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FURTHER OBSERVATIONS ON FOSSIL AND SUBFOSSIL ODOBENID MATERIAL (MAMMALIA, CARNIVORA) FROM THE NORTH SEA

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ABSTRACT

Six cranial and two postcranial fossil and subfossil odobenid remains that have come to our notice since our 1986 paper on the same subject are described and discussed. One of these can, with some confidence, be identified as *Odobenus antverpiensis* (Rutten, 1907). The others either belong to the recent species, *Odobenus rosmarus* (Linnaeus, 1758), or should simply be identified as *Odobenus* species. Some remarks are made on the morphological differences between *antverpiensis* (perhaps identical with *huxleyi*) and *rosmarus*.

GENERAL REMARKS

Since our 1986 paper a number of fossil and subfossil walrus specimens have come to our notice which have to be identified as individuals belonging to the genus *Odobenus*. Because we consider them sufficiently interesting to be recorded and described here, somewhat in continuation of our 1986 remarks, short accounts and figures of each follow in the allotted numbered sequence. The finds in question consist of:

1. An incomplete calvarium, severely damaged at the right side and without tusks and zygomatic arches, bearing the number K 8052. It belongs to the collection of the Geological Museum of Amsterdam University. It was collected in 1989 by J. C. Bout off Westkapelle, Walcheren, province of Zeeland, at a depth of 30 m.

2. A damaged calvarium with a partly broken left tusk and without the extreme part of its snout (so that presence or absence of first and second incisors cannot be verified) and without the right tusk, but still retaining the posterior half of this tusk's alveolus. It is the property of Mr S. Dekker of Winkel (N. Holland), and it was collected in 1967 or 1977 by the crew of the fishing vessel Wieringen 75, Skipper Lont, at a position to be fixed approximately as 54°30′N, 7°50′E, i.e. some 40 miles N of Helgoland and 65 miles SW from the Danish port of Esbjerg, probably about 10 miles NW of the Amrum Bank.

3 and *4*. Two rostral fragments of skulls, both in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (now part of the Nationaal Natuurhistorisch Museum). The first of these, a heavy and large individual

numbered (St) 124058, still with its two tusks (damaged at their tips), was obtained through the intermediary of the Nederlands Instituut voor Onderzoek der Zee on August 6th, 1965; it was collected by the fishing vessel HD 18 at a point some 15 miles North of Helgoland.

The second, a much smaller specimen, number (St) 137838, was recovered from the North Sea, probably somewhere in the Brown Ridge area, by a fisherman from Scheveningen. It was donated by Mr W. F. A. Guilonard on the 8th of November, 1966. The right canine has (recently) broken off at its base, but part of the left canine is still present.

5. Also a rostrum (or snout part), again from the Brown Ridge area and collected by a Scheveningen fisherman, was donated to the Zoological Museum of Amsterdam University in 1989 by Dr. P. H. de Buisonjé. It is inscribed there as number 23.910. All elements of the dentition have been lost.

6. A strongly eroded incomplete mandible (left and right vertical ramus absent) of a small, evidently female walrus, most probably subfossil or even recent, collected in the Brown Ridge area by the Stellendam Skipper P. van Es of the fishing vessel GO 27, Johannes, in January 1987, and belonging to Mr Thijs Mol. No elements of the dentition are present.

7. A (perhaps subfossil or subrecent) right femur, collected in March 1988, also by Skipper Van Es, at the edge of the Deep Water Channel to the SW of the Brown Ridge. It is inscribed as number 23.473 in the collection of the Amsterdam Zoological Museum, and it was donated by Mr D. J. Mol.

8. A heavily mineralized, almost black and slightly eroded first metatarsal bone of the right side, inscribed in the collection of the Amsterdam Zoological Museum as number 24.002 and collected at about the same locality in June 1988, again by Skipper Van Es; also donated by Mr D. J. Mol.

Regarding the geographical situations of the Brown Ridge and the Deep Water Channel the reader may be referred to our 1986 paper, figures 1a and 1b, or to our 1987 paper, fig. 1. The positions of the island of Helgoland, of the Danish port of Esbjerg, and of the Amrum Bank can, without doubt, be found on any good geographical map.

In order to give an accurate rendering of the colour encountered in each specimen we have used the revised Munsell colour charts by Oyama *et al.* (1967), as we did in 1986.

DESCRIPTIONS

1. This damaged fossil calvarium (K 8052, Pl. 1, A-E) is mainly coloured dark greyish yellow, 2.5Y 5/2, but there are numerous irregular patches of brownish black, 2.5Y 3/1, or even black, 2/1, while all over the surface of the fossil one observes colonies of Bryozoa and traces of *Balanus*-individuals, light grey in colour, 2.5Y 8/1. On top of the calvarium as well as on the palate there are rust-coloured spots of yellowish brown, 10YR 5/8. The several cranial and dental measurments taken from this and from the other specimens have been combined in tables 1, 2 and 3.

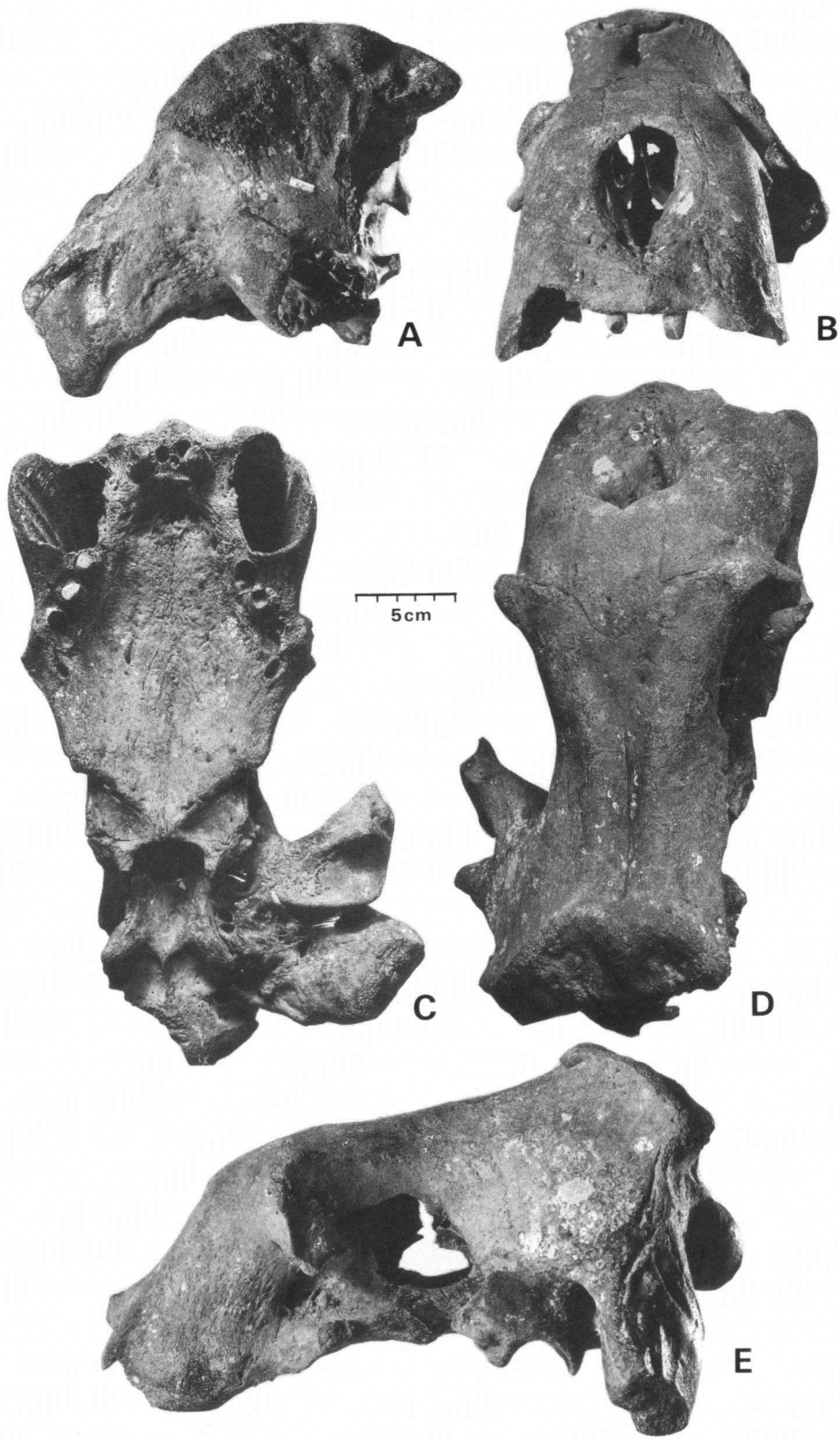
The fossil must have lain free on the bottom for a quite considerable time in view of the ubiquitously present Bryozoa and Balanidae, especially inside the left half of the braincase. The right half of this receptacle together with the right half of the occiput and even the right half of the foramen magnum, are gone. Their planes of fracture appear to be recent and still sharp in places. Inside the left half braincase one sees circumferential traces of an ossified posterior part of a tentorium cerebelli, quite as in the specimen described by one of us (B.E.) in 1972. As in that case, remains of another bony septum also indicate the former presence of a fossa lateralis (= sylvii), at least on the left side. On both sides the temporal bones have almost broken away, probably rather recently as the fractures are sharp. Part of the nasal septum is still present and visible. Only the extremities of the zygomatic arches remain, at left as well as at right. The one tympanic bulla at left that is still present, is rather flat and has an isosceles triangular to trapezoidal outline (50 mm along the contact with the slightly concave basioccipital bone and almost 45 mm at its parallel

Table 1. Cranial measurements of the described odobenid remains, in mm.

	K 8052	Coll. S. Dekker	St. 124058	St. 137838	ZMA 23.910
Rectilin. dist. in median plane at lambd. crest to tip of one of either mastoid processes	255 (sin.)	214	—	—	—
Same distance, circumferential (tape)	350	257	—	—	—
Basion - opisthocranion	129	121	—	—	—
Opisthion - opisthocranion	85	77	—	—	—
Max. width of occiput	320	265	—	—	—
For. magnum, height	36	41	—	—	—
For. magnum, width	50 ?	42	—	—	—
Distance between extern. tips of condyli, over for. magnum	104 ?	116	—	—	—
Do., between internal tips	58 ?	51	—	—	—
Width of crista lambd. in sagitt. plane	24	49	—	—	—
Do., at lateral sides	14 (sin.)	28	—	—	—
Min. width of skull between zyg. arches	95	79	106 ?	82 ?	85 ??
Prosthion - opisthocranion	390	327	—	—	—
Prosthion - back of palate	240	—	188	145 ?	175 ?
Nasion - prosthion	192	152 ?	161 ?	151	148
Nastion - lambda	169	208 ?	—	—	—
Lambda - opisthocranion	77	65	—	—	—
Nasal aperture, height	76	39	46	39	51
Nasal aperture, width	48	40 ?	51	40.5	52
Min. dist. betw. canines, internal	74	—	105	95	75
Max. width of skull over zyg. arches	320 ?	226	—	—	—
Transv. depth of palate between post. mol.	25	34	34	41	38
Proc. paroccipit. dext., length	—	31	—	—	—
Proc. paroccipit. dext., width	—	15	—	—	—
Proc. paroccipit. sin., length	36	32	—	—	—
Proc. paroccipit. sin., width	15	14	—	—	—

other side near the auditory meatus). Muscular tubercles are well-developed, in accordance with Van der Feen's (1968) descriptions. The palate is present in its entirety. As may be noted in table 1 (prosthion-back of palate) it is long, both relatively and absolutely, but at the same time (transversal depth of palate between posterior molars) relatively shallow. It is also strongly grooved and pitted.

The two tusks have fallen out long ago; the bottoms (or, rather, upper ends) of their alveoli display openings into the nasal cavity where parts of the thin bony septum between this cavity and the alveolus have broken away. At the right side, where no obstructions in the form of numerous *Balanus*-individuals are present, this alveolus can be measured to have a depth of some 160 mm. The inner surface of each alveolus possesses a number of vertical ridges, from which the conclusion may be reached that the tusks have had a distinctly fluted appearance in a longitudinal sense. In a horizontal sense, however, only very faint ripples (indications of "growth rings"; Fay, 1982: 107-111) can be discerned. The form of each alveolus indicates that its tusk has not been strongly curved; in the recent walrus this is taken to be typical of the male sex. In transverse



Pl. 1. Incomplete calvarium of *Odobenus antverpiensis* (Rutten, 1907). Coll. Geological Museum, Amsterdam University, no. K 8052. A. Occipital aspect; B. Frontal aspect; C. Palatal aspect; D. Superior aspect; E. Left side aspect.

Table 2. Dental measurements (in mm) of upper teeth of described specimens. Alveolar measurements indicated with +

	K 8052	S. Dekker	St. 124058	St. 137838	ZMA 23.910		St. 137838	St. 124058	S. Dekker	K 8052	
$C^{sup.}$ sin. ant.-post. width	68 +	62.0 +	66.0	40.5 +	57.5 +	58.0 +	39.5	69.0	—	67.5 +	$C^{sup.}$ dext. ant.-post. width
— transv. width	32 +	47.0 +	51.0	25.5 +	38 +	39.0 +	29.0	51.5	46 +	36.5 +	— transv. width
— circumfer. at base	180 +	169	190	104 +	175 +	180 +	92	193	—	170 +	— circumfer. at base
I^1 sin., length	6.0 +	—	—	1.5 +	—	—	1.5 +	—	—	—	I^1 dext., length
— width	5.8 +	—	—	1.5 +	—	—	1.5 +	—	—	—	— width
I^2 sin., length	9.0 +	7.5 +	—	2.5 +	—	—	2.5 +	—	—	9.0 +	I^2 dext., length
— width	7.5 +	8.0 +	—	2.5 +	—	—	2.5 +	—	—	7.0 +	— width
I^1 sin., length	14.0	24.5	30.0	11.5 +	21.0 +	21.5 +	14.4	27.0	24.0	14.0	I^3 dext., length
— width	14.0	20.5	20.5	9.7 +	16.5 +	13.5 +	12.4	19.0	22.5	13.0	— width
P^1 sin., length	12.8 +	20.5	15.0	14.0	22.5 +	24.5 +	13.5	16.5 +	19.5	11.5	P^1 dext., length
— width	11.0 +	20.5	20.0	10.2	14.5 +	13.5 +	12.8	20.0 +	22.5	11.7	— width
P^2 sin., length	12.8	28.5	22.0 +	17.0	23.0 +	13.5 +	21.5	28.5 +	27.5	12.5	P^2 dext., length
— width	10.0	23	19.5 +	13.0	17.5 +	11.5 +	15.1	18.0 +	22.5	10.3	— width
P^3 sin., length	14.1 +	—	18? +	14.0 +	7.0 +	—	12.0 +	18.0 +	18.5	12.5 +	P^3 dext., length
— width	10.5 +	—	16.0 +	10.5 +	5.0 +	—	11.0 +	19.0 +	16.0	8.2 +	— width
M^1 sin., length	8.5 +	—	—	—	—	—	—	—	—	7.0 +	M^1 dext., length
— width	7.3 +	—	—	—	—	—	—	—	—	5.0 +	— width

section the tusks are relatively more flattened, or more strongly oval, than those of the recent *Odobenus rosmarus*.

Between, and next to the canine sockets one encounters two peg-like incisors (Pl. 1, C), probably to be seen as I^3. The one at right has recently been slightly damaged. More sagittally there are three empty alveoli. The most central and smallest of these (table 2) has almost certainly been that of an I^1 (perhaps of the left side), the other I^1 being absent altogether. The two sockets, pushed to the front, should then be seen as those of I^2 sinister and dexter. In contrast to the situation encountered in the recent *O. rosmarus*, not even the faintest trace can be seen of any tooth on the medial side of the canine; in the recent walrus this tooth has to be explained as the I^3. According to Mohr (1952: 243) the tusks have migrated outwards in the evolution of the walrus, thanks to their degree of "over-development", and I^3, though sometimes found at the border between premaxilla and maxilla, is always implanted in the premaxilla itself.

Behind the tusks, at left and at right, a row of four subequal peg-like teeth is encountered. It is not clear whether each row should be seen as consisting of four premolars, or (slightly more preferable) as three premolars and a single, first, molar (see, however, the remarks made by one of us, B.E., in the cited 1972 paper, p. 27). In any case the most posterior of these elements has fallen out on each side. The tooth in front of it, also on each side, has recently broken off, leaving a stump inside its socket. The same has happened to the tooth most in front of the left row of four. The other peg-like elements (P^2 at left, P^1 and P^2 at right) are completely present. They, and the two I^3 (?) are somewhat concave at their worn occlusal ends, save for P^2 dexter, which is flat. They are quite sharp along their outer edges, the occlusal surfaces displaying minute wrinkles giving the effect of a lizard's skin. Exactly in the center, along the shortest distance between the canini, one observes clear traces in the palate of a foramen incisivum, accompanied at each side by accessory foramina, some six in all.

The nasal aperture, when compared to that of the recent walrus, is rather high and narrow, and inverted pyriform. Its base is much less distant from the prosthion (about 33 mm) than in the recent *Odobenus*, while the aperture is also more inclined backwards in this fossil specimen. Still, when seen from in front (Pl. 1, B), it is perfectly possible to look into the

animal's nose, apparently one of the requirements by which the Atlantic walrus can be distinguished from its Pacific counterpart.

Seen from above, the sagittal suture of the skull is clearly depressed (Pl. 1, B, D), especially in its posterior part, and not flat or ridge-like; therefore in accord with one of Van der Feen's (op. cit., p. 27) postulated features typical for the species *antverpiensis*. The lambdoid crest (crista lambdoidea transversa) is relatively high and broad, as is the entire occipital region, indicating a heavy muscled neck region. This is again one of the typical *antverpiensis*-features according to Van der Feen (loc. cit.). So is the fact that an occipital crest (Pl. 1, A) is almost absent, making it difficult to determine the opisthocranion along this weak crista occipitalis.

2. This walrus calvarium (Pl. 2, A-D) is nearly complete save for severe damage at its right anterior side. This damage is clearly of recent date as the plane of fracture is quite fresh and sharp. The colour of the specimen is a nearly uniform dull yellowish brown to dull yellow-orange, 10YR 5/3-6/3.

The anterior half of the alveolus for $C^{sup.}$ dexter is missing; so is, of course, the tusk itself. This enables the observer to look into the 150 mm deep socket up to its base, which is lined with spongious bone. In the posterior wall of the alveolus a number of about nine to ten horizontal growth rings may be counted. Next to the damaged alveolus, part of the periphery of the nasal aperture at the right side has been lost together with the premaxillary bone at its lower border. As a result the third incisor of the right side, including its root, has become uncovered over a length of 57 mm in front. The two second incisors are lost, but their alveoli, displaying sharp edges, are still present; this loss must have occurred recently. The anterior half of the socket for I^2 dexter is included in the lost premaxillary fragment already mentioned. A bone splinter on the anterior side of the alveolus of $C^{sup.}$ sinister has also broken off.

Of the dentition of this specimen there remain: $C^{sup.}$sin. (damaged during life of the individual at its tip, where a crumbling away has occurred, see Pl. 2, B, C, D); I^3 sin. and two premolars of the left side; and I^3 dext. together with three premolars on the right side.

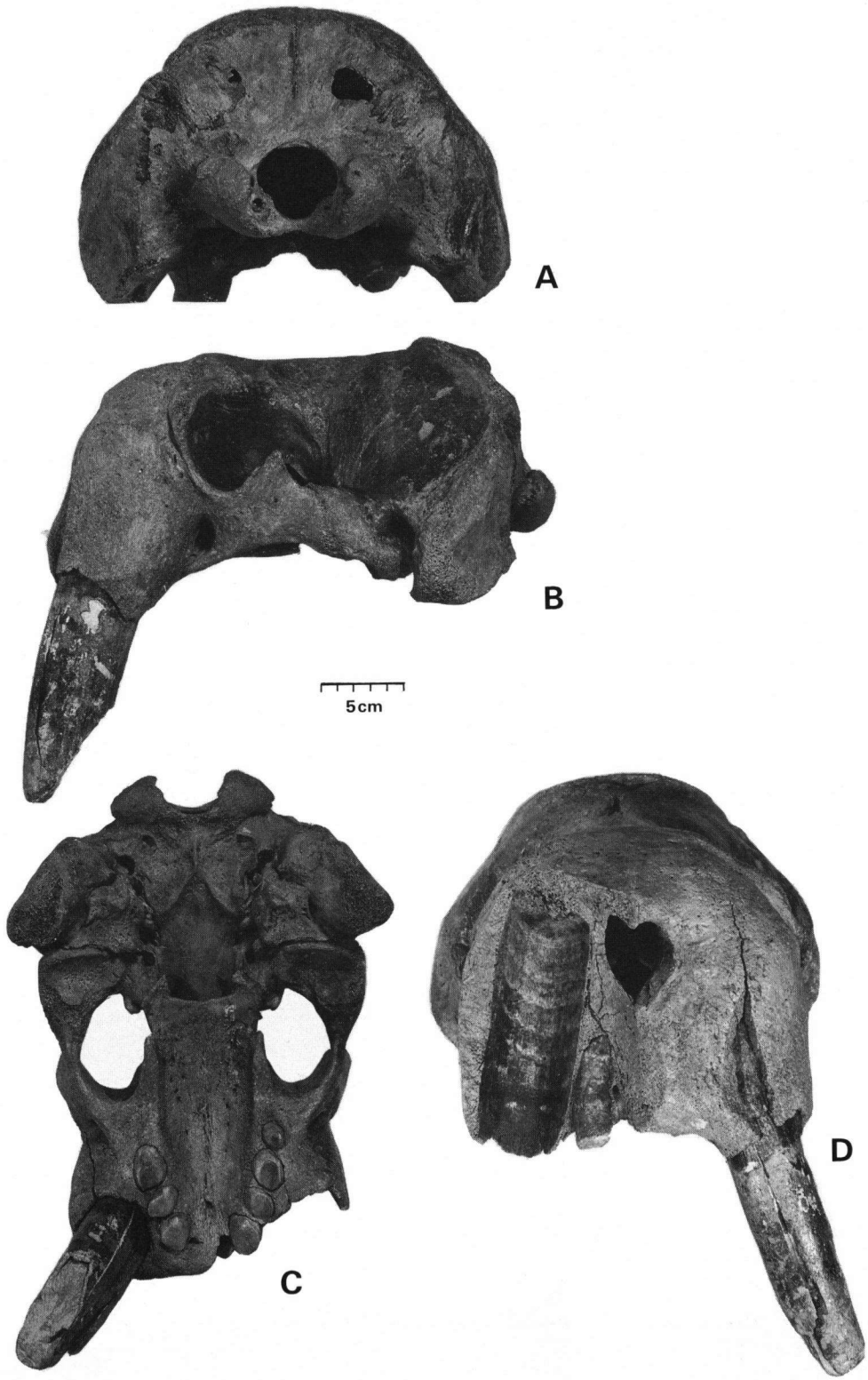
All of these elements (the canine excepted) have been worn to plate-like, lightly concave saucer-formed teeth. This is especially the case with the two hindmost left premolars and the second premolar at right.

The posterior tooth at right, P^3 dext., has a convex occlusal surface with a cusp-like prominence at its vestibular anterior side. P^2 sin. has a circumference which is not so much round or oval, but which more resembles that of a hindmost upper molar in the dentition of the genus *Ursus*. The measurable length of the left tusk is still 170 mm. The enamel on its exterior is striated and dark grey to black in colour, while the bone-coloured dentine in its centre displays a fan-shaped growth pattern.

The occipital bone (Pl. 2, A) has also recently suffered light damage as there is a small hole at centre left and a slightly larger triangular hole at centre right. The bone bears a light occipital crista. Seen from behind it is dome-like in outline with a sudden bend in the lambdoid part, by which this particular forward-leaning region displays the form of an orange segment.

Inside the braincase there are distinct traces of an ossified tentorium cerebelli, which stands out as a broad and wide balcony at the inner surface of the occipital bone. At each side rather vague traces can be detected of a formerly present fossa lateralis (= sylvii).

It appears possible to look into the nasal aperture from in front, indicative of the Atlantic subspecies *rosmarus* (Pl. 2, D). The crista lambdoidea transversa is very strongly developed, but not especially thickened at its centre. Instead of a (central) crista sagittalis a partly indistinct slot can be observed on top of the skull, which folds open in front to become lost in the region of the nasalia. There is a rather ill-defined transversal torus, which bows symmetrically inwards in an occipital direction in its centre, between the two upper limits of the orbits. The nasal aperture is somewhat wider than high, as far as can be judged (in spite of the aforementioned recent damage in front).



Pl. 2. Incomplete (damaged) calvarium of *Odobenus rosmarus rosmarus* (Linnaeus, 1758). Coll. S. Dekker. A. Occipital aspect; B. Left side aspect; C. Palatal aspect; D. Frontal aspect.

In the basal aspect (Pl. 2, C) the palate is strongly concave and covered with numerous small bony warts and knobs. There is a distinct foramen incisivum. A heavy central bony ridge divides the completely ossified and therefore no longer observable suture between basiphenoid and basioccipital bones. The bullae osseae are trapezoidal to triangular in outline and low (not inflated), covered with bony wrinkles. Although not strongly developed, a tuberculum musculare can be distinguished on either side; it more resembles a bony ridge with a central eminence. The mastoid processes each bear a processus paroccipitalis, developed into a nearly straight weak torus.

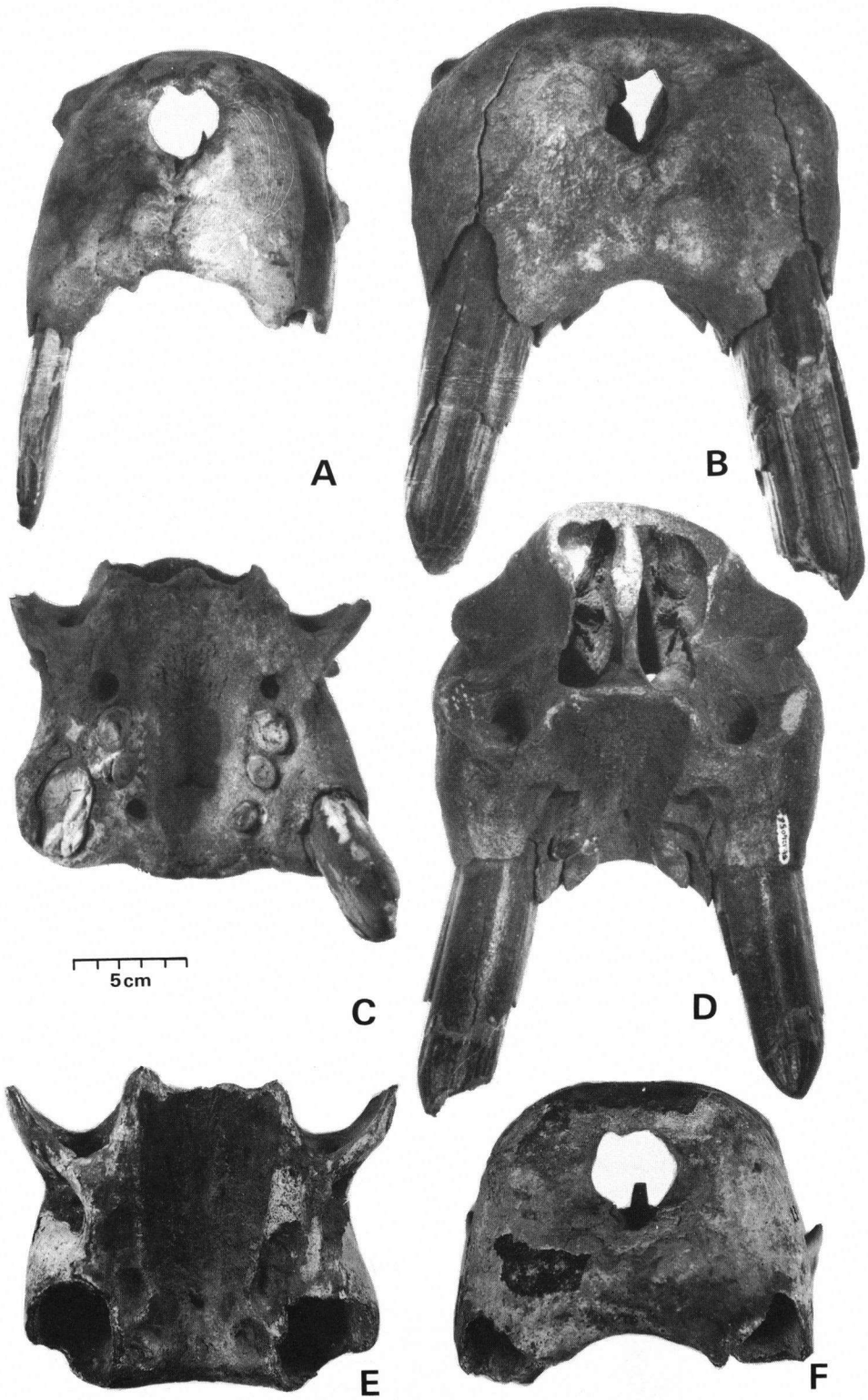
3. The third specimen, St. 124058, from a locality in the same region as *2*, consists of the snout part of a very heavy, undoubtedly male individual (Pl. 3, B, D). The colour of this well-mineralized fossil is a practically uniform brown to dark brown, 7.5 YR 4/4-3/4. The two tusks are still in place. Each has been damaged, during the lifetime of the individual as well as postmortally and even recently.

The tips of the two approximately 170 mm long tusks have each lost their enamel covering. The right canine is rounded and blunt at its end, while the left one may have had a similar form but has since suffered a sharp-edged (postmortal?) transversal break, allowing one to look into its central axis. This consists of the well-known globular dentine (light brown in colour in this case) so typical of the walrus, surrounded by concentrical dentine layers around the central core. On the sometimes almost black outside of each pillar-like dentine tusk extremity a number of distinct regular vertical flutings can be observed. These are almost of the same strength as the (negative) flutings encountered in the alveolar sheaths of the tusks of specimen *1*. In this third specimen the dentine still possesses its enamel covering more upward, in the direction of the alveolar rims. It is hard to tell whether most of the enamel has broken off postmortally and only a minor part of it *in vitam*, but it remains possible to assess the thickness of the enamel cover. This varies between 1.0 and 1.5 mm, being thicker near the alveolar rim. On the outside the enamel is almost uniformly smooth with only very faint markings of vertical and horizontal striations and flutings.

No traces are visible of first or second incisors. The two third incisors are present. They have large, sharp, ovaloid outlines and saddle-like occlusal surfaces, partly concave (in front) and partly convex (at the back). At left, a smaller P^1, recently damaged at its anterior rim, is also present. It, too, possesss a partly concave and partly convex occlusal surface.

The empty alveoli are present of P^1 dexter and of the P^2 and P^3 of both sides of the jaw. No other traces of teeth can be observed. The relatively deep palate is fairly smooth, with only faint flat bony wrinkles on its surface. There is a distinct foramen incisivum. Two more foramina on the right side and three to four at left enter the palate more to the rear, behind the posteriormost alveoli. The inner distance between the tusks, about 100 mm, the absolute size of the individual, and the heaviness of its tusks all indicate its male sex. The distance from the prosthion to the rim of the nasal aperture is 60 mm. It is possible to look into this aperture from in front (Pl. 3, B), which indicates that the specimen belongs to the Atlantic subspecies. The fully synostosed area above and to the back of the nose shows that the individual age, at death, must have been a considerable one. Part of the nasal septum is still present (Pl. 3, D). A faint and almost straight transversal bony torus runs over the top of the skull between the anterior upper corners of the orbit on each side. The sagittal part of the skull

Pl. 3. Rostra (snout parts) of *Odobenus rosmarus rosmarus* (Linnaeus, 1758). Frontal aspects of A. St. 137838 and B. St. 124058, Coll. Rijksmuseum v. Geologie & Mineralogie, Leiden. C. Palatal aspect of St. 137838. D. Oblique posterior aspect (showing the teeth) of St. 124058. E. Palatal aspect, and F. frontal aspect of ZMA 23.910 (Coll. Zoological Museum of Amsterdam University).


A
B
C
5cm
D
E
F

from the nasal aperture backwards, for as far as it is present, makes a slightly swollen impression.

4. The fourth specimen, St. 137838 (Pl. 3, A, C) is also a snout part, but of a much smaller individual with only the right (worn, but complete) tusk still in place. The left tusk has recently (in any case, *post mortem*) broken off, showing concentrical layers of dentine inside, of a dull yellow orange colour, 10 YR 7/3. The enamel has a thickness of about 1.5 mm. The rest of the fossil is mottled, displaying colours which run from dull yellow orange, 10 YR 6/3, to dull yellowish brown, 10 YR 4/3. The enamel of the remaining tusk, which has flaked off in places to show the 7/3-coloured dentine inside, has a dark reddish, almost chestnut-brown colour, 5 YR 3/4, brownish black at the tip, 5 YR 2/2. This tip (the canine still has a length of 105 mm from the rim of its alveolus) has been polished and whetted to a blunt wedge by the animal (cutting in a sagittal direction). Some seven to eight very small foramina can be observed along the front of the premaxilla; it is impossible to decide which of these should be seen as remnants of alveoli for lost incisors, or simply as foramina nutritia or foramina for tactile nerve endings. The internal distance between the two tusks is relatively great, 98 mm (pointing to a male sex?). However, the slender appearance of the tusk pleads in favour of the supposition that it is female, and its small general size is another argument for this view.

While the left I^3 and P^3 and the right P^3 have been lost (the first two of these perhaps *post mortem*, as the alveolar rims are quite sharp), the first and second premolars on each side and I^3 dexter are present. These teeth have slightly concave occlusal surfaces. Only P^2 dexter has more of a saddle-like surface, ending in a prominent and sharp cusp in front. P^2 sinister may have been similar, but this can no longer be ascertained owing to damage to which this element has been subjected during the animal's life.

The palate is relatively deep, with pronounced bony warts and ridges. A proportionally large foramen incisivum is present. The distance from the prosthion to the anterior sagittal point along the lower rim of the nasal aperture is 47 mm. Again, it is possible to look straight into the nose of the animal (Pl. 3, A). Therefore this must be *Odobenus rosmarus rosmarus*. The nasal septum has almost completely broken away. Traces of a suture run upwards from the nasal aperture to end against the faint transversal bony torus between the upper inner anterior orbital corners. This torus is slightly bowed back in an occipital direction. Too little has been preserved from this rostrum to allow for any conjectures on presence or absence of a sagittal torus, broadening or crest. The individual was probably middle-aged at the moment of death. It is well-fossilized, certainly not subfossil or (sub-)recent.

5. The last rostral fragment of the present series, ZMA 23.910 (Pl. 3, E, F), from the same general locality as *4*, is decidedly less mineralized. It may indeed very well be subfossil or (sub)recent; the bone is less heavy when weighed in the hand. Its colour is a very mottled combination of greyish yellow-brown (10 YR 6/2) with brownish black (10 YR 3/1) and even dark black (10 YR 1.7/1). There are a few spots of yellowish brown (5/8).

None of the elements of the dentition have been preserved. The sockets of each of the two tusks can be looked into up to their base. At the right side the distance from the rim of the alveolus to the spongious bone base of the tusk measures some 110 mm, at left this is 105 mm. As in specimen *4*, the transverse section of the alveolus (or of the stump of the tusk) somewhat resembles a number 8 in outline. Here, in *5*, a few (but distinct) traces of vertical fluted ridges exist along the inner walls of each alveolus. Absolutely no traces can be observed of any first or second incisors. The alveoli of I^3, P^1 and P^2 at each side, and of P^3 at left, have blunted rims and are partly filled with secondary bony growth. At right there is only a bony ridged surface where P^3 should have stood. These teeth have probably all been lost during the lifetime of the individual. The inner distance between the canine alveoli is some 80 mm (according to Mohr, 1942, 75, indicating

that this may either be an old female or a young male individual).

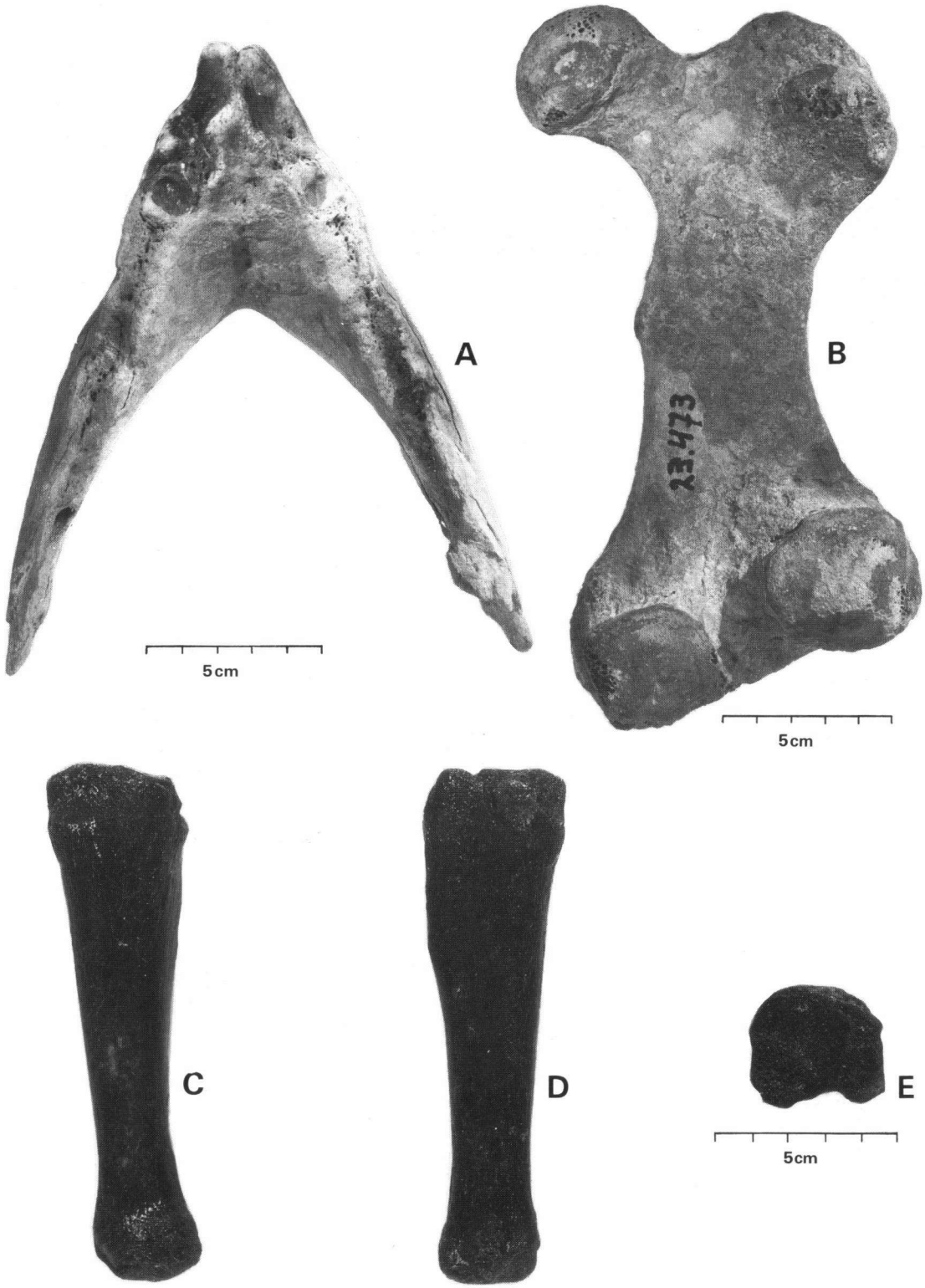
The palate is deep and covered with many longitudinal bony ridges and warts. There is a deep foramen incisivum at a level just between the two I^3 and the two P^1. Much more to the back one sees three foramina at right and three at left, arranged symmetrically with regard to the main sagittal plane. The hindmost of these six is situated at the level of the beginning of the jugal arch, while the anterior two foramina lie opposite the posterior edge of P^2. Seen from in front, the animal can be looked into its nasal aperture, showing that it belongs to the Atlantic subspecies (Pl. 3, F). The distance between prosthion and lower external rim of the nasal opening is 44 mm. A small part of the nasal septum is still in place. The backward-bowed transversal bony ridge between the two inner anterior orbital corners is rather sharply developed except in its central part. No sutural traces can be observed. Thus the individual was fully mature, possibly even old, when it died. The observations recorded above (sharp transversal interorbital ridge, small size combined with synostosis of the sutures) favour a supposition that the individual is an old female.

6. This mandibular fragment (Pl. 4, A), which is very eroded and rather light in weight, may perhaps also be subfossil. Its bone is rather flaky with a colour ranging from light grey, 7.5 YR 8/2, to orange and yellow-orange (7.5 YR 8/8-6/8). The inside of part of the alveolus for $C_{inf.}$ sinister and that of P_1 sin. are much darker, almost black. Owing to the erosion mentioned the alveoli of the lower canines can only be measured in their antero-posterior directions, while no other premolar alveoli than those of P_1 are at all measurable. The lower edges of the two horizontal rami are heavily corroded, so that the height of each ramus can hardly be estimated. At the back the horizontal rami have broken along an irregular plane of fracture. The left mental foramen displays an inner vertical bony partition, quite in the manner described by us in 1986 (p. 22). The other foramen mentale contains an ingrown oyster shell, but may possess a vertical bony partition as well. Measurements of this presumably small, female (?) specimen are given in table 3.

7. A femur of the right side (Pl. 4, B), ZMA 23.473 is recognizable as that of a walrus by its morphology and its size. We compared it with recent femora in the collection of the Amsterdam Zoological Museum. It is almost completely overgrown with Bryozoa save for some eroded areas on the "anterior" side at the caput, trochanter major and at the medial and

Table 3. Measurements of subfossil ♀ mandible, unnumbered, coll. Th. Mol (in mm).

Maximum measurable length of horiz. ramus sin.	193
Maximum measurable length of horiz. ramus dext.	194
Height of horiz. ramus sin. at P_3	46 ?
Height of horiz. ramus dext. at P_3	>44 ?
Vertical height of symphysis in nat. position	50
Sagittal width of symphysis in nat. position	82
Horiz. × vertic. dimensions of left for. mentale	12 × 6
Horiz. × vertic. dimensions of right for. mentale	12 × 8
Lower edge left mand. - lower edge left for. ment.	30
Lower edge right mand. - lower edge right for. ment.	34
Upper edge left for. ment.-edge of alv. of P_2 sin.	14
Upper edge right for. ment.-edge of alv. of P_2 dext.	13.5
Angle between sin. & dext. horiz. rami seen from above	± 55°
Sagittal length of alv. of $C_{inf.}$ sin.	25 ?
Sagittal length of alv. of $C_{inf.}$ dext.	29 ?
Length of alveolus of P_1 sin.	± 14.5
Width of same	± 12.5
Length of alveolus of P_1 dext.	± 14
Width of same	± 11



Pl. 4. A. Occlusal aspect of incomplete mandible of *Odobenus rosmarus rosmarus* (Linnaeus, 1758) ♀, subfossil or recent, unnumbered, Coll. Thijs Mol. B. 'Posterior' aspect of right femur of *Odobenus rosmarus* (Linnaeus, 1758), ssp., ZMA 23.473. C. Dorsal aspect; D. Plantar aspect and E. proximal articular aspect of right metatarsal I of *Odobenus* sp., ZMA 24.002.

lateral condyli, where the inner bony materia spongiosa have become visible. The colour of the specimen varies from orange (7.5 YR 6/8) over light grey (7.5 YR 8/2) to dark brown (7.5 YR 3/4), the colour of the bone itself. When placed upright on its condyli, the horizontal plane touching the top of the caput lies considerably higher than the tip of the trochanter major. The greater and lesser trochanters stand quite near each other on this flat, oar-like bone. No inter-trochanteric crest, nor a true trochanteric fossa seem to be developed. In place of the fossa there is a shallow trough with a nutritional foramen at its deepest point. Slightly above the middle of the diaphysis (near its "waist") a bony knob is encountered along the rounded medial keel of the shaft. This may perhaps be seen as a migrated gluteal tuberosity (or "third trochanter"), but of this we are not definitely sure. No traces exist of any bony flange starting upward from the lateral epicondyle (the "excrescentia lateralis" mentioned by us in 1987, p. 58); nor can anything be seen of a shallow single or double impression of the lowest part of the diaphysis above the patellar area, as in (many) seals. The intercondylar fossa is broad and deep. The two condyli are strongly developed, the lateral being somewhat larger and less flattened than the medial condyle. Slightly lower than the centre of the "anterior" surface (in its usual, natural position this corresponds more with an outer, lateral face) a prominent foramen nutritiae, opening in a downward direction, can be observed. Some measurements of this specimen can be found in table 4.

8. This metapodial bone, ZMA 24.002 (Pl. 4, C, D, E), has an external colour which varies between very dark brown and black (7.5 YR 2/3-2/1), while the materia spongiosa visible at some points of damage along the edge of the proximal articulation is lighter in colour, brown (7.5 YR 4/6). The bone, measurements of which have been combined in table 5, is long and heavy. It displays the same kind of very fine foramina in the compacta at each extremity observed by us in seal metapodials (1987: 60). We therefore concluded that it belonged to a

Table 4. Measurements of walrus femur dexter (in mm), ZMA 23.473.

Maximum length over caput	209
Maximum length over trochanter major	184
Proximal width (max.) caput-troch. maj.	114
Width of caput in same direction	44
'Sagittal' width of caput (right angles to previous)	± 40
'Sagittal' width of troch. major	41
'Sagittal' width of neck betw. caput & tr. major	21
Min. 'sagitt.' width, centre of diaphysis	26
Min. 'transversal' width at same location	49
'Transversal' width over condyles, at distal end	105.5
'Sagittal' width at same location	46.5
Circumference ± in centre of diaphysis (tape)	138
Angle between horiz. axes through condyles in transv. sense	162°

Table 5. Measurements of walrus metatarsale I dexter, ZMA 24.002 (in mm).

Maximum length	140
Dorso-plantar width at prox. articulation	32.5
Transversal width at proximal articulation	± 38
Dorso-plantar width at distal articulation	28
Transversal width at distal articulation	28
Dorso-plantar width at approx. centre of diaphysis	21.5
Transversal width at approx. centre of diaphysis	25
Circumference at approx. centre of diaphysis	77

pinnipede animal and, owing to its size, compared it with corresponding bones in recent walrus skeletons. This resulted in its certain determination as a first metatarsal bone of the right side of a walrus. In transverse section the bone is almost round at its central diaphyseal part. This further excludes any identification with a large land-dwelling carnivore such as lion or bear. At its base the lateral and medial edges show recent damage, but it is still perfectly visible that the articulation for the medial cuneiform bone has a shallow concave form. At the distal end of the bone the median elevation which separates the two grooved facets for a sesamoid bone at each side (the one at the right is slightly the largest) is rather broad and low.

IDENTIFICATIONS AND CONCLUDING REMARKS

The several observations and remarks made by us in the description of specimen *1* in this paper

may have made it clear that we consider this calvarium to belong to an *Odobenus antverpiensis* (Rutten, 1907). It satisfies the requirements enumerated by Van der Feen in his revision of Rutten's species (op. cit., p. 27): *a* the sagittal suture over the skull is depressed, not (inflated or) ridge-like; *b* the lambdoid crest is broad and high, not narrow; and *c* an occipital crest, while not quite absent, is certainly much less developed than in *rosmarus*. Furthermore the general size of the individual is somewhat larger than that of even a large male *rosmarus*. We refrain from attempting to give an opinion on the sex of specimen K 8052, as nothing appears to be known about (otherwise to be expected) sexually dimorphic features in the species *antverpiensis*. Once more we should like to point out that we think a conspecificity of *O. antverpiensis* with *O. huxleyi* (Lankester, 1865) highly likely, as we suggested in 1986. The more transversely compressed tusks, for instance the one in the Sekeres collection, 919 R, from the Grebbeberg along the Rhine (see figure 3B in our 1986 paper), are also indicated in K 8052, in as much as the transverse sections of the alveoli show. It is a great pity that K 8052 (once again) was found without its tusks, otherwise we might have known whether the outer dentine-cum-cement covering displayed the thinness required for *huxleyi*!

Very interesting particularities in K 8052 consist of the appearance of the present teeth and of the difference in placement of the third incisors. The last feature is no doubt linked to the lesser degree of development of the tusks (which, in *O. rosmarus*, have crowded the third incisor right to the rear of the premaxilla in between the tusks). The form of the relatively small, peg-like teeth with sharp edges, is another matter, although, as we will explain further on, it seems to be indirectly associated with Mohr's "over-"development of the tusks (rather, the development of canines into tusks). In this respect the remarks by Fay (1982: 137-138) should be taken into account. It is this author's opinion that "all but the late Miocene to Recent odobenids, however, are (or were) piscivorous. Piscivory requires a long gape that allows full use of the battery of pointed teeth for capture of fast-moving prey. Obstruction of that gape by huge, laterally placed tusks is disadvantageous in piscivory, hence evolutionary development of tusks in piscivorous mammals probably tends to be prevented by strong negatively selective pressures"... etc. We may therefore perhaps deduce from this that *O. antverpiensis* was somewhat more piscivorous than the recent *O. rosmarus*, but that the Scaldisian form already included a substantial amount of invertebrates in its diet. The described lizard-skin effect on the occlusal surfaces of the peg-like teeth may be explained through assuming that these were striated by abrasion in the way recorded by Fay of the recent walrus (op. cit., pp. 96-99): intake of microlithic particles (silt, sand) together with the diverse sucked-up invertebrate prey. Undoubtedly the "vacuum pump"-effect so well described by Fay (op. cit., pp. 167-171) in the case of the recent walrus has been less developed in *antverpiensis* because of the much more weakly vaulted palate in that ancestral form. There the still present central incisors and the relatively greater internal distance between the canines also cooperate in causing a less efficient suction apparatus that remains better adapted to the catching of fast-moving prey. Nonetheless the palate in K 8052 does again remind one of the form encountered in the Sloth Bear, *Ursus (Melursus) ursinus* Shaw, 1791, as was remarked by one of us in 1972 (p. 28), so that it probably had a comparable inhaling power. It is, incidentally, a fact that the central incisors in *U. ursinus* also usually disappear so as not to obstruct the suction faculty. Seen from aside, K 8052 displays a more bear-like profile (the angle prosthion-nasion having a value around 60°) than in the recent walrus (somewhere near 80°), which can be seen when Pl. 1, E in the present paper is compared with Pl. 2, B.

The recorded peculiarity that the distance between prosthion and lower edge of the nasal aperture is much less in *antverpiensis* than in *rosmarus* (see Pl. 1, B and Pl. 3, A, B, F) almost certainly implies a lesser development of the "moustache", the facial vibrissae, in this area

(see Fay, op. cit., pp. 64-71) and therefore, that *antverpiensis* may have had a less "rooting" habit when searching for (invertebrate) food along the bottom in murky water than *rosmarus*. This also favours the idea that *antverpiensis* has still possibly been more of a hunter of fish. Its late Miocene ancestor *Prorosmarus* with a number of sharp, relatively small mandibular teeth (the upper dentition is not yet known) has undoubtedly been piscivorous (Berry & Gregory, 1906). The figures given by Van Beneden (1877, Pl. II) of mandibular specimens, presumably of *O. antverpiensis* (= "*Alachtherium cretsii* Du Bus") in mixed-up material from different localities and stratigraphic levels around Antwerp indicate that these individuals, as does K 8052, display a somewhat piscivorous dentition also. In this respect it is interesting that observations and illustrations of relatively sharp-pointed teeth in recent captive walrus specimens given by Fay (op. cit., pp. 99-100) agree with observations made by one of us (V.B.) of the dentitions of some walrus individuals held in captivity. In each case the animals were fed on a diet of fish and shell-free clam meat, or exclusively fish, so that the abrasion of teeth by bottom sediment progressed much less than in nature. It is not clear to us in how far a carnivorous habit exhibited by certain recent individuals among Atlantic and Pacific walruses may also have played a role, where remains of seals (*Phoca hispida*, *Ph. largha*) have been encountered "with remarkable frequency" in the ingesta and faeces of 1 to 11% of researched specimens (Fay, op. cit., p. 153).

The specimens *2* up to and including *6*, according to their described morphological appearance and also to their localities of collection, may, without hesitation, be identified as belonging to the Atlantic subspecies of the recent walrus, *Odobenus rosmarus rosmarus* (Linnaeus, 1758). Specimens *2* and *3* are male, *4* and *6* female, while *5* is probably female as well. The well-mineralized condition encountered in *2*, *3* and *4* leads us to conclude that they are truly fossil and therefore very probably Upper Pleistocene in age. The rostrum without dentition, *5*, and the incomplete mandibular fragment, *6*, are more likely to be subfossil if their state of preservation allows that conclusion. Especially in the case of *5* one is reminded of, among other things, the publications by Nordmann (1952), Møhl (1974), and Ulbricht (1982). The last of these authors (in her description, pp. 19-21, of a walrus rostrum recovered from the bottom of the present harbour of Schleswig) points out that, through the commercial contacts with the Vikings, the tusks of walruses were a much-prized source of ivory. Specialized hunters killed the animals and hacked off the rostral parts of the heads containing the tusks (see also Van Bree, 1968). The rest of the animal was abandoned. It seems that not only the tusks, but also other parts of the cranial rostrum were used, for instance in the fabrication of combs. Møhl gives useful information on the dating of a considerable number of subfossil walrus finds from Denmark, together with historical information. According to this, Norsemen from Groenland paid tithes to the Pope in the form of Walrus tusks, which were transported by sailing vessel via Iceland to Bergen in Norway and from there to Flanders; around the year 890 the traveller Ottar sailed to England and brought walrus tusks with him for King Alfred. It is therefore quite possible that a subfossil specimen such as *5* formed part of such a cargo and was lost overboard or in a shipwreck in early mediaeval times. This may also be true for specimen *6*, but here it should not be overlooked that this walrus may equally well have died in a natural manner somewhere in the Brown Ridge area in the North Sea. Mandibles may have been not so interesting from a commercial point of view.

Because there is no way of identifying an isolated femur more precisely, we have to limit our identification of the subfossil specimen *7* to: *Odobenus rosmarus* (Linnaeus, 1758) ssp. (probably also of the Atlantic subspecies, in view of the locality of recovery). This may also have belonged to an individual that lived and died in the North Sea in early historical times.

The last specimen, *8*, is even more difficult to

identify. It is well-mineralized and certainly fossil. Its location, the edge of the Deep Water Channel, is known to have produced well-mineralized, heavily fossilized finds dating to Early and Middle Pleistocene times, all of which displayed the same or comparable dark to black hues and colours (see Erdbrink, 1983a, 1983b). Thus it may well be possible that this isolated metatarsal bone belonged to an early form of walrus as *Odobenus antverpiensis* or *O. huxleyi*. In this case we think it prudent not to venture beyond a determination of the specimen as *Odobenus* sp.

Finally there still is an interesting phenomenon to be discussed. This consists of the circumstance, noted in the present descriptions, that the (absent) tusks of specimen *1* must have possessed a strongly fluted exterior; while, at the same time, specimen *3*, where the outer enamel covering of each tusk may have largely been lost through abrasion (Fay, op. cit., pp. 114 *et seqq.*), displays a number of distinct vertical flutings on the outer dentine surface of either tusk. When it is considered a possibility that the recent walrus. *O. rosmarus*, has had *O. antverpiensis* (perhaps identical with *O. huxleyi*) for its ancestor, an interesting parallel may exist with a situation in recent man. Korenhof based this thesis (1960) on the discovery that the morphology of the enamel-dentine surface of human molars (made visible by his invention of "endocasts") mirrored earlier evolutionary stages encountered in the external morphology of the teeth of man's ancestors and predecessors. Since then he has extended this particular research (1978, 1982a, 1982b, 1982c). As he explained in the 1978 paper, the plane of partition between enamel and dentine, formed by, respectively, ameloblasts and odontoblasts, is a genetical blueprint, much more so than the later-formed occlusal surface.

In view of this established fact the question appears logical as to whether something of a like nature does not arise here when the morphology of the external surface of a possibly ancestral *antverpiensis* (= ?*huxleyi*) strongly resembles that of the outer dentine surface in recent *rosmarus*. By implication one might even tentatively suggest that ancestral (evolutionary) features should be present in the morphology of the enamel-dentine surfaces of mammalian teeth in general!

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RÉSUMÉ

Suite d'une publication des deux auteurs (1986). Ces pages sont une description de huit fossiles d'Odobenidés, dont trois sont plutôt subfossiles.

Deux ont été trouvés au nord de l'île d'Héligoland, cinq autres dans la partie méridionale de la Mer du Nord, et un seul crâne incomplet au fond des bouches de l'Escaut. Ce dernier est attribué à l'*Odobenus antverpiensis* (Rutten, 1907), probablement synonyme d'*O. huxleyi* (Lankester, 1865); six autres à l'espèce récent, *O. rosmarus* (L.); et un os métatarsale, par prudence, seulement à *Odobenus* sp.

Des dents plus pointues et un régime de base probablement plus piscivore chez des anciens

morses est discutée de même que la possibilité de retrouver, dans l'*O. rosmarus* et dans autres mammiféres, des stades évolutionaires dentaires anciens par observation de la surface interne séparant l'émail de la dentine.

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