P.J.H. van Bree[1], D.P. Bosscha Erdbrink[2] & F.J. Roescher[3]

[1] Zoölogisch Museum, University of Amsterdam

[2] Baarn

[3] Almere

A second find of *Aonyx antiquus* in the Netherlands, and some remarks on *Aonyx* and allied forms (Mammalia, Carnivora, Mustelidae)

A second find of a so-called clawless otter *Aonyx antiquus* (DE BLAINVILLE, 1841) from Eemian or Weichselian sands, dredged up in the Markermeer (part of the former Zuider Zee) is described and identified. The stratigraphical situation and age of the find are discussed. Some general remarks are made regarding systematics and nomenclature of clawless otters of the genus *Aonyx* and its allied forms.

Correspondence: dr P.J.H. van Bree, Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam, P.O. Box 94766,1090 GT Amsterdam, The Netherlands; dr D.P. Bosscha Erdbrink, Prinses Marielaan 27, 3743 JA Baarn, The Netherlands; F.J. Roescher, Zilvermosstraat 24, 1314 SR Almere, The Netherlands.

INTRODUCTION

Early in 1998 one of us (F.R.) collected a fossil fragment of a skull when he was searching fossils on a recently prepared building-site in the community of Almere (Province of Flevoland) in the Netherlands. At the same locality a number of other fossil animal bones were found, which were identified as belonging to mammoth, bison, rhinoceros, reindeer, giant deer, red deer, horse, wolf, hyaena, birds and fish (a.o. pike). The building-plot had been heightened and stabilised with sand suction-dredged from a nearby location, the Markermeer, part of the former Zuider Zee which has been left a lake (Fig. 1). The dredging operations were carried out by the firm of Ballast Nedam. Mr Heibloem of this firm kindly informed us that a slot-like gully had first been dredged with a width of two hundred metres and a length of approximately three to four kilometres, parallel to the

shipping-lane between Amsterdam and Lemmer, roughly opposite the Noorder Plassen near Almere in the Flevoland polder. An upper complex of layers, some twelve meters thick and mainly consisting of clay and peat with clayey sand lower down (see column in Figure 1) was removed. The sands below this set of layers were subsequently dredged up to a maximum depth of thirty metres, all along the entire gully, and transported by pipeline to the community of Almere, there to be used in heightening and stabilising an intended building-plot. After removing the sand, the gully had been refilled in part by and with the material that had initially been dredged and placed aside. According to information helpfully provided by dr W. de Gans of the Netherlands Institute for Applied Geosciences TNO (the former Government Geological Survey), the strati-

graphical age of the clay-and-peat complex dredged away in order to reach the sands below, is Holocene (Flandrian) and known as the Westland Formation (De Gans 1991, 1995). The sands below this formation, which contain some inclusions of clay lenses and locally developed peat (due to temporary ponds and small lakes, resulting from thawed permafrost soils), are known as the Twente Formation (De Gans 1983a, 1983b) and have a Weichselian (= Würm, or Devensian) age. Below that, at a depth of some twenty-five down to thirty metres, Eemian (= Ipswichian) sands appear, characteristically beginning in their uppermost part with a layer containing abundant marine shells (among these is a typical representative of the Eemian interglacial, *Venerupis aurea senescens*). Much further down one encounters glacial and periglacial deposits of the Drente Formation, Saalian (= Riss, or Wolstonian) in age, a time when about half of the Netherlands were covered by ice. Locally the marine sands and the shell layer of the Eemian interglacial

reach a considerable thickness, owing to the presence of a glacial basin formed during the Saalian when a lobe of the continental glacier bulldozed earlier sediments up to the West and Southwest into the present sandy hillrange of the Gooi and Utrechtse Heuvelrug. This basin was turned into a relatively shallow marine bay after the Saalian glaciers melted and the sea-level rose during the warmer Eemian interglacial. The bay was partly filled with sandy debris from the surrounding pushed-up morainic ridges. At present the small Eem river, which starts at Amersfoort, meanders northward through the floodplain formed above the bay sediments.

In an excellent review Van Andel & Tzedakis (1996: fig. 9) have given a sketch map of the situation during the Eemian Interglacial (= their Oxygen Isotope Stage 5e) in Europe, some 120,000 to 125,000 years ago. The following last, or Weichselian (Würm) glacial stage has known a number of short relatively warm-
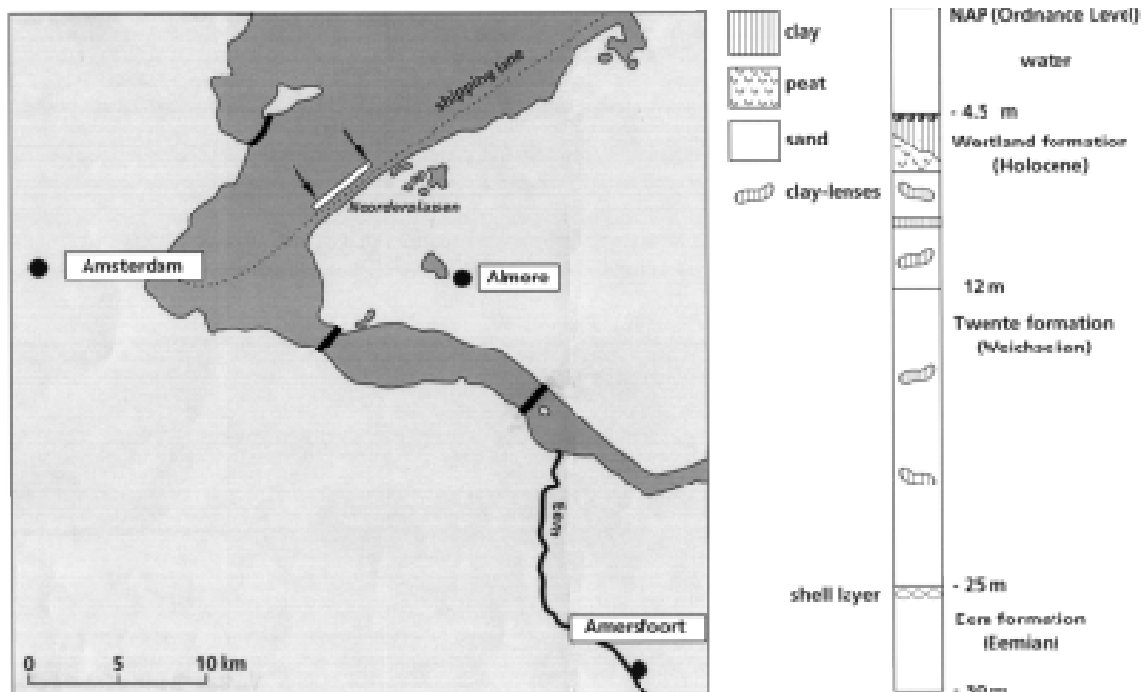

Figure 1   General situation of the dredged gully (arrows) North of the shipping lane between Amsterdam and Lemmer (beyond the map), the location of the fossil cranial fragment.

er interstadial times, as illustrated in their figure 11. Among the earlier of these interstadials are the Amersfoort interstadial (some 100,000 years ago) , the Odderade interstadial (80,000 years ago), and the Oerel interstadial (around 55,000 years ago).

DESCRIPTION

The fossil which is the subject of the present communication (Fig. 2) consists of a large part of the rostrum of the skull of an otter. In the dentition the right M1, P4, P3, P2 and the left P4, P3, P2, C, and I3-I1 are preserved while the alveoli of the two P1, the right C and the three right incisors are present as well. Most of the palatine bones, the two nasalia, the two premaxillae, the maxillae, the vomer, the anterior parts of the two orbits (up to and including each postorbital process),

and a part of the right frontal are recognisable. Curiously enough a large part of the cribriform plate, pierced by numerous fine foramina, is also still in place despite its fragility. Nothing of the nasal conchae has been left, although the very base of the nasal septum, the mesethmoid bone, can be seen when one looks into the nasal aperture from the front. The two incisive foramina are relatively large. Fairly deep concavities at each side, just behind their exits into the nasal chamber, may indicate that a once well-developed vomeronasal organ (= organ of Jacobson) has been present. The two incisive foramina stand on a line midway between the two alveoli of the first premolars, a position which is identical to that of the specimen figured by Willemsen (1992: pl. 3, c) to be mentioned later. The suture between vomer and ethmoid,
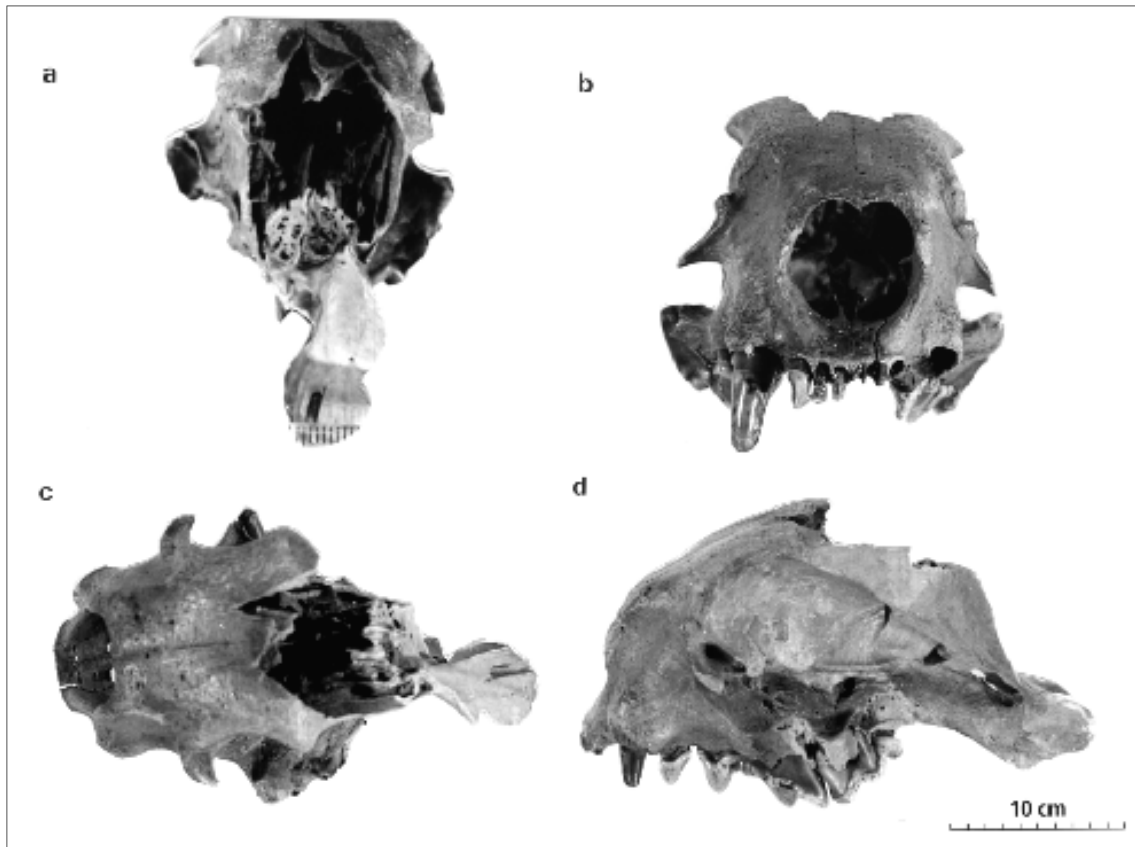

Figure 2 Four views of the cranial fragment of *Aonyx antiquus* from Almere: **a** oblique posterior view (see remains of cribriform plate) **b** frontal view; **c** dorsal view; **d** left lateral view.

a feature used by Van Zyll de Jong (1987: tab.1, p. 2539), cannot be established with certainty in the present fossil, but lies probably intermediate between P3 and P4, and therefore might be considered to represent a reasonably primitive (i.e. in the sense of original) state.

The colour and hue of the fossil bone, following the revised Munsell scale by Oyama *et al.* (1967), are a uniform 10 YR 4/4 (brown), while the enamel of the teeth runs from 7.5 Y 5/3 (greyish olive) to 4/3 (dark olive). Synostosis of the skull-bones mentioned is complete, indicating that the individual was fully adult at the time of its death. As the teeth are hardly worn, the animal was not extremely aged. It is perhaps not prudent to attempt any guess regarding its sex, although the observation regarding Jacobson's organ might point to it being male.

The first and second left incisors are small chisel-like pegs. The third incisor, the largest of the three, consists of an eccentrically placed cusp in front with, distally and only at its internal side, a distinct cingulum. The relatively small left canine (the tip of which has broken off, probably as a result of recent damage) displays a very weakly developed cingulum on its lingual side only. The single alveoli of the (now absent) first left and right premolars, each situated at the disto-lingual side of its respective canine, indicate their small, peg-like nature. The two second premolars are relatively small also, being haplodontical (with the cusp somewhat eccentrical in a forward position), but having a clearly developed cingulum around the entire tooth. In the two third premolars one observes a kind of triconodont situation, with a main cusp in a central position, a weak mesial cusplet and a slightly larger but also still weak distal cusplet, all arranged along a straight axis and again surrounded by an uninterrupted cingulum. The two fourth premolars, the carnassials, are undoubtedly the most important and largest elements of the

Table 1 Cranial measurements of some *Aonyx* specimens, following Willemsem (1992) and Desse *et al.* (1986), with additions, in mm. BM = British Museum (Natural History): the Tornewton specimens; ZMA = Zoological Museum Amsterdam: recent specimens.

	Almere specimen	'C.'antiqua BM M34370 (Willemsen 1992)	Aonyx capensis ad. male ZMA 24.687	Aonyx congicus ad. female ZMA 13.533
Lfac (facial length)	± 59	62.0	71.6	67.4
Wc (snout width, outer sides of C)	30.2	31	36.1	31.5
Wio (interorbital width)	28.2	30.5	28.9	26.2
D9 (nasion-prosthion)	± 50	-	53.0	51.3
D10 (long.lat.du museau)	29.1	-	36.1	33.1
D11 (staphylion-prosthion)	± 63	65.3	65.0	52.8
D12 (long.du palais)	± 61	-	64.6	52.1
D23 (Diam.max.du palais)	± 45	-	48.8	37.9
D24 (d.t. du palais alv. can.)	29.6	-	36.5	31.8
D1 (d.t. face entre for. inf.orb.)	30.2	-	33.2	28.5
D2 (long. max. orb.:ectorb-ectorb,)	21.0	-	22.4	18.5
Max. width nasal aperture	17.2	-	17.4	16.3
Cran.height between ectorbitalia	31.0	-	35.2	33.5
Mesiodist. width of talon of P⁴	11.4-11.3	-	11.5-11.4	9.2-8.9

upper dentition. Their outline, seen occlusally, more or less conforms to a capital D. A high trenchant ridge runs along the vestibular side of each premolar, the highest point of which is formed by the paracone with a distinct parastyle in front and a somewhat more prominent metacone at its rear. A slight ridge runs down from the lingual side of the paracone to the edge of the tooth, where a low

cusp represents the protocone. A cingulum completely surrounds the premolar, but its most conspicuous part lies along the lingual edge. A hardly observable eminence on it, opposite the metacone, should be regarded as the hypocone. Several wrinkles in the enamel between paracone, metacone, protocone and hypocone provide a rugose nature to the occlusal surface. The tip of the metacone of

Table 2 Dental measurements in mm of some *Aonyx* specimens. Data taken from Willemsen (1992: table 8) are underlined.

	Almere specimen	BM M34370	BM M34373	BM M34374	BM IM50707	Verona specimen	*A.capensis* ad. male ZMA 24687	*A.congicus* ad. female ZMA 13533
I³ sin. m-d.	4.0						4.3	3.2
a-p.	4.6						5.2	4.3
I³ dext m-d	3.0 alv						4.5	3.0
a-p.	4.8 alv						5.6	4.5
C⁺⁺ sin. l.	6.8						8.3	8.5
w.	6.2						7.8	7.0
C⁺⁺ dext. l.	8.1 alv						8.3	8.1
w.	7.9 alv						7.9	7.3
P¹ sin. l.	2.2 alv						2.2	*
w.	1.9 alv						2.2	-
P¹ dext. l.	2.1 alv						1.9	2.1
w.	2.0 alv						1.9	2.0
P² sin. l.	5.0	_5.2_					4.2	4.6
w	3.6						3.5	3.1
P² dext. l.	5.3						4.4	4.4
w.	4.1						3.8	3.1
P³ sin. l.	8.0						7.0	6.0
w.	4.6						5.0	4.7
P³ dext. l.	8.2						7.1	6.1
w.	5.1						5.1	4.3
P⁴ sin. L	13.6	_11.2_				_11.8_	13.0	11.0
w.	10.6	_9.5_				_10.0_	12.6	9.2
P⁴ dext. l.	13.8		11.3	11.6	11.0		12.9	10.6
w.	10.7		_9.4_	_10.0_	_9.4_		12.8	9.3
M¹ sin l.	*						11.2	9.1
w.	-						15.6	10.6
M¹ dext. l.	8.9						11.0	9.3
w.	11.6						15.7	11.1

the left P4 has broken off owing to recent damage. The distal external roots of each of the two fourth premolars, as well as the two vestibular roots of the single remaining first molar (on the right), are largely visible at the side of each maxilla, because the thin bony cover there has broken away. The right first molar, with an outline of its occlusal surface which resembles a parallelogramme, is a smaller dental element than the fourth premolar. Whether this has also been the case in Willemsen's (1992: pl. 3, c) specimen already cited, cannot be verified, as the first molar there has been lost. In the present, Almere, specimen it displays a paracone (the highest cusp) and a metacone at its vestibular side, and a distinct protocone and hypocone on its lingual side, with a well-visible protoconule between protocone and paracone. The tooth is surrounded by an insignificant cingulum, while here again the central part of the enamel surface is somewhat rugose. The enamel along the lingual side of the cingulum has been worn away in part, but this is the only sign of wear in the whole dentition, indicating that the individual, though adult, cannot have been very old at the time of its death. The dentition does not display any indication of crowding ('Kulissen-Stellung' of German authors). Cranial and dental measurements can be found in Tables l and 2 (where we partly follow Desse *et al.* 1986 and Willemsen 1992).

DISCUSSION AND IDENTIFICATION

As has already been stated above, there can hardly be any doubt that the skull fragment is that of an otter of fairly large dimensions. It is, however, certainly no common otter; the morphology of its dentition is peculiar in that the posterior (distal) elements are relatively large with a rather flat surface beset with proportionally small cusps. Such an aspect is encountered at present among the so-called 'clawless' otters of Africa and Southeast Asia, the Aonychini or Aonyxini. It has to be seen as an adaptation to their preferred diet of hard-shelled prey such as crabs, crayfish and molluscs, though this does not mean that the animals will disdain occasional fish, amphibians, birds or small mammals or insects. Willemsen (1992: 9) as well as Davis (1978) and Sokolov (1973) place this group together in a Tribus and include the genera *Aonyx* (in Africa) and *Amblonyx* (in S.E. Asia). Willemsen also includes the fossil genus *Cyrnaonyx* (proposed by Helbing in 1935). Helbing has proposed this generical name for a single species, uniting three mandibular fragments, a fragment of a lower first molar, and two maxillary teeth, namely a fourth premolar (indicated by him as P1) and a first molar. The first of the three mandibular specimens is a fragment of a right mandible containing m1, p3 and p4, and the alveoli of m2, p2, p1, c and two or three incisors. It was collected from one of the caves at Lunel-Viel (or Lunel-Vieil) in the Département Hérault, S.E.France, described and figured by De Serres *et al.* (1829, 1839) as belonging to an otter but differing in several aspects, such as being of a larger size, from the recent *Lutra lutra*. No specific name was given by them, but according to De Blainville (1841: 59) they intended to name the find *Lutra antiqua*. Correctly, therefore, Willemsen (1992: 44 et seqq.) and others mention the find as '*Lutra*' *antiqua* DE BLAINVILLE, 1841. Willemsen remarks that Helbing did not give a formal diagnosis, only a detailed description of his material, from which that first-mentioned author concluded that it should henceforth be known as *Cyrnaonyx antiqua* (DE BLAINVILLE, 1841). He also pointed out that Symeonides & Sondaar (1975) appear to have been the first to criticise the conspecificity of Helbing's material, especially that of the two maxillary teeth, collected at the Grotta del Margine in Corsica by Forsyth Major and presented by him (= FM) in 1920 to the Muséum des Sciences Naturelles in Lyon, France, with the mandibular fragment from Lunel-Viel. Functional occlusion between the lower teeth of the type specimen from Lunel-Viel and the two maxillary Corsican teeth seems highly improbable indeed, as

Symeonides & Sondaar (1975) pointed out. The Corsican teeth have therefore now been established by Malatesta & Willemsen (1986) as type specimina (within the Tribus Aonychini) for a new genus and species, *Algarolutra majori*. The specimen from Lunel-Viel remains as the holotype specimen of '*Cyrnaonyx antiqua*', while the other, mandibular, specimina described by Helbing, from the Roter Berg near Saalfeld (Thuringia, Germany), from the Carrière d'Aurensan at Bagnères-de-Bigorre (Hautes-Pyrénées, France) and from Montsaunès (Haute-Garonne, France), resemble very much the Lunel-Viel specimen and should be ascribed to that same species. To be added to this material are several pieces discovered later, namely a left m1 from Weimar-Ehringsdorf in Germany, a left p4 from Verona, Italy, a left half mandible with p3, p4 and m1 from the Maasvlakte near Rotterdam in the Netherlands, and a rather extensive material excavated in 1960 and 1968 from the Tornewton cave in Devonshire, England. It is this last-mentioned material consisting of a skull, skull fragments, isolated upper and lower teeth as well as some postcranial bones, which is of particular importance because it was found together and thus serves to extend the knowledge of the morphology of the dentition of the species. A good and thorough description with figures has been given by Willemsen (1992: 50-55, pls. 2-5). Although Helbing (1935) recognised and pointed out the affinity of his fossil material with the recent *Aonyx* and *Amblonyx* group (he rather curiously expressly mentioned the Corsican P4 which, as we have seen, should be separated from the Lunel-Viel species), he stated that he had been unable to find any exactly analogous traits among either fossil or recent otters, 'so that the establishment of a new genus had to be necessary' (Helbing 1935: 571) and proposed the name *Cyrnaonyx*. Quite apart from the fact that his Corsican material and that from Lunel-Viel (and other localities) cannot be considered to belong together, nor to be exactly contempo-

raneous, by which it becomes inadmissible as a base for a new genus, Helbing has nowhere given any particulars of his quest to compare the traits of his fossil material with that of other fossil or recent (clawless) otters, which he stated to have ended with negative results. Other authors evidently have thought differently; for instance Kurtén (1968, 1971) mentions the species from Lunel-Viel as *Aonyx antiqua*.

A nomenclatorial error, already pointed out some time ago by Van Zyll de Jong (1987), which seems to have eluded most authors, is the fact that the generical names *Aonyx* and *Amblonyx* are both derived from the Greek ονυξ (onux; meaning nail, claw, hoof), which is a masculine substantive. The species name is a Latin adiective and has to agree in gender with the generical name (Art. 31, b, of the International Code of Zoological Nomenclature). Therefore, in the case of the recent clawless otters, the names *Amblonyx cinereus* (not: *cinerea*) and *Aonyx congicus* (not: *congica*) should be used, and, for the fossil: *Aonyx antiquus* (not: *antiqua*).

That we are of the same opinion as Kurtén (1968, 1971), namely, that the fossil otter has to be placed within the genus *Aonyx*, is based upon the degree of likeness which it shows with the recent Cape clawless otter. For instance, when a comparison is made of the dentition of *Aonyx capensis* (SCHINZ, 1821), specimen ZMA 24.687, an adult male collected in the Cape Province (the general area whence Schinz obtained his type) with that of our Almere find (Fig. 3), the resemblance is striking. The detailed description of the teeth given by us above, almost completely fits that of the recent Cape specimen. The only differences (in the Cape animal) are found in the less outspoken, but still observable degree of triconodontism of the third premolars (mesial and distal cusplets are much smaller), in the smaller parastyles of the fourth premolars and the practically absent hypocones and ridges between paracone and

protocone in those same carnassials. The first molars have larger, not smaller, occlusal surfaces than the P4's and a much stronger developed cingulum but a very insignificant protoconule. These differences may well be explained by assuming that the recent Cape otter shows a more advanced stage of adaptation to a diet of hard-shelled prey. Yet another, perhaps minor, difference between the fossil and *A. capensis* lies in the fact that the amount of flatness (or height) of the skull, in the rostral part, is less in the recent animal than in the Almere fossil. To demonstrate this we measured the main sagittal height of the skull along the vertical midline from the palatum upward between the two orbital processes (Table 1). Van Zyll de Jong (1972: 62) has remarked that a dorso-ventral flattening of the skull is observable in several unrelated mammalian groups adapted to an aquatic existence, that the skulls of *Aonyx* and *Amblonyx* are high in comparison to those of American river otters, and that it seems that the flattened skull is restricted to stream-dwelling forms that feed on fast-moving prey (fish), as is the case with the common *Lutra lutra*.

But also when we compare the dentition of the fossil to that of an equally (closely) allied form, *Aonyx congicus* (LÖNNBERG, 1910), specimen ZMA 13.533, an adult female from Loa-Loa near Makokou in N.E. Gabon, the close resemblances are immediately apparent. In the recent specimen the differences consist of an evidently further reduction of P1 (only the one of the left side, minutely small, is present), crowding of the teeth, overall much smaller sizes of each dental element, a degree of trenchantness of the separate cones of the teeth which stands in between that of *A. capensis* and the fossil, and an almost equal amount of occlusal surface of P4 and M1 (while, as we have seen, the fossil has a M1 which is definitely much smaller in surface than its P4).

A third comparison of the fossil with another allied form, *Amblonyx cinereus* (ILLIGER, 1815), in this case specimen ZMA 6968, an adult female from Tanjung Karang, S. Sumatra, results in our observation that this, much smaller, species does not possess any P1 and that the general configuration of cones and cingula in the other elements of its dentition are the same as described above in the fossil and in *A. capensis*, but that the degree of trenchantness is the same as in the fossil. This outspoken trenchant nature of the teeth, in which *Amblonyx* resembles recent American otters such as *Lutra provocax* and *L. felina*, is discussed by Van Zyll de Jong (1972: 51).

The already mentioned good description and figures of the Tornewton fossil material in Willemsen (1992) show that our present specimen belongs, beyond doubt, to the same species. Thus it constitutes a second case of occurrence of *Aonyx antiquus* (DE BLAINVILLE, 1841) in the Netherlands, after the description of a mandible from the Maasvlakte, now in the Kerkhof collection, by Willemsen in 1992 (mentioned by him in 1984). Stratigraphically the Almere find more or less agrees with Willemsen's analysis (1992: 45) of its occurrence from the Holsteinian Interglacial (the probable age of the Lunel-Viel cave deposits is final Holsteinian or beginning Saalian according to Bonifay & Bonifay 1965) up to Eemian or even Weichselian (interstadial) times. If the Almere fossil, assuming that it occupied a freshwater habitat, happens to be Eemian in age, as might be indicated by the many Eemian shells occurring as an upper border horizon in the Eemian marine sands, and found scattered nearby at the building-site, one has to suppose that the otter was washed down, as a cadaver, from nearby higher ground (in particular the Gooi morainic hills nearby) into the shallow bay at the mouth of the Pleistocene river Eem. If, on the other hand, it should be Weichselian, it has to be
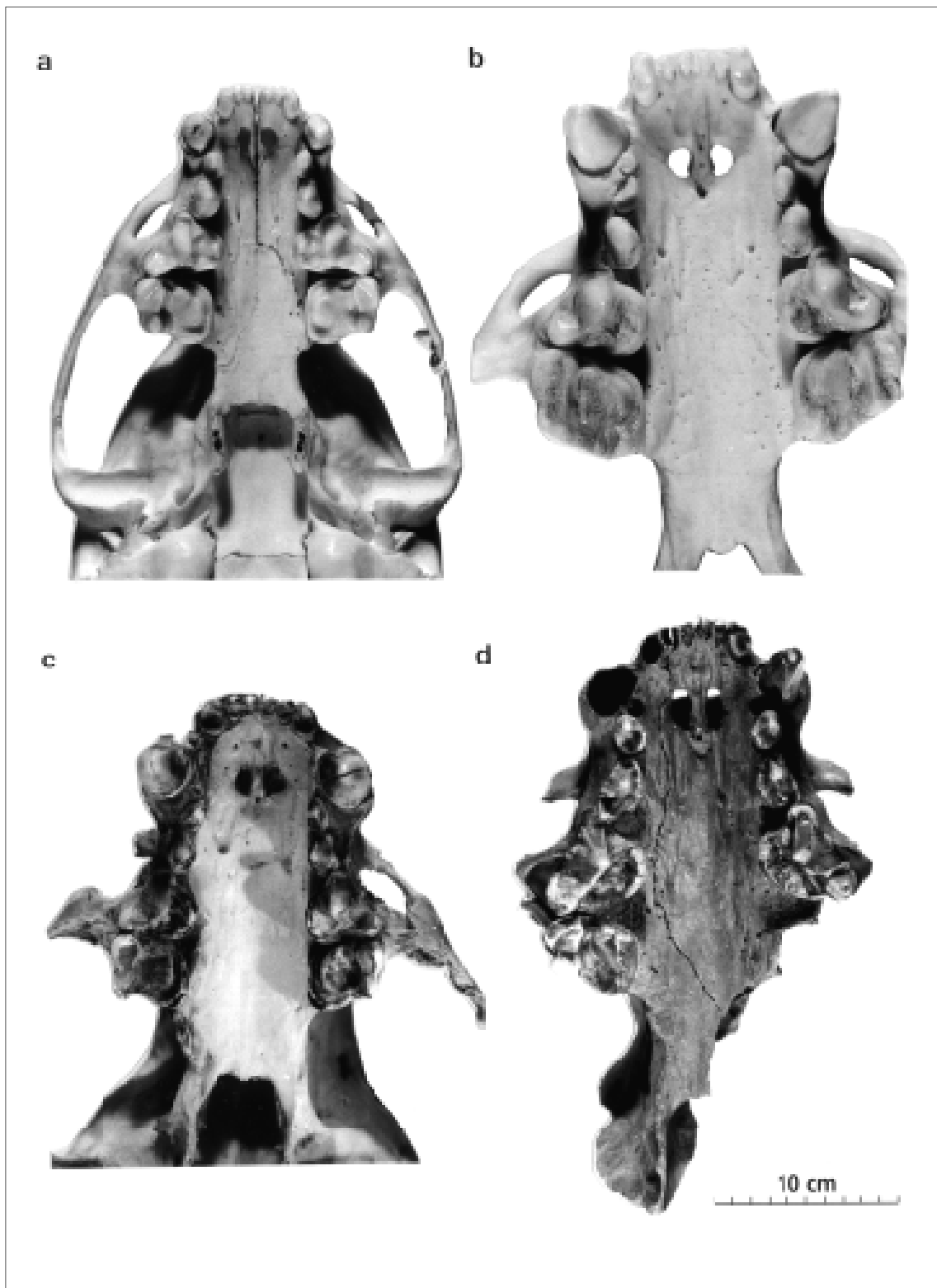
Figure 3 Palatal aspects, to show the mastication surface of the teeth, of : **a** *Amblonyx cinereus*, ZMA 6968; **b** *Aonyx capensis*, ZMA 24.687; **c** *Aonyx congicus*, ZMA 13.533; and **d** *Aonyx antiquus* from Almere, coll. Roescher.

explained as a more or less *in situ* find from one of the several shallow ponds or lakes formed during one of the Early Weichselian interstadials, such as the Amersfoort or Odderade interstadial (Van Andel & Tzedakis 1996: fig. 11), the alternative possibility. The fossil bones of several mammalian species collected at the building-site, mentioned earlier in the present paper, constitute an argument in favour of this.

CONCLUSION
The fossil snout of an otter found at a building-site in Almere and dredged up from Eemian or Early Weichselian sands in front of the Noorder Plassen in the Marker meer is identified as *Aonyx antiquus* (DE BLAINVILLE, 1841).The generical name *Cyrnaonyx* is inadmissible and has to be abolished. Contrary to Willemsen (1992: 45) we are of opinion that the differences with recent *Aonyx* are insufficient to justify a generic separation. The more flattened skull of the fossil (a feature also noted by Willemsen) has to be explained as an adaptation to life in swiftly flowing water and to a diet containing more fish than in the case of the recent *Aonyx*. The eyes of the fossil do not impress us as being more dorsally set than in recent *Aonyx* or *Amblonyx*, of which we have inspected more than forty skulls. Nor do other features mentioned in Willemsen's diagnosis of '*Cyrnaonyx*' strike us as sufficiently particular and absent among recent individuals of *Aonyx* or *Amblonyx*. A typical feature of *A. antiquus* may be that its M1 has a smaller occlusal surface than its P4, but more material will be necessary to verify this supposition. It might indicate an ancestral and conservative trait, as *Potamotherium valletoni* GEOFFROY, 1833 from the French Oligocene shows the same feature; but according to Savage (1957) this fossil form should not be seen as the ancestor of all later otters. The more trenchant upper teeth of *A. antiquus* (compared to recent *Aonyx*), of a similar degree as in *Amblonyx*, may indicate a diet containing more fish, but it could also

mean that *antiquus* retains some features (the absence of crowding in the upper dentition is another possible case) that could point to the (or a) common ancestor of *Amblonyx cinereus, Aonyx capensis* and *Aonyx congicus* (see the Adams-2 consensus tree, fig. 5 in Van Zyll de Jong, 1987: 2542), a supposedly Pliocene or Early Pleistocene form. Geographically such a form would probably have lived somewhere at approximately equal distance from S.E. Asia, tropical Africa and W. Europe, therefore at a location within the 'plantain- or boomerang-shaped region along the eastern and northern limits of the Indian Ocean' mentioned in Erdbrink (1988: 155).

The climate of the area in which *A. antiquus*, our Almere fossil, lived, may have resembled that of the present-day Cape Province in S. Africa. According to Van Andel & Tzedakis (1996: p. 490, OIS 5e, the Eemian; and pp. 491-492, OIS 5c and 5a, the Brørup and Amersfoort, and the Odderade interstadials) temperatures did not differ very much from the values of around 20º C in summer to about 10º C in winter which are those with which *Aonyx capensis* has to cope at its type locality.

REFERENCES

Bonifay, M.-F. & Bonifay, E., 1965 - Age du gisement de mammifères fossiles de Lunel-Viel (Hérault). Comptes Rendus de l'Académie des Sciences, Paris 260 (9): 3441-3444

Davis, J.A., 1978 - A classification of otters - in: Duplaix, N. (ed.) - Otters - Proceedings of the first working meeting of the Otter Specialist Group, Paramaribo, Surinam, March 1977 - Morges: I.U.C.N.: 14-33

De Blainville, H.M. Ducrotay, 1841 (1839-1864) - Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récents et fossiles pour servir de base à la zoologie et à la géologie. T. Iime (secundatès) avec atlas (folio), 117 pls., Paris, I: 54-60

De Gans, W., 1983a - Permafrost en permafrost ver-schijnselen in arctische gebieden - Grondboor & Hamer 37 (6): 165-174

De Gans, W, 1983b - Fossiele permafrost verschijnselen in Nederland - Grondboor & Hamer 37 (6): 175-184

De Gans, W., 1991 - Kwartairgeologie van West-Nederland - Grondboor & Hamer 45 (5/6): 103-114

De Gans, W., 1995 - Een geologisch overzichtsprofiel van Ridderkerk naar Urk - Grondboor & Hamer 49 (3 /4): 90-93.

De Serres, M., Dubreuil, J. & Jeanjean, B., 1829 - Recherches sur les ossemens fossiles des cavernes de Lunel-Vieil (Hérault) Troisième Art., Ch. V: des différentes espèces de mammifères terrestres - Mémoires du Muséum d'Histoire Naturelle 18: 313-356

De Serres, M., Dubreuil, J. & Jeanjean, B., 1839 - Recherches sur les ossements humatiles des cavernes de Lunel-Viel - Montpellier: 1-275

Desse, J., Chaix, L. & Desse-Berset, N., 1986 - 'Ostéo', Base-réseau de données ostéométriques pour l'Archéozoologie - Paris: Éditions du C.N.R.S.: 1-161

Erdbrink, D.P. Bosscha, 1988 - *Protoryx* from three localities East of Marâgheh, N.W. Iran - Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B 91 (2): 101-159

Helbing, H., 1935 - *Cyrnaonyx antiqua* (Blainv.), ein Lutrine aus dem europaeischen Pleistocaen - Eclogae Geologicae Helvetiae 28 (5): 563-577.

Kurtén, B., 1968 - Pleistocene mammals of Europe London: Weidenfeld & Nicholson: 1-317

Kurtén, B., 1971 - The Age of Mammals. The World Naturalist - London: Weidenfeld & Nicholson: 1-250

Malatesta, A. & Willemsen, G., 1986 - *Algarolutra* g.n. established for a fossil otter of the Sardinia island - Geol. Romana 25: 285-286

Oyama, M., Takehara, H. & Ooi, Y., 1967 - Revised Standard Soil Color Charts - Tokio: 1-12 + 17 pls.

Savage, R.J.G., 1957 - The anatomy of *Potamotherium*, an Oligocene lutrine - Proceedings of the Zoological Society London 129: 151-244

Sokolov, I.I., 1973 - Napravleniya evolyutsii i estestven naya klassifikatsiya podsemeistva vydrovykh - Bull. Mosk. O. Ispyt Prirody, Otd. Biol. 78 (6): 45-52

Symeonides, N. & Sondaar, P.Y. 1975 - A new otter from the Pleistocene of Crete - Annales géologiques des Pays Helléniques 27: 11-24

Van Andel, T.H. & Tzedakis, P.C., 1996 - Palaeolithic Landscapes of Europe and Environs, 150,000 - 25,000 Years ago. An Overview - Quaternary Science Reviews 15: 481-500

Van Zyll de Jong, C.G., 1987 - A phylogenetic study of the Lutrinae (Carnivora; Mustelidae) using morpholo-gical data - Canadian Journal of Zoology 65: 2536-2544.

Van Zyll de Jong, C.G., 1972 - A Systematic Review of the Nearctic and Neotropical River Otters (Genus *Lutra*, Mustelidae, Carnivora) - Life Science Contributions, Royal Ontario Museum 80: 1-104

Willemsen, G.F., 1984 - Europese otters door de tijden heen - Lutra 27: 11-18

Willemsen, G.F., 1992 - A revision of the Pliocene and Quaternary Lutrinae from Europe - Scripta Geologica 101: 1-115