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Het Gat: preliminary note on a Bavelian fauna from the North Sea with possibly two mammoth species

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We describe the fossil vertebrate remains from a site ('Het Gat') on the bottom of the North Sea, between the United Kingdom and the Netherlands. The site is a maximally c. 46 m deep gully that cuts through layers of Holocene and Eemian sediments and reaches into the Yarmouth Roads Formation. This part of the Yarmouth Roads Formation is a complex of fluvial sediments of late Early-Pleistocene, most probably Bavelian, age. The age of the Bavelian is considered to be some 1.000.000 - 750.000 years (1 - 0.75 Ma). As the fossils originate from the Yarmouth Roads Formation, the fauna is thus attributed a late Early Pleistocene age; we correlate it to localities such as Untermassfeld (Germany) and Saint-Prest (France), which both have an estimated age of c. 1 Ma. The faunal content of the site 'Het Gat' is provisionally as follows: (Proboscidea) Mammuthus meridionalis and/or Mammuthus trogontherii; (Artiodactyla) Hippopotamus antiquus, Alces latifrons, Megaloceros dawkinsi, Megaloceros savini, Eucladoceros ctenoides, Bison menneri; (Perissodactyla) Equus major, Stephanorhinus etruscus; (Carnivora) Homotherium cf. latidens, Ursus cf. etruscus. These finds necessitate us to discuss whether or not two different species of mammoth can have coexisted and can thus be present in one fossil faunal assemblage. There appears to have been a continuous evolutionary development leading from Early Pleistocene M. meridionalis to Late Pleistocene and Holocene M. primigenius. Most authors recognise an intermediate species M. trogontherii, of supposedly Middle Pleistocene age. The differences are in the dentition, while postcranially the taxa are difficult to distinguish. The molars we found in 'Het Gat' can either be interpreted as advanced M. meridionalis or as M. trogontherii. Until the taxonomy of Pleistocene Mammuthus species is clarified we doubt the presence of two species in one locality.

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INTRODUCTION

Early and/or Middle Pleistocene mammalian fossils from the bottom of the North Sea were first recognised by Kortenbout van der Sluijs (1970-1971, 1971). Drees (1986) attempted to give a paleontological and geological context to these 'black and heavy' fossils. In the most recent and detailed treatment of this subject an early Early Pleistocene association (with mastodon and southern mammoth) is described in addition to a late Early and/or early Middle Pleistocene association (Van Kolfschoten & Laban 1995). This latter association comprised Mammuthus meridionalis, Mammuthus trogontherii, Equus major, Stephanorhinus etruscus, Hippopotamus antiquus, Alces latifrons, and an (as yet) unidentified deer and bison. The fauna would date to a period between Late Tiglian (TC5-6) and Early Cromerian. According to Van Kolfschoten & Laban (1995) the fossils originate from several associations with different geological ages. This conclusion was substantiated by doubting the occurrence of both Mammuthus meridionalis and Mammuthus trogontherii within a single fauna.

All such studies about the oldest mammalian fossils from the North Sea are based on accidental finds without accurate locality data. Often it is only known that the fossils originate from the deeper parts of the southern North Sea, and as a rule the term 'Deep Water Channel' is used for the lack of better. In reality the rare finds originate from several different deeper pits. The distances between these pits (of up to 40 nautic miles) and the complex geological situation of the bottom of the southern part of the North Sea necessitate a critical evaluation of the general conclusions published so far.

Most fishermen do not discriminate between older (Early and Middle Pleistocene) fossils and the ones from the Late Pleistocene and hence precise locality data are rare. Yet an increasing interest among the fishermen led to a better localisation of the fossils and to a wealth of new data. The importance of the present paper is the restriction to data collected

by one single ship on one single locality, named Het Gat. Geological details of this site are known and the Cerpolex/Mammuthus Expedition 2001 thoroughly investigated the locality, enabling us to be reasonably exact about the geological context of the fossils.

THE LOCALITY AND ITS GEOLOGICAL CONTEXT

Nearly all localities of fossil bones (both Late Pleistocene and older) are situated S or SW of the so-called Brown Bank. The fauna described in the present paper, however, originates from an aberrant, narrow and very elongate trench N and NE of the Brown Bank. The site is situated between 52°35'-52°50' N and 3°20'-3°25' E (Fig. 1). Fishermen call this trench 'Het Gat' or 'Het Gat binnen de Bruine Bank' (meaning The Pit or The Pit within the Brown Bank). The Brown Bank itself lies at c. 18 m below sealevel and the sides of the Bank steeply dip to c. 36-40 m. The maximum depth of Het Gat is about 46 m.

Fishermen consider the area to be difficultly fishable due to the presence of small erratic boulders and irregularly folded layers of coarse brown sands and fine clays. The folded sediments and the erratica are caused by, and deposited by, glacial action. They cause damage to the nets or even the loss of entire equipments. The trench Het Gat therefore is only rarely visited and the vessel that provided our fossils is the only ship that frequents the trench on a regular basis. The vessel, GO41 with captain G. 't Mannetje, always follows the same route: a N-S directed stretch at 40-42 m depth, at 3°20'30" E and 52°41' N to 52°36'30" N. Below 42 m depth, problems arise with lots of stones. Turning the ship is to be avoided. After five subsequent pulls the bottom becomes too loose and fishing is halt-

The geological map of the area (Cameron *et al.* 1984) shows that thin layers of Eemian and Holocene sediments lay directly on top of the Yarmouth Road Formation (YRF). As these layers are being exposed, both Eemian

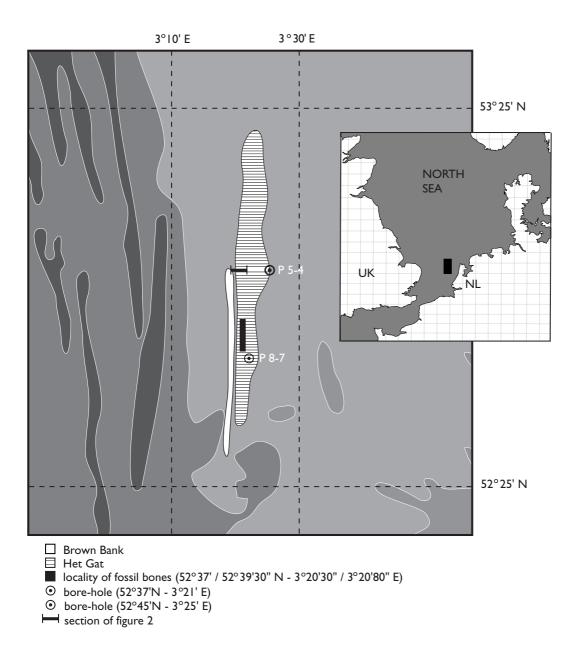


Figure I Map of the Brown Bank area with Het Gat and indications of the locations of borings P 8-7, P 5-4 and of the profile of Figure 2.

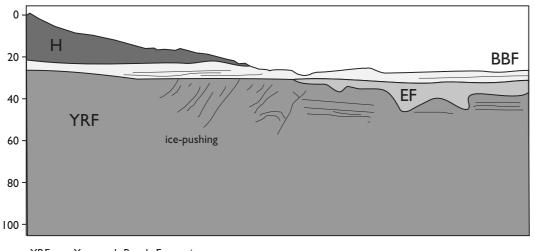
sediments and YRF sediments can be found at or near the surface. Profile 4 of Cameron et al. (1984; our Figure 2) cuts through the middle part of the trench (52°43' N, 3°18'-3°22' E) and shows that glacial pushing during the Elsterian brought the YRF at or near the bottom surface. Comparison with Profiles 2 at 52°48' N and 3 at 52°18' N (Cameron et al. 1984; here not reproduced) shows that the YRF is present throughout Het Gat and that the lowermost depth of the YRF lies at 60 - 200 m below sea level. Thus, older layers can not have been exposed.

The YRF must be interpreted as a fluviatile sedimentary complex deposited between the Early Waalian and the Early Cromerian. Laban (1995) shows that the boulders and the irregular structures are due to glacial pushing by Elsterian ice. The gravel and the stones are most probably of Scandinavian origin. Two borings by the Rijks Geologische Dienst (RGD, the Dutch Geological Survey) are an important reference. Boring P5-4 at the NE

border of Het Gat (52°45' N - 03°25' E; water depth 33.80 m) contained the YRF at 30 -47.20 m below the bottom surface (RGD report 560). Boring P8-7 in the centre of Het Gat (52°37' N -03°21' E; water depth 40 m) has the YRF directly at the bottom surface. Zagwijn (1971) performed a pollen analysis of a clay layer at 2.45 m below the bottom surface (RGD report 581). He found a flora with a characteristically interglacial composition (comprising e.g. Tsuga, Eucommia and Azolla filiculoides) that is typical for either the Waalian or the Bavelian.

Three fossil faunas

At least three fossil faunas are to found in Het Gat. These are the Mammoth Steppe Fauna, a warmer Eemian fauna and a possibly older fauna from the YRF. The wellknown Late Pleistocene fossils of mammoth and its companions are rarely encountered. Sometimes animals are found that could date from the Eemian (such as beaver, boar, deer



YRF = Yarmouth Roads Formation ΕF = Fem Formation

BBF = Brown Bank Formation

= Holocene Sediments (Brown Bank)

Figure 2 Profile through Het Gat, after Cameron et al. 1984, see Figure 1.

and a large rhino). These slightly mineralised fossils show a degree of fossilisation and a colour that largely differs from the bulk of heavily mineralised fossils normally found in Het Gat. In addition, these heavily mineralised fossils all belong to older and extinct mammal taxa. We thus have to conclude that the latter group of taxa -subject of the present paper- originates from the YRF. An additional and interesting fact is the presence of as yet unstudied fossil wood, known from no other place in the North Sea.

THE CERPOLEX/MAMMUTHUS EXPEDITION

Cerpolex/Mammuthus chartered the fishing vessel SL27 from June 5-8 2001 in order to search for fossils in the depression known as Het Gat and to properly map the area. The expedition was led by the first author (DM) and by Mr Bernard Buigues (Cerpolex). The vessel and its able crew were assisted by a team of divers, a robotic camera and a second ship called Togo. Scientists and journalists could follow the expedition from the Togo and come aboard SL27 in order to study the fossils caught. The expedition collected a wealth of geological and paleontological details. Most of this still has to be studied, but some preliminary conclusions can here be drawn.

The entire area of Het Gat was sampled in 31 drags. The geological results of these confirm the suppositions that were made on the basis of the geological maps and the data collected by the GO41. The heavily mineralised bones were found in a relatively small part of Het Gat, situated between 52°37' N - 52°39'30" N and 3°20'30" - 3°20'80" E (Fig. 1), at depths of 42 to 44 m. Large lumps of ferrugineous fossil wood (> 30 pieces) were found in addition to 161 heavily mineralised bones corresponding to those previously discovered by the GO41. Outside of this area no older bones were found, only Late Pleistocene, possibly Eemian fossils.

THE FAUNA

The fossils found in Het Gat are heavily mineralised and of a brownish to blackish-brownish colour. These fossils are often broken and the impression is that many of the fractures are old. Fracture surfaces can appear glass-like and often contain traces of iron. Identification of a certain taxon is done on the basis of the morphology. Yet the degree of fossilisation does play a certain role in the process. The heavily mineralised specimens produce a high-pitched sound when tapped upon with a hard object. This indicates that we should look for Early or early Middle Pleistocene taxa.

So far, nearly one thousand fossils of this fauna have been collected from Het Gat. Identifications of the taxa mentioned in this study are based on the presence of one or more characteristic fossils. In the following short accounts the fossils are compared with specimens from other Early or early Middle Pleistocene faunas in Europe.

Hippopotamus antiquus DESMAREST, 1822

At least two species of hippo are known from the Pleistocene of NW Europe: *Hippopotamus antiquus* and the somewhat smaller *H. amphibius incognitus* FAURE, 1984. The latter is considered a subspecies of the hippo still existing in Africa and was mentioned from Dutch continental and North Sea territory (Mol 1993, 1994). Fossils collected on the Maasvlakte area originate from the dredged sands from the Rotterdam area and are commonly considered of Bavelian age (Vervoort-Kerkhoff & Van Kolfschoten 1988).

Remains of *Hippopotamus antiquus* are morphologically almost indistinguishable from the Late Pleistocene (Eemian) hippo, but they are considerably larger. The species is restricted to the Early and Middle Pleistocene. In this case, identification is based on the degree of fossilisation in combination with the size of the material. Hippo remains from Het Gat are mostly parts of manus, pes, and dentition. Larger bones are nearly always damaged, with the exception of

a fine cervical vertebra.

H. antiquus is known from e.g. the Arno Valley, Tuscany, Italy. Large collections are present in the paleontological museums of Florence (e.g., a mounted skeleton) and Montevarchi. From the beginning of the Pleistocene onward H. antiquus was part of a fauna dominated by the southern mammoth (M. meridionalis). Another important locality where this hippo was found is Untermasssfeld in Thuringia, Germany. Here, fluviatile sediments are being systematically searched and over 700 hippo remains were decribed by Kahlke (1995). The Untermassfeld fauna is dated around the end of the Early Pleistocene (Late Waalian) to the beginning of the Middle Pleistocene (Early Bavelian), c. 1 Ma ago.

Another locality with an important Early/Middle Pleistocene fauna is Saint-Prest (Eure-et-Loir), France (Guérin 1999). Here, H. antiquus was found in association with Mammuthus meridionalis, Stephanorhinus etruscus, Equus stenonis, Alces carnutorum, Megaloceros verticornis, two unidentified deer, a large bovid (Bos or Bison), and Trogontherium cuvieri. The age of Saint-Prest is nearly the same as of Untermassfeld. The remains, found some 150 years ago, are in the Natural History Museum of Chartres (France). Nowadays hippos live in a warm environment, but this can not be used to indicate a high paleotemperature. Faure (1985) showed that hippos are mostly to be seen as a species of humid circumstances.

The mammoths

Three species of mammoth as well as the forest elephant are known from the bottom of the North Sea (Mulder 1973; Hooijer 1984; Mol 1989, 1991; Van Essen & Mol 1996; Mol *et al.* 1999). The presence of these four proboscideans is shown by the respective dental elements. Two species are known from Het Gat: the southern mammoth *Mammuthus meridionalis* and the steppe mammoth *M. trogontherii*.

Mammuthus meridionalis (NESTI, 1825)

Southern mammoth is known in the Netherlands from the Tegelen and Oosterschelde faunas. In the Oosterschelde it occurs together with the mastodon Anancus arvernensis (Mol & De Vos 1995). This indicates that the Oosterschelde fauna is older than Tegelen, where the mastodon was no longer present. The Oosterschelde fauna with the two proboscideans is considered contemporaneous with the fauna from Chilhac (Auvergne, France), c. 1.9 Ma of age (De Vos et al. 1998). M. meridionalis is also regularly found on other locations on the bottom of the North Sea. Van Essen & Mol (1996) showed that there existed a 'primitive' and an 'advanced' form, the advanced being the younger of the two. The forms are distinguished by their

Fossils of the southern mammoth are quite common from Het Gat, mostly molar fragments and sometimes a complete molar (Fig. 3).



Figure 3 Mammuthus meridionalis. Right mandibular m2, coll. KP no. 2701. bar = 3 cm.

The molars indicate a very advanced stage and thus rather young representatives of the species. Many post-cranial remains are attributed to southern mammoth based on their large sizes, although it should be mentioned that it can be difficult to differentiate southern mammoth from steppe mammoth on the basis of isolated bones only. Smaller parts of the skeleton are found complete, larger bones (such as humeri, femora etc.) are found mostly fragmented. Both the complete bones and the fragments confirm the large size of the mammoths concerned.

The *M. meridionalis* from Saint-Prest was also of an advanced form (Coppens & Beden 1982). It was described as a distinct subspecies: *Mammuthus meridionalis depereti* COPPENS & BEDEN, 1982. The age of the Saint-Prest fauna is estimated around 1 Ma (Guérin 1999) and this age is considered the beginning of the Middle Pleistocene in France.

Mammuthus trogontherii (POHLIG, 1881)

The steppe mammoth is seen by many researchers as the link between the southern mammoth M. meridionalis and the woolly mammoth M. primigenius (Lister 1996). As a rule, steppe mammoth is considered an indicator for the Middle Pleistocene; it is a rather little known species (Hooijer 1984). The few known complete skeletons cause considerable discussion. For example, the skeleton found in the 1930's in Edersleben (Germany; now on display in the Spengler Museum, Sangerhausen) was attributed to the steppe mammoth but is now considered a female southern mammoth. Another important find in this respect is the nearly complete skeleton found in fluviatile sediments at the East Anglian coast near West Runton (Norfolk, UK; Stuart no date, Lister & Bahn 2000). It is a male with a shoulder height of c. 4 m, dated to an interglacial some 600,000-700,000 y ago. Southern mammoth is also reported from West Runton, but the two molars from the Upper Fresh Water Bed on which this is based (kept in the Natural

History Museum, Londen) could originate from a different level (A. Lister, pers. comm. dd. 26 February 2001).

Until recently, remains of *M. trogontherii* were considered great rarities. However, fragmentary or even complete molars are often found in Het Gat (Fig. 4, 5). Possibly the rarity of the species is caused by the difficulty to recognise the molars/molar fragments as they resemble strongly fossilised woolly mammoth teeth. Postcranially there is great resemblance to the southern mammoth.

M. trogontherii is considered derived from M. meridionalis. In this framework the early Middle Pleistocene locality of Kärlich in the Neuwied basin (Germany) is of importance. Van Kolfschoten & Turner (1996) mention M. trogontherii from this locality in strata that



Figure 4 *Mammuthus trogontherii*. Right upper molar M1, coll. KP no. 2700, in buccal and occlusal view. bar = 3 cm.

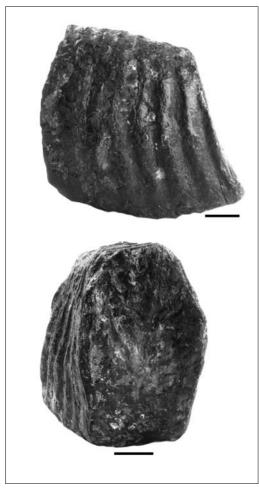


Figure 5 Mammuthus trogontherii. Right fragmentary mandibular m3, coll. C/M no. CME 2001/002, in lingual and posterior view har = 3 cm

are older (!) than strata where *M. meridionalis* occurred. Lister (1996) mentions the same phenomenon 'from Britain and Germany', but this is probably based on hearsay as the reference to these remarks is 'unpublished observations'. This stratigraphic reversal seems quite strange, but can be explained by the scarcity and the very fragmented character of the molars ascribed to *Mammuthus trogontherii*.

Azzaroli (1966, 1977) does accept *trogon-therii* as the precursor of the *primigenius*, but denies *meridionalis* to be the precursor of *trogontherii*. He bases this hypothesis on the

skull shape. This vision implies that *trogon-therii* originated allopatrically (Lister 1996). Also Lister & Sher (2001) implied allopatric speciation to have occurred, starting with a speciation event in Eastern Siberia around 1.0 My ago, with *trogontherii* subsequently spreading over Eurasia in a westward direction. This scenario may have its merits, but still it seems unlikely for two mammoths to have coexisted in more or less the same ecological niche. Also, one species a browser and the other one a grazer seems unlikely as this would imply the presence of two different habitats. There are no other fossil taxa to support such hypotheses.

Artiodactyla

Deer remains are the most frequently encountered fossils in the Het Gat area. Especially the resistant proximal parts of antlers are common. The most frequent is the Tiglian deer Eucladoceros ctenoides. Many deer species are known from the Early and Middle Pleistocene. Over a hundred years ago, during the ascent of mammalian paleontology, many species were described and nearly every European locality had its own species. We now know that many taxa are synonyms, but still many species 'exist'. Since we deal mostly with fragmentary antlers and only few post-cranial remains, it is difficult to simply identify our material to the species level. Complete skeletons from many (Early and Middle) Pleistocene species are unknown, therefore descriptions are often based on (fragmentary!) antlers only. Hence good identifications are often impossible.

Alces latifrons (JOHNSON, 1874)

Two moose species are known from the Early and Middle Pleistocene of Europe: *Alces gallicus* (AZZAROLI, 1952) and *A. latifrons*; the former considered a precursor of the latter and having a gigantic antler of some 3 m width with a blade-like shape like modern moose (*A. alces*). The beam was extremely long and rounded in the oldest representati-

ves; it shortened during the course of the Pleistocene to the shorter beam of *A. latifrons*. The Late Pleistocene to Recent *A. alces* has the shortest beam, facilitating manoeuvring in forested areas. Another species is known, *Alces gallicus*, of which a complete mounted skeleton from Sénèze (France) is on display in the building of the University Claude Bernard, Lyon.

Alces latifrons is the largest deer found in the European Pleistocene, its range was large: from England to NE Siberia. An m3 was found on the Maasvlakte (the Netherlands, Vervoort-Kerkhoff & Van Kolfschoten 1988). Early 2000 an antler fragment with part of the skull was found in Het Gat; this fragment of 15 kg weight proved the presence of A. latifrons in the locality. Moose is also known from the contemporaneous localites of Saint-Prest and Untermassfeld. In both cases however, it was described as Alces carnutorum (LAUGEL, 1862), a species being much more slender than A. latifrons. This is clear from the Untermassfeld fossils; for Saint-Prest we have doubts on the species identification.

Megaloceros dawkinsi (NEWTON, 1882)

At least three species of giant deer (genus Megaloceros) are known from the Early ad Middle Pleistocene. Two of these, M. dawkinsi and M. savini, are known from Het Gat; the third species (*M. verticornis*) was not found. M. dawkinsi differs from M. verticornis by having a considerably smaller skull. The species was described based on an antler of a young individual. The antler, especially at its base, is characterised by a round-oval circumference and by the presence of a knob as a rudimentary brow-tine. Sometimes this knob is lacking. The species is known mostly from East Anglia (UK); a complete skeleton is unknown. The best (antler) material of this insufficiently known species is in the London Natural History Museum. Most of the material from Het Gat is here attributed to M. dawkinsi. It is supposed to have been a common faunal element.

Megaloceros savini DAWKINS, 1887

M. savini is characterised by an antler consisting of a small number of long, rounded and distally flattened tines. It is less common than the previous species. We identified the species in Het Gat on the basis of some antler fragments. Yet we need more material to properly identify the deer species in the fauna. The presence of both species here mentioned is likely; both species have a considerable geographical range in the Early and Middle Pleistocene and were found in East Anglia, which is not far from our locality. Surprisingly, no Megaloceros was found in Untermassfeld; in Saint-Prest on the contrary, Megaloceros verticornis was found next to two as yet unidentified species.

Eucladoceros ctenoides (NESTI, 1841)

This so-called Tiglian deer was large and comparable to recent *Cervus elaphus*. *Eucladoceros* antlers vary in size from moderate to large and the major axis is only slightly bent. Many species have been described within the genus *Eucladoceros*. Many of these are very similar and are now considered *E. ctenoides*, e.g. the specimens from Tegelen formerly called *E. tegulensis* (De Vos *et al.* 1995). The species from Untermassfeld is considerably larger and is called *E. giulii* KAHLKE 1997.

Most deer remains in Het Gat belong to *Eucladoceros*. This means that this taxon was a common faunal element. The biotope was generally wooded, hence we assume that the vast plains between the present UK and Holland, some 1 Ma ago, contained forests bordering the rivers in a furthermore steppic landscape.

Bison menneri SHER, 1997

One of the least known and largest bovids from the Early and early Middle Pleistocene is *Bison menneri*. This cattle species was described by Sher (1997) based on extensive material from Untermassfeld. Cattle are living in herds, hence the abundance of material from this German locality. In Het Gat,

however, only few remains have been trawled. Only the smaller parts of the feet (metapoda, calcanea and astragali) and two horn cores are identified with certainty. These remains are provisionally indentified as *Bison* cf. *menneri*. A very large, black and heavily fossilised metatarsale from the collections of Naturalis, first identified as *Bison priscus*, and later as *Bos primigenius* (Guérin, in litt.) is now also ascribed to *Bison menneri* (Mol 1998; Drees 1999).

Perissodactyla

Equus major BOULE, 1927

The smaller skeletal elements of a large horse (such as phalanges, vertebrae and some longbones like ulna, radius and metapodia) were trawled from Het Gat; some material still awaits identification. Although Pleistocene horses range from small and slender to large and sturdy, it is clear that our material belonged to a rather large horse, such as also known from e.g. the Oosterschelde. Often the name *E. bressanus* VIRET, 1954 is used, and this name was used earlier for North Sea material (Hooijer 1985). However, the name *E. major* BOULE, 1927 has priority.

Stephanorhinus etruscus (FALCONER, 1868)

Pleistocene rhino remains are common from the North Sea. Most of these can be ascribed to Coelodonta antiquitatis (BLUMENBACH, 1799) on the basis of morphology and degree of fossilisation. Other NW European taxa were the etruscan rhino Stephanorhinus etruscus, the forest rhino Stephanorhinus kirchbergensis (JÄGER, 1839), and the steppe rhino Stephanorhinus hemitoechus (FALCONER, 1868), see Mol & De Vos 2001. Future research must show whether or not all these species are known from the North Sea. S. etruscus is known for some time from the North Sea, and the Cerpolex/Mammuthus expedition proved its presence in het Gat, as three characteristic parts were trawled. S. etruscus is an Early Pleistocene rhino that was common from c. 2.0 - 0.8 Ma ago. From

the Netherlands it is known from the Oosterschelde, from clay pits near Tegelen, from the Maasvlakte and from Westerhoven (Rutten 1909, Loose 1975, Guérin 1980, Van Kolfschoten 1989, Mol & De Vos 2001). A comparison with faunas from other early and early Middle Pleistocene localities (Table 1) shows that the etruscan rhino was present in many of them.

DEINSEA 9, 2003

The species lived in a savanna biotope, with shrubby grasslands mixed with forests. The same biotope was favoured by Mammuthus meridionalis. Both taxa were browsers as can be deduced from the lowcrowned dentition; also the position of the head of S. etruscus was more forward (horizontally) directed and it was rather longlegged. This latter condition was proved by a complete and extremely slender radius found by the SL27 elsewhere in the Southern North Sea. All known remains of the species from the North Sea as well as from the Oosterschelde (Hooijer 1981a,b) are as a rule brownish/blackish in colour and strongly fossilised.

Carnivora

Remains of Carnivora are usually quite rare in a fossil fauna association. Yet remains of large Late Pleistocene carnivores such as cave lion, cave bear and hyena are regularly found on the bottom of the North Sea. Early and Middle Pleistocene carnivore remains, however, are rare both in the Netherlands and the adjacent North Sea area.

Homotherium cf. latidens OWEN, 1914

Sabretooth cat was first recognised in January 2001, when the GO41 crew made four one-hour pulls in Het Gat. In addition to remains of *Mammuthus meridionalis*, several deer species, and the large horse, they found part of the distal articulation of a left humerus. This small but characteristic piece could be identified with the aid of a cast of a *Homotherium* humerus from Artenac (Charente, France). The humerus fragment is

Table I Comparison of the mammals from Het Gat with some Early and Middle Pleistocene mammal faunas; only those taxa that were found in Het Gat are used in this table. **Ch** = Chilhac (France, Early Tiglian), **Teg** = Tegelen (Netherlands, Late Tiglian), **Un** = Untermassfeld (Germany, Early Bavelian), **SP** = Saint Prest (France, Late Bavelian), **Vo** = Voigtsted (Germany, Early Cromerian), **WR** = West Runton (England, Middle Cromerian), **Sb** = Süssenborn (Germany, Late Cromerian), - = absent, **s** = same species, **g** = same genus, but other species or species uncertain.

Ch	Teg	Un	SP	Vo	WR	Sb
-	-	s	s	-	-	-
s	S	S	S	S	S	-
-	-	-	-	S	S	S
-	-	g	g	S	S	S
-	-	-	_	g	g	g
S	s	g	g	-	-	-
-	-	S	g	g	g	g
g	g	g	g	g	g	g
s	s	s	s	S	s	S
-	-	S	-	-	-	-
S	S	s	-	-	-	-
4	4	6	3	4	4	3
I	1	3	5	3	3	3
5	5	9	8	7	7	6
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here identified as *Homotherium* cf. *latidens*, this species was present throughout the Pleistocene. A mandibular fragment of sabretooth cat (*Homotherium* cf. *latidens*) is known from the Oosterschelde (Hooijer 1962); Van Hooijdonk (1999) described a *Homotherium calcaneum* from the same area, a location called 'Onrust', N of Walcheren, found by the suction-dredging vessel 'Eemshoorn'.

Ursus etruscus Cuvier, 1823

Etruscan bear is typical for the Early Pleistocene; in the Netherlands it is known from the classical Tegelen locality in Limburg. This bear, considered the ancestor of the cave bear *U. spelaeus*, is better known from the Arno river valley in Tuscany, Italy. Part of a right humeral diaphysis was found by the GO41 in July 2000; it is black and strongly fossilised and could be ascribed to a relatively small bear. Comparison with literature data makes an identification as *U. etruscus* plausible. Yet the fragment is smaller than half the complete humerus, so some caution is required.

DISCUSSION

Geological data, data collected by the GO41 and the results of the Cerpolex/Mammuthus expedition let us conclude that no fossils older than the YRF are found in Het Gat. Thus, the lower boundary for dating the fossils is the beginning of the Waalian. Eemian layers lay directly on top of the YRF in Het Gat, intermediate layers are absent. These could theoretically have been eroded away, but fossils from such intermediary layers have never been found.

Both pollen analysis and the identification of the fossils show that the fossils date from an interglacial of the Waalian or the Bavelian. Comparison of the fauna with faunas from other Early or Middle Pleistocene localities (Table 1) shows that the presence of *Eucladoceros ctenoides*, *Hippopotamus antiquus* and *Mammuthus* sp. are of great importance. Our fauna should be somewhat older than the Early Cromerian, as in none of the Cromerian faunas the genus *Eucladoceros* and the hippo *Hippopotamus antiquus* still occur. Other elements are found in these fau-

nas that are lacking in Het Gat, such as *Cervus* and *Castor*. The fauna also appears slightly younger than the Early Bavelian Untermassfeld as *Megaloceros* species do not occur in this fauna.

We saw that the mammoths pose problems in this unmixed fauna. The molars from Het Gat can be interpreted either as *M. meridionalis* or as *M. trogontherii*, but also as an intermediate form showing characters of both. In this framework we can present the following models.

Model 1 *Mammuthus meridionalis* is the ancestor of *M. trogontherii*

If this were true, then finding both taxa in Het Gat in one single layer makes this supposition rather unlikely.

Model 2 *M. meridionalis* is the ancestor of *M. trogontherii* and sometimes both taxa occur together in one faunal association.

The presence of both 'species' in one fauna (such as known from Germany, England and Siberia) is explained by an 'overlap' between the taxa (Sher 1986). This would be in accordance with the hypothesis of Lister & Sher (2001) that *trogontherii* originated in E. Siberia and subsequently replaced *meridionalis*.

Model 3 *M. meridionalis* is the ancestor of *M. primigenius*.

Some fossils from Het Gat have characters of both *M. meridionalis* and *M. primigenius*. We also observed that *M. trogontherii*, in the past and now, causes problems. Do we need to maintain it as a valid taxon? In case this model were true, then *M. trogontherii* would not be a real species. This would be in accordance with gradualistic models such as proposed by Lister (1996), who accepted *trogontherii* as a species but failed to show its clear delimitation from *meridionalis*.

Lister & Sher (2001) concluded a rather punctuated equilibrium-like model for the

succession of the three mammoth species in Europe, driven by (allopatric) speciation events in NE Siberia. We have two objections to this model, however elegantly presented. (1) the number of observations per locality is often rather low, which does not facilitate a good and statistically sound comparison, and (2) the sequence of the crucial localities around 1.0 My is rather arbitrarily chosen, another sequence might have given other results. We therefore hesitate to accept the sudden replacement of *M. meridionalis* by *M. trogontherii* around 1.0 My, and cannot exclude the possibility that *M. trogontherii* is nothing but an advanced *meridionalis*.

CONCLUSION

A combination of all available data sets (geology, boring results, information from the vessel GO41, the Cerpolex/Mammuthus expedition, and faunal comparisons) seem to justify the conclusion that the fossils from Het Gat represent an interglacial fauna of larger mammals most probably Middle or Late Bavelian in age. The fauna also necessitates us to reconsider the taxonomic validity of the steppe mammoth *M. trogontherii*, described in 1881. It can not be excluded that in the future (after more late Early and early Middle Pleistocene material can be studied) the evolution of the mammoth will show a direct line from *M. meridionalis* to *M. primigenius*.

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