decide whether this is an effect of the already mentioned erosion or a remnant of an alveolus for a supernumerary molar. A relatively large mental foramen is present at right as well as left. The left one is the largest of the two. A vertical bone partition can be seen to exist inside each cavity, dividing the foramen into two subequal parts. Another small foramen is visible, left and right, more to the front about 14 to 15 mm above the lower edge of the mandible and only 18 mm in a horizontal direction from the vertical symphyseal plane. The symphyseal region is extraordinary massive, as is usual in the walrus. On the inner side of the mandible one observes a relatively large mandibular foramen opening obliquely forward, left and right, and situated approximately below the highest point of the low and rounded coronoid process and almost at the horizontal level of the upper edge of the condylar process. The left foramen possesses a small lingula. The very wide angle between the low vertical and horizontal mandibular rami has a value of some 122 to 123 degrees. Additional mandibular and alveolar measurements are given in table II.

The postcranial remains consist of an incomplete left radius, a fragment of a right humerus and another, also right one which is far more complete, a slightly damaged left calcaneum, and most of the right half of a pelvic girdle. The first-mentioned find, ZMA no. 21.076, was donated to the Amsterdam Zoological Museum by Mr D. J. Mol; the two humeral specimens, numbered N.Z. and N.Z. 53, belong in the Stolzenbach collection, as does the pelvic fragment N.Z. 50, while the calcaneum belongs in the Van Tuyll van Serooskerken collection (no. 5237).

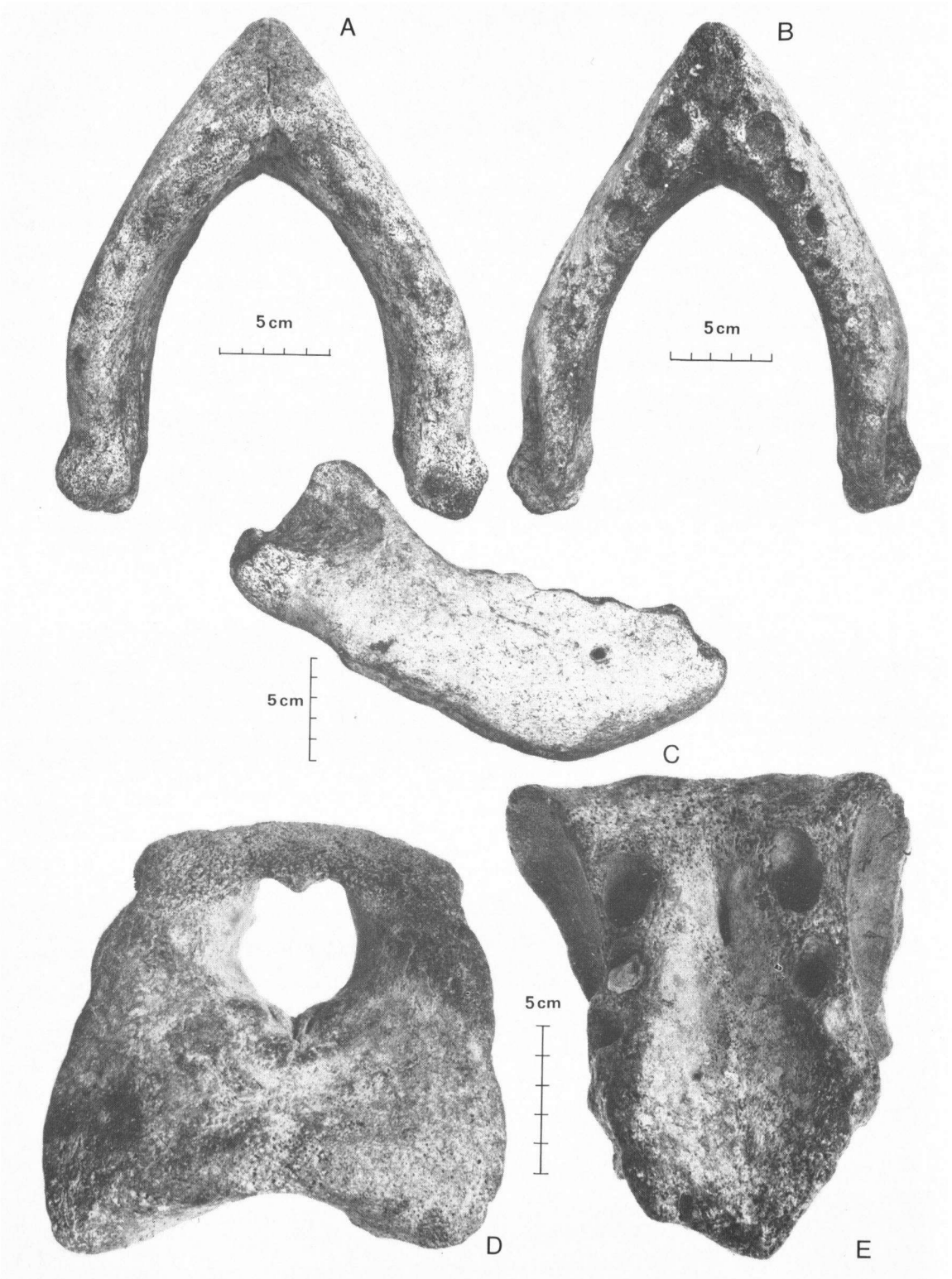

Fig. 5. A, B, C, nearly complete mandible, Coll. S. Boersen. A, seen from below; B, occlusal aspect; C, external aspect from right side. D, E, cranial fragment N.Z. 63, Stolzenbach Collection. D, frontal aspect, showing nasal aperture; E, occlusal aspect of palate.

Table II. Measurements of female mandible, coll. Boersen.

Max. length of left half mandib. ramus	247 mm
Max. length of right half mandib. ramus	246 mm
Height of horiz. left ramus at P_3	74 mm
Height of horiz. right ramus at P_3	73 mm
Height of vertic. left ramus	83 mm
Height of vertic right ramus	85 mm
Vertical height of symphysis in natural position	62 mm
Sagittal width of symphysis in natural position	79 mm
Distance between centres of left and right proc. coronoidei, seen from above	144 mm
External distance between left and right proc. condylares, seen from above	197 mm
Horiz. × vert. dimensions of left for. mentale	10 × 5 mm
Horiz. × vert. dimensions of right for. mentale	8 × 6 mm
Lower edge left mandib. - lower edge left for. mentale	38 mm
Lower edge right mandib. - lower edge right for. mentale	38 mm
Upper edge left for. mentale - edge of alv. of P_2sin.	20 mm
Upper edge right for. mentale - edge of alv. of P_2dex.	22 mm
Horiz. × vert. dimensions of left for. mandibule.	12 × 7 mm
Horiz. × vert. dimensions of right for. mandibulae	12 × 7 mm

Alveolar measurements of:	ant.-post.	transv.
M_1sin.	+ 9 mm	+ 8.5 mm
M_1dext.	7 mm	6.6 mm
P_3sin.	+ 17 mm	+ 13.5 mm
P_3dext.	10 mm	6.3 mm
P_2sin.	+ 19 mm	14 mm
P_2dext.	+ 11 mm	9.5 mm
P_1sin.	+ 17.5 mm	16 mm
P_1dext.	+ 17.5 mm	17 mm

9. Starting with this last piece (fig. 5, F, H), which displays a largely uniform external colour (10YR 5/2, or middle greyish yellow-brown), it can be said that the only missing part consists of the recently broken-off lateral processus of the tuber calcanei. Thereby it affords a view of the spongiosa inside; while part of this has the same colour as the external compacta, the remainder can be described as being orange to yellow-orange, 7.5YR 6/8. The fossil was collected in February 1983, West of the Brown Ridge along the 52nd degree of N. latitude (c on fig. 1b).

The bone carries a possibly symmetrical tuber calcanei at the back. This can no longer be fully ascertained, but the now absent lateral process may well have been equally large and high as the still present medial process (a small dorsal area of which has been superficially damaged too). Near the centre of the bone, at its dorsal side, a relatively long and narrow oval posterior facet for the astragalus can be remarked, with a surface which is convex anteroposteriorly. This articular surface is separated medially from another oval facet, the anteroposteriorly concave middle articular surface for the astragalus, by a rough groovelike sulcus calcanei. The sulcus contains four to five transverse bony ridges and a number of foramina. The dorsal surface in front of the posterior astragalar facet and the sulcus contains a number of diverging robust bony ridges and furrows, interspersed with more nutritional foramina. The middle articular surface for the astragalus continues without interruption in an oblique anterior direction into a small, also oval and weakly concave articular surface for the cuboid bone at the anterior surface of the calcaneum. This articular surface stands at right angles to that of the anterior articulation for the

astragalus, and it contains a triangular concavity just below the above-mentioned sharp ridge. The sustentaculum astragali runs practically continuous with the medial border of the articular surface for the cuboid. No other remarkable processes or ridges, only numerous large and small foramina nutricia and anteroposteriorly oriented bony streaks and furrows can be seen on the medial and plantar aspects of the bone. The following four measurements can be taken from this interesting fossil, which morphologically fully resembles some calcanei of recent walruses in the ZMA collection:

Maximum total length	127	mm
Maximum mediolateral width over sustentaculum astragali	67.5	mm
Transversal width over cuboid facet	45	mm
Height of bone at the same place	37	mm

Table III. Measurements of right half pelvic fragment N.Z. 50, Coll. Stolzenbach.

Diameter of acetabulum in the direction of the obturator foramen	80 mm
Diam. of acetabulum at right angles to previous measurement	72 mm
Maximum depth of acetabulum	49 mm
Thickness of bone at edge of acetabulum	58 mm
Maximum length of specimen	340 mm

10. The next specimen, the right half pelvic fragment N.Z. 50 in the Stolzenbach collection (fig. 5, G, I), found in 1985 in the general area between Smith's Knoll and the Brown Ridge, has been impregnated with a colourless artificial resin by the owners to counteract the almost inevitable flaking and desintegration to which the bone would otherwise have been subjected, even after desalinization. The present colour can be described as 10YR 2/2 to 2/3 (brownish black) with occasional spots of 3/4 (dark brown). The acetabular area is complete; the acetabulum is relatively deep. From its rim some eight centimetres' length of the illium is still present up to a fresh transverse fracture through this pelvic part, allowing a view of the dark-brown spongiosa inside. Also measured from the acetabular rim some eighteen centimetres (nearly the entire length) of the ischium can be oberved. Only an insignificant fracture along the extreme edge at the "inner" (obturator) side is present. Of the pubis a length of some eleven centimetres (starting at the acetabular rim) is still in existence. Its extremity is irregularly broken along a recent plane of fracture. The edge along the obturator foramen is quite sharp. Other measurements of the fossil are given in table III.

The Stolzenbach collection contains two items to be identified as partial or nearly complete right humeri. They were found in the same general area as the pelvic fragment N.Z. 50, and more or less at the same time.

11. The first of these (fig. 5, E), N.Z. 53, is only a fragment of a diaphysis. Its present colour (as in the previous and in the following cases it has been impregnated with colourless resin) can be called 10YR 2/2 to 2/3 (brownish black) or even 1.7/1 (black). Proximally an irregularly plane of fracture through the diaphysis, just above the damaged deltoid tuberosity, forms the upper limit of the specimen. The sulcus for the radial nerve can be traced. The dark brown spongiosa is everywhere present, indicating that the fracture has occurred recently. Distally the medial epicondyle is complete, as is the medial supracondylar ridge. Juste below the epicondyle a recent, irregular, but nearly horizontal plane of fracture forms the lower border. Measurements of this specimen are combined with those of the next one in table IV.

12. The next fossil, unnumbered but marked N.Z. (fig. 5, A, B), is only somewhat damaged at its proximal extremity. The lateral part of

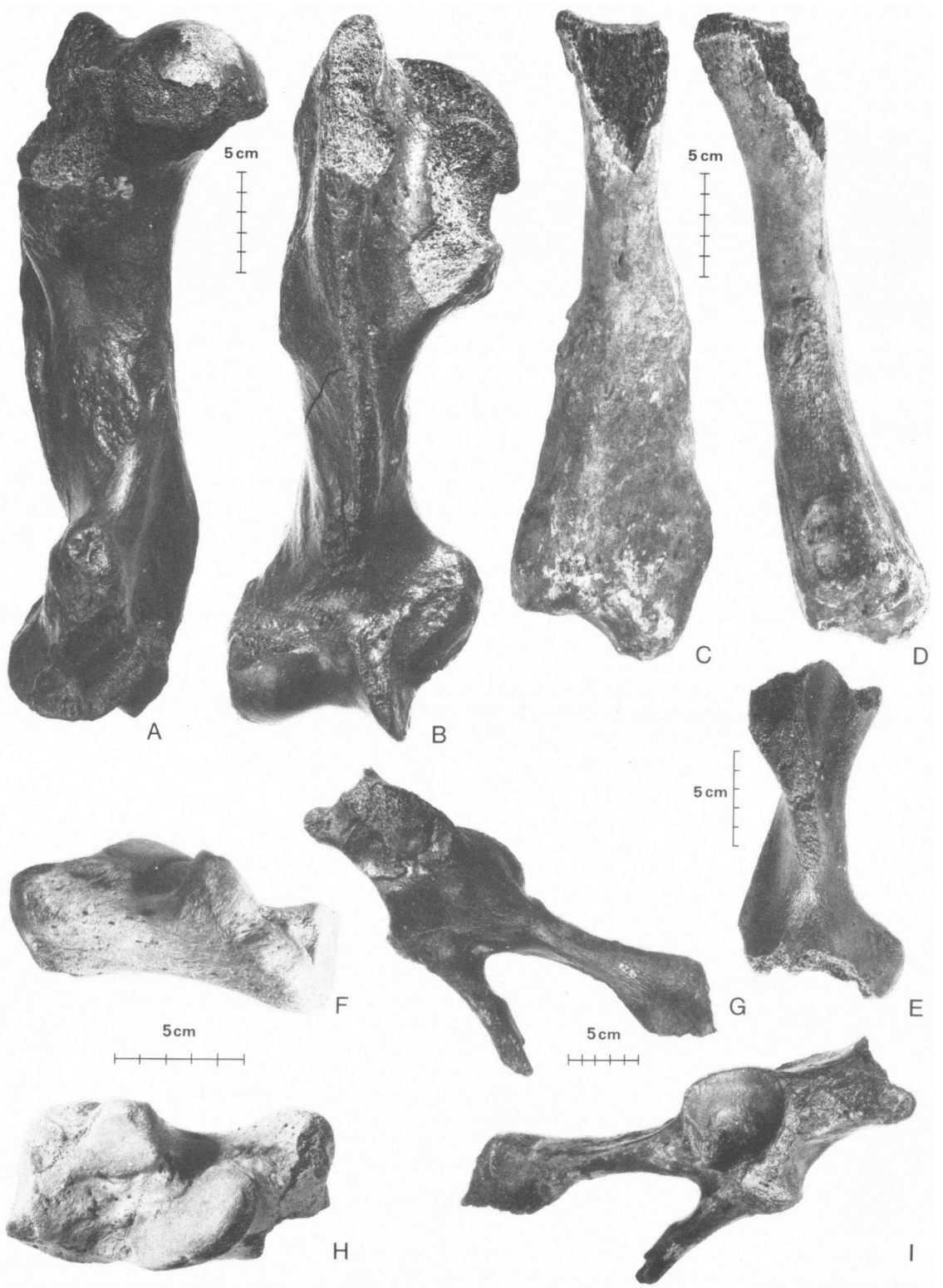

Fig. 6. A, B, giant right humerus N.Z., Stolzenbach Collection. A, internal side view; B, frontal aspect. C, D, nearly complete left radius ZMA 21.076. C, internal side view; D, posterior aspect. E, fragment of right humerus N.Z. 53, Stolzenbach Collection; frontal aspect. G, I, right half pelvic fragment N.Z. 50, Stolzenbach Collection. G, internal, and I, external side views. F, H, slightly damaged left calcaneum, Coll. Van Tuyll van Serooskerken no. 5237. F, external side view; H, seen from above.

Table IV. Measurements of right humeri, in mm.

	N.Z. 53	N.Z. (no number), (Coll. Stolzenbach)	ZMA 22.648	ZMA 22.649 (recent, Edgeøya)
Maximum length	189	378	329	349
Proximal width, trans.	—	116	114	107
Distal width, trans.	91	144	117	119
Distal width, sag.	—	74	68	73
Min. width, centre of diaphysis, sag.	35	49.6	40	46
Min. width, centre of diaphysis, trans.	35	53	—	—
Min. circumference of diaphysis	152	205	—	—
Max. width, sag., over deltoid ridge	72	118	—	—

Table V. Measurements of left radius ZMA 21.076 (don. D. Mol).

Length along ulnar side (at right angles to ulnar notch)	295 mm
Length along anterior side, over crista	320 mm
Circumference of caput radii	150 mm
Anteroposterior diameter of caput radii	52 mm
Mediolateral diameter of caput radii	44 mm
Height of ulnar notch	43 mm
Horizontal width of ulnar notch	30 mm
Anteroposterior width of distal extremity (= long axis of articular basin for carpus)	102 mm
Width of same at right angles to previous measurement	56 mm
Minimum circumference of diaphysis (70 mm below caput)	111 mm
Diameter at same place (ant.-post. and transversally)	35 mm
Width of diaphysis at 30 mm above distal extremity (at right angles to the two flat planes)	57 mm

the greater tubercle, most of the lesser tubercle (except its base), and some areas along the periphery of the head have been damaged, showing the spongiosa everywhere. This displays the same uniformly brown colour, 5YR 2/4, as the compacta and the exterior of the fossil. A few presumably recent cracks in the compacta at the anterior and posterior faces of the diaphysis indicate that impending disintegration of the bone has been successfully halted by impregnation with artificial resin.

The morphological similarity of this humerus with the previous fragment, N.Z. 53, makes it superfluous to reiterate the description of that part of the fossil. It should be stated, however, that the distance between the medial epicondyle and the (preserved) deltoid tuberosity in the present fossil is markedly larger, as are most of its other measurements. Perhaps it should be stressed here that there is absolutely no question of a supratrochlear perforation. The coronoid, radial and olecranon fossae are only very shallowly indicated or even practically absent. Nor is there any trace of an entepicondylar foramen, such as can usually be encountered in humeri of the Phocidae. Some Bryozoan colonies adhere to the surfaces of the deep intertubercular sulcus, of the posterior base of the lesser tubercle, and of the spongiosa of the fractured areas around the base of the caput humeri. It can be inferred that the highest part of the greater tubercle, now absent, has slightly exceeded the uppermost level of the caput. The same morphological particularity is observable in two very large recent right humeri

of *Odobenus rosmarus* in the collection of the Amsterdam Zoological Museum, ZMA 22.648 and 22.649, collected at a seventeenth-century walrus butchery emplacement at Cape Lee on the island of Edgeøya in the Spitsbergen archipel in the year 1977 (leg. Rees 77 Exp.). It can be seen (table IV) that the fossil humerus in the Stolzenbach collection, compared with these two recent specimens, appears to be a truly gigantic piece. All three are presumably ascribable to male individuals because of their size; the specimen N.Z. 53 may have been female, as it is much smaller.

13. The nearly complete left radius ZMA 21.076 (fig. 5, C, D) was collected near the Brown Ridge in 1980 by Mr P. van Es and donated to the Amsterdam Zoological Museum by Mr D. J. Mol of 's-Heerenberg. There is only some damage just below the medial side of the caput, where a triangular piece of compacta with sides of about 6.5 cm length has recently broken off. Light erosion allows the spongiosa to be visible everywhere around the caput radii and on the distal anterior crista, slightly above the articulation for the bones of the pollex. This spongiosa has a dark reddish-brown colour (2.5YR 3/4), darker than the compacta, which, on the planes of fracture, is dull yellowish-brown (10YR 5/4), while, on the external surface, it is more greyish-brown (7.5YR 4/2 to 5/2). On the flat lateral (external) side some twelve irregular scratches or notches in the compacta can be observed near the center of the diaphysis. The surface makes the impression of having been gnawed by scavengers, while traces caused by roots may also be thought possible. A large number of nutrient foramina in the proximal and distal epiphyseal extremities have imparted a sponge-like surface to these parts of the bone. Slightly above the centre of the diaphysis and on its medial side a larger foramen nutricium is visible, forming the entrance to a 30 mm deep perpendicular inward channel. The already mentioned recent damage at the proximal end has resulted in the loss of most of the radial tuberosity; only its lower extremity is still in place. Distally, the ulnar notch is entirely present, as is the shallow oval articular basin for the carpal bones. The strongly developed lengthwise cristae on the anterior and posterior edges of this flat, oarlike bone may perhaps indicate that it belonged to a male individual. Measurements of the specimen are given in table V.

DISCUSSION

Lankester (1865) described the fossil walrus species *Trichecodon huxleyi* from material consisting of at least twelve complete and fragmentary tusks collected at a number of localities in Suffolk, from deposits believed to belong to "the" Red Crag. Following Van der Feen (1968), amongst others, these deposits include what has more recently become known as the Butleyan, Newbournian and Waltonian stages of the Lower Pleistocene period. The Waltonian stage (op. cit., table, p. 25) is considered by him to be contemporaneous with the base of the Merxemian (formerly: Poederlian) stage found around Antwerp in Belgium, while there the Scaldisian stage, the earliest Pleistocene stage, precedes it. He thinks it probable that Lankester's syntypes were collected near Woodbridge (Suffolk), while similar tusks were found at Felixstowe and at Fox Hall near Ipswich. This walrus lived during the Waltonian stage or earlier.

Other, similar tusks were gathered from the Cromer Forest Bed formation (Cromerian stage complex) at Norfolk and from marine laminated beds directly above (in a stratigraphical sense). In a somewhat more modern review by Stuart (1982: 6-8) the Red Crag is correlated with the (cold) Waltonian and (temperate) Ludhamian stages, separated by a successional gap. The possibly about 2 million years old Waltonian is preceded by the Pre-Ludhamian stage, the beginning of the Pleistocene; it may therefore be contemporaneous with the Scaldisian stage of the Low Countries. The Cromerian and its preceding stage, the Beestonian, are thought to represent the beginning of Middle Pleistocene times, perhaps some 350,000 year ago. Thus the time span during which Lankester's walrus occurred, stretches from 2,000,000 to 350,000 years B.P. That it is indeed a walrus rests upon a number of observations by Lankester, one of which is the

presence of globular osteodentine in the pulp cavity, a characteristical feature for which he cites the anatomical description of a walrus by Cuvier in a 1805 treatise. He observes, however, that the layers of dentine and cementum that surround the filled-in pulpal cavity are very much thinner in his fossil material than in the recent walrus. The "minor development of cement" (op. cit., p. 230) is stated to be a specific point of distinction between the fossil and the recent walrus. Two other such points of the fossil form mentioned by him (but not quantified) are the greater curvature at the point of the tusk and (its) greater lateral compression.

In a later publication, Lankester (1880) reviews the anatomy of fossil and recent walrus tusks more thoroughly, and consequently declines the further use of the generic name *Trichecodon* for his Red Crag fossils. He is of opinion that the difference between them and the recent walrus is too small to warrant generic distinction. Therefore he proposes to apply the (misspelt) name *Trichecus* for both species. As has fully been expounded by Van der Feen (op. cit., paragraphs 2 & 3) the correct generic name for the walrus is not *Trichechus* Linnaeus, 1766, but *Odobenus* Brisson, 1762. This nomenclatorial knot seems partially to have escaped Ray (1960: 129, footnote 2) in his otherwise very thorough and valuable paper. Ray prefers to keep on using Lankester's original name *Trichecodon* for the species *huxleyi* while he states that "Whether *Trichecodon* is congeneric with *Odobenus* must be determined on the basis of the European material...". That Lankester himself should have done that already in 1880 makes things more simple. Consequently Hooijer (1957), amongst others, correctly writes *Odobenus huxleyi*. In Lankester's 1880 publication it is inferred that the distinctive points of difference formed by greater lateral compression and greater curvature of the fossil tusks may only be an expression of "special factors..." accounting for the differences of form (such as less rocky sea-bottoms and seashores in the case of *huxleyi*).

It is stated that these distinctions may only "*possibly* indicate a Walrus-like animal distinct from that with less-compressed tusks". Also the greater overall size of the complete tusks of *huxleyi* and their stronger and deeper degree of fluting are no longer seen as typical, since Lankester gives the measurement of a recent tusk (34¾ inches along the greater curvature, i.e. 882.7 mm) that is larger than his fossil ones. The upshot of the very thorough 1880 anatomical study of tusks is, that greater curvature, larger overall size, more intense grooving and fluting, and greater lateral compression are features apparently occurring more frequently in the fossil form *huxleyi* than in the recent walrus; but that, individually, they may be encountered here too in no lesser degree (two enormous recent tusks, ZMA 14.640 A & B, for instance, measure 79 and 80 cm along the anterior or greater curvature). They should not be used as distinctive points for the separation of *huxleyi* from *rosmarus* as species. A valid differential feature between the two forms appears to be the much thinner dentine-cum-cement covering in *huxleyi* of the pulp cavity filled with globular osteodentine.

It seems quite likely that *huxleyi* may have occupied a relatively "warmer" range than the recent walrus, as is supposed by Ray (op. cit.). The fossil form existed during the first part of the Pleistocene period along the western and eastern shores of the Atlantic Ocean. From a palaeoecological point of view it should not be forgotten, as Ray points out, that the recent form has been recorded as breeding in historical times on Sable Island off Nova Scotia and, possibly, on the Orkney Islands; its present status as an Arctic animal is due, to a large part, to man.

Regarding another fossil form, described by Rutten (1907) as *Trichechus antverpiensis*, found near Antwerp, Belgium, in deposits of (presumably) Scaldisian age, we are in full agreement with Van der Feen (op. cit.) on its systematic position, having been renamed *Odobenus antverpiensis* (Rutten, 1907). Possibly the same form, *Alachtherium cretsii* Du Bus, 1867 is insufficiently described and figured and thus should be seen as a nomen nudum. The clear differences of cranial characters of *O. antverpiensis* from those of modern (Van der Feen's 'Late-Pleistocene' skulls V 24, V 31) walruses are given in tabular form by Van der Feen (op. cit., base

of :27); the occipital aspect illustrates the differences very clearly and we agree with his observations.

We have been fortunate in having been enabled to re-view the walrus specimen described by Rutten (op. cit.) as *Trichechus huxleyi*, most of a grey-black skull with the two tusks, collected by a fisherman near Breskens at the mouth of the Scheldt in 1906. It is in the collection of the Instituut voor Aardwetenschappen (the former Geological Institute) of Utrecht University and we want to extend our thanks to Drs. M. van Kolfschoten for his mediation in making the specimen available to us. The principal result of this study consists of our recording the facts that the strongest curvature, that along the anterior sagittal side of each tusk does not have a radius of 27 cm, as maintained by Rutten, but one of 45 cm; the curvature along each posterior sagittal side is one of 48 cm. A still more important observation is formed by the measurement of the thickness of the outer covering (of dentine-cum-cement) of the filled-in pulp cavity, measured at the beginning of each tusk: this is, in each case, some 10 to 11 mm. The form of the palate in front is that of a rather narrow triangle, with no great distance between the two tusks (we refrain from measuring this as the tusks are more or less loosely placed in their sockets). From this a female sex of the individual is no doubt indicated. In turn this may explain the several somewhat weakly developed basal features of the skull, seen as typical characters with which to distinguish between the skulls of *huxleyi* and *rosmarus* by Rutten as well as by Van der Feen. The skull described by Rutten, in our opinion, should not be regarded as belonging to *Odobenus huxleyi*, but to *O. rosmarus*, the recent form. Thereby the known and authentic material on which the species *huxleyi* is based, is again restricted to the syntypes used by Lankester in 1865. We do not, with certainty, know what the skull to which these tusks belonged, looked like. However, there is a possiblitity offered by stratigraphical circumstances: might not the definitely different cranial remains (alas without tusks) of *Odobenus antverpiensis* (Rutten, 1907), of which Van der Feen described an additional specimen also with no tusks (op. cit.), be of the same species as that to which Lankester's type-material of *Odobenus huxleyi* has to be referred? We have seen that the two forms may very likely be almost contemporaneous. Until a skull which is recognizable as *O. antverpiensis*, but containing tusks recognizable as those of *O. huxleyi*, has been found, we shall have to wait and keep the two species apart. It is, of course, possible that *antverpiensis* is a Scaldisian form and *huxleyi* one that existed in Post-Scaldisian times up to the Cromerian. Clearly *huxleyi* is the oldest of the two specifical names, the one to be used in case conspecificity is demonstrated.

The two more or less complete walrus skulls described by Van Deinse (1943-'44 and 1964), collected by fishermen prior to 1911 somewhere near Breskens and at present in the Provincial Museum (of the Zeeuwsch Genootschap) at Middelburg, Zeeland, are no *Odobenus huxleyi* either, but *O. rosmarus* too, in our opinion. It can be seen that the one skull figured in each of the two papers is that of a male walrus, because of the considerable distance between the inner edges of the two tusks. It is possible to look into the nasal opening when the specimen is viewed from in front, thus demonstrating its affinity to the recent Atlantic subspecies. Regarding the identification of the other walrus-like fossils from several Dutch localities, enumerated and mentioned by Van Deinse especially in his 1964 paper (tables on pp. 191 and 197), this is no easy matter. Van Deinse does not question the validity of the genus *Alachtherium*, evidently impressed by a lengthy paper written by Hasse (1910). We do not consider this last publication sufficiently convincing for that purpose. In our opinion it is only demonstrated that the uppermost Tertiary and lowermost Pleistocene deposits around Antwerp contain fossil remains of a walruslike animal which clearly differs from the recent form. At the same time fossils of more modern representatives of *Odobenus* seem to have been collected at (other) Antwerp localities, and the entire mass of material has been irretrievably mixed up, as is conceded by Van Beneden (1877) in a treatise with a separate atlas containing excellent figures in natural size. One of these, Plate VI, fig. 8,

is a picture of a tusk fragment of "*Trichecodon Koninckii*". One sees that the core of globular osteodentine is entirely surrounded by a 10 mm thick outer cover of dentine and cement, as in the modern *Odobenus rosmarus*; we can only conclude that it is or was part of a tusk of the modern form. Once again, as long as it is not demonstrated that the early Antwerp walrus with its definitely different skull (see the figures in Rutten's and Van der Feen's cited papers) and mandible (see the Van Beneden atlas, cited above), usually larger-sized than the recent walrus, is identical with the East Anglian *Odobenus huxleyi* (as we suspect), it should be known as *Odobenus antverpiensis* (Rutten, 1907). From a stratigraphical point of view it seems feasible to suppose that the finds numbered 3 up to (and including) 7 in Van Deinse's table (p. 197, in his 1964 paper), and perhaps the numbers 4, 6, 7, and 8 in the table on p. 191 too, may belong to this species. The numbers 5 of p. 191, and 1 and 2 of p. 197, could very well be remains of a much earlier, Upper Miocene form, *Prorosmarus* species. It falls outside the scope of the present paper to solve this separate problem, which should, nonetheless, be pursued.

When the specimens described by us here are evaluated in the light of the data summed up above, we can only conclude that number 919R in the Sekeres collection, from the Grebbeberg, has to be identified as *Odobenus huxleyi* (Lankester, 1865), because of the thinness of the dentine-plus-cementum layer which surrounds the core of globular osteodentine of this tusk fragment. We have seen that the species *huxleyi* seems to have existed up to Cromerian times. This may well be an acceptable date for some of the deposits in the core of the ice-pushed morainic ridge at Rhenen. We should point to the discovery of Waalian sediments in the nucleus of the same morainic ridge at Kwintelooijen, slightly further to the North of Rhenen, where palynological and mineralogical evidence indicates this age for a clay containing extremely primitive human flint artefacts (additional specimens have been collected since the description of a first one, Bosscha Erdbrink, 1981).

A second specimen, perhaps referable to *huxleyi*, is the tusk in the Mulder collection. Although it is only very modestly sized, which might plead against such an identification, the extreme thinness of the dentine-and-cement covering of the globular osteodentine filling of the pulp cavity forms a strong argument in favour of the proposed determination. Because of its tentative nature (nothing is known, for example, about its stratigraphical position or age), the correct identification should read: *Odobenus* cf. *huxleyi* (Lankester, 1865).

The other fossils described by us should all be identified as remains of the recent walrus species, *Odobenus rosmarus* (Linnaeus, 1758), ssp. in those cases in which it does not appear to be possible to attempt a determination with regard to the particular subspecies. Only in two instances, number 1076 of the Mol collection and number N.Z.63 in the Stolzenbach collection, we are confident that even the Atlantic subspecies is indicated, so that there the correct name to give to each fossil is: *Odobenus rosmarus rosmarus* (Linnaeus, 1758).

When the variation in colour existing among the several pieces is reviewed, it is interesting to note that a certain conformity between a number of finds is observable, perhaps indicating a somewhat identical matrix. The dark brown external colour 10YR 3/3 or 10YR 3/4 is shared by the specimens 1075 and 1076 of the Mol collection with N.Z.63 of the Stolzenbach collection; almost the same hue can be detected in the mandible (10YR 4/4), the calcaneum (no. 5237 of the Van Tuyll collection, 10YR 5/2), the radius (ZMA 21.076, 10YR 5/4), the pelvic fragment (N.Z. 50, 10YR 2/2-2/3-3/4) and the humerus fragment (N.Z. 53, 10YR 2/2-2/3), both of the Stolzenbach collection. The nearly complete humerus of giant size displays the aberrant hue 5YR 2/4, but this and its size do not constitute valid arguments for an identification as ? *antverpiensis*. Nor is that the case with the two periotic fragments of the Stolzenbach collection (7.5R 2/2-3/2 and 7.5YR 4/4-4/6), which could have a certain affinity with the tusk of the Mulder collection (7.5YR 4/6-5/8). The two fragments are too small, however, to permit the reaching of any

other conclusion than that of having belonged to a species of walrus, presumably the most frequently occurring one, *O.* cf. *rosmarus*.

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RÉSUMÉ

Treize fossiles d'Odobenidés sont décrits, dont douze trouvés au fond de la mer du Nord et un dans une sablière près de Rhenen aux Pays-Bas. Ce dernier, un fragment de défense, et à titre provisoire l'un des autres fossiles, sont attribués à l'*Odobenus huxleyi* (Lankester, 1865), espèce Pléistocène ancienne. Le reste appartient à la forme récente, *O. rosmarus* (L.); deux fossiles même à la sous-espèce atlantique, *O. rosmarus rosmarus*. La position systématique des genres *Trichecodon* et *Alachtherium* et de l'espèce *antverpiensis* (Rutten, 1907) est discutée. Cette dernière pourrait être identique à *O. huxleyi*.

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Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam,
P.O. Box 20125, 1000 HC Amsterdam, The Netherlands.