Extinct beaver *Trogontherium cuvieri* Fischer, 1809 (Mammalia, Rodentia, Castoridae) from the Deep Water Channel between England and The Netherlands

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Abstract

A proximal part of a femur of the extinct beaver Trogontherium cuvieri *is described. The heavily mineralized fossil was trawled from Early Pleistocene or early Middle Pleistocene sediments of the so-called 'Deep Water Channel', a 30 to 40 m deep gully in the North Sea between England and The Netherlands. The exact stratigraphical position of the fossil remains is, however, unknown. Some remarks are made concerning the geographical and stratigraphical distribution of the species. It remains enigmatic why* Trogontherium *became extinct during the early Saalian, while the contemporaneously living* Castor *survived into recent times.*

Introduction

Early in 1994 Mr. Gert Jan van Veen, a crew member of the fishing vessel GO 31 (the 'Morgenster'), trawled a femur fragment of the extinct beaver *Trogontherium cuvieri* from the floor of the North Sea. The site from which the fossil was trawled is situated in the southern part of the 'Deep Water Channel', a deep gully running in a north-south direction, situated SW of the so-called 'Brown Bank' or 'Brown Ridge'. Here the North Sea reaches a depth of about 30 - 40 metres. The discovery of this *Trogontherium cuvieri* fossil is remarkable since this beaver species was previously known from the North Sea floor (Mol & De Vos, 1995). In this paper the fossil femur will be described and some remarks concerning this extinct beaver will be made.

Description of the femur

The right femur (Figure 1) belongs to the collection of Mr. Kommer Tanis at Havenhoofd (Goedereede), where it is stored as inv. no. 390. The distal part of the femur is missing, and the fossil is heavily mineralized. The trochanter tertius is situated just below the trochanter major, on the lateral side. The trochanter major rises above the caput femoris; it is situated close to the length axis of the diaphysis. The trochanter minor is weakly developed. The diaphysis is not markedly flattened.

Since the skeletal elements of the two beaver genera that are found in the European Quaternary, *Trogontherium* and *Castor,* show superficial resemblances, the femur from the North Sea must be compared with the femurs of both *Trogontherium* and *Castor.* The differences between the femur of *Trogontherium* and *Castor* can be summarized as follows (Schreuder, 1929): in *Trogontherium* the trochanter tertius is situated just below the trochanter major, at the lateral side of the femur whereas in *Castor* it is situated halfway along the diaphysis. In *Trogontherium* the trochanter major rises above the caput femoris and it is situated close to the length axis of the diaphysis; in *Castor* on the other hand, it is situated more towards the lateral side. In *Trogontherium* the trochanter minor is more weakly developed than it is in *Castor,* and the diaphysis as a whole is less flattened.

Morphologically, the femur fragment thus shows the major characteristics of a *Trogontherium* femur, and it is therefore identified as belonging to *Trogontherium cuvieri.* The femur fragment measures 86 mm in length, the largest width of the proximal part is 43 mm, the smallest diameter of the diaphysis in anterior-posterior direction is 13 mm, and in lateral-medial direction it measures 29 mm, the diameter of the caput femoris amounts to 17 mm.

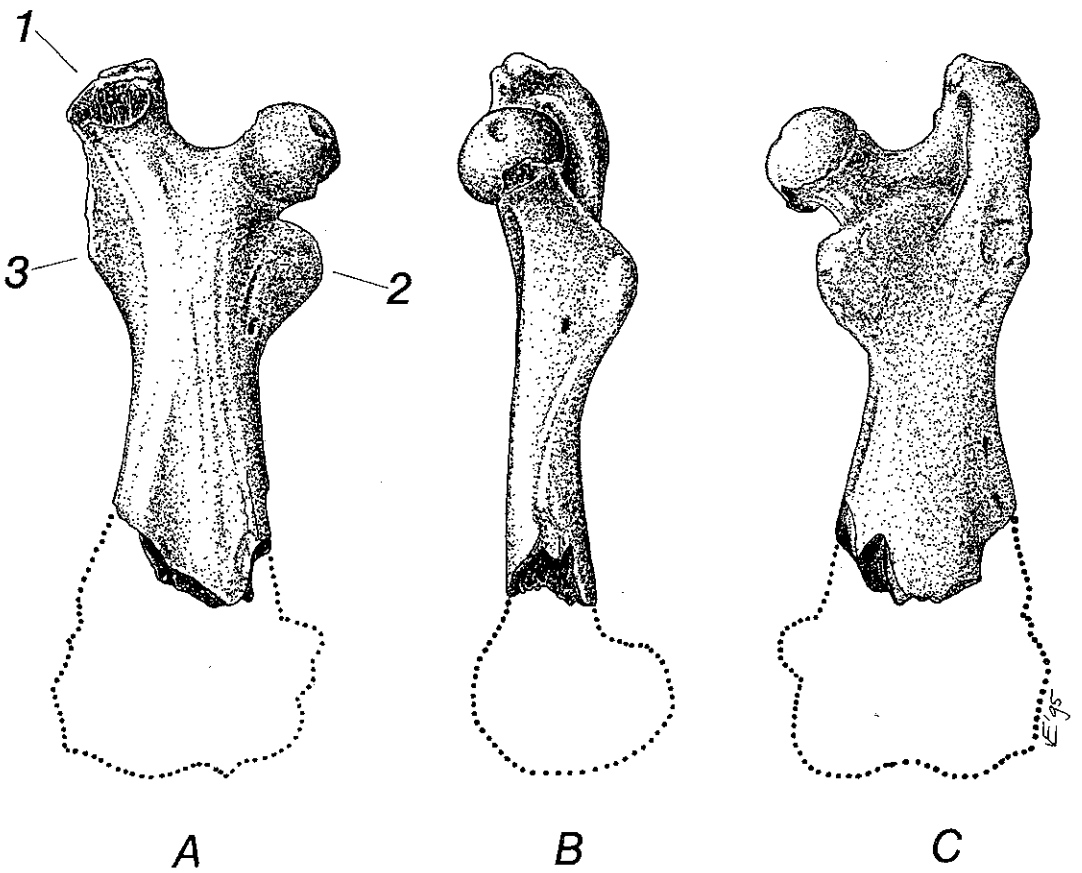

Figure 1
The fragmentary right femur of Trogontherium cuvieri. *North Sea floor, Deep Water Channel, 1994. Collection K. Tanis (Havenhoofd), inv. no. 390.*
A: anterior view,
B: medial view,
C: posterior view,
1: Trochanter major,
2: Trochanter minor,
3: Trochanter tertius.
Drawing: Hans van Essen.

Geographical and stratigraphical distribution

The species *Trogontherium cuvieri* Fischer von Waldheim 1809 was described on the basis of a fragmentary skull from Taganrok, located on the Sea of Azov, Russia (Figure 2). Schreuder (1929) mentioned finds from England, France, Germany and The Netherlands. Since, many new finds have become available, and the taxon is now known from the following areas: in England, *Trogontherium* has been found in the Upper Freshwater Bed and the Cromer Forest Bed Formation along the coast of Norfolk (localities include Cromer and Bacton) and of Suffolk (e.g. Kessingland). Furthermore, there were finds from the Weybourne Crag (East Runton), the Norwich Crag from Thorpe and sites such as Copford in Essex and Greenhithe in the Thames valley (Kent, Schreuder, 1929). Stuart (1982) added sites including Trimingham, Clacton and Hoxne. From France, the taxon has been recovered from the valleys of the Saône, the Seine and the Meuse (Schreuder, 1929); in Germany from the classical sites such as Mosbach, Jockgrim (Guenther & Mai, 1977) and Mauer (Schreuder, 1929; Mai, 1979), and from Erpfingen (Lehmann, 1953), Voigtstedt, Süssenborn, Bilzingsleben (Mai, 1978), Miesenheim I (Van Kolfschoten, 1990) and Schöningen 12 (Van Kolfschoten, 1995). In The Netherlands it is known from Tegelen (Schreuder, 1929), Neede (Hooijer, 1959), the Maasvlakte (Vervoort-Kerkhoff & Van Kolfschoten, 1988), Rhenen (Van Kolfschoten, 1990) and the North Sea (this paper). Furthermore *Trogontherium* is known from Hungary (Vértesszöllös: Kretzoi & Vértes, 1965), and from Bohemia (Czechia), southern Russia (Mariopol), and Siberia (Kazachstan; all Schreuder, 1951), and even from China (Choukoutien: Young, 1934). On the basis of current knowledge, and as already noted by Schreuder (1929), there are no sites from southern France, Spain or Italy. The distribution area thus has a rather northern and belt-like character, ranging from England in the west to China in the east (Figure 2).

Table 1 provides an overview of most of the English, Dutch and German localities, arranged in stratigraphical order. According to Stuart (1988), *Trogontherium* is known in England from the Hoxnian Interglacial (sites such as Hoxne and Clacton), as well as from the Cromerian Interglacial (s.s.) (West Runton). The finds from Trimingham are thought to pre-date the Cromerian. The German Schöningen 12 locality appears to be the youngest; it is placed in the Early Saalian Reinsdorf Interglacial (Urban, 1995). The finds from the German site of Bilzingsleben have been assigned to the Holsteinian. A number of German sites with *Trogontherium*, such as Miesenheim I, Mosbach, Mauer, Voigtstedt and Süssenborn, are placed in the Cromerian. The oldest finds in Germany are probably those from the clay-pits at Jockgrim. However, it is not known from precisely which layers they originate; the age of the sediments probably ranges from Eburonian to Menapian (Von Koenigswald, 1983). Based on the presence of *Mammuthus trogontherii*, it appears that the Jockgrim fauna is younger than that from Tegelen.

Trogontherium is known primarily in The Netherlands (Figure 3) from the clay-pits near Tegelen (Schreuder 1929). This is the locality stratotype of the Tiglian Stage. The main fauna is dated to the TC5 pollen substage and is thought to be about 1.7 Ma old.

Hooijer (1959) described two *Trogontherium* mandible fragments and some other material from Neede (the Needse Berg), which is placed in the Middle Pleistocene Holsteinian Interglacial by Van Kolfschoten (1990). Other remains collected from the Maasvlakte (Vervoort-Kerkhoff & Van Kolfschoten, 1988) are dated to the late Early Pleistocene by Van Kolfschoten (1990). However, the present authors would like to be more cautious about this dating, since the fossils were found washed ashore and hence were not recovered in situ.

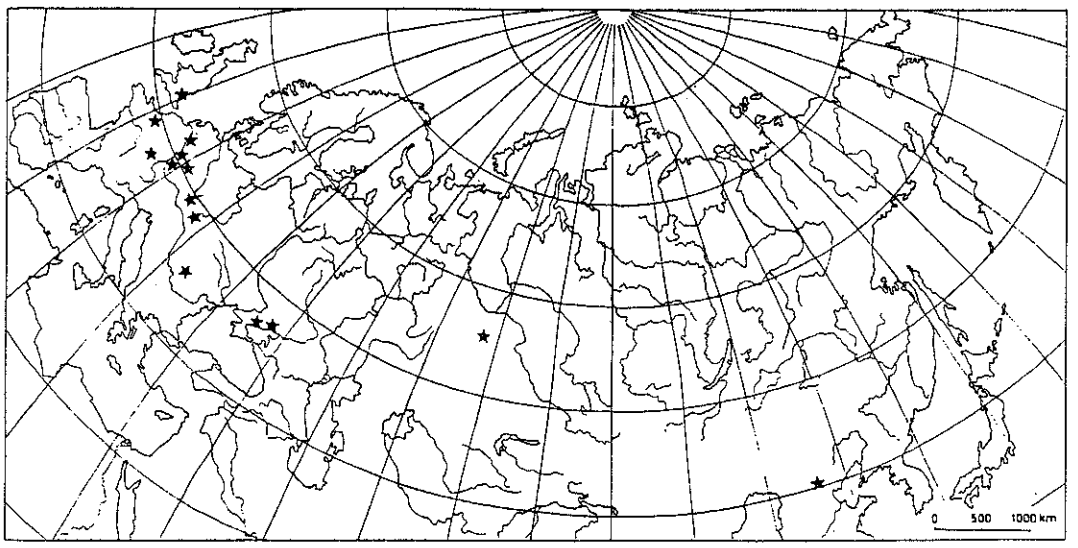

Figure 2
Map showing some selected localities of Trogontherium cuvieri, *occurring in a belt-like distribution through Eurasia.*

Age	British stages	West European stages	British localities	West European localities
Middle Pleistocene	*Wolstonian*	*Saalian Complex*		Schöningen Bilzingsleben
	Hoxnian	Holsteinian	Hoxne Clacton	Neede
	Anglian	*Elsterian*		
	Cromerian (s.s.)	Cromerian Complex	West Runton	Miesenheim I Mauer Mosbach Voigtstedt Süssenborn
Early Pleistocene		Bavelian Complex	Cromer Forest Bed Formation	
		Menapian		
		Waalian	Trimingham (?)	Jockgrim (?)
		Eburonian		
	Beestonian Pastonian Pre-Pastonian/ Baventian Bramertonian/ Antian Thurnian Ludhamian	Tiglian	Crags	Tegelen
	Pre-Ludhamian	*Praetiglian*		

Table 1
Stratigraphical distribution of Trogontherium. *Glacials printed in italics.*

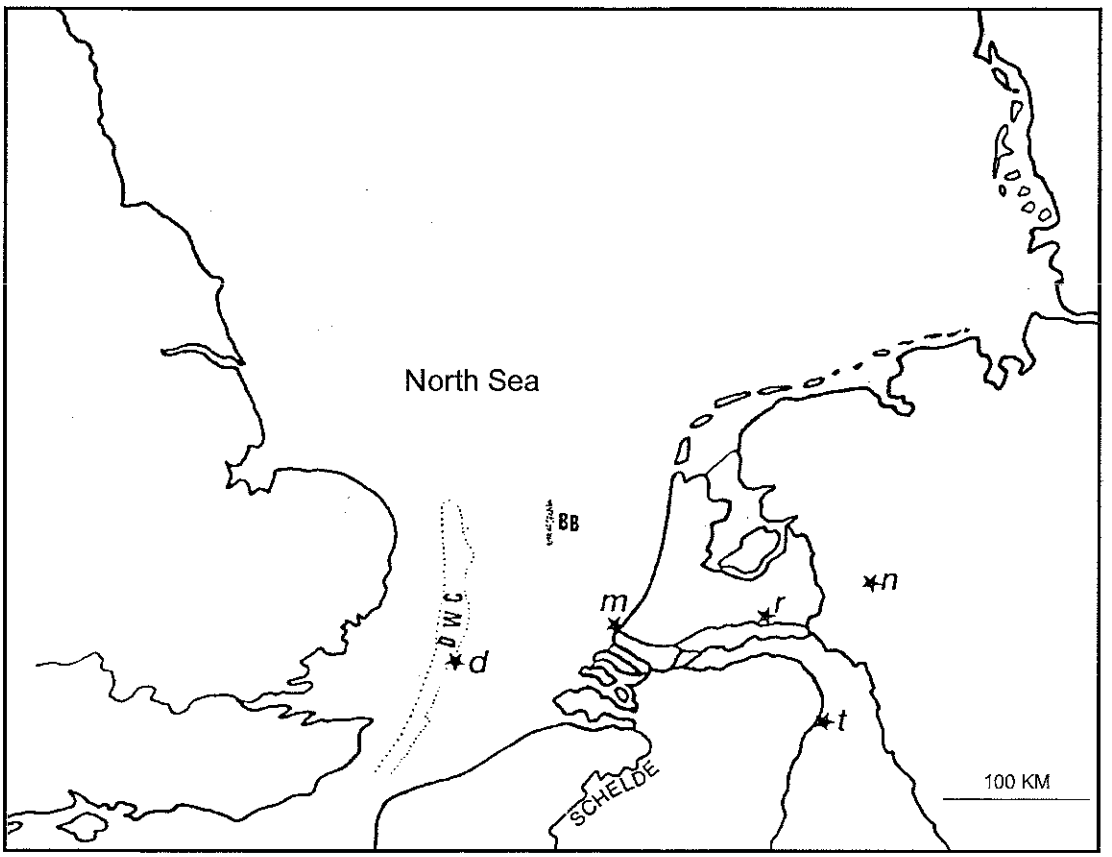

Figure 3
Map of The Netherlands and part of the North Sea.
DWC = Deep Water Channel, BB = Brown Bank or Brown Ridge.
Localities where Trogontherium was found are
m = Maasvlakte,
r = Rhenen,
n = Neede,
t = Tegelen.

The exact stratigraphical position of the material from the ice-pushed ridges of Rhenen (The Netherlands) is also not known. It may be of late Early or early Middle Pleistocene age (Van Kolfschoten, 1990). Only one *Trogontherium* mandible was found at this site.

Although there may be uncertainties concerning the stratigraphical position and the age of much of the *Trogontherium* material, it can be safely stated that *Trogontherium cuvieri* lived from the Tiglian up to the Early Saalian (Reinsdorf). *Trogontherium* thus lived during a long period of about 1.4 Ma, and in a rather restricted belt-like area (Figure 2).

Discussion

The question now arises whether it is possible to determine the stratigraphical position and thus the age of the femur from the bottom of the North Sea. Van Kolfschoten & Laban (1995) divided the terrestrial mammals from the North Sea into four faunal associations: I) an Early Pleistocene association with the proboscideans *Anancus arvernensis* and *Mammuthus meridionalis;* II) a late Early Pleistocene to early Middle Pleistocene terrestrial association with *Mammuthus meridionalis* (advanced type) and *Mammuthus trogontherii;* III) a Late Pleistocene terrestrial association with *Elephas antiquus* and *Mammuthus primigenius;* and IV) a Holocene terrestrial association lacking proboscideans but containing, among others, *Castor fiber* and *Homo sapiens*. Material of the two oldest associations can be recognized by their high degree of fossilisation: they are almost completely mineralized, producing a high-pitched sound when tapped with a hard object. Furthermore the material is a black brown to grey in colour (Mol & Van Essen, 1992). The *Trogontherium* femur described in this paper shows these two fossilisation characteristics: strong mineralization and dark colour, which means that it could belong to either the Early or the Middle Pleistocene associations. A closer stratigraphical attribution does not seem possible.

It is interesting to notice that *Trogontherium* lived together with *Castor fiber* for a very long period. There are two exceptions to this co-occurrence: *Castor* also lived in more southerly latitudes, and did survive into recent times, while *Trogontherium* became extinct after the Reinsdorf Interglacial (attributed to the Early Saalian; Urban, 1995). Why, therefore, did two beavers that lived sympatrically over a large area and during a long period experience a different fate by the end of the Middle Pleistocene. Evolution does not seem to have played a role: both taxa virtually remained in stasis. Schreuder (1929, 1951) supposed the existence of two Trogontherium species: *T. boisvilletti* and *T. cuvieri,* living west of the River Rhine (France, England and Tegelen), and east of this river (e.g. in Mosbach and Mauer) respectively. Mayhew (1978) reduced these two taxa to the subspecies level within *T. cuvieri;* Fischer (1991) stated that the teeth from Mosbach were somewhat larger than those from Tegelen; while Mai (1978) reached the conclusion that *Trogontherium* virtually remained in stasis in the Early and Middle Pleistocene (see also Heinrich, this volume). The same applies to *Castor fiber:* there is no noticeable difference between the European beaver from Tegelen and modern animals. Therefore, there must have been an ecological difference, which can be deduced from differences in the dentition and the postcranial skeleton. The most striking character is the absence in *Trogontherium* of the flat tail that is so characteristic of *Castor,* the former genus had a round tail, much like the modern *Myocastor.* The ecological differences in combination with the long co-occurrence of the two beavers exclude competition as a cause of extinction. The latest occurrence of *Trogontherium* is in the Reinsdorf Interglacial. The subsequent stadial apparently caused its extinction. It remains an enigma to us why the European beaver apparently could find refuge in more southern latitudes, while *Trogontherium* became extinct.

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