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FOSSIL APPENDICULAR SKELETAL WALRUS MATERIAL FROM THE NORTH SEA AND THE ESTUARY OF THE SCHELDE (MAMMALIA, CARNIVORA)

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ABSTRACT

Seventeen fossil, and two recent odobenid remains belonging anatomically to the appendicular skeleton, encountered by us in two public and two private collections since the publication of a number of earlier papers, are described and discussed. Most specimens should be identified as *Odobenus rosmarus* or simply as *Odobenus* sp., but in some cases identification as either *Odobenus antverpiensis* (Rutten, 1907) or as *Odobenus huxleyi* (Lankester, 1865) appears to be justified.

INTRODUCTION

Following upon our previous description of fossil odobenid remains belonging to the axial skeleton, in the collections of "Naturalis", the Nationaal Natuurhistorisch Museum at Leiden, and of Mr Klaas Post, of 8321 EJ Urk, Klifweg 6, we now describe and discuss more fossil material encountered by us in those same collections, as well as in the private collection of Mr Kommer W. Tanis of 3252 LC Goedereede, Breenstraat 12. In addition, two Recent walrus femora in the collection of the Zoological Museum of the University of Amsterdam are also shortly described and figured in order to serve as comparison with the fossil specimens. The Leiden specimens are indicated by the prefix St. (from "Stamboek", the original register of the collection of the Rijksmuseum van Geologie en Mineralogie, now incorporated into that of "Naturalis"), those from Amsterdam by the prefix ZMA, and those in the (private) Post and Tanis collections by, respectively, the prefix KP and T.

As in our 1986, 1990 (a, b) and 1999 (a, b) papers, the accurate rendering of the colours and hue(s) of each specimen has been attempted through the use of the revised Munsell colour charts by Oyama et al. (1967). This practice, as far as we know, has been initiated by Louwe Kooijmans (1972). Its purpose, together with that of recording the degree of mineralization of each fossil bone, is to enable future researchers to arrange dredged or fished-up fos-

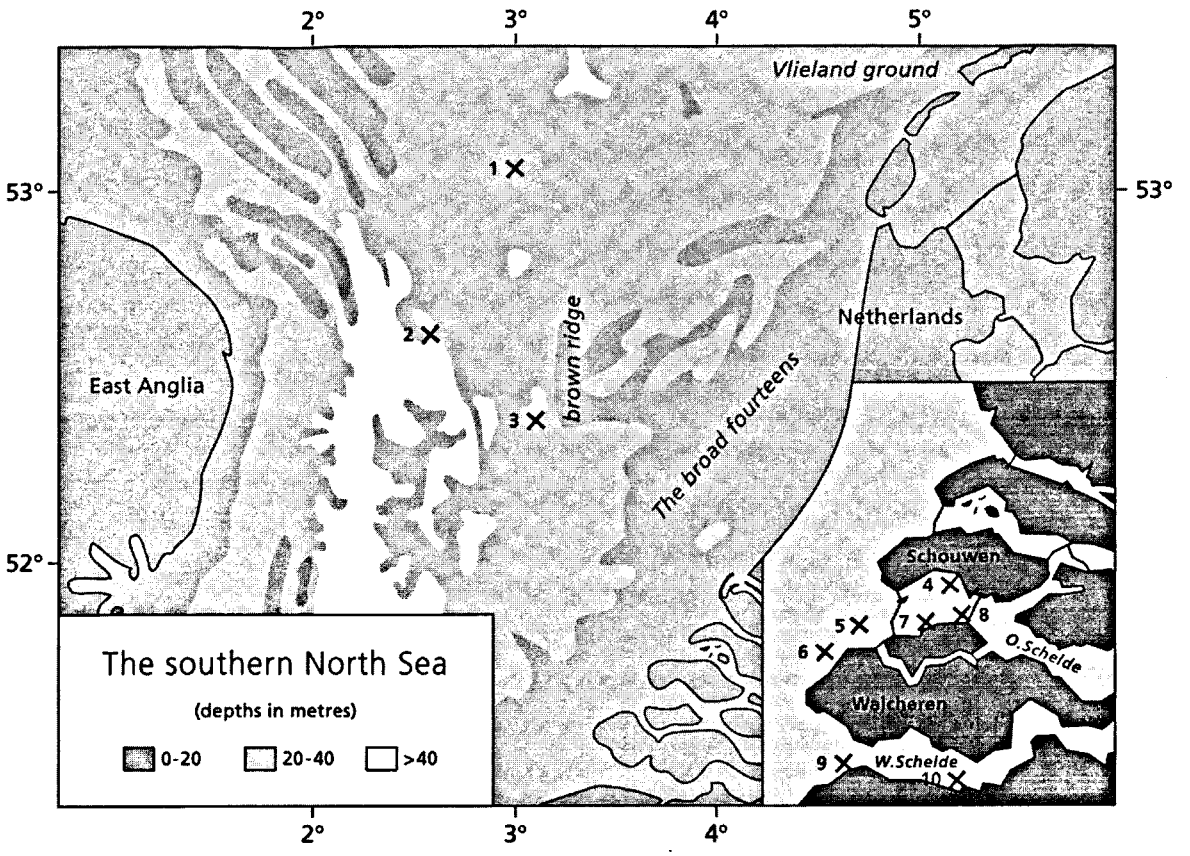

Fig. 1. Localities of collection of described specimens in the southern part of the North Sea: 1, N.W. of Brown Ridge (West Hole?), ZMA 24.613. 2, 52°40'N 2°50'E, T333. 3, S.E. of Brown Ridge (Brown Ridge area), KP 472 and KP 499A. 4, in front of the Flaauwerspolder, Oosterschelde, not numbered incomplete femur and tibia. 5, gully near Domburg (Oosterhoofd, island of Walcheren), St. 118849, St. 118963, St. 147040, St. 147067. 6, pit of Oostkapelle, St. 42340. 7, in front of Wissenkerke, Oosterschelde, not numbered fragment of tibia. 8, Schaar of Colijnsplaat, Oosterschelde, St. 170510. 9, in front of Nieuwe Sluis, Westerschelde, St. 122611. 10, the "Ree" in front of the Braakman (creek), W. Schelde, St. 145446.

sils without exactly known data regarding their provenance, in groups together, something which Kortenbout van der Sluijs (see Louwe Kooijmans, 1972: 69) has ventured upon to do from the very beginning when fossil bones of mammals were offered to him for determination. A short review of these colour- and fossilization problems can be found in Bosscha Erdbrink (1982: 13). We are firmly convinced that, in any description of a fossil specimen, every observable feature should always be registered, including colour and degree of mineralization. Measurements of the fossils (Tables 1-3) were taken in the same manner as in our two last publications. In some cases the measuring practices are identical with those advocated by Desse et al. (1986, mainly: 116-120). These were again largely based upon those recommended by Von den Driesch (1976). In those instances a letter D, followed by a number, marks the particular numbered measurement in one of Desse's tables. We are not convinced that each measurement advised by Desse et al. for Carnivora does indeed make sense in the case of the Odobenidae, because there appears to remain too much room for inaccuracy when measuring.

Fifteen of the fossil specimens have been collected at more or less exactly recorded localities (see Fig. 1). The two other ones come from unknown sites in the southern part of the North

Sea. We refer the reader to figures 1a and 1b in our cited 1986 paper, and to a more recent publication by Laban (1995: Fig. 17), for an impression of the very uneven surface of the sea-bottom (the only exceptions being the areas of the Broad Fourteens = Breeveertien, and the Vlieland Ground), reason why we abstain from using the term sea-floor.

DESCRIPTION

Humeri

A series of four humeri (Fig. 2f, g, h, i, j; Fig. 5a, b, c, d; Table 1) comprises two of the left side and two of the right. One of each belongs in the Leiden collection: St. 122611 (left) and St. 170510 (right). The other right humerus, ZMA 24.613, formerly KP 550, was donated by Mr Post to the Amsterdam museum. The remaining left humerus is numbered KP 270.

One label of St. 122611 states that the fossil, identified there as '*Odobenus huxleyi* (Lank)', is a humerus of the right side (which is incorrect, as is the identification). A second label only bears the identification as '*Odobenus* spec.' It is furthermore noted that the fossil was fished up from the Westerschelde in front of Nieuwe Sluis, and acquired through Mr J.P. Jacobs on 8 July 1964. Colour and hue of the compacta and spongiosa of the fossil are a uniform 10 YR 3/4 (dark brown), with several patches of -5/4 (dull yellowish brown). Save for some slight damage, undoubtedly the result of erosion in sand-laden water, along the rim of the caput, the greater tubercle, the deltoid ridge, and the medial edge of the trochlea, this massively mineralized left humerus is anatomically complete. As in the specimens described by us in 1986, the coronoid, radial and olecranon fossae are very shallow or absent, while there is absolutely no question of any supratrochlear perforation or of an entepicondylar foramen. The intertubercular sulcus (= bicipital groove) is strongly marked and deep. The greater tubercle considerably exceeds the uppermost level of the caput in its height. There is a well-defined supinator ridge.

The label of St. 170510 states that this left humerus (which is incorrect, as it is from the right side) was fished up from the Oosterschelde at the "Schaar" of Colijnsplaat and that it was donated to the Rijksmuseum van Geologie en Mineralogie on 18 September 1970 by the Rijksmuseum van Oudheden at Leiden. Colour and hue are 10 YR 4/4 (brown), with several patches and areas of -7/4 (dull yellow orange) and -7/1 (light grey). The description given above of St. 122611 also holds for this specimen. It has, however, suffered considerably more damage through erosion. Its diaphysis has broken, but is glued together again. The compacta at the point of breaking has a slightly darker internal colour than on its exterior. Erosion has demolished the upper extremity of the greater tubercle, which still slightly exceeds the uppermost level of the caput in height. The tip of the lesser tubercle has also broken off. The bicipital groove, if anything, is still deeper and more finely bordered than in St. 122611. The supinator ridge is also more sharply defined. Rims and edges around the medial epicondyle and trochlea have been damaged by erosion. This is true also along the base of the greater tubercle and along the upper part of the deltoid ridge. The measurements of this specimen (Table 1) show that there are no great differences from St. 122611. They are somewhat less than the comparable dimensions of two large Recent walrus humeri, ZMA 22.648 and ZMA 22.649, from Edgeøa (Spitsbergen), given by us in 1986, Table IV.

ZMA 24.613, formerly KP 550, a fossil right humerus, was trawled up on March 18, 1993, from a deep hole (possibly the West Hole in our sketch map, Fig. 1) to the north-west of the Brown Ridge at about 53°10' N 3°20' E, donated to Mr Post by skipper M. de Boer of the vessel UK 95. Its colour and hue are 10 YR 4/3 (yellowish brown), with patches of -3/2 (brownish black) and -7/4 (dull yellow orange). This specimen is quite considerably larger than the two humeri described above. It is complete save for some erosional damage to the top of the greater tubercle (which is still higher than the uppermost level of the very large caput), to a short part of the deltoid ridge and to some of the edges of the trochlea, and the lateral epicondyle. The bicipital groove is very broad and deep and must have housed an enormous biceps muscle. There are numerous (at least more than ten) nutrient foramina in its upper part between the greater and lesser tubercle and on the lesser tubercle itself, as well

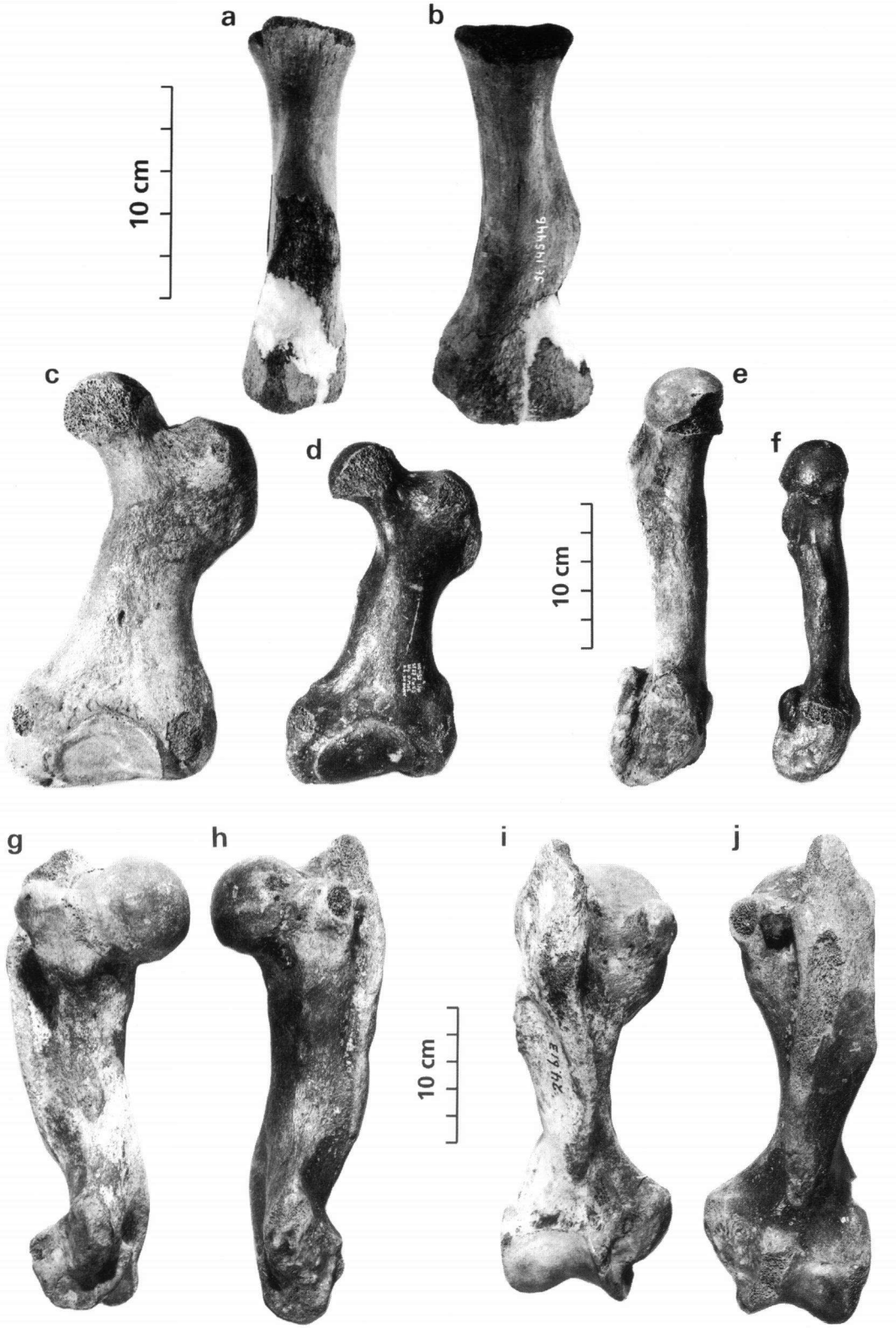

Fig. 2 . a, lateral, and b, frontal aspects of St. 145446 (diaphysis of radius sin., subad. individual). c, d, anterior, and e, f, medial aspects of left femora, resp. KP 472 and KP 499A. g, h, medial, and i, j, anterior aspects of two humeri, resp. ZMA 24.613 (= KP 550) (dext.) and KP 270 (sin.).

Table 1. Measurements of humeri, in mm, partly following Desse et al. (1986).

	St. 122611	St. 170510	ZMA 24.613	KP 270
	(sin.)	(dext.)	(dext.)	(sin.)
D.1 Greatest length	302	312	352	391
D.4 Transversal proximal width	90	86	119	121
D.7 Transversal distal width	110	109	137	136
Sagittal distal width	64	63	80	66
D.6 Sagittal min. width at centre of diaphysis	39	49	45	53
Transversal min. width at centre of diaphysis	41	39	52	52
Min. circumference of diaphysis	164	158	214	207
Sagittal max. width across deltoid ridge	88	86	118	>86

as below the caput and the trochlea. The deltoid ridge is strongly developed; so is the supinator ridge. The coronoid and olecranon fossae are hardly indicated. The entire bone makes a massive and heavy impression and falls in the same category as the giant right humerus N.Z. of the Stolzenbach collection described by us in 1986.

The fourth humerus, KP 270, is by far the largest ever encountered by us. It is from the left side, collected between 1990 and 1992 somewhere in the southern part of the North Sea. Its colour and hue are 10 YR 3/2 (brownish black) with patches of -4/6 (brown). Erosional damage has occurred at the tips of the greater and lesser tubercles, at the upper part of the deltoid ridge, and at the edges of the trochlea and the lateral and medial epicondyles. The lowest point of the deltoid ridge lies at a relatively much more distal position than in the three specimens described earlier, and only some 70 mm from the uppermost point of the medial epicondyle. The bicipital groove, although deep and strong, makes a slender, gradually proceeding and more elegant impression than its counterpart in ZMA 24.613. Opposite the lesser tubercle an ironstone concretion has blocked the groove, in which some bryozoan colonies attest to the fact that the fossil lay free on the bottom for a considerable time. The top of the greater tubercle exceeds the uppermost level of the caput in height, although relatively less so than in ZMA 24.613. The caput itself, though large, is not as enormous either. There are numerous foramina nutricia around the base of the caput and at the bases of the two tubercles. The bony outer surfaces of the diaphysis display a curiously ramified pattern of very fine ripples, especially in the area above the olecranon fossa, but also elsewhere. This fossa, and the coronoid fossa, are relatively better developed than in ZMA 24.613. The medial epicondyle is very prominent and the supinator ridge starting from it is well-defined. When the bone is placed upright on a plane through its most distal epicondylar extremities, the long axis through the centre of the diaphysis stands at an angle of some eighty degrees with that horizontal plane. This is a rather remarkable difference from the three humeri described above, and from the giant right humerus N.Z. of our 1986 publication, where this angle at most differs only some two degrees from the vertical, if at all.

Radius

The damaged diaphysis of a left radius, St. 145446 (Fig. 2a, b; Table 2), was fished up at the "Ree" in front of the Braakman (Fig. 1). The colour and hue of the find are 10 YR 4/6 (brown) to -3/4 (dark brown), with lighter areas where the fossil has been restored with some resinous material. The item was acquired through Mr J.P. Jacobs on December 20, 1967. On the label its determination does not go beyond '*Odobenus* spec.' As is evident in the figures, the proximal and distal epiphyses are absent and the extremities of the diaphyseal piece are roughly those of the planes along which a final synostosis should have taken place after adulthood would have been attained. From this, and because the few

Table 2. Measurements of the diaphysis of left radius St. 145446, in mm, partly following Desse et al. (1986).

Length along ulnar side (at right angles to ulnar notch)	173
D.11 Length along anterior side, over cristal	82
D.14 Maximum proximal width	>76
D.16 Minimum width of diaphysis (= diameter at min. circumference)	30
D.17 Minimum circumference of diaphysis	106
D.18 Maximum distal width	>52
Distal anteroposterior width of diaphysis	75
Width of diaphysis above distal extremity, at right angles to the two flat planes	54

comparable measurements (Table V, p. 27 in our 1986 paper) are smaller than in the fossil described earlier by us, the bone appears to be that of a subadult individual. A large ovaloid fragment of bone at the distal anterior end is missing as a result of recent damage. This has in part been repaired with a waxy or resinous substance (as mentioned above). The visible materia spongiosa has the same colour as the rest of the bone. A relatively much smaller nutrient foramen than in ZMA 21.076, described by us in 1986, occurs at the same position slightly above the centre of the diaphysis and at its medial side.

SCAPHOLUNAR

T 333, identified by us as a scapholunar bone of the anterior left extremity, has a colour and hue that run from 7.5 YR 4/4 (brown) over -3/4 (dark brown) to -2/3 (very dark brown). It appears to be the first of its kind (as far as we know) to have been collected from the bottom of the North Sea.

This typical bone of the manus in all Carnivora is a product of the fusion of scaphoid (or radiale) and lunar (or intermedium), and also includes the centrale, as is so clearly described by Cornwall (1956: 150). In the case of *Odobenus*, most resemblances seem to lie with the scapholunar of the Ursidae (see plates 14 and 18 in the Anatomical Atlas of Pales and Lambert, 1971). Here the pollex is developed almost equally with the other digits; the thumbbones are not more mobile than the other digits or opposable to them, but they articulate in the same plane. This is undoubtedly also the case with the walrus.

According to Mr Tanis the fossil was collected in 1993 near 52°40'N 2°50'E (Fig. 1). It is pictured on Fig. 3a-c. Slight erosional damage to the surface of the bone, so that the -4/4 coloured spongiosa has become visible, occurs all around the scaphoidal part, on the posterior edge of the lunar (or lunate) part, and along some of the distal edges of this latter and of the central part. A small series of bryozoan colonies exists in a pit near the articulation of the trapezoid bone, in some pits at the posterior side and in one on top of the bone; the fossil lay free on the bottom for

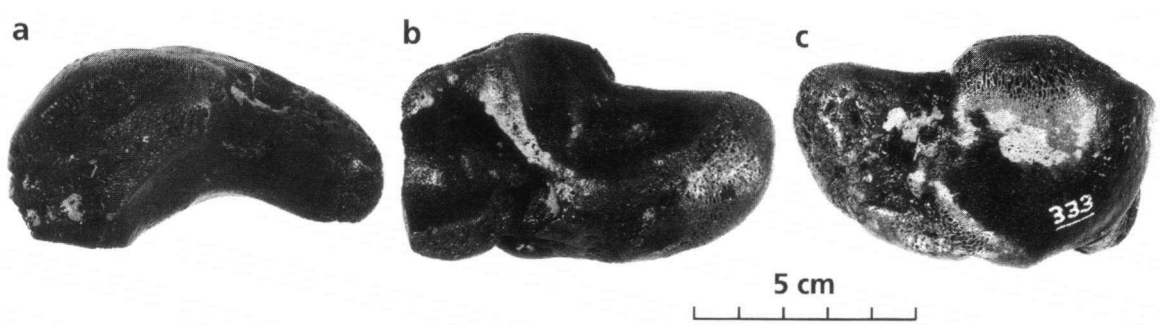

Fig. 3. Left scapholunar bone T 333: a, posterior, b, distal, and c, proximal aspects.

some time. Measurements of the specimen are: maximum transverse width 84 mm; maximum ventro-dorsal (sagittal) width 53 mm; maximum height (or proximo-distal width) 43 mm.

FEMORA

The Post collection contains three femora (Fig. 2c-f; Fig. 4a-f ; Fig. 5a-d; Table 3) with measurements that are comparable to those of ZMA 23.473 (Table 4 in our 1990b paper). KP 472, from the Brown Ridge area, was collected between 1985 and 1990. KP 499A, collected in January 1993 by skipper P. van Es (of the fishing vessel ST 27), obtained through Mr D. Mol, is stated to have been found south-east of the Brown Ridge. KP 826 lacks a date of collection, but has an inscription in white ink with the name of its collector, P. de Jonge, and the notice Zd. Noordzee (southern North Sea).

KP 472 has a colour and hue of 5 YR 3/6 (dark reddish brown) with some patches of -6/3 (dull orange). KP 499A has a uniform dark reddish brown colour and hue, 5 YR 3 /4 to-3/6. KP 826 is uniformly glossy black, 10 YR 1.7/1, while some areas of the spongiosa visible at damaged places are 10 YR 2/3, brownish black. Most resemblances with the specimen ZMA 23.473 are found in KP 499A, a left femur. It is almost equal in size, and complete but for minor erosional damage to the anterior neck, the anterior base of the trochanter major, the region above the medial condyle, and the base of the patellar area. The spongiosa, visible at these points, has the same colour as the rest of the bone. The tip of the trochanter major lies considerably below the horizontal plane over the top of the caput. No true intertrochanteric crest, nor a trochanteric fossa appear to be developed. Some foramina nutricia occur at, and below, their expected locations. As in ZMA 23.473, a bony knob, the equivalent of a trochanter minor, exists on the rounded medial keel of the diaphyseal shaft, slightly above its middle half. There are only faint traces of a ridge (the intertrochanteric crest) from this knob towards the base of the trochanter major. A large and a small nutritional foramen stand some 25 mm below the supposed trochanter minor on the rounded keel of the shaft. There are some short bony crests along the lateral and medial keels of this oar-like bone, above the epicondyli. The intercondylar fossa is deep and broad and the condyli are strong. The lateral one is larger and less flattened than the medial. The patellar area is a single saddle-like plane, not a double one as in seals.

The left femur KP 472 differs from KP 499A and ZMA 23.473 in several respects. Not only is it larger, but it also possesses a definite lesser

Table 3. Measurements of femora in mm, partly following Desse et al. (1986: 138-139).

	KP 472	KP 499A	KP 826	St. 42340	St. 118849	St. 118963	St. 147040	St. 147067	St Fl.pold	ZMA 23.395	ZMA 23.396
D.2 Length over caput	269	220	181	164	-	-	-	234	-	181	226
D.1 Length over troch. major	235	199	163	164	-	-	-	210	-	172	219
D.3 Width over caput & troch. major	136	111	91	108	-	-	-	100	-	95	116
D.5 Trans. width of caput	59	49	±47	46	50	-	-	51	-	48	55
Sagitt. width of caput	±55	46	46	42	43	-	-	51	-	44	51
Min. sagitt. width, centre of diaphysis	48	31	29	34	-	-	-	37.5	-	27	35
D.6 Transv. min. width, centre of diaphysis	65.5	50.5	51	61	-	-	-	58	-	52	62
D.8 Transv. width over condyles	129	108	±98	-	-	135	>87	117	65	97	116
Sagitt. width, ibidem	70	58	±50	-	-	67	-	59	-	51	59
D.7 Circumference, centre of diaphysis	173	134	142	160	-	-	-	156	-	140	154
Angle between transversal horiz. axes through condyli	161°	155°	152°	-	-	155°	±152°	153°	156°	145°	166°

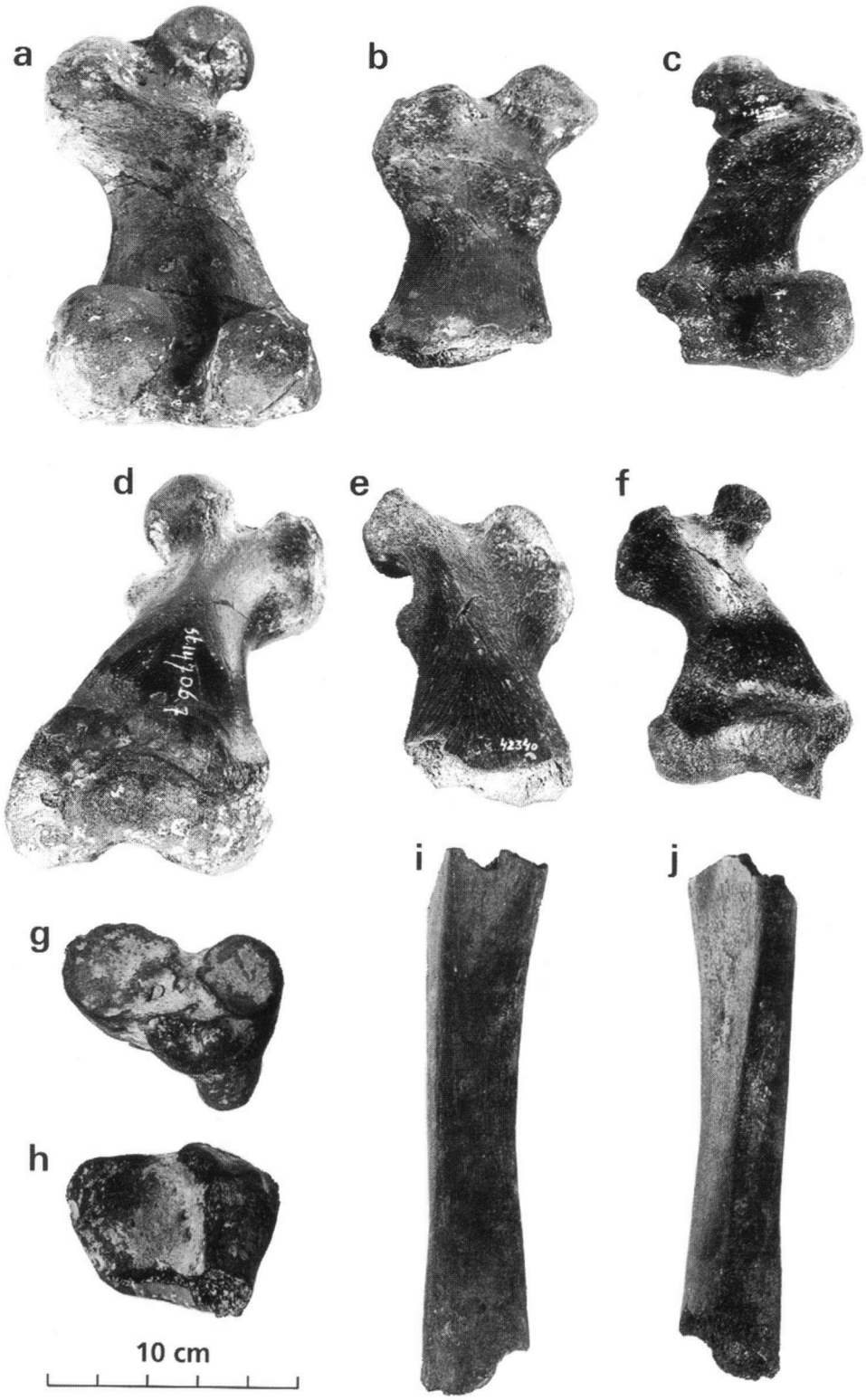

Fig. 4. a, posterior, and d, anterior aspects of left femur St. 147067. b, posterior, and e, anterior aspects of incomplete left femur St. 42340. c, posterior, and f, anterior aspects of right femur KP 826. g, proximal articulation surface, and h, anterior aspect of not numbered proximal fragment of left tibia/fibula (Leiden collection) from in front of Wissenkerke. i, posterior, and j, anterior aspects of not numbered diaphysis of left tibia (Leiden collection) from in front of the Flaauwerspolder.

trochanter on what might be termed the posterior face of its diaphysis, at a distance of some 70 mm from the caput and the greater trochanter. From there, a somewhat roughened area runs down to the medial keel of the diaphysis, which is more rounded, not so flattened, as in the other two femora. Only a very indistinct ridge connects the trochanter minor with the base of the trochanter major. No traces of a trochanteric fossa exist; the surface where this feature might have occurred is, instead, strewn with a number of foramina nutricia which are also present below the caput and, in front, in the area between the greater trochanter and the caput. The femoral head itself has suffered some recent damage on its anterior side, displaying spongiosa with the same colour and hue as the rest of the bone. Slight damage of a comparable nature has occurred at the tip of the trochanter major, and, in front, to each side of the very strongly developed saddle-like patellar area. The intercondylar fossa is very deep and strong, with a roughened surface containing many foramina. This surface continues above the medial and lateral condyli along the entire posterior base of the diaphysis. The lateral condyle is again the largest of the two condyli, but neither is as markedly flattened as are the condyli in the two earlier-described femora. A large (3 x 5 mm) nutrient foramen is present on the anterior face of the diaphysis at some 60 mm above the patellar area. It opens in a downward direction. No clear traces of bony ridges or flanges on either side of the "keels" at the diaphyseal sides above the epicondylar region are observable. There are some indistinct traces of a ramified bony surface of the diaphysis on its anterior and posterior planes, much less clear than in the humerus KP 270. Finally it should be mentioned that we tried to fit the femoral heads of KP 499A and KP 472 to the acetabulum of St. 400978. To our surprise the caput of KP 472 appeared to be of almost the correct size.

The right femur KP 826 has suffered some recent damage. About half of the caput has broken away at the anterior side and opposite the greater trochanter, as well as medially near its base. A small part of the greater trochanter, also anteriorly, has gone too. Two-thirds of the medial epicondyle, on the medial side, a fraction of the upper posterior region of the lateral epicondyle, and a piriform region just above that latter feature on the anterior side, are all broken off, displaying the brownish-black spongiosa inside. This right femur, which has almost the same size as a presumedly female Recent walrus femur from the same side, ZMA 23.395 from Kap Lee on Edgeøa in the Spitsbergen (Svalbard) archipelago (Fig. 5f, h), differs from it morphologically. In the fossil the greater and lesser trochanters are very much more distinct, and stand separated some distance from each other. They are linked by a rounded, broad and flat intertrochanteric crest, on which faint traces of a quadrate tubercle can be made out. The very shallow trochanteric fossa just above the crest contains a few relatively large foramina nutricia at its upper end near the greater trochanter. Traces of a flat and shallow spiral line are observable lower down on the posterior face of the bone. A large nutrient foramen occurs laterally from the middle line on the anterior face of the diaphysis almost at its narrowest point, somewhat halfway and just below the level of the lesser trochanter. No traces of a gluteal tuberosity can be seen. The intercondylar fossa is broad and deep and contains a number of foramina. Traces of a crestlike feature exist above the lateral epicondyle along the lateral side of the bone, perhaps to be equated with the "Excrescentia lateralis" which we have observed on femora of the Phocidae (Van Bree & Bosscha Erdbrink, 1987: 50).

One of the largest of the presently described fossil femora is St. 147067, a specimen of the left side (Fig. 4a, d). According to its label it was fished up in front of the Oosterhoofd (East Head) near Domburg on the isle of Walcheren (Fig. 1). No date of collection is given, but it is identified as '*Odobenus Antwerpiensis* (rutten)' (sic!). Colour and hue are 10 YR 3/3 to 2/2 (dark brownish black). There are some balanid encrustations on this almost complete, heavily mineralized fossil. It appears that it has recently broken in three pieces, which were glued together again. Very slight erosional damage occurs at, and on the medial epicondyle, above the lateral epicondyle and on several places on the caput. A very pronounced, large and strong lesser trochanter is present, which is linked to the greater trochanter by a flat and extremely broad intertrochanteric crest. The trochanteric fossa and the neck of the

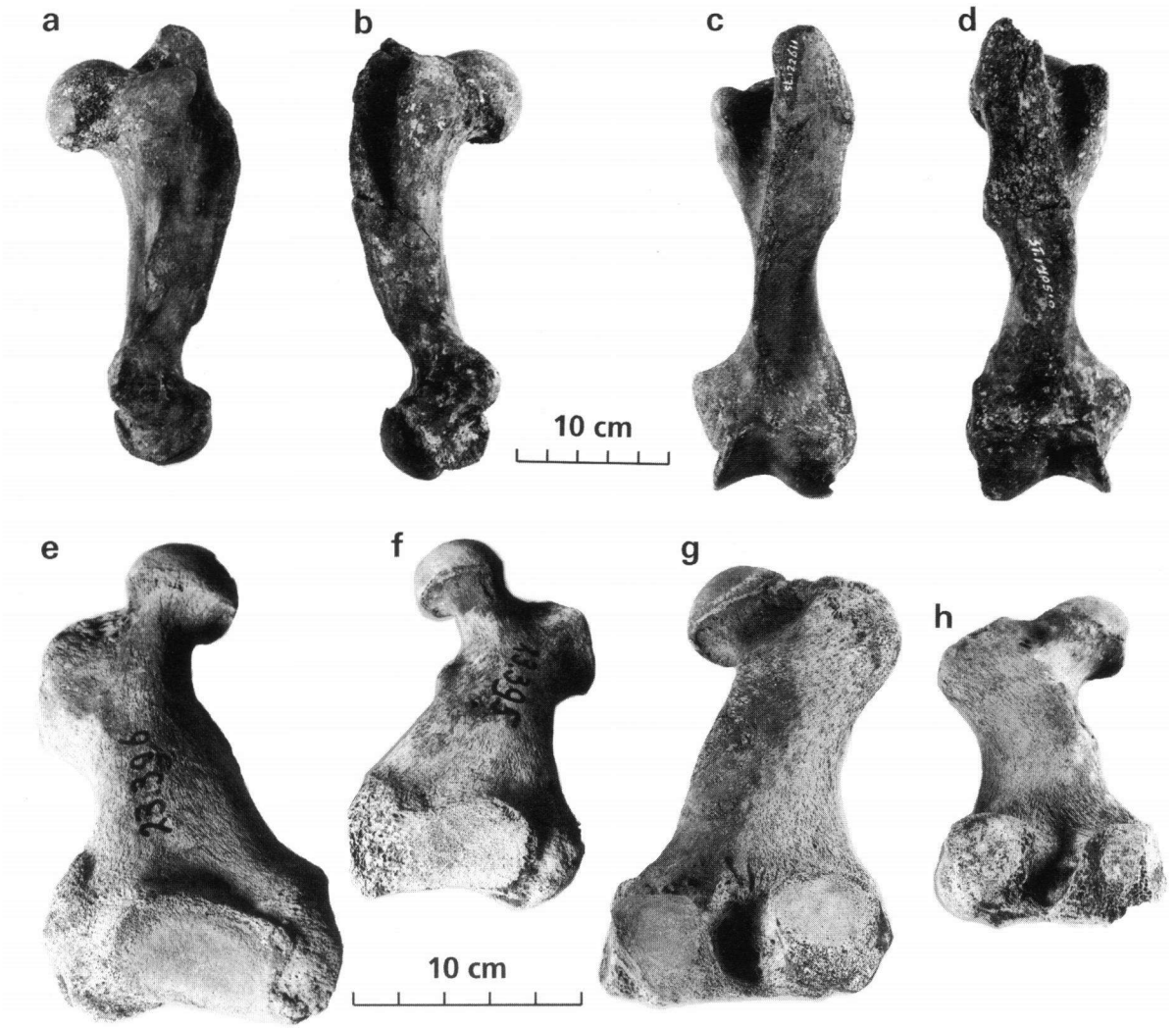

Fig. 5. a, b, frontal and c, d, distal (= external) aspects of humeri St. 122622 (sin.) and St. 170510 (dext.). e, f, anterior, and g, h, posterior aspects of recent femora ZMA 23.396 (dext., male?) and ZMA 23.395 (sin, female?).

caput are strewn with many nutrient foramina. This is also the case in the large and deep intercondylar fossa. The lateral epicondyle is larger than the medial one. It is slightly irregular at its lateral side (where a relatively big foramen occurs at the bottom of a shallow pit), while a distinct crest ("Excrescentia lateralis") can be found running from there upwards along the lateral edge of the diaphysis over a distance of some 80 mm. The upper end of the trochanter major lies below the horizontal plane over the top of the caput. No traces exist of a nutrient foramen halfway down the anterior side of the diaphysis. The surface of the patellar articulation is a single convex plane, as in Recent walruses, indicating that the patella must have been a single bone, not a double one as in seals.

From the same locality, the Oosterhoofd near Domburg, according to its two labels, comes St. 118963 (Fig. 6d; Table 3). This is the distal part of a right femur, collected on June 26, 1961, during trawls numbers 116 to 118, of the vessel ZZ 8. The fossil is identified on its labels as '*Alachtherium* spec.'. Colour and hue are 10 YR 2/3 (brownish black), while its many (mainly balanid) encrustations are 10 YR 7/3 (dull yellow orange). As can

be gathered from the few measurements that we took, the size of the femur may even have surpassed that of the one from the same locality described just previously. The specimen is eroded and rolled. The break through the diaphysis is ancient, as its edges are encrusted with Balanidae. Whatever is left of the spongiosa has the same colour as the rest of the bone. The medial and lateral epicondyles were also damaged prior to fossilization in several places, although not at their medial and lateral extremities. The intercondylar fossa is broad and deep and contains some nutrient foramina. Local (ancient) damage precludes the observation of a possibly present "Excrescentia lateralis".

St. 118849, from the same locality and again collected by the ZZ 8 during trawls 200 to 203 on June 30, 1961, is also identified as '*Alachtherium* spec.' on its two labels (Fig. 6c; Table 3). Colour and hue are 10 YR 4/6 (brown) to -3/4 (dark brown), while a few encrustations are -6/4 (dull yellow orange). The specimen is a fragment of a right femur consisting of a much damaged head and neck and the medial portion of its diaphysis just below the caput, so that a very pronounced lesser trochanter has been preserved in its entirety. The spongiosa on the inside has the same colour as the rest of the bone. The entire femur must have had almost the same size as St. 147067.

Again from the same locality, collected on July 12, 1961, during trawls 357 to 361 by the ZZ 8, and identified as '*Alachtherium* spec.' on its two labels (Fig. 6a; Table 3), is a small fragment of the distal extremity of a left femur, numbered St. 147040. Its colour and hue are 10 YR 1.7/1 (black), while its balanid encrustations are -6/3 (dull orange). Only parts of the two epicondyles are preserved. The intercondylar fossa is broad and deep and contains some large nutrient foramina. The spongiosa along the ancient planes of fracture has the same colour as the exterior of the bone.

From near the previous locality comes St. 42340 (Fig. 4b, e; Table 3), an incomplete left femur without its distal extremity. It is identified on its two labels as '*Alachtherium* spec.' and it was collected at an unspecified date and donated to the Rijksmuseum van Geologie en Mineralogie by Dr A.B. van Deinse. Its provenance is from the "pit of Oostkapelle" (Fig. 1), at a depth of about 20 m. Colour and hue of this strongly mineralized fossil are 10 YR 2/2 (brownish black), with some patches of 4/1 (brownish grey). There are a few encrustations of *Balanus* on the proximal extremity of the bone. The femoral caput is very eroded and anciently damaged, but a horizontal plane over its top still lies higher than the highest point of the greater trochanter. The base of this feature on the anterior side is also eroded, displaying spongiosa with the same colour as the rest of the bone. The neck of the caput, in front, and the upper area of the broad intertrochanteric fossa, at the back, contain a number of relatively large foramina nutricia. The lesser trochanter is distinctly developed and is connected to the

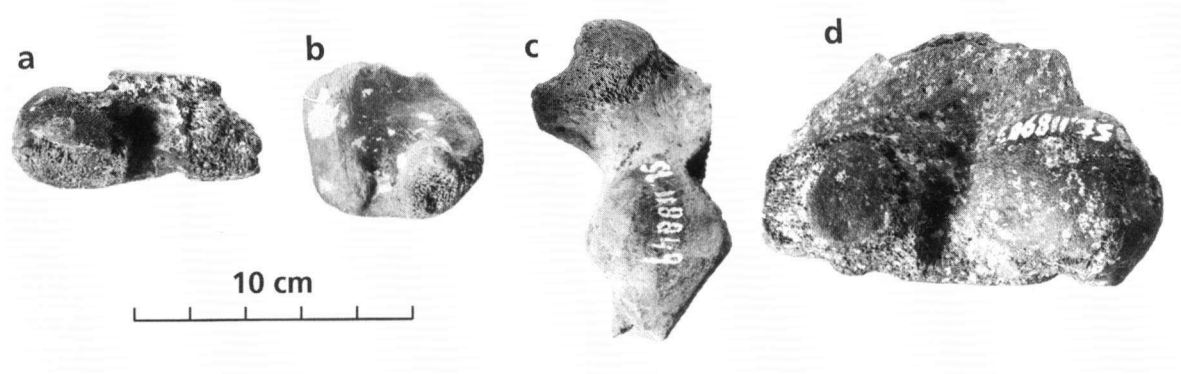

Fig. 6. a, posterior view of small distal fragment of left femur St. 147040. b, posterior view of small, possibly distal fragment of not numbered right femur from in front of the Flaauwerspolder (Leiden collection). c, posterior aspect of proximal fragment of right femur St. 118849. d, posterior view of distal fragment of right femur St. 118963.

trochanter major by a very broad and barely prominent intertrochanteric crest. In the centre of the diaphysis, on the anterior side, a large nutrient foramen is present amidst a fan-like structure of superficial lines in the materia compacta, a phenomenon also observable on the posterior surface of the bone.

A last, possibly femoral, fragment in the Leiden collection (Fig. 6b; Table 3), unnumbered but identified on its label as '*Odobenus* spec.', was fished up by the ZZ 8 on August 31, 1991, in front of the Flaauwerspolder (Fig. 1). It may well be a very much eroded part of the distal extremity of a right femur. Its colour and hue are 10 YR 3/1 (brownish black) to -5/1 (brownish grey, on the worn surfaces only). The intercondylar fossa, which is not particularly broad or deep, is entirely preserved. The two epicondyli have been largely abraded, as has the anterior part of the fragment.

This is perhaps a suitable place to describe two Recent walrus femora (Fig. 5e-h). These two specimens, ZMA 23.395 and ZMA 23.396, respectively a left and a right femur, were collected in 1977 at a seventeenth-century russian slaughtering place of seals at Kap Lee on the island of Edgeøa in the Spitsbergen (Svalbard) archipelago by the 1977 Rees expedition. Although the sex of each specimen is not known, we think that the smaller of the two, 23.395, may probably be female, and the other, 23.396, possibly male. The figures demonstrate that, in each case, the horizontal plane over the top of the caput lies very considerably higher than a comparable plane over the top of the trochanter major. The neck is relatively slender and directed in a somewhat oblique direction with relation to the horizontal axis through the greater trochanter. A trochanter minor is barely developed in each case; in other instances among the material in the Amsterdam collection it is even absent. In ZMA 23.395 the trochanter minor is more of a slight crest. This continues, feebly, as a kind of intertrochanteric crest, towards the greater trochanter. The feature is completely absent in ZMA 23.396, where the locus of the trochanter minor is represented only by a bony rugosity. In this latter bone a slight crest above the lateral epicondyle is observable ("Excrescentia lateralis"), which is entirely wanting in ZMA 23.395. In most other respects the femoral morphology conforms to the descriptions of fossil specimens given above, although some length/width relations may differ, as follows from the data in Table 3.

TIBIAE

Two unnumbered tibial fragments in the Leiden collection are identified on their labels as '*Odobenus* spec.' (Fig. 4g-j). One is a large piece of a left tibia, with a maximum length of 196 mm. It was fished up from "pit G1" in front of the Flaauwerspolder, by the ZZ 8 on August 28, 1982. Its colour and hue are uniformly 10 YR 3/4 (dark brown). Approximately at the center of the diaphysis the transverse width is 33 mm and the sagittal width 30 mm, while the circumference at the same place measures 105 mm.

The other unnumbered specimen consists of an upper (proximal) fragment of a left tibia/fibula. It is usual in adult walrus individuals that synostosis of the proximal parts of tibia and fibula is complete, as we remarked in our short communication (1990a) on a similar fossil fragment from the island of Sylt in northern Germany. The present fossil was collected by the Tholen fishing vessel TH 6 in front of Wissenkerke (Fig. 1) and donated to the Rijksmuseum van Geologie en Mineralogie by the Rijksmuseum van Oudheden at Leiden in August 1972. The colour and hue of this fossil are 10 YR 1.7/1 (black) with encrusted bryozoan areas of 10 YR 7/4 (dull yellow orange). The maximal height of the fragment is 61 mm. The proximal surface, which contains two separate ovaloid flat articulations, separated by a slightly deeper roughened area in the form of a letter T, has a transversal maximum width of 81 mm and a sagittal one of 54 mm. The lateral ovaloid articulation measures 41 by 38 mm and the medial articulation 37 by 28 mm. The fragment is heavily mineralized. The spongiosa, visible at the distal plane of fracture, has the same colour as the rest of the bone. The surface of the compacta displays the curious web-like structure mentioned above for some of the other fossil bones.

RECAPITULATION

Before proceeding with the identification of the

fossils described above, it may prove useful to review some of the facts, opinions and problems relative to the occurrence of walrus and walrus-like fossils of the southern North Sea region. Much of this has already been mentioned by us in some of our earlier publications (1986, 1990a,b, 1999a, b), but a recapitulation may serve to illustrate our motives in identifying the material treated in the present paper and in the two previous ones.

One of the first descriptions with figures of fossil walrus-like remains from the North Sea region appears to be that by Lankester (1865) of (at least) twelve tusks and tusk fragments, to which the name *Trichecodon huxleyi* was given by its author. The generic name *Trichecodon* had been suggested *in tutters* to him by his belgian colleague Van Beneden. The fossils had been found at a number of mentioned localities in Suffolk in deposits of what was known at that time as the Red Crag. In Recent stratigraphical concepts, according to, for instance, Stuart (1982), Laban (1995: Table 6), and others, these coastal sediments have to be correlated with the Waltonian (a cold stage) and the Ludhamian (a temperate stage) at the very beginning of the Pleistocene period. The Waltonian stage is preceded by a Pre-Ludhamian stage, the start of the Pleistocene, which should be correlated with the Scaldisian stage at the opposite, eastern border of the southern North Sea basin. Lankester's material is, therefore, datable to the earliest part of the Pleistocene, some two million years ago. Morphologically, these tusks and tusk fragments are characterized, according to its describer, by being generally larger and laterally more flattened than those of the Recent walrus, usually with more pronounced fluting in a vertical sense, while the cover by layers of dentine and cementum of the central vertical core of globular vasodentine (also encountered in the Recent walrus) is much thinner than in the latter case ("minor development of cement", Lankester, 1865: 230). We have shown (1986: 29) that size and lateral flattening in tusks of Recent *Odobenus rosmarus* may occur occasionally in a quite comparable degree, so that only the thinner cover of the globular dentine core remains as a specific point of distinction.

In 1867 the Vicomte du Bus published a description (without illustrations) of a right half-mandible of a walrus-like animal, collected in 1863 at Wijneghem, Antwerp "dans le crag supérieur" at the locality of F(or)t 1 in the inset-map of Antwerp in Van Beneden (1877: between pp. 38 and 39), by a Captain of Military Engineers, Crets. Du Bus invented the generic and specific names *Alachtherium cretsii* for this fossil, which he himself had carefully cleaned of its completely surrounding crag-like matrix (according to van Beneden, 1876: 794, 1877: 50), whereby the dentition appeared, consisting of two cylindrical peg-like incisors, a relatively small canine, and four somewhat smaller post-canine teeth, each resembling the canine in form. This half-mandible was again mentioned by Van Beneden in 1871 (when it was stated to be still the only find of its kind), 1876 and 1877, and figured in the last- mentioned publication. In the two last-mentioned papers he ascribed a number of other, cranial and postcranial specimens to this same species, despite the fact that they had not been found together or in connection, nor at the same place or at the same time. It appears that his main reason for doing so was based upon their larger size and supposedly different morphology in comparison to their counterparts in the Recent walrus. Van Beneden also described and figured part of a tusk, found "in the environs of Antwerp" by Nyst several years before 1871, and a thoracic vertebra with a tarsal bone and a phalanx, collected at a later date. All this material was thought by him to represent yet another walrus-like animal of large size, to which he gave the name *Trichecodon koninckii*. Van Beneden (1876) remains rather vague with regard to the differences between this *T. koninckii* and the about equally large *A. cretsii*, stating (1871: 18) that they both belong to the "family of Morses", that they must have lived together, and that they "evidently were different because of the form and size of their tusks". From this it might be concluded that Van Beneden, who had visited Lankester and seen his material of *T. huxleyi*, was (at that time) of opinion that *T. huxleyi* and *A. cretsii* were identical. This is also what Lankester states in a later publication (1882: 215; the paper is the text of a lecture given by Lankester in 1880). Correctly, Lankester differs from him in declaring: "...I cannot admit that there is the remotest evidence for

the connexion of the Suffolk tusks with the bones called *Alachtherium* rather than with any other Walrus-bones, since no Walrus-tusk has been found in connexion with Walrus-bones in either Suffolk or Belgium." In that same 1882 paper, Lankester retracts the generic name *Trichecodon* (which would have precedence over *Alachtherium* in case the two species might prove to be identical, as he remarks) in favour of '*Trichecus*' (the misspelt generic name, as he thought, for the Recent walrus, *Trichechus*). He was convinced that the slight differences between tusks of his Suffolk fossils and those of the Recent walrus did not warrant a generic distinction. As Simpson (1945) remarked, the valid generic name of the Recent walrus is not *Trichechus* Linnaeus, 1766, but *Odobenus* Brisson, 1762. Van der Feen (1968) restated this also. Therefore the Suffolk fossil tusks described by Lankester should be known as those of *Odobenus huxleyi* (Lankester, 1865), as was written by Hooijer (1957), and followed by us (1986: 29).

In 1907 Rutten described an incomplete cranium (without mandible) of a walrus-like fossil collected somewhere in or around Antwerp, in Van Beneden's collection (and presently, according to Demeré (1994: 118), in the collection of the Institut Royal des Sciences Naturelles de Belgique at Antwerp, under number M.169), differing from its Recent relative, as *Trichechus antverpiensis*. The points of difference have been summed up (in tabular form) by Van der Feen (1968: 27) in a revision of Rutten's species. Another find which Rutten described, in the same paper, as *Trichechus huxleyi*, collected near Breskens in 1906, has to be relegated to a female specimen of the Recent species, *Odobenus rosmarus*, as we argued in 1986 (: 30).

Three years later, in 1910, a lengthy paper appeared by Hasse, on several finds of fossil walrus-bones made during the construction of new harbour basins at Antwerp between 1902 and 1905, in the Steenborgerweert polder, at present in the northern part of the city. The deposits whence the fossils were found, according to Hasse, were of Pliocene age, belonging to the upper part of the Poederlian stage (as also illustrated by his photograph, Fig. 2). The Poederlian (chronostratigraphical) stage is nowadays known as the Merxemian stage (as we stated in 1986: 28). It is directly preceded, as already in Hasse's description, by the Scaldisian stage. Presently the Scaldisian is considered to represent the beginning of the Pleistocene. The Merxemian has to be correlated with the Waltonian (cold) stage in Suffolk, some two million years ago. In a very thorough manner Hasse enumerates and describes the (in all) sixty-two fossil cranial and postcranial walrus remains and records their exact finding localities. In tabular form they are compared with their counterparts in the skeleton of the Recent species. Among them are four fragments of juvenile crania and one almost complete adult cranium, but no mandibular remains. Hasse considers the entire lot to belong to a single species, which he compares with *'Trichecus' huxleyi* (only known from its tusks) and with *Alachtherium cretsii* (only known from a single half-mandible). He arrives at the conclusion that most similarities seem to lie with *A. cretsii*, although there are sufficient differences (he thinks) to warrant the institution of a new species, *Alachtherium antwerpiensis*. He only mentions Rutten's description of a specimen of a *'Trichecus' huxleyi*, from Breskens, but that of a *'Trichecus' antverpiensis*, from Antwerp, is ignored. We explained (1986: 29) that this latter form should, correctly, be called *Odobenus antverpiensis* (Rutten, 1907), and that this name has (at least) two years precedence over Hasse's *Alachtherium antwerpiensis*. It follows from Hasse's excellent and detailed cranial descriptions and figures that there can be very little doubt that the two forms are one and the same species. Its differences from the Recent walrus were given, in tabular form, by Van der Feen (1968), and these should be compared with Hasse's tables.

When, furthermore, our remarks made in our 1986 and 1990b papers are taken into consideration, it is possible to conclude that, formally according to the rules of Nomenclature, **three** Early Pleistocene "species" can be distinguished: *Odobenus huxleyi* (Lankester, 1865), *Odobenus cretsii* (Du Bus, 1867), and *Odobenus antverpiensis* (Rutten, 1907). The first of these is exclusively known from a number of its tusks, the second solely from a right half-mandible, and the third from a partial cranium, to which some more identical cranial material has been added at a later date. As long as there is no definite proof (such as finding sep-

arate skeletal elements in connection with each other), we have to remain in doubt whether certain postcranial bones are indeed those of an *O. antverpiensis* or an *O. cretsii*, larger and earlier form(s) than the Recent walrus. We have already frequently stated that we are, privately, convinced that *O. huxleyi, O. cretsii* and *O. antverpiensis* are, in reality, a single species, which lived in the northern Atlantic region during the Early Pleistocene and was larger in size, a better and perhaps swifter swimmer, and more piscivorous than the Recent *Odobenus rosmarus*. We hope that this conviction may soon be proved right, when a connected find will be made of a specimen with its tusk(s), complete cranium with mandible, and the necessary postcranial bones. Albeit it appears reasonable to agree with Hasse that the postcranial remains and cranial specimens, found close together, belong to a single species, a remark by Du Bus (1867: 574-575) should be kept in mind: "Les ossements du crag ne se rencontrent pas toujours dans les mêmes conditions. Dans toutes les couches, on les trouve ordinairement disséminés, brisés, roulés et portant quelquefois des traces d'un séjour prolongé dans les eaux de la mer, comme des bases adhérentes de balanes ou de polypiers. Très souvent on trouve confondus pêle-mêle des fragments de différentes espèces de baleines, de ziphius, de dauphins et même de phoques. Ce n'est que par exception que l'on découvre des groupes isolés d'ossements appartenant ˆ un même individu, et le plus souvent c'est dans le crag noir ou inférieur."

Van Beneden's *'Trichecodon koninckii'* as we already remarked (1986: 30, 31) is simply based upon a tusk fragment wich does not, morphologically, differ from that of the Recent *O. rosmarus*, but in this case of an extremely large individual. One might conjecture that, **if** there is any evolutionary connection between the large *O. huxleyi* = *O. cretsii (?)* = *O. antverpiensis (?)* and the younger, Recent walrus, the earliest individuals of *O. rosmarus* were frequently of the same huge size as their direct forerunners. This would also explain the isolated finds, among the fossil North Sea material, of a few very big bones (such as femora and humeri), otherwise morphologically indistinguishable from those of Recent walruses.

In the light of this recapitulation it may be clear that we disagree with some of the remarks made by Deméré (1994: 118, 119, 121) with respect to *Alachtherium cretsii, Odobenus huxleyi* and *O. koninckii sensu lato*. In our view the "Scaldisian sands" or the Poederlian mentioned there are certainly not Pliocene, but Pleistocene; the pieces referred by Van Beneden to *cretsii* have been done so incorrectly and should certainly not be used for any diagnosis or characterization; and *O. koninckii*, even when meant *sensu lato*, should be dismissed completely, as a *nomen nudum*.

IDENTIFICATION AND FINAL REMARKS

The sequence is repeated in which the fossils were described above. With regard to the fossils recovered from the Westerschelde and from, and around, the harbour basins at Antwerp, it should be stressed that the sediments there consist of reworked examples of delta bedding, resulting from frequent and repeated changes of sealevel and containing Miocene, Pliocene, Pleistocene and Holocene layers and lenses, transsected by some particularly deep gullies and troughs. One may therefore expect a very diverse combination of fossils of varying age. We have pointed this out already in our 1999a paper.

St. 122611, a left humerus from in front of Nieuwe Sluis on the Westerschelde, is not especially large, but fits into the range of Recent walrus humeri (see Table IV, p. 27, in our 1986 paper). It may well be female. As there appear to be no significant morphological differences from the Recent species, we suggest a determination as *Odobenus* cf. *rosmarus* (Linnaeus, 1758), ssp. Identification as *Odobenus huxleyi* (Lankester, 1865), evidently based on the locality of collection only, is decidedly erroneous. The well-defined supinator ridge mentioned in our description is a feature which is similar to that encountered in the same bone of the Ursidae. This may be a convergence, but it may also point to a common ancestry.

More or less the identical arguments apply in the case of the right humerus St. 170510 from the Oosterschelde and identified on its label as *Odobenus* spec.; its size may indicate that it is female.

The right humerus ZMA 24.613, a larger and heavier one, and possibly collected from the West Hole in the North Sea (Fig. 1), could be seen as a

bone of a male walrus of great size, but of the Recent species, as the very large right humerus N.Z. in the Stolzenbach collection, which we described in 1986. The two latter humeri in the present description should be identified as *Odobenus* cf. *rosmarus* (Linnaeus, 1758), ssp.

The left humerus KP 270 from the southern North Sea is a special case, as we remarked above. Its morphology, compared to that of the Recent walrus, differs in that its caput is relatively smaller and that the bone appears more slender in spite of its much larger size. This could indicate a better and swifter swimming ability; so may the differing angle, made by the long axis through the diaphysis, with the basal line through the epicondyli. Such arguments lead us to adopt a very tentative ascription to *Odobenus* cf. *antverpiensis* (Rutten, 1907), possibly a better swimmer and larger in size than *Odobenus rosmarus.*

St. 145446, a diaphysis of a subadult left radius from the Westerschelde, was collected opposite Ellewoudsdijk on the island of Walcheren, a known locality of many terrestrial mammalian fossils which date back to the second half of the Pleistocene, usually recognizable as possessing the same colour and state of mineralization as this St. 145446. Although the left radius fragment is morphologically atypical, it appears to us that identification as *Odobenus* cf. *rosmarus* (Linnaeus, 1758), ssp., is acceptable.

The scapholunar bone T 333 is also (for lack of knowledge of the morphology of this bone in *O. antverpiensis*) considered by us to be morphologically atypical. It much resembles the bone in Recent *O. rosmarus*, although quite large in size. Taking into account its state of fossilization, colour, and general locality of collection (in the southern part of the North Sea), we like to suggest an identification as *Odobenus* cf. *rosmarus* (Linnaeus, 1758), possibly a male individual.

The description of the several fossil femora shows that there exist definite differences in the morphology of the somewhat larger KP 472 and St. 147067 compared to KP 499A, while this last specimen has many points of resemblance with Recent walrus femora. The slightly smaller KP 826 displays the same morphological traits as KP 472 and St. 147067, by which it stands apart from Recent, presumedly female, walrus femora. We suggest that KP 472, St. 147067, and KP 826 might possibly be ascribed to *Odobenus* cf. *antverpiensis* (Rutten, 1907); the first two of these, the largest, perhaps being male specimens, and KP 826 a female one; assuming that the Early Pleistocene form showed a sexual dimorphism comparable to that found in the Recent walrus. On the other hand, KP499A may very well belong to the Recent species and could be a male individual of *Odobenus* cf. *rosmarus* (Linnaeus, 1758), ssp.

Because of what is still observable regarding their morphology, despite their fragmentary state and incompleteness, we think that St. 118963, St. 118849, and St. 42340, resemble most of all the features to be expected of the suggested *Odobenus* cf. *antverpiensis* (Rutten, 1907).

The very incomplete and small fragment St. 147040, and the unnumbered fragment (of the right side) collected in front of the Flaauwerspolder, are each too atypical to be definitely identified. The first piece can only be assigned to *Odobenus* species, the second to cf. *Odobenus* sp. This same argumentation also applies to the two unnumbered parts of tibia/fibula bones, one from in front of the Flaauwerspolder and the other from in front of Wissenkerke. These should therefore also be identified as *Odobenus* species.

Concluding, we have reached the impression, based upon the material described here as well as in our 1986, 1990a, 1990b, 1999a and 1999b papers, to which should be added the information in earlier papers by Van Deinse (1964), Bosscha Erdbrink (1972), Van der Feen (1968), and in short notices by Van Bree and Post (1994; on a fossil walrus baculum) and Post (1994; on yet another walrus mandible), that the sediments on the bottom of the southern part of the North Sea and in the Schelde estuary (around Zeeland and in the Antwerp area) contain fossils of:

1, subfossil, subrecent and historical walrus individuals which date back to, at most, the Early Holocene (= Preboreal);
2, truly fossil walrus individuals of the Recent species (in many cases clearly the Atlantic subspecies), in which occasional specimens attain large sizes, exceeding those of present times; these may date back to, at most, the end of the Early Pleistocene;
3, heavily fossilized walrus individuals of (possi-

bly) one (perhaps three) different species, namely *Odobenus huxleyi* (Lankester, 1865) (perhaps identical with *O. antverpiensis* and *O. cretsii*), of a larger size than most *O. rosmarus*, which occurred during (final?) Pliocene and Early Pleistocene times on both sides of the Atlantic Ocean (Ray, 1960; basing himself exclusively on tusk-fragments, comparable to Lankester's type material) and possibly occupied a more southerly range than its (or their?) presumed descendant *rosmarus*;

4, very strongly fossilized, frequently silicified early walrus individuals which lived during warmer Miocene to Early Pliocene times and were the ancestors of the form(s) mentioned under 3, and are usually indicated in literature as *Prorosmarus*. We contest the necessity of instituting such a separate genus for a form already showing many general similarities with the genus *Odobenus*.

This arrangement into four categories of increasing stratigraphical age agrees nicely (at least with regard to the first three of them) with the arguments in Bosscha Erdbrink (1982, 1983: 427-430). As is remarked there, this is again based on papers and observations by Houbolt (1968), Jelgersma (1961), Kortenbout van der Sluijs (1971, 1972, in an appendix to Louwe Kooijmans, 1972), Oele (1969, 1971), Van Straaten (1954), and Stuart (1982). The oldest category of walrus fossils, 4, collected from very deeply scoured-out gullies or from cores of Pleistocene push-moraines (as at the island of Sylt, N. Germany) shows that a shallow marine environment with abundant shellfish and fish existed in the southern part of what is, at present, the North Sea. This is also indicated by the presence of the typical greenish mica-mineral glauconite, formed in shallow and coastal environments. This is present in the Schelde estuary in the sands of the (lithostratigraphical) unit of the (Miocene) Breda Formation; and also in the sandstone of the cliff at Sylt whence the tibia/fibula fragment was collected which we described (1990a) and which still contained a rock-hard concretion of this sandstone.

It may perhaps be speculated here that the relative frequency with which fossil and subfossil remains of walruses are nowadays collected and brought to our notice by fishermen might be the result of (former) seasonal migrations during the Upper Pleistocene and the Early Holocene, sometimes accompanied by large-scale mortality as described from present walrus populations by Fay & Kelly (1980).

Du Bus' generic name (1867) *Alachtherium* should, in our opinion, be relegated to the *nomina relinquenda*. Although the institution of new generic names is largely a matter of taste, and we are aware that *de gustibus non est disputandum*, Systematic Zoology is an artificial human invention intended to obtain a comprehensive oversight of all zoological forms, living and extinct, and it should therefore be kept as simple as possible so as not to obstruct that general view. Especially vertebrate palaeontologists frequently appear to be prone to the habit of instituting new genera, either from a kind of personal vanity, or because it seems easier than the making of a study of the intraspecific variability of a species!

An interesting development is formed by the recent description by Geraads (1997) of a discovery at the Moroccan site of Ahl al Oughlam (formerly known as the Deprez quarry) near Casablanca. Here some eight isolated fossil remains of a walrus-like animal were collected: parts of a cranium, an incomplete right half-mandible, another mandibular fragment, isolated teeth, two distal parts of left humeri, a left scapholunar, and the distal part of a tibia. The describer identified all this as belonging to a single, and new, species, to which the name *Alachtherium africanum* was given. Its size was that of a small Recent walrus, therefore smaller than *A. cretsii*, to which it certainly appears to be related, as follows from the figure of the half-mandible and from its anatomical description. Attribution of all the collected remains to a single species seems to be very plausible, as there appear to be no other contemporary forms with which there is a possibility of confusion.

The fossils were collected from deposits of the local C1 level, with an age of about 2.5 Ma. According to Raynal et al. (1990) these are continental sandy deposits containing a rich vertebrate fauna, with an age between 2.0 and 2.5 million years and overlying an eollanite and a marine conglomerate. In another publication Geraads (1993) estimates the age of this C1 level at 2.4 Ma. As the other carnivores from this level are all

terrestrial (amongst which there are Hyaenidae), it might be suggested that the walrus remains were those of a few individuals preyed upon or scavenged from beach deposits quite nearby. The proposed age of 2.4 to 2.5 Ma, Late Pliocene, which, in our view seems to be very much acceptable, is certainly older than that of the larger Antwerp relative (Early Pleistocene, probably at most 2.0 Ma). We would therefore like to suggest the possibility of an evolutionary link from the older, smaller Moroccan form with the younger and larger north-west European form, perhaps caused by a quest for more abundant fishy prey in somewhat cooler or even colder marine environmental conditions. In case the generic name *Alachtherium* should have to be abandoned, the Moroccan form has to be named *Odobenus africanus* (Geraads, 1997).

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