

Records of *Trogontherium cuvieri* Fischer, 1809 (Castoridae) from the Pleistocene of the Netherlands and the North Sea

Bram W. Langeveld^{1,4}, Ingrid de Bruijn², Rob van den Berg³ & Peter de Bruijn²

¹ Natural History Museum Rotterdam, Westzeedijk 345, 3015 AA Rotterdam, The Netherlands

² Dam 6, 3214 AD Zuidland, The Netherlands

³ Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands

⁴ Corresponding author: langeveld@hetnatuurhistorisch.nl

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This paper provides new records of the extinct beaver *Trogontherium cuvieri* Fischer, 1809 from the Pleistocene of the Netherlands and the North Sea and summarizes earlier reports. We recorded *T. cuvieri* from 4 new sites and found 19 more in the literature, totalling 23 Dutch sites. We identified over 1000 new specimens, mostly in citizen scientist collections and predominantly from Maasvlakte 2, the artificial extension to the port of Rotterdam constructed from dredged sediments. Statistical tests indicate that many of the specimens from Maasvlakte 2 are significantly larger and those samples have a larger (coefficient of) variation than those from the classical locality of Tegelen. This suggests the *ex situ* Maasvlakte 2 and by extension the North Sea record consists of a mix of different populations of *T. cuvieri*, which fits with the temporally mixed North Sea Pleistocene record in general. The North Sea appears to be one of the richest sources of *Trogontherium* fossils available worldwide, possibly including some of the largest individuals known to date.

Key words: citizen science, *ex situ*, Maasvlakte 2, Rotterdam, Tegelen

Introduction

Trogontherium cuvieri Fischer, 1809 is an extinct beaver (Castoridae), known from the Late Pliocene and Early and Middle Pleistocene of Eurasia (Fostowicz-Frelik, 2008), with a tentative youngest record from the Late Pleistocene of China (Yang *et al.*, 2019). Its body size was roughly similar to the modern Eurasian beaver *Castor fiber* Linnaeus, 1758, but its head was relatively larger and its tail was not flattened (Schreuder, 1929). Its extremities were less well adapted to swimming than in *Castor fiber* and its dentition did not allow it to cut down trees (Fostowicz-Frelik, 2008). Over the past decade, *T. cuvieri* fossils were recovered *ex situ* in some numbers by citizen scientist fossil collectors from the novel site of Maasvlakte 2, Rotterdam, The Netherlands, from sediments dredged from the North Sea. This prompted us to review the occurrence of *T. cuvieri* in the Netherlands, including its stratigraphy. This paper presents an up-to-date list of Dutch sites yielding *T. cuvieri*, including those located in the North Sea. We compare measurements of selected material from the classical locality of Tegelen with those of the finds from Maasvlakte 1 and Maasvlakte 2 and try to retrieve information about the geological age and/or the degree of stratigraphical mixing of the Maasvlakte 2 material. This is a more in-depth analysis with a more extensive dataset than the preliminary analysis published earlier (Van den Berg *et al.*, 2022).

Geological setting

Although we identified *Trogontherium* Fischer, 1809 from numerous sites, just three sites yielded the vast majority of specimens: Tegelen, Maasvlakte and Maasvlakte 2 (Fig. 1). Therefore, their geological setting is briefly expanded upon. To avoid confusion, for the remainder of this paper, Maasvlakte is referred to as Maasvlakte 1.

The classical locality of Tegelen is well-known from the literature: especially in the first half of the twentieth century, numerous fossils were collected from clay deposits of the Waalre Formation near the village of Tegelen, as these deposits were dug by hand for the ceramics industry. Although the various clay pits of Tegelen each exposed a slightly different part of the record (spatially, but also temporally), generally, the record is Early Pleistocene (Tiglian) in age, at *c.* 2 million years (Van den Hoek Ostende & De Vos, 2006; Westerhoff *et al.*, 2020). The Tegelen *Trogontherium* remains were detailed by Schreuder (1929).

The artificial peninsula Maasvlakte 1 is part of the Rotterdam harbour and was created by dredging sediments from various areas in the vicinity of the site, including both on-shore and offshore areas, in some cases up to considerable depth. Especially between 1970 and 2010 the beach was accessible to fossil collectors, some of which collected quite abundant material. The fossils represent different faunas from the entire Pleistocene and Holocene (Kerkhoff, 1984; Hordijk & Janse, 1987; Vervoort-Kerkhoff & Van Kolf-

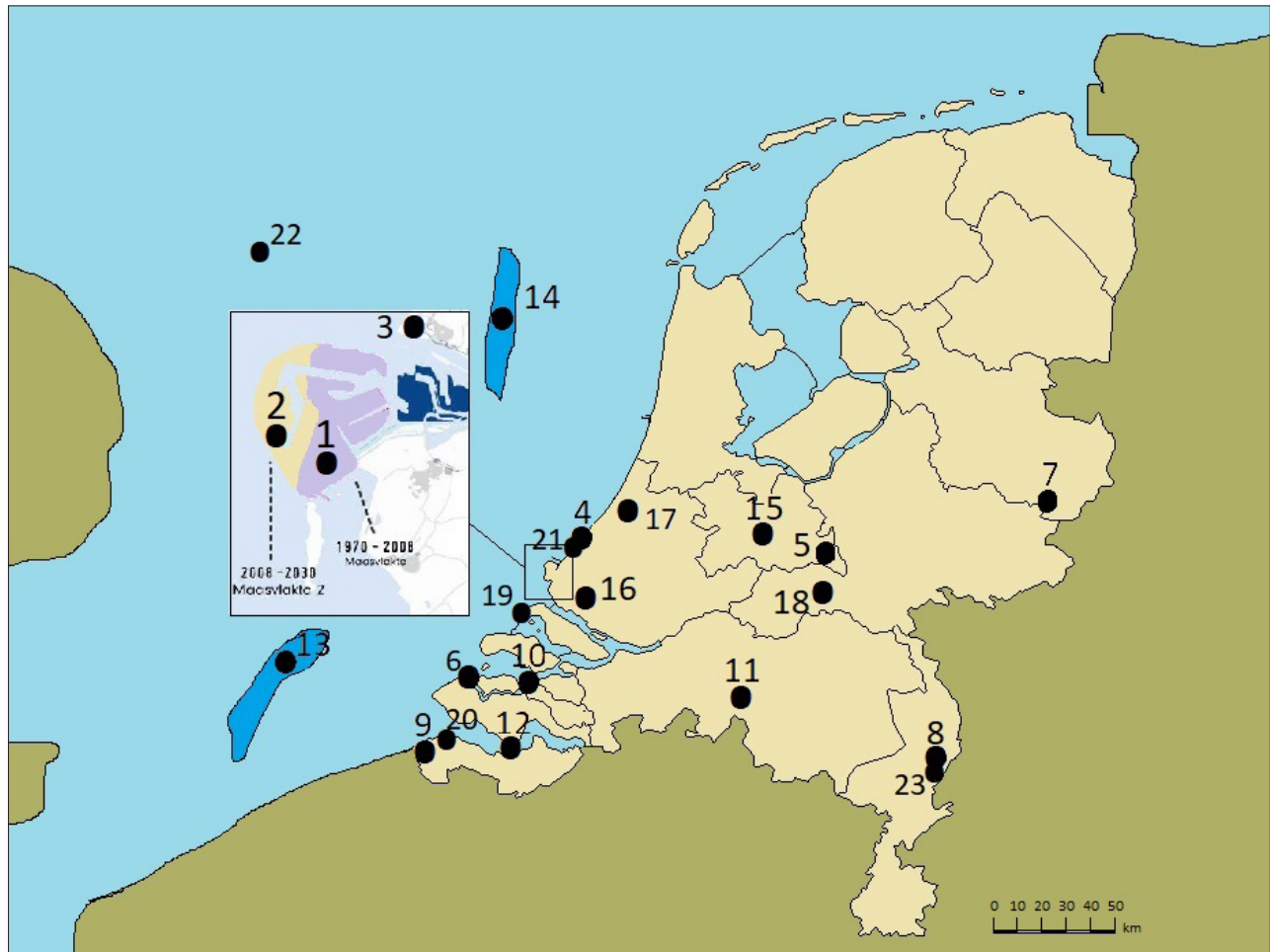


Figure 1. Dutch (and adjacent North Sea) records of *Trogontherium cuvieri* Fischer, 1809, based on new material and a literature survey (details in Table 1). 1 Maasvlakte 1; 2 Maasvlakte 2; 3 Hoek van Holland; 4 Zandmotor; 5 Rhenen; 6 Banjaardstrand; 7 Needse Berg; 8 Tegelen; 9 Cadzand; 10 Oosterschelde; 11 Goirle; 12 Ellewoutsdijk, Westerschelde; 13 Deep Water Channel, North Sea; 14 Het Gat, North Sea; 15 Nieuwegein, Put van Weber; 16 Zuurland 19 borehole; 17 Valkenburg borehole; 18 Dreumel; 19 Oud-dorp; 20 Zwarte Polder; 21 Monster; 22 Southern bight of the North Sea; 23 Maalbeek.

schoten, 1988; Van Kolfschoten & Vervoort-Kerkhoff, 1999; Janse, 2014). Although not officially named that way, since the creation of Maasvlakte 2 (see below), the Maasvlakte site is now usually referred to as Maasvlakte 1. Maasvlakte 2 is the most recent addition to the port of Rotterdam and was completed in 2012. It was built directly attached to Maasvlakte 1. Maasvlakte 2 consists of 240 million cubic metres of sediment that was dredged from the nearby North Sea. The sediment was retrieved from an underwater sand dredging pit (coordinates *c.* 52.01, 3.92) just offshore the Rotterdam harbour, from as much as 20 metres below the seafloor level (Reumer *et al.*, 2010; Busschers *et al.*, 2013; Kuitems *et al.*, 2015). These are predominantly fluvial deposits from the Upper and Middle Pleistocene Kreftenheye Formation and upper Lower or Middle Pleistocene deposits of the Urk Formation or Waalre Formation (Busschers *et al.*, 2013). The Maasvlakte 2 beach is publicly accessible and has proven a popular locality for fossil collecting, yielding mammalian taxa representative of various parts of the Pleistocene and Holocene (Dieleman, 2013; Mol & Langeveld,

2014; Langeveld *et al.*, 2022). After the initial creation, starting in 2014 the beach was nourished with additional sediment about once every two years. This sediment was dredged from roughly the same sand source area, but mostly from shallower depths and contains fewer (if any) Early/Middle Pleistocene fossils (Langeveld & Roosen, 2022).

Methods

The large and active community of Dutch citizen scientist fossil collectors (*e.g.* Haug *et al.*, 2020) was actively approached at meetings of Dutch palaeontological societies and through social media. They were invited to present their (possible) *Trogontherium* fossils to us for study. We organized several semi-public identification sessions at various natural history museums and other locations (Mol *et al.*, 2021). As comparative material, we used specimens from the Natural History Museum Maastricht, Teylers Museum (Haarlem), Naturalis Biodiversity

Center (Leiden) (*Trogotherium cuvieri*, mostly from Tegelen), and the Natural History Museum Rotterdam (a recent skeleton of *Castor fiber*: NMR99900003574). The dissertation of Schreuder (1929) was regularly consulted.

Measurements were based on Von den Driesch (1976). As dimensions and appearance at the occlusal surface of (pre-)molars vary markedly based on wear stage (e.g. Schreuder, 1929; Heinrich & Maul, 2020), we did not measure them at that surface. Instead, we attempted to measure (pre-)molars at the base of the crown (base of the enamel). This, however, proved difficult, due to common damage to the base of specimens and a variable and irregular lower boundary of the enamel, as already noted by Schreuder (1929). We therefore included only measurements of premolar 4 inf., which has the largest sample size in our analysis. We measured the shortest distance between the anterior and posterior of the premolar at the base of the enamel; often, these points were not at equal heights relative to the occlusal surface and the measurement may therefore be oriented at an angle. It, however, seemed the most appropriate way of measuring these objects, while excluding any differences due to wear stage. For the tibia, the distal width (Bd) in many cases could not be reliably measured due to damage (as Mayhew (1978) already observed in his material). Therefore, instead, the width of the distal articular surface was taken, which could be much more reliably measured, here designated as Bd*. In the astragalus, the greatest length (GL) does not follow Von den Driesch (1976) exactly. Instead, we took the greatest length obtainable at all on the bone. Incisor fragments were measured similarly to Mayhew (1978). Width and length of a fragment were taken anywhere along the curve (except at the occlusal surface, if present). However, per specimen, the length and width were taken at the same place. For bones and premolar 4, each measurement was taken three times and then averaged. That average is used in the analysis. For the incisors, each measurement was taken only once.

Statistical analysis was confined to selected skeletal parts and sites with a reasonable number of observations: incisor inf., premolar 4 inf., astragalus, calcaneum, and tibia from Tegelen, Maasvlakte 1 and Maasvlakte 2 were selected. Analysis was performed in PAST 4.04 (Hammer *et al.*, 2001) and consisted of Shapiro-Wilk tests for normality, followed by ANOVA and Tukey's pairwise comparison (for measurements on bones, incisor inf. length and premolar 4 inf.) and ANCOVA (for incisor inf. length and width). Results were considered statistically significant at $p < 0.05$.

Results

During our research, several new sites emerged where remains of *Trogotherium cuvieri* were found. This gives us the opportunity to provide an update of all Dutch sites. We identified 23 Dutch sites that yielded *Trogotherium cuvieri* (Fig. 1; Table 1). Four of them are new:

- 1) The site of Ellewoutsdijk concerns shells and (other) fossils dredged from the Westerschelde estuary at Ellewoutsdijk and processed elsewhere. Although Kerkhoff (1988) could not confirm the presence of *Trogotherium* from Ellewoutsdijk, specimen NMR999100001734 in the Natural History Museum Rotterdam from that site is a heavily worn premolar 4 sup. that allows attribution to *T. cuvieri* based on its well-developed roots and the complete lack of striids running to the base of the tooth (Fig. 2A).
- 2) The Valkenburg borehole concerns a borehole from close to a road near Valkenburg (province Zuid-Holland) (e-mail F.P. Wesselingh, 3 July 2023): it yielded a *T. cuvieri* p4 inf. dex. (which shows an anterolingual striid) that is kept in Naturalis Biodiversity Center (Fig. 2C).
- 3) The beach of Monster has yielded one fragmentary *T. cuvieri* dental element (NMR999100003784) in 1986, originating from sediments dredged from the nearby North Sea used to nourish the beach (Fig. 2B).
- 4) From an unspecified locality in the southern bight of the North Sea, a femur in collection Tanis (3261) was identified as *T. cuvieri* (Fig. 2D). In addition to these new sites, our literature survey yielded 19 sites. From the site of Goirle, only a tentative record of *Trogotherium* was published (De Jong, 1998) which could not be verified by the present authors. It is listed here for the sake of completeness. Almost all material was obtained either *ex situ* (the majority of sites), or its exact stratigraphic provenance was inaccurately recorded (in the case of Tegelen: Van den Hoek Ostende & De Vos, 2006, except for some material reported by Freudenthal *et al.*, 1976). Notable exceptions are the *in situ* records from Maalbeek, the Zuurland 19 borehole and Valkenburg borehole; the stratigraphy of the latter two is currently under investigation.

The remainder of this paper focusses on the three richest Dutch *Trogotherium* sites: Maasvlakte 1, Maasvlakte 2 and Tegelen. In total, we attributed more than 1000 new fossil remains in 42 citizen scientist fossil collections to *Trogotherium cuvieri* from Maasvlakte 2. The material predominantly consists of dental elements, but quite substantial post-cranial material is also available. However, that is often damaged. Most of the material from the North Sea (including beach locations, such as Maasvlakte 2) shows some signs of (local) reworking or weathering/polishing.

In a sample of 16 specimens of premolar 4 inf. from Maasvlakte 2 (collections Natural History Museum Rotterdam, De Bruijn and Ter Steege), we recorded the presence/absence of an anterolingual striid (Maul & Heinrich, 2007). We could not assess the presence/absence due to damage in 4 specimens and advanced wear in another. Of the 11 remaining specimens, an anterolingual striid was well-developed in 7 specimens (64%) and clearly absent in 4 (36%).

Shapiro-Wilk tests demonstrated our data follows normal distribution ($p > 0.05$), except for incisor data from Maasvlakte 2 ($p < 0.05$). Our incisor inf. measurements (Fig. 3) showed a gap between the five smallest ones and all other measurements. These are by far the smallest specimens from Maasvlakte 2. Cluster analysis (un-

Nmbr	Site	Source/primary reference(s)	Volume of material	Stratigraphy
1	Maasvlakte 1 (beach)	Vervoort-Kerkhoff & Van Kolfshoten, 1988	< 1000 specimens	ex-situ
2	Maasvlakte 2 (beach)	Mol & Langeveld, 2014	> 1000 specimens	ex-situ
3	Hoek van Holland (beach)	Langeveld, 2013	< 20 specimens	ex-situ
4	Zandmotor (beach)	Langeveld, 2013	< 20 specimens	ex-situ
5	Rhenen	Van Kolfshoten, 1990; Mol & De Vos, 1995	1 specimen	unclear, ice-pushed sediments
6	Banjaardstrand (beach)	Cardol, 2023	1 specimen	ex-situ
7	Needse Berg	Hooijer, 1959; Pierik <i>et al.</i> , 2010	2 specimens	Urk Formation, Needse Klei (Neede Clay)
8	Tegelen	Schreuder, 1929; Meijer, 1973; Westerkhoff <i>et al.</i> , 2020	> 1000 specimens	Waalre Formation, Tegelen Member
9	Cadzand (beach)	Nijholt & Van den Hoek Ostende, 2004	1 specimen	ex-situ
10	Oosterschelde	Mayhew <i>et al.</i> , 2008	1 specimen	ex-situ
11	Goirle	De Jong, 1998	< 10 specimens	ex-situ
12	Ellewoutsdijk, Westerschelde	this study (NMR999100001734)	1 specimen	ex-situ
13	Deep Water Channel, North Sea	Mol & De Vos, 1995	1 specimen	ex-situ
14	Het Gat, North Sea	Mol & Post, 2007	1 specimen	ex-situ
15	Nieuwegein, Put van Weber	Van Kolfshoten, 2001a	< 10 specimens	ex-situ
16	Zuurland 19 borehole	Hordijk, 2022	1 specimen	under investigation
17	Valkenburg borehole	this study (Naturalis Biodiversity Center)	1 specimen	under investigation
18	Dreumel	Liscaljet, 2018	< 10 specimens	ex-situ
19	Ouddorp (beach)	Dieleman, 2013	1 specimen	ex-situ
20	Zwarte Polder (beach)	Dieleman, 2013	< 10 specimens	ex-situ
21	Monster (beach)	this study (NMR999100003784)	1 specimen	ex-situ
22	Southern bight of the North Sea	this study (coll. Tanis 3261)	1 specimen	ex-situ
23	Maalbeek	Van Kolfshoten (2020); e-mail Th. van Kolfshoten (10 December 2021)	1 specimen	Waalre Formation, Tegelen Member

Table 1. Dutch sites (including the adjacent North Sea) that have yielded remains of *Trogontherium cuvieri* Fischer, 1809, based on a literature survey and new material. Numbers refer to Figure 1. NMR: Natural History Museum Rotterdam.

weighted pair-group average with euclidean similarity index) clustered these five specimens very closely together, but at a large distance from all other clusters. HTSM00933 is the smallest specimen (length 8.08 mm; width 6.85 mm). It is a mesial fragment (total length 42.68 mm) of an incisor, preserving the occlusal surface on one end and the base (most mesial part) of the pulp cavity on the other end. The specimen lacks longitudinal grooves in the dentin; its pear-shaped cross-section is more triangular. This is a characteristic of juvenile specimens (Schreuder, 1929). Furthermore, the pulp cavity extends significantly further into the tooth than in similar fragments of larger

sized incisors (also in comparison with Heinrich & Van Kolfshoten (2007: Abb. 97)). Therefore, HTSM00933 is ascribed to a very young/juvenile specimen, but based on the rough texture of the enamel, undoubtedly of *Trogontherium* (Schreuder, 1929). By extension, the cluster of the five smallest specimens was thus ascribed to juvenile *Trogontherium* and excluded from ANOVA/ANCOVA. Shapiro-Wilk tests demonstrated the remaining measurements of incisor inf. follow normal distribution ($p > 0.05$). ANOVAs of measurements (Table 2; Figs 3, 4) of incisor inf. length (F 37.55, p 8.988E-13), premolar 4 inf. (F 6.642, p 0.002636), astragalus (F 6.218, p 0.004792), calcaneum



Figure 2. Selected Dutch/North Sea fossils of *Trogontherium cuvieri* Fischer, 1809. A: premolar 4 sup., dredged from the Westerschelde at Ellewoutsdijk, NMR999100001734 (Natural History Museum Rotterdam); B: fragmentary dental element, beach of Monster, originating from sediments dredged from the nearby North Sea, NMR999100003784; C: premolar 4 inf., Valkenburg borehole (province Zuid-Holland), Naturalis Biodiversity Center; D: femur, unspecified locality in the southern bight of the North Sea, 3261, private collection Tanis; E: incisor inf., Dreumel, from sediments dredged from the Meuse, collection Stichting Expeditie Over de Maas. Scale bar 2 cm for A-C and 4 cm for D-E. Photos: Isaak Eijkelboom (D) and Hans Wijnstekers (E).

(F 7.665, p 0.008745) and tibia (F 12.32, p 3.48E-05) showed statistically significant differences between the collecting sites. Results of Tukey's pairwise comparisons of these ANOVAs (Table 3) showed the mean size of the specimens from Tegelen to be significantly different (smaller) than the mean size of the specimens from Maasvlakte 2. There is no significant difference

between both Maasvlakte sites. The summary statistics (Table 2) and boxplots (Fig. 4) showed that measurements of specimens from Maasvlakte 1 and Maasvlakte 2 generally have a larger (coefficient of) variation than those from Tegelen. ANCOVA of the incisor length and width showed a significant difference between the equal adjusted means (F 11.68, p 2.915E-05).

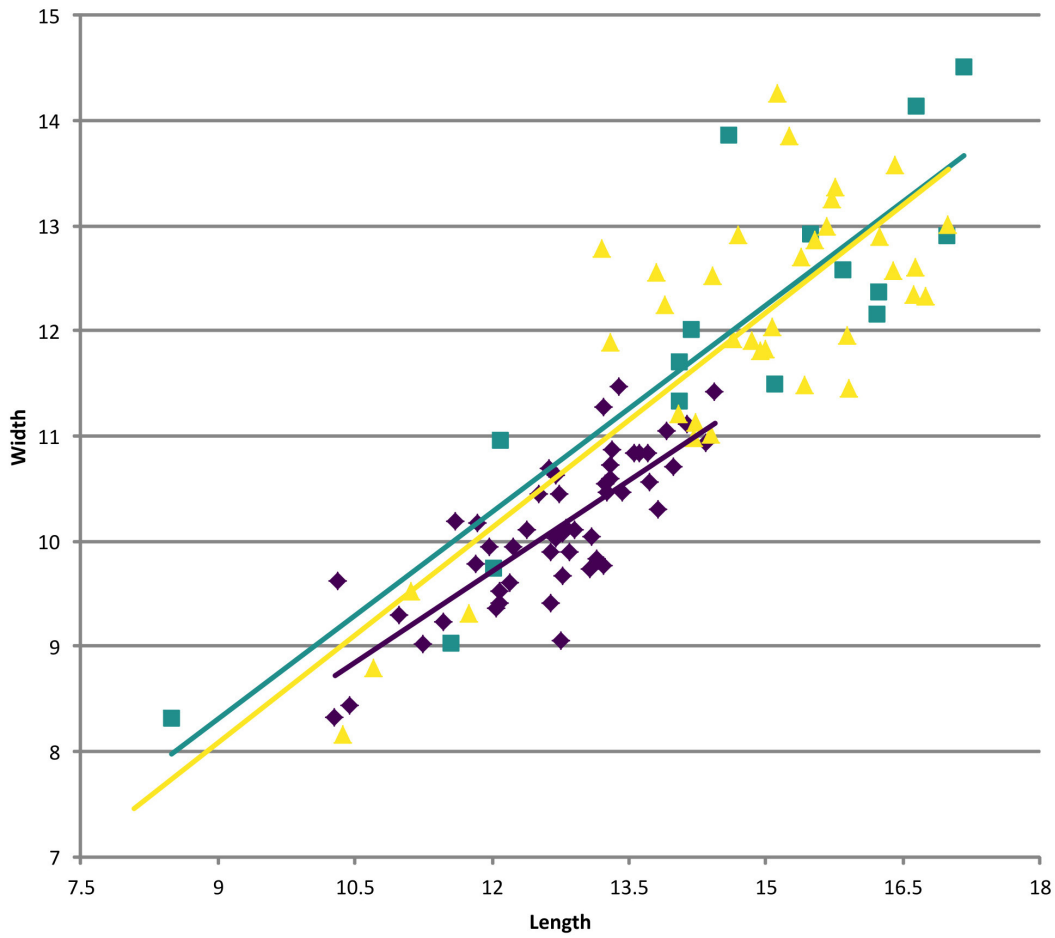


Figure 3. Regression of *Trogontherium cuvieri* Fischer, 1809 incisor inf. length versus width. Purple diamonds: Tegelen (r^2 : 0.63604); green squares: Maasvlakte 1 (0.79575); yellow triangles: Maasvlakte 2 (0.72078).

		Tegelen	Maasvlakte 1	Maasvlakte 2
Astragalus	Tegelen		0.08256	0.003633
F 6.218	Maasvlakte 1	3.129		0.9954
p 0.004792	Maasvlakte 2	4.934	0.1300	
Calcaneum	Tegelen			0.008745
F 7.665	Maasvlakte 2	3.915		
p 0.008745				
Tibia	Tegelen		0.1358	1.98E-5
F 12.32	Maasvlakte 1	2.748		0.5658
p 3.48E-05	Maasvlakte 2	7.001	1.446	
Incisor inf.	Tegelen		4.40E-5	4.29E-10
F 37.55	Maasvlakte 1	6.454		0.1390
p 8.988E-13	Maasvlakte 2	11.89	2.714	
Premolar 4 inf.	Tegelen		0.3812	1.73E-3
F 6.642	Maasvlakte 1	1.891		0.6324
p 0.002636	Maasvlakte 2	5.152	1.296	

Table 3. Results of ANOVAs (left column) and Tukey’s pairwise comparisons of maximum length of astragalus and calcaneum, maximum width of the distal articulation of tibia, incisor inf. length and premolar 4 inf. length of *Trogontherium cuvieri* Fischer, 1809 from Tegelen, Maasvlakte 1 and Maasvlakte 2. The test statistic Q is given below the diagonal, the p value above.

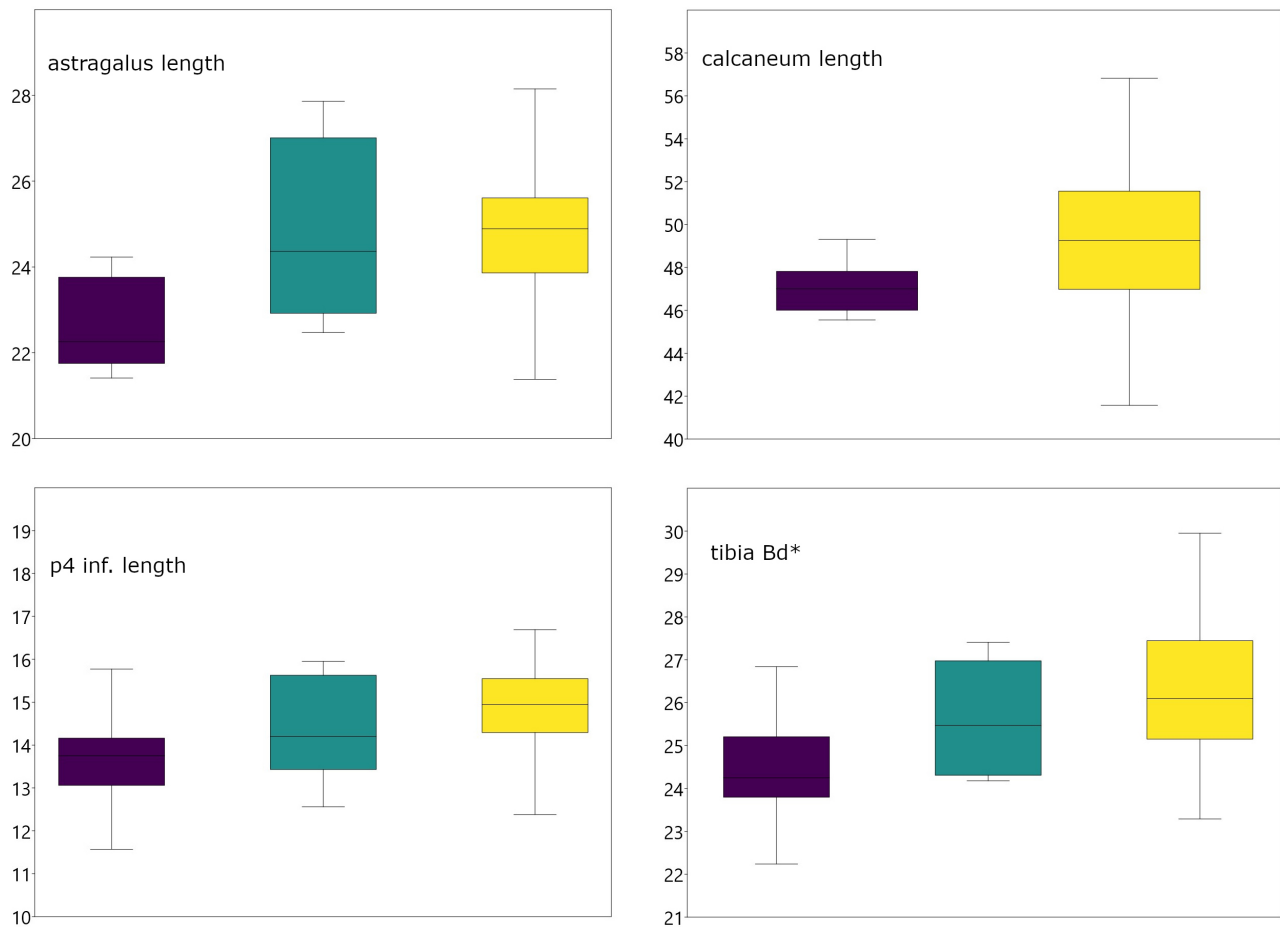


Figure 4. Boxplots of measurements (mm) of *Trogontherium cuvieri* Fischer, 1809 skeletal remains. Purple (left): Tegelen; green (centre): Maasvlakte 1; yellow (right): Maasvlakte 2.

Discussion

Having been recovered *ex situ*, obviously stratigraphic and palaeoecological data is lacking from the dredged material. However, its abundance and partially rather good preservation justify scientifically studying it, as is indeed the case with many other vertebrate fossils from the North Sea (e.g. Van Kolfschoten, 2001b; Mol *et al.*, 2008 and references therein). We found that Maasvlakte 2 may well be the richest Dutch site for *Trogontherium* fossils, or at least tied with the classical locality of Tegelen. Contrary to Tegelen however, from Maasvlakte 2 specimens are still being recovered by citizen scientist fossil collectors on an almost daily basis. Hence, the North Sea record of *Trogontherium* will most likely grow further. The abundance of its fossils from the North Sea holds promise for future, more in-depth anatomical or biomechanical studies of *Trogontherium*. Therefore, the Dutch/North Sea *Trogontherium* record is also important on an international scale.

Our quantitative comparison showed that the majority of the samples of the Maasvlakte 1 and Maasvlakte 2 material have a larger range and variation and the specimens are on average larger than the Tegelen material, even though our sample size was rather similar between sites (Maas-

vlakte 1 was underrepresented; Table 2), hence making natural variation in a larger assemblage due to sample size effects an unlikely explanation. Vervoort-Kerkhoff & Van Kolfschoten (1988) already observed this larger size on dental elements of *Trogontherium cuvieri* from Maasvlakte 1 compared to Tegelen. Mayhew (1978) observed a size increase of *Trogontherium* through the Pleistocene, attaining a maximum in the Cromerian (late Early Pleistocene) before a slight decrease in size before final extinction in the late Middle Pleistocene. The Tegelen material is (by definition) Tiglian in age, which is c. 2 million years (Westerhoff *et al.*, 2020). The significantly larger material from Maasvlakte 2 as compared to Tegelen, may suggest that at least a significant part of those specimens are much younger than the Tegelen specimens. The common occurrence (64%) of an anterolingual striid in premolar 4 inf. is an additional indicator that a significant part of the material is of relatively young geological age, as this character is virtually absent in Tegelen material and common in later faunas (Mayhew, 1978; Heinrich, 1997; Heinrich & Van Kolfschoten, 2007; Maul & Heinrich, 2007). Many *Trogontherium* remains from Maasvlakte 2 thus may originate from the late Early or Middle Pleistocene. Some of the smaller specimens (not including the five specimens judged as juveniles) from Maasvlakte 1/Maasvlakte 2

may well be of an age similar to Tegelen, as their sizes do overlap. This fits with some of the other taxa recovered from Maasvlakte 2, which are assigned a Tiglian age (Dieleman, 2013; Langeveld *et al.*, 2022). This suggests the Maasvlakte 1/Maasvlakte 2 records consist of a mix of different populations of *Trogotherium cuvieri*, which matches with the mixed North Sea Pleistocene record in general (*e.g.* Mol *et al.*, 2008) and that of Maasvlakte 1 (Kerkhoff, 1984; Vervoort-Kerkhoff & Van Kolfshoten, 1988; Van Kolfshoten & Vervoort-Kerkhoff, 1999) and Maasvlakte 2 (Dieleman, 2013; Mol & Langeveld, 2014; Langeveld *et al.*, 2022) in particular, which consists of taxa (or their evolutionary stages) from various parts of the Pleistocene.

Our analysis of the incisors yielded results similar to the analysis by Mayhew (1978). We found that incisors inf. from Maasvlakte 1 and Maasvlakte 2 are roughly one millimetre wider for any given length than the Tegelen specimens. Mayhew (1978) and Mai (1979) found this exact result when they compared Tegelen specimens to specimens from the Middle Pleistocene of Mosbach. Mayhew (1978) found a similar maximum size in both Tegelen and Mosbach. Our specimens from Maasvlakte 1 and Maasvlakte 2, however, are significantly (demonstrated by ANOVA of length) larger than those from Tegelen. They fit best with specimens from the Upper Freshwater Bed of the Cromerian, although our largest specimens are larger still (compare Mayhew, 1978: fig. 5). *Trogotherium* long bones from both Maasvlakte sites were often damaged due to taphonomical or sand dredging processes. Hence, we do not have many measurements of the post-cranial skeleton that we can compare directly with Schreuder (1929) or Mayhew (1978), but based on the incisor data (compare Mayhew, 1978: fig. 5), the Maasvlakte 1/Maasvlakte 2 *Trogotherium* record seems to contain the largest specimens of the genus known to date. Apart from the absolute dimensions, the difference in incisor shape between the specimens from Tegelen and those specimens provides further evidence for a relatively young age (*e.g.* late Early or Middle Pleistocene) of a significant part of the Maasvlakte 1 and Maasvlakte 2 material, when compared to the observations of Mayhew (1978). Mayhew (1978) observed the size increase of *Trogotherium* through the Pleistocene especially in the dentition and not as clearly in the post-cranial skeleton. Our analysis, which has larger sample sizes for selected bones, did find the size difference between Maasvlakte 2 and Tegelen both in the dentition (incisor inf. and premolar 4 inf.) and in the analyzed post-cranial bones, further suggesting that the pattern observed by Mayhew (1978) and utilized by Mayhew *et al.* (2008) and the present contribution indeed holds for total *Trogotherium* body size and not just its dentition, although we cannot provide definitive proof as we lack stratigraphic data.

Conclusions

We recorded *Trogotherium cuvieri* from 4 new sites and found 19 more in the literature, totalling 23 Dutch sites.

We identified over 1000 new specimens (both cranial and post-cranial), mostly in citizen scientist collections and predominantly from Maasvlakte 2, demonstrating the Maasvlakte 2 locality as one of the richest sources of *T. cuvieri* fossils worldwide. Based on the fossils' dimensions and known evolutionary size trends of the genus, we assume that the Maasvlakte 2 assemblage is stratigraphically mixed, and represents Pleistocene populations that differ in age. The assemblage includes some of the largest *Trogotherium* individuals known to date. The abundance of fossils recovered by a great number of citizen scientist fossil collectors from the nourished Dutch beaches provides a unique opportunity to study a normally inaccessible fossil record. Although lack of stratigraphy may hamper some types of research, this is more than made up for by the abundance of the fossil material through the combined enormous search effort and the easy accessibility through close cooperation with the citizen scientists. This wealth of fossils holds promise for future, more in-depth anatomical or biomechanical studies of *Trogotherium*.

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Table 2A-E. Incisor length and width (2A), premolar 4 inf. length (2B), maximum length (GL) of astragalus (2C) and calcaneum (2D), and maximum width of the distal articulation of tibia (Bd*) (2E) in mm of *Trogontherium cuvieri* Fischer, 1809 from Tegelen, Maasvlakte 1 and Maasvlakte 2. Collections: Kruizinga (AE, CI, DB2, DF, ED, EG, EJ, FB, MK), Medendorp (AM), Korf (BK), Langeveld (BL), Heins (CH), Maas (CM), De Bruijn (DB), Mol (DM), Van der Lee (ER), Vis (EV), De Boer (FdB), Houtgraaf (HH), Ter Steege (HTSM), Tanis (KT), Van Steijn (M), Sman (MES), Simmelink (MS), Venema (MVT), Van Eemeren (NE), Reehorst (NEZHMV), Natural History Museum Maastricht (NHMM), Liscaljet (NL), Natural History Museum Rotterdam (NMR), Mouthaan (RM), Van Reijmersdal (RR.MV), Wolhuis (RW), Schouten (San), Naturalis Biodiversity Center (RGM, ZMA), Passchier (TH), Teylers Museum (TM), Graper (VG), Van den Broek (WB) and Van Wingerden (WVW).

Table 2A									
Incisor inf. length and width									
	Tegelen			Maasvlakte 1			Maasvlakte 2		
	Collection	Length	Width	Collection	Length	Width	Collection	Length	Width
N		51	51		16	16		37	37
Min.		10.28	8.32		8.50	8.31		8.08	6.85
Max.		14.44	11.47		17.17	14.50		17.00	14.26
Mean		12.72	10.14		14.43	11.87		14.55	11.86
Stand. dev.		0.98	0.71		2.37	1.74		1.97	1.58
Coeff. var.		7.69	6.98		16.41	14.68		13.53	13.31
	ZMA.MAM.25960	10.28	8.32	NMR999100205278	8.50	8.31	HTSM00933	8.08	6.85
	ZMA.MAM.25936	10.32	9.62	KT5260	11.57	9.02	ED23	10.36	8.16
	RGM.53046	10.45	8.44	NMR999100161045	12.02	9.74	MS106	10.70	8.79
	RGM.52952	10.99	9.30	KT5262	12.10	10.95	DB2071	11.11	9.53
	RGM.103149	11.25	9.03	KT5263	14.07	11.70	MS103	11.74	9.32
	RGM.47417	11.46	9.23	KT5265	14.07	11.32	BL2341	13.20	12.79
	RGM.86599	11.60	10.19	KT5261	14.20	12.00	M4	13.30	11.89
	RGM.28163	11.83	9.79	KT5274	14.60	13.85	MS107	13.80	12.55
	RGM.52998	11.85	10.17	KT5269	15.10	11.49	HTSM00003	13.89	12.25
	RGM.10593 specimen 2	11.98	9.94	KT5273	15.49	12.91	San0216	14.05	11.21
	RGM.53047	12.04	9.36	KT5272	15.86	12.57	DB1779	14.21	10.99
	RGM.449148 specimen 1	12.08	9.52	KT5264	16.23	12.15	DB1966	14.23	11.13
	RGM.93275	12.08	9.41	KT5266	16.25	12.37	CM002	14.39	11.01
	RGM.47420 specimen 2	12.20	9.60	KT5271	16.66	14.13	MS105	14.42	12.52
	RGM.53044	12.24	9.95	KT5268	16.99	12.89	DB2331	14.64	11.93
	RGM.52969	12.39	10.11	KT5267	17.17	14.50	MS104	14.70	12.92
	RGM.64912	12.51	10.45				RR.MV.048	14.84	11.91
	ZMA.MAM.25959 specimen 1	12.62	10.69				KT4268	14.93	11.81
	RGM.47412	12.64	9.41				M5	14.99	11.82
	RGM.85760 specimen 1	12.65	9.90				MS101	15.06	12.04
	ZMA.MAM.25949 specimen 1	12.70	10.63				DB2659	15.12	14.26
	RGM.85760 specimen 2	12.70	10.03				MS102	15.25	13.86
	ZMA.MAM.25941	12.74	10.45				San2386	15.38	12.70
	RGM.85690	12.76	9.05				AM006	15.42	11.49
	RGM.53039	12.77	9.67				NMR999100213955	15.54	12.86
	RGM.36599	12.78	10.07				NL001	15.66	12.99
	RGM.10593 specimen 1	12.81	10.13				HTSM00934	15.73	13.26
	RGM.52985	12.85	9.90				KT4424	15.76	13.36
	RGM.449148 specimen 2	12.91	10.11				MK285	15.89	11.96
	ZMA.MAM.25958	13.07	9.74				DB2287	15.91	11.45
	RGM.93193	13.10	10.05				DF5	16.24	12.90
	RGM.95979	13.15	9.84				FdB002	16.40	12.57
	RGM.40351 specimen 1	13.22	11.28				HTSM00686	16.42	13.58
	RGM.85683	13.22	9.77				San0813	16.61	12.34
	ZMA 25872	13.24	10.55				FdB003	16.63	12.61
	ZMA 25959 specimen 2	13.26	10.46				MS100	16.74	12.33
	RGM.47420 specimen 1	13.29	10.73				BK4354	17.00	13.01
	RGM.52950 specimen 2	13.30	10.59						
	RGM.95019	13.32	10.87						
	RGM.53063	13.39	11.47						
	RGM.52950 specimen 1	13.43	10.46						
	RGM.95444	13.55	10.84						
	RGM.52947	13.61	10.84						
	ZMA 25949 specimen 2	13.71	10.84						
	RGM.94501	13.72	10.56						
	RGM.52951	13.82	10.30						
	RGM.40351 specimen 2	13.92	11.05						
	RGM.52991	13.99	10.71						
	RGM.52936 specimen 1	14.14	11.11						
	RGM.62916	14.34	10.94						
	RGM.52936 specimen 2	14.44	11.43						

Table 2B	Premolar 4 inf. length					
	Tegelen		Maasvlakte 1		Maasvlakte 2	
	Collection	Length	Collection	Length	Collection	Length
N		23		6		28
Min.		11.57		12.56		12.38
Max.		15.77		15.95		16.69
Mean		13.72		14.36		14.79
Stand. dev.		1.02		1.23		1.03
Coeff. var.		7.43		8.58		6.99
	RGM.53785	11.57	RGM.1341224	12.56	RM012	12.38
	RGM.52999	11.76	KT5288	13.72	RM010	12.79
	NHMM002235	12.82	RGM.1341223	14.14	ER4	13.30
	RGM.52984	12.87	RGM.1341167	14.26	HTSM00761	13.54
	TM16236f	12.98	KT5279	15.52	ER3	13.56
	NHMM002291	13.06	RGM.1341125	15.95	DM1541	14.06
	TM16236b	13.19			CH22	14.26
	ZMA.MAM.25695 Ref.nr. 23	13.35			RM009	14.39
	NHMM198497-15	13.41			DB2218	14.40
	ZMA.MAM.25869 Ref.nr. A19d	13.56			CH19	14.49
	RGM.36614	13.59			MVT0440	14.56
	TM16236a	13.75			CH20	14.59
	ZMA.MAM.25964 Ref.nr. 22	13.92			RW182	14.90
	ZMA.MAM.25695 Ref.nr. 23	13.95			RW464	14.93
	NHMM002350	13.97			DB2216	14.95
	ZMA.MAM.25972 Ref.nr. 30	14.06			MS013	14.95
	ZMA.MAM.25970 Ref.nr. 28	14.16			VG6	15.00
	NHMM002322	14.16			RW405	15.02
	RGM.53785	14.18			NMR999100213936	15.06
	ZMA.MAM.25695 Ref.nr. 23	14.75			CH21	15.47
	TM15543e	15.13			WB32611-12	15.54
	RGM.53785	15.51			MVT0355	15.55
	ZMA.MAM.25883 Ref.nr. A127	15.77			DM1544	15.65
					M1	15.77
					CH18	16.01
					MVT0467	16.03
					HTSM01028	16.29
					RM007	16.69

Table 2C	Astragalus GL					
	Tegelen		Maasvlakte 1		Maasvlakte 2	
	Collection	GL	Collection	GL	Collection	GL
N		8		4		27
Min.		21.41		22.47		21.38
Max.		24.23		27.86		28.15
Mean		22.61		24.77		24.84
Stand. dev.		1.05		2.25		1.62
Coeff. var.		4.63		9.08		6.52
	NHMM002380	21.41	RGM.1341205	22.47	DB2048	21.38
	RGM.62888	21.62	RGM.1341218	24.27	RW149	22.21
	RGM.95403	22.14	RGM.1341204	24.46	EV013	22.30
	NHMM001513	22.20	KT2876	27.86	DB2020	22.73
	TM15570b	22.32			HTSM00796	23.66
	RGM.52955	22.92			ER8	23.84
	RGM.95430	24.04			MS033	23.86
	NHMM001712	24.23			RW919	24.02
					DB2972	24.25
					CH48	24.31
					MVT0673	24.65
					DB2230	24.69
					San0516	24.74
					RW750	24.89
					HH014	24.91
					MES174	24.99
					DB2174	25.10
					RR.MV.040	25.34
					CI8	25.46
					DB2	25.50
					MVT0071	25.61
					RW198	26.52
					AM001	26.59
					WVW042	26.63
					RW224	26.69
					TH32	27.75
					CH49	28.15

Table 2D	Calcaneum GL			
	Tegelen		Maasvlakte 2	
	Collection	GL	Collection	GL
N		18		21
Min.		45.55		41.57
Max.		49.31		56.82
Mean		46.99		49.30
Stand. dev.		1.00		3.41
Coeff. var.		2.13		6.92
	RGM.63302	45.55	CH47	41.57
	RGM.63302	45.81	MVT0092	45.70
	NHMM1986181	45.89	San1232	46.25
	NHMM001485 specimen 2	45.92	San2090	46.40
	NHMM2429	46.03	MES175	46.74
	NHMM001485 specimen 1	46.32	CH44	47.22
	TM15570a	46.52	EJ31	47.51
	ZMA.MAM.25901 Ref.nr. A147	46.83	CH43	47.89
	NHMM001515	47.00	NE nn	48.09
	TM15572b	47.01	MS032	48.27
	ZMA.MAM.26007 Ref.nr. 65	47.05	EG6	49.26
	TM16241	47.18	CH46	49.80
	RGM.63986	47.42	NEZHMV 2020 001	50.04
	RGM.53022	47.81	DB2253	50.42
	RGM.53022	47.84	MVT0119	50.88
	TM15573	48.05	CH48	51.54
	NHMM1986166	48.21	WB32611-14	51.58
	RGM.95459	49.31	DB3083	51.73
			DB2484	51.94
			DB2017	55.61
			DB2221	56.82

Table 2E	Tibia Bd*					
	Tegelen		Maasvlakte 1		Maasvlakte 2	
	Collection	Bd*	Collection	Bd*	Collection	Bd*
N		25		6		30
Min.		22.24		24.18		23.29
Max.		26.84		27.41		29.95
Mean		24.47		25.62		26.21
Stand. dev.		1.03		1.40		1.47
Coeff. var.		4.19		5.48		5.60
	NHMM1986160	22.24	KT3201	24.18	RW715	23.29
	RGM.119929	23.11	RGM.1341489	24.35	FB16	24.12
	RGM.95397	23.42	KT3202	24.62	VG12	24.17
	NHMM002219	23.61	KT3200	26.33	MS020	24.54
	NHMM1986161	23.65	RGM.1341484	26.83	DB2588	24.66
	TM16240	23.79	RGM.1341483	27.41	WB32611-43	24.84
	RGM.52989	23.80			MS019	25.15
	NHMM1986177	23.97			WB32611-30	25.15
	RGM.85590	24.02			MES26	25.24
	TM15568b	24.05			EV122	25.34
	ZMA.MAM.25900 Ref.nr. A21	24.15			CM001	25.64
	NHMM1986165	24.19			HTSM01067	25.73
	RGM.93435	24.25			San0147	25.80
	ZMA.MAM.25900 Ref.nr. A22	24.41			CH42	25.96
	RGM.52988	24.61			HTSM00917	26.04
	RGM.86704	24.71			MS018	26.15
	RGM.85697	24.80			VG13	26.21
	TM15568a	24.86			DB2526	26.36
	TM15588a	25.19			DB3092	26.49
	RGM.95461	25.22			HTSM01066	26.89
	NHMM002421	25.27			CH41	27.35
	ZMA.MAM.26003 Ref.nr. 61	25.45			DB3124	27.44
	RGM.47409	25.95			MS016	27.44
	ZMA.MAM.25900 Ref.nr. A144	26.30			AM002	27.46
	TM15568c	26.84			MS017	27.46
					AE138	27.51
					RW218	27.67
					DB1992	28.15
					NMR999100016686	28.19
					AM003	29.95