

**Pleistocene macrofauna from NW Europe: Changes in response to
Pleistocene climate change and a new find of *Canis etruscus*
(Oosterschelde, the Netherlands) contributes to the 'Wolf Event'**

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Abstract

Milanković cycles and/or the related sea level fluctuations have been thought to be responsible for mammalian events (migrations and/or extinctions) on a large geographical scale. One of those events was the so-called '*Wolf Event*'. A recent find of *Canis etruscus* (this study) shows that the tribe Canini was dispersed further than Central-southern Europe, up to the Northwestern part of the continent. In addition it appears that palaeontologists have to reconsider the diachroneity of the '*Wolf Event*', which seems that it occurred during a longer time span than originally thought.

Moreover, extensive literature research combined with the study of several Dutch and other European faunal assemblages (Chilhac, Oosterschelde, Tegelen, Untermassfeld, Het Gat, Eurogeul and Maasvlakte-2) indicate that Milanković cycles and/or the related sea level fluctuations can cause mammal events. This is confirmed by the faunal elements themselves, which show a certain pattern of adaptation according to different climatic regimes during (inter-)glacial periods.



1. Introduction

The classical definition of palaeontology states that '*Palaeontology is the science that studies the forms of life that existed in geologic times, as represented by fossils*'. They may represent a small percentage of the organisms that used to be part of this planet, but they provide us with useful information about several factors of the Earth's history. Some of them are the evolution of the living organisms themselves, environmental conditions, topography and geography, and much more. In short, fossils contribute significantly to the reconstruction of the Earth's history.

Mammals have been one of the most successful forms of life in the geologic history. They first appeared during the Upper Triassic (van den Berg *et al.*, 2012) and since the Cretaceous Mass Extinction they have dominated the Earth. Since then many different forms have evolved as is presented in the fossil record. Although the early forms of mammals are playing a key role to their overall evolution, more recent forms (e.g. of Pleistocene age) are of great significance, too. Furthermore, younger fossils are numerous and usually better preserved than the older ones, which allows us to have a better knowledge of the younger geological history and the regime under which the organisms were living (palaeoecology).

Climate has always been the controlling factor of the organisms. This means that the organisms are climate-dependent as it controls their nutrition (type of food, food availability, etc.), habitats (sea-level fluctuations, desertification, etc.) and other aspects that are crucial for their life. Climate, though, has varied constantly during the past. There are many factors contributing to this climate variability, but for the time span that is of interest for this project (Pleistocene-Recent), those variations have been mainly attributed to astronomical climate forcing (Hays *et al.*, 1976).

Astronomical climate forcing takes place mainly in the form of the so called Milanković oscillations, which are caused by changes in the geometry of the Earth's orbit. Those changes affect the interaction of regional climatic systems and the amount of insolation (the solar radiation that arrives at the atmosphere) and cause cyclic variations. The dominant cycles (oscillations) in the Pleistocene are climatic precession (ca. 21 Ka), obliquity (ca. 41 Ka) and eccentricity (ca. 100 Ka and ca. 400 Ka) (Hays *et al.*, 1976).

Sea level changes are caused mainly by tectonic (millions of years) and climatic processes/changes (thousands of years) and they can be either regional or global (Lambeck & Chappell, 2001). Moreover, those changes are affecting the regional climates and the habitable areas by altering the climatic conditions and increase or



decrease the habitable areas. They can connect continental areas with other continental areas or with islands, or disrupt such connections, causing isolation.

Milanković cycles together with sea level fluctuations have thought to lead to various events, either global or regional, regarding the fauna and flora of the Earth. More specific mammalian events, like the appearance of *Homo erectus* in Africa (Hopley *et al.*, 2007), out-of-Africa events (Muttoni *et al.*, 2010), rodents turnover in central Spain (van Dam *et al.*, 2006), the establishment of new environmental conditions at the western Palaeartic during E.-M. Pleistocene and the reaction of mammal communities (Kahlke *et al.*, 2011), are just some examples that indicate a relation with Milanković cycles and/or sea level fluctuations.

One interesting example of turnover events occurring in faunal assemblages is the 'Turnover Pulse Hypothesis' (Vrba, 1995). The main idea of this hypothesis is the occurrence of turnover events in multiple taxa, that are statistically pronounced compared with other events, that are considered to occur due to physical changes. The time scale of those turnover events depends on the event itself. In addition, it is expected that a turnover pulse is occurring during another turnover pulse, which has as an effect to produce an internal cyclic pattern. This internal cyclic pattern can reveal a frequency in time and consequently faunae can be tested for this. Unfortunately, the available data for this project and the time period of interest, do not allow us to test this hypothesis and as a result it will no longer be discussed.

Another intriguing event of the Pleistocene is the reappearance of canids in Europe and their dispersal. The genus *Canis* first appeared in Europe at late L. Miocene (ca. 7 Ma) at E Spain (Pons Moya & Crusafont Pairo, 1978; Sotnikova & Rook, 2010). Although, "*Canis*" *cipio* is still a questionable taxon due its scarce record (one fragmented maxilla and an isolated tooth) (Sotnikova & Rook, 2010). Another early appearance of *Canis* (*Canis* sp.) is recorded from the site of Viallette, France, (three fragmented mandibles, two isolated teeth and one tibia) resulting in an age of ca. 3.1 Ma (Lacombat *et al.*, 2008). Nevertheless, those finds can only be addressed as doubtful (Garrido & Arribas, 2008).

In E. Pleistocene together with the *Canis arnensis* (a small sized coyote-like canis) appeared a larger wolf-like form, *Canis etruscus*, which is believed to later have evolved into *Canis mosbachensis*, which in turn gave rise to *Canis lupus* (wolf) (Garrido & Arribas, 2008). This appearance is the so called 'Wolf Event' and occurred at the E. Pleistocene/L. Villafranchian (Azzaroli, 1983; Azzaroli *et al.*, 1988; Sardella & Palombo, 2007). This event is characterized by the disappearance of the genus *Nyctereutes* (raccoondog) and its replacement by *Canis arnensis* in the Mediterranean region and *Canis etruscus* in the



rest of the European continent. During this event other taxa were also replaced by other ones (e.g. *Cervus rhenanus* by *Dama nestii*, *Leptobos stenometopon* by *Leptobos etruscus*, etc.) (Azzaroli *et al.*, 1988).

In September 2012 the annual expedition at the Oosterschelde was carried out with purpose to find mammalian fossils (for the technique used see Mol *et al.*, 1999; Reumer *et al.*, 2005 and others). During this expedition a fragment of a carnivore's mandible was brought to the surface. This mandible is thought to belong to *Canis etruscus* (Reumer and van Zelst, personal communication). As a result, this sample could be the oldest find of the genus *Canis* in the Netherlands and it might be related to the so-called 'Wolf Event' (Azzaroli, 1983; Azzaroli *et al.*, 1988; Sardella & Palombo, 2007).

The purpose of this research is to investigate whether mammalian events could be triggered by Milanković oscillations and resulting climatic and environmental variations, to what extent (global and/or regional) they do so and the significance of those mammalian events for the Earth's history. The 'Wolf Event' is the starting point, due to a recent discovery of a wolf's mandible (**Chapter 3**) at the locality of Oosterschelde (the Netherlands), a locality that is dated at the time range of E. Pleistocene/L. Villafranchian. Additionally, attention is paid on several key fossil localities from the Netherlands and the surrounding area (**Chapter 4**) for which we will try to identify the effect of Milanković cycles that emerges from the different faunae (**Chapter 5**).



2. Material and Methods

In this chapter is provided information concerning the methodology and the data that was used for the needs of this project. This research started with the study of the wolf's mandible (see **Chapter 1**) aiming to identify the specimen and check its relation to the 'Wolf Event', it was continued with the study of several faunal assemblages from the Netherlands and nearby areas and ended with an investigation of the Milanković effect that might be presented by the studied faunae.

2.1. Wolf's mandible

First we studied the wolf's mandible found in the Oosterschelde, to provide its description according to palaeontological methods and understand the reasons for the occurrence of this specimen at Oosterschelde.

The mandible fragment (sinistral) consists of part of the ramus, two premolars (P_1 and P_2), part of the canine and part of the third premolar (P_3). The mental foramen is also visible. It is stored at the National Museum of Natural History (Naturalis, Leiden; Registration number: RGM631800).

All the measurements were taken with a Vernier caliper, the photographs with a Canon Digital IXUS 65 camera and the statistical analysis was carried out in Microsoft Excel 2010.

In order to identify the mandible fragment, material was used from several collections and published data. The collections that were studied are from the National Museum of Natural History (Naturalis, Leiden), Natuurhistorisch Museum Rotterdam and Laboratory of Paleontology (Department of Geology, Aristotle University of Thessaloniki). The inventory of the studied material is in Appendix (**Table A1** and **A2**). The published data that were used for the purpose of this task are from Del Campana (1913), Kerkhoff (1992), Rook (1993), Baryshnikov & Tsoukala (2010) and Baryshnikov (2012). (**Note that the Canis mandible will be described and discussed in a separate chapter (**Chapter 3**) from the rest of the conducted research.*)

2.2. Faunal assemblages

The next step was to choose which faunal assemblages would provide us with a lot of information concerning the aims of this project. After thorough search it was believed that the Pleistocene localities of Oosterschelde, Tegelen, Het Gat, Eurogeul, Maasvlakte-2 (The Netherlands), Chilhac (France) and Untermassfeld (Germany) are suitable for our purposes (**Figure 1**). The main criteria, amongst others, for choosing those localities



were based on: (1) the significance/importance of the faunae for regional/global palaeontology, (2) the completeness of the faunal records, (3) previous research that has been done on those localities, (4) the accessibility to the collections (5) their age and (6) the resemblance between the different faunae.

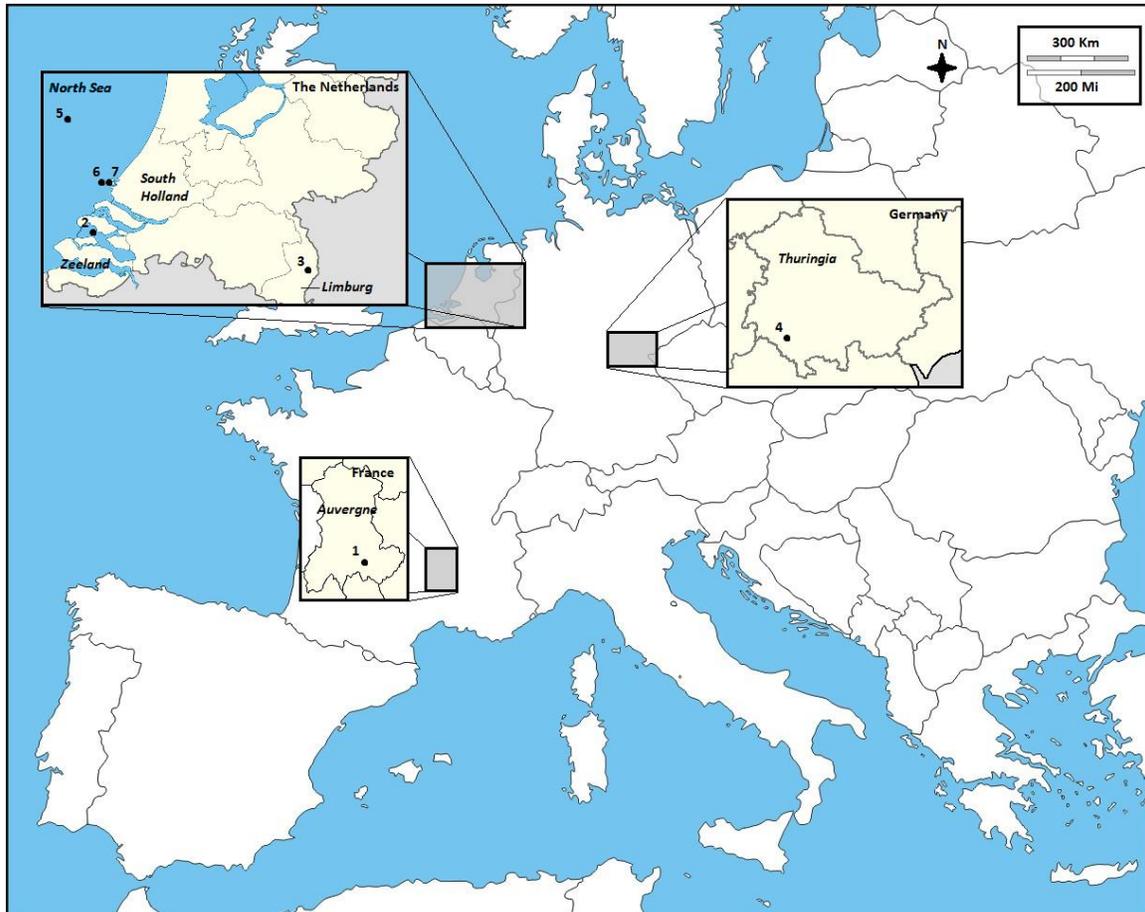


Figure 1. Map showing the studied faunal assemblages, ordered according to the age of the faunae (1: Chilhac, 2: Oosterschelde, 3: Tegelen, 4: Untermassfeld, 5: Het Gat, 6: Eurogeul, 7: Maasvlakte-2).

National Museum of Natural History (Naturalis, Leiden) and Natuurhistorisch Museum Rotterdam gave us access to their collections in order to have a better insight of as many faunae as possible. The Oosterschelde and Tegelen faunal assemblages were studied at National Museum of Natural History (Naturalis, Leiden) and the Eurogeul and Maasvlakte-2 at Natuurhistorisch Museum Rotterdam. For the purpose of this study were taken into account only the terrestrial mammals. The faunae of the aforementioned localities can be seen in **Tables 1, 2, 3** and **4** and they indicate the taxa as they were recorded from the museums' collections.



Table 1. *The Oosterschelde faunal assemblage as it was recorded from the National Museum of Natural History (Naturalis, Leiden) collections during the period 05-09/11/2012.*

Oosterschelde Faunal Assemblage	
Carnivora:	
<i>Crocuta crocuta</i>	<i>Felis catus</i>
<i>Ursus spelaeus</i>	<i>Canis familiaris</i>
Perissodactyla:	
<i>Equus caballus</i>	<i>Dicerorhinus</i> sp.
<i>Equus robustus</i>	<i>Rhinocerotidae</i> sp.
<i>Coelodonta antiquitatis</i>	
Artiodactyla:	
<i>Cervus rhenanus</i>	cf. <i>Leptobos</i> sp. (<i>elatus</i>)
<i>Eucladoceros ctenoides</i>	<i>Bison</i> sp.
<i>Eucladoceros tigliensis</i>	<i>Ovis aries</i> or <i>Capra hircus</i>
<i>Megaloceros giganteus</i>	<i>Cervidae</i> (gen. indet. sp. indet.)
<i>Cervus elaphus</i>	<i>Rangifer tarandus</i>
<i>Cervus falconeri</i> (<i>Eucladoceros ctenoides</i>)	<i>Capra hircus</i>
<i>Sus scrofa</i>	<i>Bos</i> or <i>Bison primigenius</i> or <i>priscus</i>
<i>Bos taurus</i>	<i>Hippopotamus</i> sp.
<i>Alces</i> sp.	<i>Capreolus capreolus</i>
<i>Bos taurus</i> or <i>primigenius</i>	
Proboscidea:	
<i>Mammuthus primigenius</i>	<i>Mammuthus</i> sp.
<i>Elephantidae</i> gen. indet.	<i>Anancus arvarnensis</i>
<i>Mammuthus archidiskodon meridionalis</i>	<i>Mammuthus meridionalis</i>
Primates:	
<i>Homo sapiens</i>	
Soricomorpha:	
<i>Galemys kormosi</i>	<i>Sorex</i> (<i>Drepanosorex</i>) <i>praeearaneus</i>
<i>Beremendia fissidens</i>	
Rodentia:	
<i>Castor fiber</i>	<i>Mimomys tigliensis</i>
<i>Trogontherium</i> sp.	<i>Mimomys newtoni</i>
<i>Mimomys pliocaenicus</i>	<i>Microtus oeconomicus</i>
<i>Mimomys reidi</i>	

Table 2. *The Tegelen faunal assemblage as it was recorded from the National Museum of Natural History (Naturalis, Leiden) collections during the period 05-09/11/2012.*

Tegelen Faunal Assemblage	
Carnivora:	



<i>Enhydriactis ardea</i>	<i>Ursus etruscus</i>
<i>Mustela palerminea</i>	<i>Crocuta perrierii</i>
<i>Panthera gombaszoegensis</i>	
Perissodactyla:	
<i>Dicerorhinus etruscus</i>	<i>Tapirus arvernensis</i>
<i>Equus robustus</i>	
Artiodactyla:	
<i>Cervus rhenanus</i>	<i>Eucladoceros tegulensis (ctenoides)</i>
<i>Leptobos cf. elatus</i>	<i>Sus strozzii</i>
Proboscidea:	
<i>Anancus arvernensis</i>	<i>Mammuthus meridionalis</i>
Primates:	
<i>Macaca florentina</i>	
Soricomorpha:	
<i>Desmana thermalis</i>	<i>Sorex (Drepanosorex) praeearaneus</i>
<i>Galemys kormosi</i>	<i>Sorex minutus</i>
<i>Talpa minor</i>	<i>Beremendia fissidens</i>
<i>Petenya hungarica</i>	<i>Sorex gen. indet.</i>
Rodentia:	
<i>Trogontherium boisvillettii</i>	<i>Mimomys pliocaenicus</i>
<i>Castor fiber</i>	<i>Mimomys tigliensis</i>
<i>Hylopetes debruijini</i>	<i>Mimomys reidi</i>
<i>Muscardinus pliocaenicus</i>	<i>Mimomys pitymyoides</i>
<i>Glirulus pusillus</i>	<i>Ungaromys dehmi</i>
<i>Apodemus cf. sylvaticus</i>	<i>Clethrionomys kretzoi</i>
<i>Micromys sp.</i>	<i>Dicrostonyx cf. torquatus</i>
Lagomorpha:	
<i>Hypolagus brachygnathus</i>	
Chiroptera:	
<i>Chiroptera sp.</i>	

Table 3. The Eurogeul faunal assemblage as it was recorded from the Natuurhistorisch Museum Rotterdam collections during the period 17-18/11/2012 and 31/05/2013.

Eurogeul Faunal Assemblage	
Carnivora:	
<i>Canis sp.</i>	<i>Panthera leo spelaea</i>
<i>Ursus cf. arctos</i>	<i>Crocuta crocuta spelaea</i>
Perissodactyla:	
<i>Coelodonta antiquitatis</i>	<i>Equus caballus</i>
<i>Stephanorhinus kirchbergensis</i>	<i>Equus sp.</i>



Artiodactyla:	
<i>Bison priscus</i>	<i>Cervus cf. elaphus</i>
<i>Megaloceros giganteus</i>	<i>Alces alces</i>
<i>Rangifer tarandus</i>	<i>Ovibos moschatus</i>
Proboscidea:	
<i>Mammuthus primigenius</i>	<i>Elephas antiquus</i>
Rodentia:	
<i>Castor fiber</i>	
Soricomorpha:	
<i>Desmana cf. moschata</i>	

Table 4. The Maasvlakte-2 faunal assemblage as it was recorded from the Natuurhistorisch Museum Rotterdam collections during the period 17-18/11/2012 and 31/05/2013.

Maasvlakte-2 Faunal Assemblage	
Carnivora:	
<i>Lutra lutra</i>	<i>Panthera leo spelaea</i>
<i>Ursus cf. arctos</i>	<i>Crocuta crocuta spelaea</i>
<i>Canis sp.</i>	
Perissodactyla:	
<i>Coelodonta antiquitatis</i>	<i>Equus caballus</i>
<i>Stephanorhinus etruscus</i>	<i>Equus sp.</i>
Artiodactyla:	
<i>Bison priscus</i>	<i>Megaloceros giganteus</i>
<i>Cervus sp.</i>	<i>Rangifer tarandus</i>
<i>Cervus cf. elaphus</i>	<i>Hippopotamus incognitus</i>
<i>Sus scrofa</i>	<i>Alces alces</i>
<i>Cervus elaphus</i>	<i>Bos primigenius</i>
<i>Bos sp.</i>	
Proboscidea:	
<i>Mammuthus primigenius</i>	
Primates:	
<i>Homo sapiens</i>	
Rodentia:	
<i>Castor fiber</i>	<i>Arvicola cantiana</i>
<i>Arvicola sp.</i>	<i>Mimomys savini</i>
<i>Microtus agrestis</i>	<i>Microtus sp.</i>

This was aimed on the better understanding of the Dutch faunae, identification of (dis)similarities, comparison and in turn the update of the faunal lists of those fossiliferous localities.



Furthermore an extensive literature study was done in order to extend the region of the study, as it was believed that the Dutch faunae may give us a good insight for the purpose of this project, but it was thought that by expanding the data the results would be of greater reliability. Therefore, faunae from several localities around Europe were taken into account, mainly from the British Islands and the North Sea region, Western, Northwestern and Central Europe.

The time span that was selected for this is E. Pleistocene-Recent, but emphasis was given on the E.-M. Pleistocene boundary due to the faunal turnover that has been observed at the end of the Villafranchian (Azzaroli, 1983; Rook & Martínez-Navarro, 2010 and others).



3. Canis mandible

Order: Carnivora (Bowdich, 1821), Suborder: Caniformia (Kretzoi, 1943), Family: Canidae (Fischer de Waldheim, 1817), Subfamily: Caninae (Fischer de Waldheim, 1817), Tribe: Canini (Fischer de Waldheim, 1817), Subtribe: Canina (Fischer de Waldheim, 1817), Genus: *Canis* (Linnaeus, 1758)

Canis etruscus (Forsyth-Major, 1877)

Material: RGM631800 (**Figure 2.a, 2.b, 2.c, 2.d and 2.e**)

Locality: Oosterschelde (Zeeland, the Netherlands)

Age: E. Pleistocene (ca. 1.9 Ma)

Description: This partial mandibula has two complete premolars (P_1 and P_2) the anterior part of P_3 and the canine, which is broken on the level of the alveolus. Moreover, the ramus is broken at the level of the canine at the anterior part and at the level of P_3 at the posterior part. The rest of it is complete. There is one mental foramen beneath the anterior root of P_2 . The measurements of the various characteristics of this sample can be seen in **Table 5**.

Table 5. Measurements of RGM631800 (L: Length in mm, W: Width in mm, H: Height in mm, D: Depth in mm, R- P_1 : Ramus under P_1 , R- P_2 : Ramus under P_2).

	L	W	H	D
C (approx.)	11.8	7.0	-	-
P_1	5.0	4.4	-	-
P_2	12.5	6.0	-	-
R-P_1	-	-	21.7	12.0
R-P_2	-	-	24.2	12.0
Diastema	7.3	-	-	-



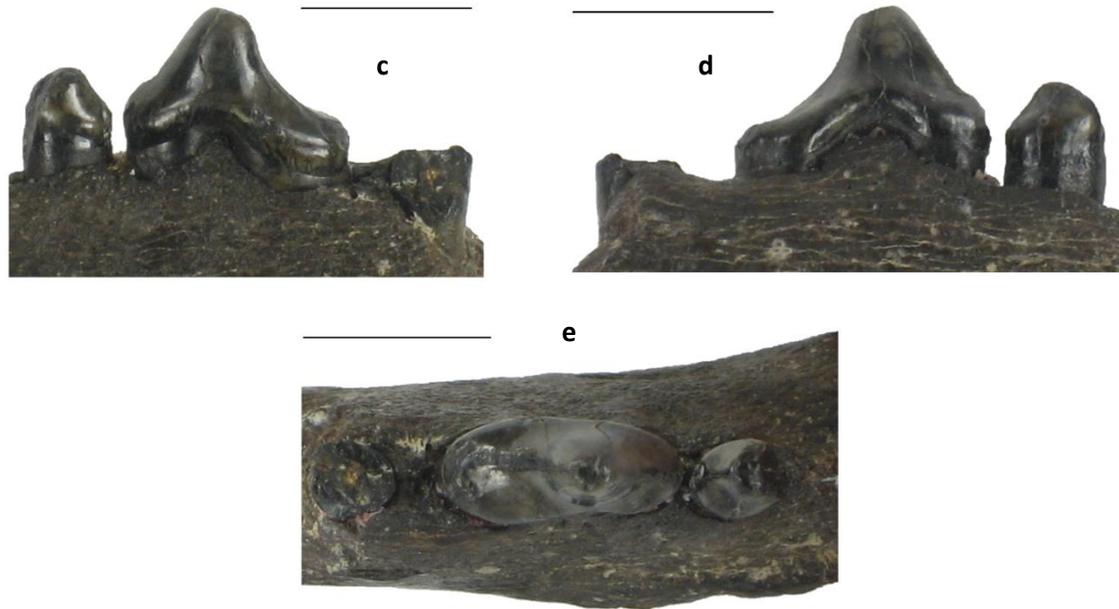


Figure 2. *Canis etruscus* – *sinistral* mandible fragment with part of *C*, complete *P*₁ and *P*₂ and part of *P*₃ (RGM631800) **a)** labial and **b)** reversed view of the mandible, **c)** labial and **d)** reversed view of the premolars, **e)** occlusal view of the premolars. Scale = 1 cm.

Comparison: The studied mandible fragment points to a robust large-sized canid. The basic difference that has with *Canis lupus*, *Canis familiaris* and the *Canis* (*Xenocyon*) subgenus is that the aforementioned taxa have one extra cuspid a bit above the lower part of the posterior end of *P*₂ (e.g. **Figure 3**). Similarities in the tooth morphology are

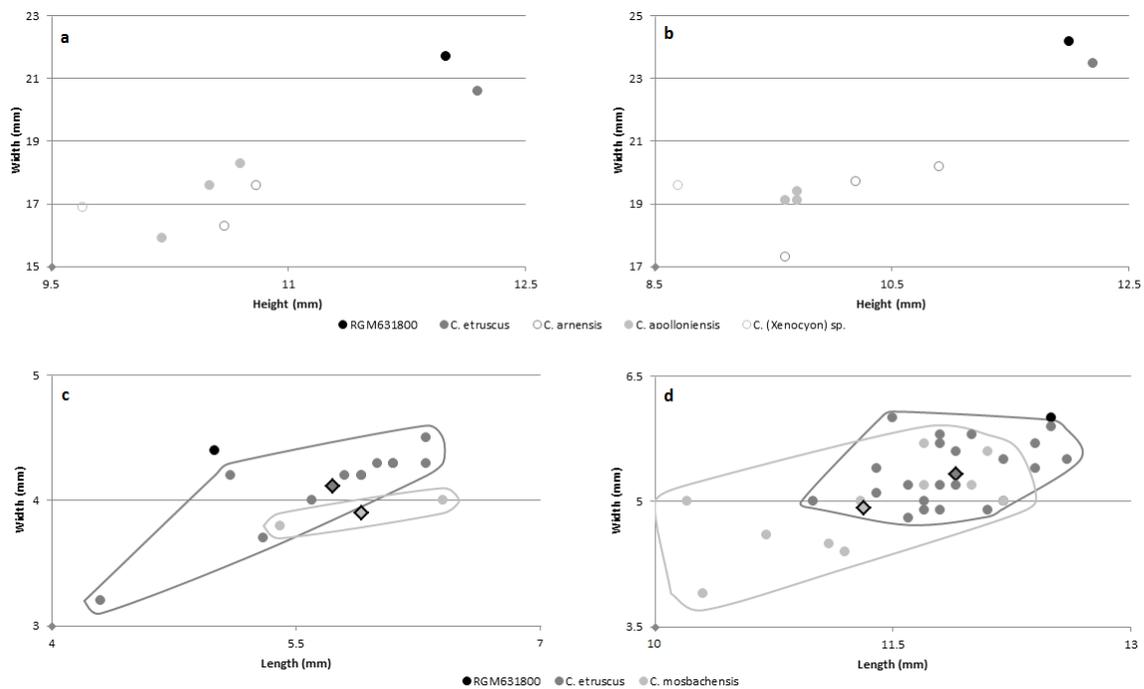


Figure 3. *Canis lupus* (St.445834). Note the extra cuspid (arrow) on *P*₂. Scale = 5 cm.

apparent with *Canis arnensis*, *Canis etruscus*, *Canis apolloniensis* and *Canis mosbachensis*. However, there is a significant size difference with the small-sized *Canis*



arnensis and *Canis apolloniensis*, which is indicated not only by the dentition, but also by the ramus width-height measurements (**Plot 1.a** and **1.b**). Moreover, P_1 of *Canis arnensis* and *Canis apolloniensis* are more elongated (length>>width) compared to the P_1 of *Canis etruscus* and *Canis mosbachensis*, which tends to be more circular (length>width). In addition, the small-sized specimens are considerably more slender than RGM632800. As a result, all the aforementioned point either to *Canis etruscus* or to *Canis mosbachensis*. Beginning by comparing the teeth dimensions (**Plot 1.c** and **1.d**) it is evident that it is closer to *Canis etruscus*, with *Canis mosbachensis* being slightly smaller. Moreover, the ramus height and width measurements indicate a close relation to *Canis etruscus* as well (unfortunately, no *Canis mosbachensis* was included in the studied collections; as a result the measurements were taken only from the literature). The comparable characteristics though, do not show any morphological difference between them, apart from the size. As a result this mandible fragment is attributed to *Canis etruscus*.

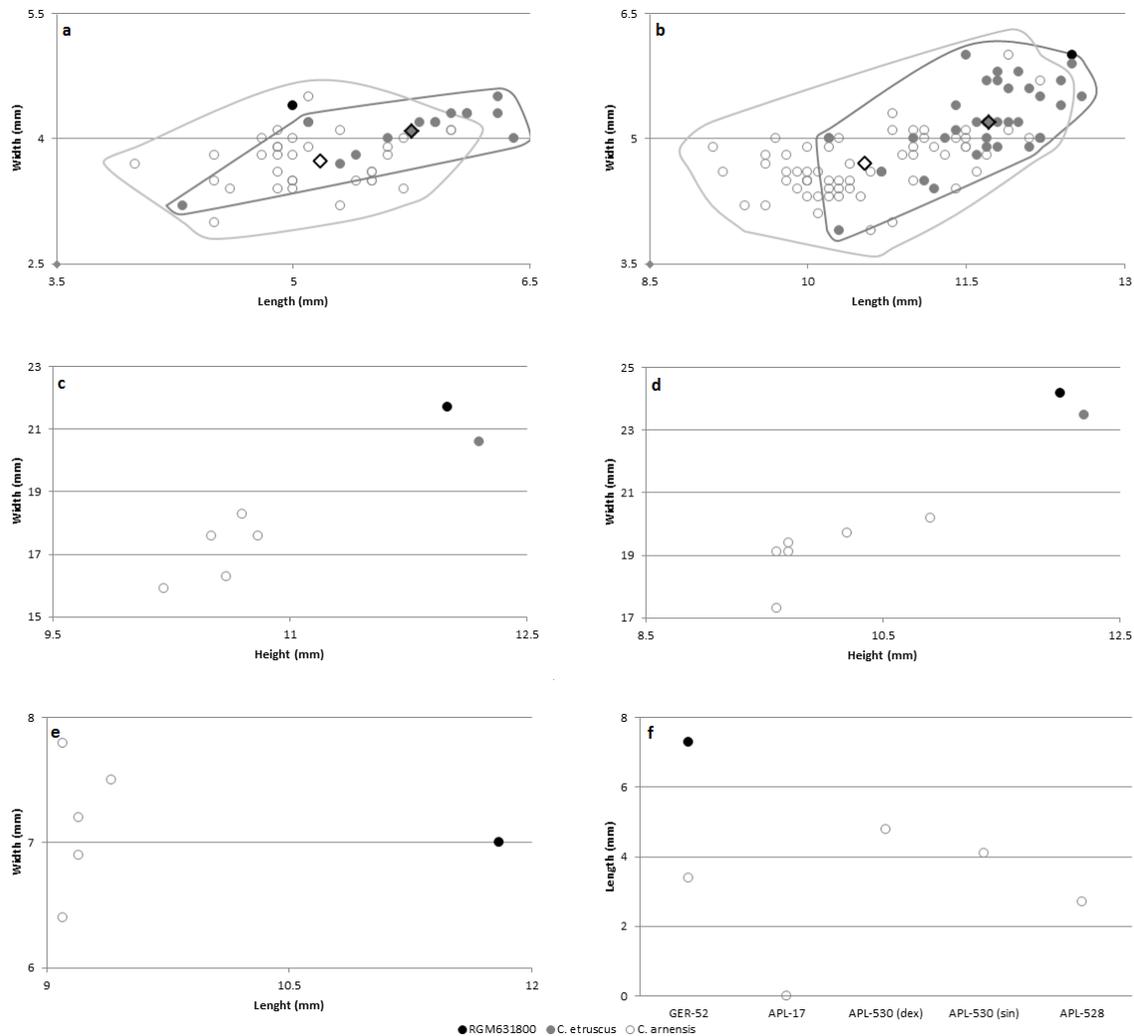


Plot 1. Comparison of ramus width-height below **a)** P_1 and **b)** P_2 between RGM631800, *Canis etruscus*, *Canis arnensis*, *Canis apolloniensis* and *Canis (Xenocyon) sp.* and comparison of **c)** P_1 and **d)** P_2 between RGM631800, *Canis etruscus* and *Canis mosbachensis* with Convex Hulls. *The diamonds indicate the average values for each specimen.

Additional remarks: This conclusion is further supported by a recent suggestion by Brugal & Boudadi-Maligne (2011), who point to a simplification of the taxonomy of the Pleistocene *Canis* genus by the recognition of only two species, the small-sized *Canis*



arnensis (which will include *Canis accitanus* and *Canis apolloniensis*) and the large-sized *Canis etruscus* (which will include *Canis mosbachensis*). This suggestion is mainly based on the fact that the morphological characteristics of the aforementioned groups are the



Plot 2. Comparison of **a)** P₁ and **b)** P₂ between RGM631800, *Canis etruscus* and *Canis arnensis* with Convex Hulls; comparison of ramus width-height below **c)** P₁ and **d)** P₂ between RGM631800, *Canis etruscus* and *Canis arnensis*; comparison of **e)** C between RGM631800 and *Canis arnensis* and comparison of **f)** diastema between RGM631800 and *Canis arnensis*. ***e)** and **f)** no available data for *Canis etruscus*.

same apart from the body size and the body size variability is not a factor of phyletic differentiation. By accepting this suggestion, the results point to *Canis etruscus* phyletic group as it can also be seen in **Plot 2.a, 2.b, 2.c, 2.d, 2.e** and **2.f**. P₁ falls in the *Canis arnensis* group, although due to the length-width difference that was described before,



it has a closer relation to *Canis etruscus*. In the case of P_2 , it falls in the *Canis etruscus* group, with the *Canis arnensis* group showing a clear overlap. Although, if we take into account the averages for both cases, the latter is considerably smaller. Unfortunately, the studied collections or the literature did not contain any information about the canine and consequently the diastema of *Canis etruscus*. Nevertheless, by taking into account the extracted results (**Plot 2.e** and **2.f**) it is expected that RGM631800 is closer to *Canis etruscus* rather than *Canis arnensis*, due to the significant size difference that occurs. Consequently, RGM631800 is attributed to *Canis etruscus*.



4. The Localities – Results

This research that started with the study of the wolf's mandible was followed by the investigation of the museums' collections, as it was stated before, aiming to provide an up-to-date record of the fossiliferous localities. The next step was to find relevant information in the literature and compare them with the present results in order to provide the best explanation for the faunal assemblages.

The North Sea region has provided palaeontologists with a large amount of fossils the past decades and thus it is considered a region rich in mammalian (and other) fossils. Fossils are literally fished by fishing vessels either accidentally during the working hours of the vessels or intentionally during organized expeditions for fossils retrieval. The problem that is usually encountered with this technique is that the fossils lack stratigraphic position (van Kolfschoten & Laban, 1995). The situation though is even more complicated, as a lot of re-sedimentation and reworking of the fossils has occurred (Slupik *et al.*, 2013). Although, the past years an intensive work on the stratigraphy of the Netherlands led to a better understanding of the formations that comprise the southern North Sea basin, which in turn gave more insight concerning the biostratigraphy of the region. On the other hand, the regions apart from the southern North Sea basin were easier to be described. Those localities were part of rivers' palaeobanks, which resulted in a continuous stratigraphical record that yields a significant amount of information.

After the study of the faunal assemblages and several literature resources, it was observed that synonymity occurred between several taxa. The nomenclature used in this project is described for all the faunal elements that are under debate, but for synonyms or names that have been used incorrectly in the past see Appendix **Table A3**.

4.1. Chilhac (Auvergne, France)

In 1875 farmers that were working in the close vicinity of Chilhac (Massif Central) found the first fossils of this important locality. The fossiliferous locality is situated in a river valley, ca. 1 Km NNE from the village of Chilhac (Boivin *et al.*, 2010).

4.1.1. Biostratigraphy

The fossiliferous locality of Chilhac is situated close to the northwestern end of the Devès Plio/Pleistocene volcanic complex (Boivin *et al.*, 2010). This complex is comprised of basaltic flows, scoria cones of strombolian type and maar craters (Mergoïl & Boivin, 1993). Devès complex sits on top of a metamorphic basement (gneisses of Variscian orogeny) with the oldest lava flows dated at ca. 2-3 Ma and the youngest ones at ca. 1-2



Ma. The fossils have been found in sediments intercalated in the Devès lavas. Furthermore, there have been recognized lava flows below and above the fossiliferous sediments dated at ca. 2.5 Ma (for the lower one) and ca. 1.8 Ma (for the one above the sediments). Additionally, there happened two major events, an erosion event which occurred shortly before the younger lava flow and a major landslide shortly after the fossiliferous sediments were deposited (Boivin et al., 2010).

4.1.2. The fauna

The taxa that are included in the fauna can be seen in **Table 6**.

Table 6. Updated faunal list of the Chilhac fossiliferous locality (according to Mol et al., 1999 and Boivin et al., 2010 – authors that have discussed this faunal assemblage).

Chilhac Faunal Assemblage	
Carnivora:	
<i>Ursus aff. minimus</i>	<i>Megantereon megantereon</i>
<i>Nyctereutes megamastoides</i>	<i>Pliocrocuta perrieri</i>
<i>Homotherium crenatidens</i>	
Perissodactyla:	
<i>Stephanorhinus etruscus</i>	<i>Equus stenorhinus</i>
Artiodactyla:	
<i>Cervus rhenanus</i>	<i>Gallogoral meneghini</i>
<i>Croizetoceros ramosus</i>	<i>Gazellospira torticornis</i>
<i>Eucladoceros ctenoides</i>	
Proboscidea:	
<i>Anancus arvernensis</i>	<i>Mammuthus meridionalis</i>
Rodentia:	
<i>Hystrix</i> sp.	<i>Castor</i> sp.

Boivin et al. (2010) state for the bear that was found, that it is closer to *Ursus minimus* rather than *Ursus etruscus*. Moreover, *Megantereon megantereon* is a synonym for *Megantereon cultridens*. The same applies to *Pachycrocuta perrieri* and *Pliocrocuta perrieri* and to *Dicerorhinus etruscus* and *Stephanorhinus etruscus*. For the case of *Cervus philisi* (Schaub, 1941), *Cervus rhenanus* (Dubois, 1904) has priority. Mol et al., (1999) referred to *Eucladoceros senezensis*, but they concluded that the large deer *Eucladoceros senezensis* and *Eucladoceros ctenoides* (= *Eucladoceros tegulensis*) is the same species and *Eucladoceros ctenoides* (= *Eucladoceros tegulensis*) (Nesti, 1841) has priority to *Eucladoceros senezensis* (Deperet, 1910). Furthermore, something that is worth noting about Chilhac fauna is the coexistence of *Anancus arvernensis* (MN 16-17)



and *Mammuthus meridionalis* (MN 17), which is the main characteristic of this fauna (Boivin *et al.*, 2010).

Concerning the medium-sized deer, Croitor & Bonifay (2001), Boivin *et al.* (2010) and others consider that this deer belongs to the genus *Metacervoceros* due to significant morphological differences from the genus of *Cervus*. Although, by judging the arguments of both sides (de Vos *et al.*, 1995), it is concluded that the two genera do not differ significantly, at least not until new material will be discovered which will enable researchers to further investigate that controversy. In this study the genus *Cervus* will be used.

4.1.3. Age of the fauna

The Chilhac fauna was found intercalated in volcanic sediments, which made the radiometric dating of the fauna possible. Boivin *et al.* (2010) suggest an age of 2.2 Ma (2.47-1.8 ±0.2 Ma). Kahlke *et al.* (2011) consider the fauna to be slightly younger with an age of ca. 2.0 Ma. Furthermore, an age of ca. 1.9 Ma was suggested by Slupik *et al.* (2007), Drees (2005) and Mol *et al.* (1999). From all the aforementioned it is concluded that the fauna is typical of the MN 17 biozone (L. Villafranchian), despite the MN 16 taxa present, with an age of ca. 2.0 Ma.

4.1.4. Palaeoenvironment

According to the faunal elements of the Chilhac faunal assemblage it is apparent that the palaeoenvironment of the region was an open grassland with forested patches, high temperatures and humid. This is shown by the occurrence of *Mammuthus meridionalis* and *Anancus arvernensis*, two species that their habitat preference is indicative of forested environments with temperatures ranging from mild-warm. *Cervus rhenanus* and *Eucladoceros ctenoides* are faunal elements representative of woodland, too. On the other hand, the Bovidae and the Perissodactyls of this fauna are representatives of open environment. Furthermore, the presence of water masses (lakes, rivers, etc.) is highly probable due to the presence of *Hystrix* and *Castor*.

4.2. Oosterschelde (Zeeland, the Netherlands)

The first to find and describe fossil material from the Oosterschelde estuary was de Man (1875). Since then, fossils are 'fished' from the bottom of the estuary (annually after 1950). This collecting method leads to a significant problem, which has to do with the stratigraphic position of the fossils. Another drawback that occurs with this method is that the fishing nets bring to the vessel only large bones, which are also significantly fragmented (de Vos *et al.*, 1995). Nevertheless, after 1997, started an effort to retrieve



micromammals with the addition of new equipment to fishing nets, something that led to new material (Reumer *et al.*, 2005). The fossils from Oosterschede have a characteristic dark colour, are heavily mineralised, have high density and produce a metallic sound when tapped on by a hard object. All those led many authors to describe them as the 'Black Bone Fauna' (Gibbard *et al.*, 1991; de Vos *et al.*, 1995; Mol *et al.*, 1999), but this term is not preferred.

4.2.1. Biostratigraphy

Oosterschelde is a deep-water channel where fossiliferous submarine sediments are dredged (Mayhew *et al.*, 2008; Kahlke *et al.*, 2011). More specific fossils are fished from the bottom of this channel from depths of ca. 35-40 m (Maassluis Formation) (Slupik *et al.*, 2007; 2013). The top of Maassluis Formation is comprised of aeolian and channel-fill deposits. Those deposits are medium- to fine-grained arenite with a small amount of lithic grains (for the aeolian deposits) or arenite mixed with small particles of clay, manganese and shell fragments (for the channel-fill deposits). The taphonomic and preservational characteristics of the fauna indicate that it was not found *in situ* or that at least, no long transport occurred (Slupik *et al.*, 2007; 2013).

4.2.2. The fauna

The Oosterschelde faunal list is given in **Table 7**.

Table 7. Updated faunal list of the Oosterschelde fossiliferous locality (according to own observations from the National Museum of Natural History, Naturalis, Leiden collection (**Table 1**); Gibbard *et al.*, 1991; de Vos *et al.*, 1995; Mol *et al.*, 1999; Mol *et al.*, 2003; Reumer *et al.*, 2005; Slupik *et al.*, 2007; Mayhew *et al.*, 2008; Reumer *et al.*, 2010 and Kahlke *et al.*, 2011 – authors that have discussed this faunal assemblage).

Oosterschelde Faunal Assemblage	
Carnivora:	
<i>Pliocrocuta perrieri</i>	<i>Canis etruscus</i>
<i>Ursus spelaeus</i>	<i>Homotherium cf. latidens</i>
<i>Felis catus</i>	
Perissodactyla:	
<i>Equus caballus</i>	<i>Stephanorhinus sp.</i>
<i>Equus robustus</i>	<i>Rhinocerotidae sp.</i>
<i>Coelodonta antiquitatis</i>	<i>Stephanorhinus etruscus</i>
Artiodactyla:	
<i>Cervus rhenanus</i>	<i>Bos taurus</i> or <i>primigenius</i>
<i>Eucladoceros ctenoides</i>	<i>Leptobos cf. elatus</i>



<i>Megaloceros giganteus</i>	<i>Bison</i> sp.
<i>Cervus elaphus</i>	<i>Ovis aries</i> or <i>Capra hircus</i>
<i>Sus strozzii</i>	<i>Cervidae</i> (gen. indet. sp. indet.)
<i>Bos taurus</i>	<i>Rangifer tarandus</i>
<i>Alces</i> sp.	<i>Capra hircus</i>
<i>Bos</i> or <i>Bison primigenius</i> or <i>priscus</i>	<i>Capreolus capreolus</i>
<i>Hippopotamus</i> sp.	
Proboscidea:	
<i>Mammuthus meridionalis</i>	<i>Mammuthus</i> sp.
<i>Mammuthus primigenius</i>	<i>Elephantidae</i> gen. indet.
<i>Anancus arvarnensis</i>	
Primates:	
<i>Homo sapiens</i>	
Soricomorpha:	
<i>Galemys kormosi</i>	<i>Sorex (Drepanosorex) praeearaneus</i>
<i>Beremendia fissidens</i>	
Rodentia:	
<i>Castor fiber</i>	<i>Mimomys reidi</i>
<i>Trogontherium cuvieri</i>	<i>Mimomys tigliensis</i>
<i>Mimomys pliocaenicus</i>	<i>Borsodia newtoni</i>

At the Oosterschelde was found a saber-toothed cat, which was identified as *Homotherium* cf. *latidens* by Mol *et al.* (2003). There was also found and a hyaena which has caused a lot of confusion in terms of its taxonomy. Here this specimen has been attributed to the taxon *Pliocrocuta perrieri*, as all the non-crocutoids of M. Villafranchian are grouped in the genus of *Pliocrocuta* (Palombo *et al.*, 2008). Furthermore, the fragmentary material of an equid made the identification of this specimen a complicated task. At the collection of Naturalis there are referred two species, *Equus caballus* and *Equus robustus*. Mol *et al.* (2003) assigned it as *Equus major*. Although, the uncertainty levels for this (these) heavily built horse(s) are high enough, something that should be considered in any case. To continue with the horses, Kahlke *et al.* (2011) state that *Equus bressanus* (= *Equus major* = *Equus robustus*). On the other hand *Equus robustus* was named by Pomel (1853), *Equus major* by Boule (1927) and *Equus bressanus* by Viret (1954). Concerning all the aforementioned, for the purpose of this research it will be referred as *Equus robustus*, because it has priority. There was also confusion about the rhinoceroses that were found, as at the Naturalis collection it was assigned to *Dicerorhinus* genus, but according to Fortelius *et al.* (1993) all the Plio/Pleistocene rhinos from Europe that were assigned as *Dicerorhinus* are temporarily



now assigned to the *Stephanorhinus* genus. In addition, *Cervus* or *Eucladoceros falconeri* is a synonym for *Eucladoceros ctenoides* (de Vos *et al.*, 1995).

The genus *Leptobos* was also found in Oosterschelde and it was assigned as *Leptobos* cf. *elatus* according to the collection of Naturalis. Reumer *et al.* (2005) agree with this identification. On the other hand, Mayhew *et al.* (2008) recognize the material only up to the genus level. It is becoming clear then that this taxon remains partly unidentified on a species level. In this project it will be followed the *Leptobos* cf. *elatus* identification. According to the collection of Naturalis and Gibbard *et al.* (1991), there is an elephant, which was identified as (*Mammuthus*) *archidiskodon meridionalis*. Although, according to Maglio (1973) and Lister (1996), *Mammuthus* is a synonym with *Archidiskodon*. For the purpose of this research it will be agreed that this elephant is *Mammuthus meridionalis* (Mol *et al.*, 1999; Mol *et al.*, 2003; Reumer *et al.*, 2005; Slupik *et al.*, 2007; Mayhew *et al.*, 2008 and Kahlke *et al.*, 2011).



Figure 4. *Coelodonta antiquitatis* mandible (dextral) (dentition formula from the right side to the left: $(P_2), P_3, P_4, M_1, M_2, M_3$). Scale = 5 cm.

As it can be easily seen from the taxa that were found, Oosterschelde represents a composite faunal record of E.-L. Pleistocene age. Thus, the fauna can be divided in two groups, with the main faunal elements of E. Pleistocene age and with *Ursus spelaeus*, *Coelodonta antiquitatis* (**Figure 4**), *Megaloceros giganteus*, *Mammuthus primigenius*, *Cervus elaphus*, *Bos* or *Bison primigenius* or *priscus*, *Bos taurus* or *primigenius*, *Bison* sp., *Ovis aries* or *Capra hircus*, *Rangifer tarandus*, *Capra hircus* and *Homo sapiens* representing younger than E. Pleistocene taxa.



Furthermore, it was found one molar of *Microtus oeconomus*, which exists only since the L. Pleistocene/Holocene till Recent and especially at the vicinity of the fossiliferous location. As a result it was considered a contamination (Reumer *et al.*, 2005).

Contamination: *Microtus oeconomus*.

It is worth to note that the Oosterschelde and Chlhac faunal assemblages are well correlated with each other, which are considered to be contemporaneous (Mol *et al.*, 1999; Mol *et al.*, 2003; Slupik *et al.*, 2007). This hypothesis is confirmed after examination of both localities, as many similarities arise between them (see **Section 4.8.** and **Chapter 5**)

4.2.3. Age of the fauna

The age of the Oosterschelde locality is more or less well constrained as well. Gibbard *et al.* (1991) placed Oosterschelde faunal assemblage at M. Tiglian (\pm TC3). This comes to an agreement with all the researches that have been done onwards. An age of 1.9 Ma is suggested by Mol *et al.* (1999, 2003), Slupik *et al.* (2007, 2013) and Reumer *et al.* (2010). Moreover, Mayhew *et al.* (2008) gave an age of ca. 1.8 Ma and Kahlke *et al.* (2011) of ca. 2.0 Ma. Additionally, Reumer *et al.* (2005) states that the fauna has to be placed at MN 17 and that an age of TC3 remains still questionable. According to the aforementioned information, the most appropriate age of the fauna should be ca. 1.9 Ma (L. Gelasian, TC1-4b) with a fauna typical of MN 17 (M.-L. Villafranchian).

4.2.4. Palaeoenvironment

Gibbard *et al.* (1991) stated that there was a gradual decrease in the temperature during TC1-4b, with the occurrence of a climatic optimum at TC3. This comes in an agreement with later studies by Slupik *et al.* (2007) and Kahlke *et al.* (2011), who state that Oosterschelde had a moderately temperate palaeoenvironment. As a result the Oosterschelde faunal assemblage is probably younger than the TC3 warm stage.



Figure 5. *Anancus arvernensis* M^1 (sinistral) Oosterschelde. Scale = 5 cm.



This temperate environment is furthermore confirmed by the faunal elements of this fossiliferous locality. *Cervus rhenanus*, *Eucladoceros ctenoides*, *Mammuthus meridionalis* and *Anancus arvernensis* (**Figure 5**) confirm the presence of forested/wooded environments with temperatures ranging from mild-warm, as in Chilhac. Moreover, *Homotherium latidens* is also indicative of interglacial stages. In addition, the presence of water masses (lakes, rivers, etc) is apparent due to the presence of *Trogotherium cuvieri*, *Castor fiber* and *Galemys kormosi*. Furthermore, both warm and humid environment is represented by the occurrence of *Hippopotamus* and more specific this shows an interglacial stage with warm summers and mild-humid winters. All those point to a temperate forest with few open areas on the close proximity of a river (most probably an estuary).

4.3. Tegelen (Limburg, the Netherlands)

The classical locality of Tegelen has yielded and provided a highly diverse fossil record. The first time that fossils were found was at the early 1900's by workers of the clay pit (van den Hoek Ostende & de Vos, 2006). Eugène Dubois was the first who studied fossils from this locality and published his work in 1904 and 1905. Beyond this point, many palaeontologists studied the fauna from Tegelen, but the one that did remarkable job on it was Antje Schreuder during 1930's-1940's (Schreuder, 1935, 1945 and more). Moreover, during the 1970's it was the first time that expeditions were organized aiming to collect micromammal fossils (van den Hoek Ostende, 2004), which have been only incidentally collected until then. Nevertheless, the Tegelen clay pit has given a significant amount of fossils for over a century. Unfortunately, most of the material is extremely fragmentary due to the bad preservation and the way of collection (van den Hoek Ostende, 2004; van den Hoek Ostende & de Vos, 2006).

4.3.1. Biostratigraphy

The famous Tegelen clay, which has been exploited since ancient times, is in fact a set of pits with the occurrence of a clay bed that lies on top of gravels and sands (O'Regan & Turner, 2004; van den Hoek Ostende & de Vos, 2006). More specific the clay beds are a blend of channel-fill deposits and oblique floodplains (van den Hoek Ostende & de Vos, 2006). Although the presence of faults is significantly dense, the aforementioned clay beds are considered to be one unit, which is composed of silty clay and was deposited due to the Rhine and Meuse Rivers (O'Regan & Turner, 2004). The up to 10 m thick Tegelen clay is rich in faunal and floral fossils and after the studies that were carried out on pollen it became the Tiglian type locality (O'Regan & Turner, 2004; Drees, 2005).



4.3.2. The fauna

An updated faunal list (for the mammals only) is given in **Table 8**.

Table 8. Updated faunal list of the Tegelen fossiliferous locality (according to own observations from the National Museum of Natural History, Naturalis, Leiden collection (**Table 2**); Azzaroli et al., 1988; Reumer & van den Hoek Ostende, 2003; O'Regan & Turner, 2004; van den Hoek Ostende, 2004; Drees, 2005; van den Hoek Ostende & de Vos, 2006; Kahlke et al., 2011 and van den Hoek Ostende & Reumer, 2011 – authors that have discussed this faunal assemblage).

Tegelen Faunal Assemblage	
Carnivora:	
<i>Enhydrictis ardea</i>	<i>Ursus etruscus</i>
<i>Mustela palerminea</i>	<i>Panthera (onca) gombaszoegensis</i>
<i>Pliocrocuta perrieri</i>	
Perissodactyla:	
<i>Stephanorhinus etruscus</i>	<i>Equus robustus</i>
Artiodactyla:	
<i>Cervus rhenanus</i>	<i>Eucladoceros ctenoides</i>
<i>Leptobos cf. elatus</i>	<i>Sus strozzii</i>
Proboscidea:	
<i>Mammuthus meridionalis</i>	
Primates:	
<i>Macaca sylvanus florentina</i>	
Soricomorpha:	
<i>Desmana thermalis</i>	<i>Sorex (Drepanosorex) praeareneus</i>
<i>Galemys kormosi</i>	<i>Sorex minutus</i>
<i>Talpa minor</i>	<i>Beremendia fissidens</i>
<i>Petenya hungarica</i>	<i>Sorex gen. indet.</i>
Rodentia:	
<i>Trogontherium cuvieri</i>	<i>Mimomys reidi</i>
<i>Castor fiber</i>	<i>Mimomys pitymyoides</i>
<i>Hylopetes magistri</i>	<i>Ungaromys dehmi</i>
<i>Muscardinus pliocaenicus</i>	<i>Clethrionomys kretzoi</i>
<i>Glirulus pusillus</i>	<i>Dicrostonyx cf. torquatus</i>
<i>Apodemus cf. sylvaticus</i>	<i>Spermophilus primigenius</i>
<i>Micromys sp.</i>	<i>Sciurus sp. indet.</i>
<i>Mimomys pliocaenicus</i>	<i>Hystrix refossa</i>
<i>Mimomys tigliensis</i>	
Lagomorpha:	
<i>Hypolagus brachygnathus</i>	



Chiroptera:

Chiroptera sp.

Panthera (onca) gombaszoegensis is a chronosubspecies as it has been stated by Hemmer *et al.* (2001) for the Eurasian jaguars of E.-early M. Pleistocene. At the collection of Naturalis the hyaena was assigned as *Crocuta crocuta*, but for reasons that have already been discussed, it is considered *Pliocrocuta perrieri* for this project. There is also another big debate about the rhinoceros(es) of Tegelen. Guérin (1980) recognized two species, *Stephanorhinus etruscus* and *Stephanorhinus kirchbergensis*. Although, the occurrence of the latter is not very likely, as *Stephanorhinus kirchbergensis* is a species from the M. Pleistocene and the Tegelen fauna is of E. Pleistocene age (van den Hoek Ostende & de Vos, 2006) (details on the age of Tegelen will follow in **Section 4.3.3.**). Also, several authors considered it to be of the *Dicerorhinus* genus, but for the reasons discussed, here it is considered as *Stephanorhinus*. To sum up, in this project and according to the criteria that were mentioned before it is considered only one species of rhinoceros, *Stephanorhinus etruscus* (**Figure 6**). For the large deer, it is considered to be *Eucladoceros ctenoides* (= *Eucladoceros teguliensis*) for the reasons stated in **Section 4.1.2.**



Figure 6. *Stephanorhinus etruscus* mandible (dextral) (dentition formula from the right side to the left: P_3, P_4, M_1, M_2, M_3). Scale = 5 cm.

The collection of Naturalis contains also a molar of *Anancus arvernensis* and material from *Tapirus arvernensis*, which are excluded from the Tegelen fauna as they were found in Maalbeek pit. Azzaroli *et al.* (1988) include these taxa also in the faunal list that they presented. Despite the fact that Maalbeek pit is close to Tegelen, the layer at which was found the material is considered to be a bit older than the Tegelen clay (Drees, 2005; van den Hoek Ostende & de Vos, 2006). Another worthnoting element of the fauna was the macaque. According to Castaños *et al.* (2011), all the macaques of the E. Pleistocene are classified as *Macaca sylvanus florentina*. This is a chronosubspecies classification of the taxon *Macaca sylvanus*, which also includes *Macaca sylvanus prisca* during Pliocene and *Macaca sylvanus pliocena* during M.-L. Pleistocene.



Trogontherium cuvieri (a large beaver) is an important part of the Tegelen fauna. Naturalis, O'Regan & Turner (2004) and van den Hoek Ostende (2004) suggested the name of *Trogontherium boisvillettii*, which was initially used by Schreuder in order to make a distinction between an Eastern European and a Western European species, as well as by Mayhew (1978) as chronosubspecies (*Trogontherium cuvieri* being younger than *Trogontherium boisvillettii*). Here we follow the perspective of Azzaroli *et al.* (1988) and van den Hoek Ostende & de Vos (2006), because the different elements do not show significant morphological differences to be divided in two taxa.

Finally, *Hylopetes debruijni* that was identified at Tegelen (Reumer & van den Hoek Ostende, 2003), was preoccupied by a taxon of Miocene age that was found in France and is totally different from the aforementioned one. As a result a new name was assigned for this species, *Hylopetes magistri* (van den Hoek Ostende & Reumer, 2011).

4.3.3. Age of the fauna

The age of the Tegelen faunal assemblage has yielded a lot of uncertainties. Azzaroli *et al.* (1988) and O'Regan & Turner (2004) agree that the age of this locality is between 2.2-1.7 Ma (M.-early L. Villafranchian). Van den Hoek Ostende (2004) and van den Hoek Ostende & de Vos (2006) state that the age of Tegelen is Plio/Pleistocene (former Plio/Pleistocene boundary), but this is still uncertain because the exact stratigraphic position of many fossils is not known. An age of L. Tiglian (TC5-6) is suggested by Reumer & van den Hoek Ostende (2003), Mol *et al.* (2003), Drees (2005) and Kahlke *et al.* (2011). All these suggest an age of ca. 1.8 Ma.

4.3.4. Palaeoenvironment

The rich and diverse Tegelen faunal assemblage is indicative of an interglacial palaeoenvironment (van den Hoek Ostende, 2004; Kahlke *et al.*, 2011), with warm climate (Azzaroli *et al.*, 1988; O'Regan & Turner, 2004), forested landscape (Reumer & van den Hoek Ostende, 2003; O'Regan & Turner, 2004) and with strong presence of water (Drees, 2005).

All this information is derived from the presence of *Mammuthus meridionalis*, *Cervus rhenanus*, *Eucladoceros ctenoides*, *Sus strozzi*, *Macaca sylvanus florentina* and *Sciurus*, which are faunal elements representative of a temperate woodland habitat. Furthermore, the presence of water bodies is indicated by the occurrence of *Trogontherium cuvieri*, *Castor fiber*, *Galemys kormosi*, *Desmana thermalis*, *Hystrix refossa* and *Talpa minor*. On the other hand the horses represent an open habitat. As a result, the palaeoenvironment in that case is similar to Oosterschelde (temperate woodland with open areas in the close vicinity of an estuary).



4.4. Untermassfeld (Thuringia, Germany)

This locality was discovered in 1978 in Central Germany and since then it has yielded a significant amount of palaeontological information, as it comprises a nearly complete fauna (Kahlke, 2000). Its significance is summarized by the same author (Kahlke, 2000), who states that the '*Untermassfeld fossil assemblage illustrates an important step in the transition from Latest Villafranchian to Early Middle Pleistocene faunas in Europe*'.

4.4.1. Biostratigraphy

The Pleistocene fossiliferous deposits of Untermassfeld have been found in fluvial sands at the eastern bank of the Werra River, which lay on top of M.-L. Triassic limestones (Kahlke, 2000; Kahlke & Gaudzinski, 2005). The sequence that can be seen in **Figure 7** is from the

bottom to the top: a 7-8 m layer of coarse gravels, a ca. 12 m thick bed of floodplain deposits, a 4 m bed of channel-fill deposits and a 1-2 m bed of silty clay. The aforementioned indicate significant flood events, which can also be confirmed by the high accumulation of vertebrate skeletons at the banks of the river (Kahlke, 2000). The fossiliferous sediments are the floodplain deposits, which are divided in the Lower Fluvial Sands and the Upper Fluvial Sands (Kahlke & Gaudzinski, 2005).

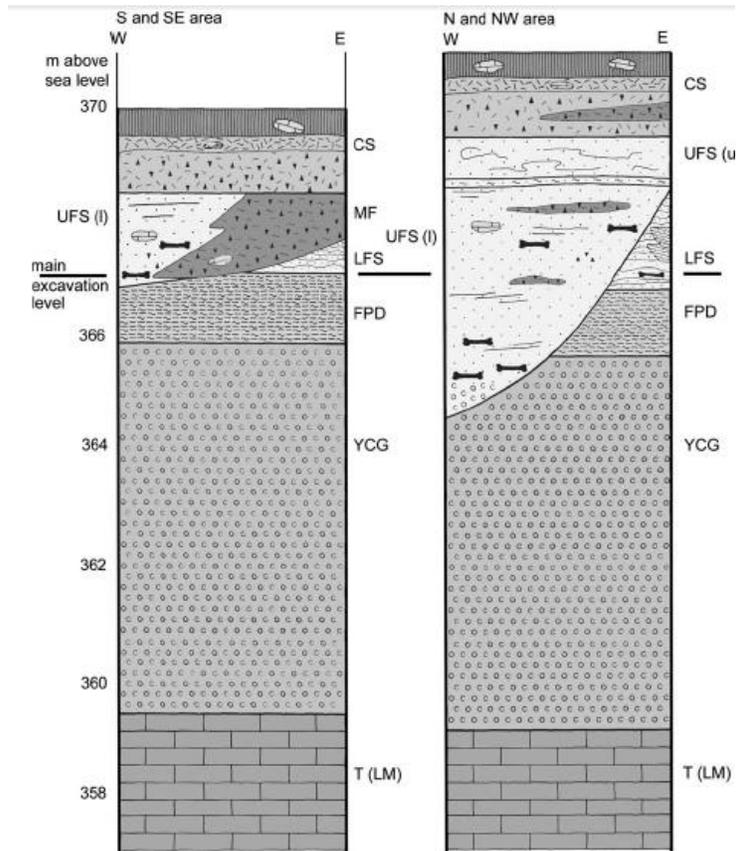


Figure 7. Diagrammatic sections of the Untermassfeld excavated area (T (LM): M. Triassic limestone, YCG: 'Younger Coarse Gravels (Eburonian deposition-Waalian weathering), FPD: E. Pleistocene floodplain deposits, LFS: Lower Fluvial Sands, UFS (l): lowermost Upper Fluvial Sands, MF: coarse clastic mudflow, UFS (u): uppermost Upper Fluvial Sands, CS: post-L. Pleistocene cover sediments) (Kahlke & Gaudzinski, 2005).



4.4.2. The Fauna

An updated faunal list of Untermassfeld (for mammals only) is given in **Table 9**.

Table 9. Updated faunal list of the Untermassfeld fossiliferous locality (according to Kahlke, 2000; Kahlke, 2004; Breda & Marchetti, 2005; Kahlke & Gaudzinski, 2005 and Kahlke et al., 2011 – authors that have discussed this faunal assemblage).

Untermassfeld Faunal Assemblage	
Carnivora:	
<i>Panthera (onca) gombaszoegensis</i>	<i>Homotherium crenatidens</i>
<i>Lycaon lycanoides</i>	<i>Pachycrocuta brevirostris</i>
<i>Acinonyx pardinensis pleistocaenicus</i>	<i>Ursus cf. dolinensis</i>
<i>Puma pardoides</i>	<i>Canis mosbachensis</i>
<i>Megantereon cultridens adroveri</i>	<i>Meles hollitzeri</i>
<i>Lynx issiodorensis ssp. ex aff. spelaeus</i>	
Perissodactyla:	
<i>Stephanorhinus hundsheimensis</i>	<i>Equus wuesti</i>
Artiodactyla:	
<i>Bison menneri</i>	<i>Alces carnutorum</i>
<i>Eucladoceros giulii</i>	<i>Capreolus cusanoides</i>
<i>Hippopotamus antiquus</i>	<i>Sus scrofa priscus</i>
<i>Dama nestii vallonnetensis</i>	
Proboscidea:	
<i>Mammuthus sp. (advanced M. meridionalis and/or M. trogontherii)</i>	
Primates:	
<i>Macaca sylvanus florentina</i>	
Soricomorpha:	
<i>Talpa cf. europaea</i>	<i>Sorex runtonensis</i>
<i>Talpa cf. minor</i>	<i>Beremendia cf. fissidens</i>
<i>Sorex (Drepanosorex) ex gr. margaritodon - savini</i>	
Rodentia:	
<i>Castor fiber</i>	<i>Apodemus cf. sylvaticus</i>
<i>Trogontherium cuvieri</i>	<i>Sciurus cf. whitei</i>
<i>Clethrionomys cf. hintonianus</i>	<i>Glis sackdillingensis</i>
<i>Pliomys episcopalis</i>	<i>Cricetus cf. runtonensis</i>
<i>Mimomys savini</i>	<i>Microtus thenii</i>
<i>Mimomys (Cseria) pusillus</i>	<i>Hystrix sp.</i>
<i>Spermophilus (Urocitellus) ex gr. primigenius/polonicus</i>	
Lagomorpha:	
<i>cf. Lepus sp.</i>	
Erinaceomorpha:	



Erinaceus cf. europaeus

The occurrence of *Puma pardoides* at Untermassfeld (**Table 9**) is the earliest specimen of this taxon that has been found so far in Europe (Kahlke, 2004). Its origin though is still questionable (African or Eurasian) (Hemmer *et al.*, 2004). *Puma pardoides* should have replaced *Megantereon cultidrens adroveri* (*Megantereon megantereon*) and been replaced by *Panthera pardus* (Kahlke, 2004).

The Untermassfeld faunal assemblage has been thoroughly studied since it was first discovered. This has resulted in a well-defined faunal list that does not contain inaccuracies. This is due to the fact that it was studied mainly by Ralf-Diedrich Kahlke and his colleagues who supported this avoidance of misidentifications. As a result we found no reason to argue with the authors (see **Table 9**) that provided information for this faunal assemblage.

Something that has to be distinguished though is about the genus *Cervalces*. There is a debate concerning this matter, as many authors recognize *Alces alces* as the only species of that genus and they refer to the earlier forms as *Cervalces* (Breda & Marchetti, 2005). This distinction is made because of some differences in skull shape between the two genera. However, the observed differences are not significant enough to make a distinction between *Alces* and *Cervalces*, due to the absence of intermediate forms which could give us useful information about the evolution of those genera. As a result, here it will be excluded the genus *Cervalces*.

Contamination: *Ursus cf. dolinensis*, *Mammuthus trogontherii*, *Talpa cf. europaea*, *Clethrionomys cf. hintonianus*, *Mimomys savini*.

4.4.3. Age of the fauna

Magnetostratigraphic analysis gave an age slightly younger than the onset of the Jaramillo subchron, which occurs ca. 1.05 ± 0.11 Ma for the Untermassfeld faunal assemblage (Kahlke, 2000 and 2004; Breda & Marchetti, 2005; Kahlke & Gaudzinski, 2005; Kahlke *et al.*, 2011).

4.4.4. Palaeoenvironment

The well-studied Untermassfeld faunal assemblage is indicative of a distinct warm interval, which is apparent by the warm-adapted and thermophilous faunal elements (Kahlke & Gaudzinski, 2005; Kahlke *et al.*, 2011). This interpretation is supported by the fact that the Untermassfeld Faunal Assemblage lacks cold-adapted faunal elements. Summer temperatures at that site were higher than today's ones (Kahlke *et al.*, 2011).



To be more specific, the palaeoclimate of the region was characterized by temperate winters, with the lowest temperatures not less than a few degrees Celsius below zero and warmer than today's summers, with more than 60 days with temperature more than 25°C (Kahlke, 2000; Kahlke & Gaudzinski, 2005; Kahlke *et al.*, 2011). Furthermore, the palaeohabitat is indicative of a river valley with humid (forested areas) and dry (shrub and grasslands) patches as it is indicated not only by the faunal assemblage, but also from the palaeoflora (Kahlke & Gaudzinski, 2005; Kahlke *et al.*, 2011). Moreover, there should have been several flood events that were caused by intensive rainfalls (mainly during autumn and winter). In addition, the whole biosystem should have been largely influenced by the Atlantic Ocean and the Mediterranean Sea (Kahlke, 2000).

The faunal elements that indicate the aforementioned palaeoenvironmental properties are the following: *Mammuthus trogontherii* and *Stephanorhinus hundsheimensis* (open grasslands influenced by continental conditions during interglacials); Cervidae, *Sus scrofa priscus*, *Panthera (onca) gombaszoegensis* and *Canis mosbachensis* (fully temperate wooded interglacial); *Macaca sylvanus florentina* (temperate woodland-mixed environment); *Sciurus cf. whitei* (woodland); Bovidae (open environment); *Hippopotamus antiquus* (warm-humid environment, with warm summers and mild-humid winters); Talpidae and Castoridae (water bodies).

4.5. Het Gat (North Sea, the Netherlands)

Het Gat (Dutch for 'The Pit') is a narrow trench at the bottom of the North Sea, which has accumulated a considerable amount of fossils. The fossils that are retrieved by fishing vessels are heavily mineralized and they come from the Yarmouth Roads Formation (Mol *et al.*, 2003; Kahlke *et al.*, 2011).

4.5.1. Biostratigraphy

Het Gat (**Figure 8**) is an elongated narrow trench that is adjacent to the Brown Bank in the southern North Sea. The maximum depth of Het Gat is 46 m and at the bottom of the area are boulders, coarse-grained brown sands that are irregularly folded and fine-grained clays. All those are structures and depositions indicative of a glaciation phase, which were most probably formed during the Elsterian glaciation. Eemian and Holocene sediments sit on top of the Yarmouth Roads Formation. The lower limit of this formation is at ca. 60-200 m, which means that no formations underneath it can be exposed as they are completely covered by the Yarmouth Roads Formation. Moreover, it is comprised by fluvial sediments of E. Waalian-E. Cromerian. Pollen analysis that was carried out on the top layers of the Yarmouth Roads Formation shows that the palaeoflora is characteristic of an interglacial period (Waalien or Bavelian) (Mol *et al.*,



2003). The fossils found come from the Yarmouth Roads Formation (Mol *et al.*, 2003; Kahlke *et al.*, 2011) and no older faunae have been retrieved. As a result the fossils cannot be older than the Waalian. Beds of Eemian age lay directly on top of the Yarmouth Roads Formation, while beds of intermediate age are absent (Mol *et al.*, 2003).

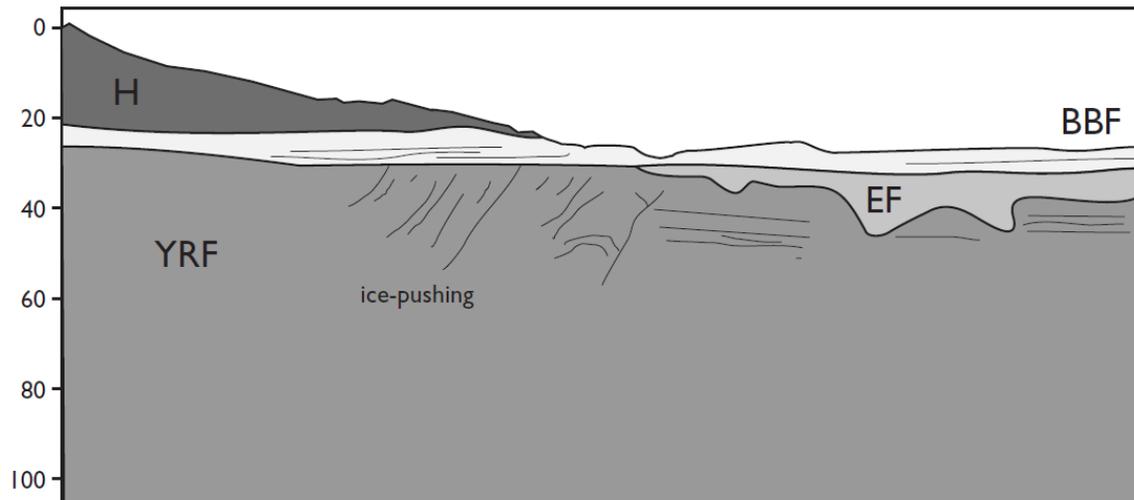


Figure 8. Profile through Het Gat. (YRF: Yarmouth Roads Formation, EF: Eem Formation, BBF: Brown Bank Formation, H: Holocene Sediments (Brown Bank)) (Mol *et al.*, 2003).

4.5.2. The fauna

An updated faunal list of this locality is given in **Table 10**.

Table 10. Updated faunal list of the Het Gat fossiliferous locality (according to Mol *et al.*, 2003 and Kahlke *et al.*, 2011 – authors that have discussed this faunal assemblage).

Het Gat Faunal Assemblage	
Carnivora:	
<i>Homotherium cf. latidens</i>	<i>Ursus etruscus</i>
Perissodactyla:	
<i>Stephanorhinus etruscus</i>	<i>Equus robustus</i>
Artiodactyla:	
<i>Alces latifrons</i>	<i>Bison cf. menneri</i>
<i>Hippopotamus cf. antiquus</i>	<i>Megaloceros dawkinsi</i>
<i>Eucladoceros ctenoides</i>	<i>Megaloceros savini</i>
Proboscidea:	
<i>Mammuthus trogontherii</i>	<i>Mammuthus meridionalis</i>



Het Gat faunal assemblage is well defined and significant misinterpretations seem absent. As a result there is no reason to debate with the aforementioned authors (**Table 10**).

Contamination: *Equus robustus*, *Mammuthus trogontherii*.

4.5.3. Age of the fauna

Mol *et al.*, (2003) suggest an age of M.-L. Bavelian for the Het Gat faunal assemblage. Kahlke *et al.*, (2011) place this assemblage at the Jaramillo normal subchron (Bavel interglacial). As a result, this locality has an estimated age of ca. 1.07-0.99 Ma. Furthermore, the faunal assemblage of this locality is well correlated to Untermassfeld faunal assemblage according to faunal and chronological criteria (see also **Section 4.8.** and **Chapter 5**).

4.5.4. Palaeoenvironment

Het Gat faunal assemblage is indicative of an interglacial stage (Mol *et al.*, 2003). More specific it is of a Bavelian interglacial stage and it is characterized of a warm palaeoclimate and an open with forested patches palaeohabitat (Kahlke *et al.*, 2011). In addition, the presence of water bodies is highly probable due to the presence of the hippopotamus (Mol *et al.*, 2003).

Among the taxa that have been indicated in earlier chapters concerning their palaeoenvironmental preferences, *Homotherium cf. latidens* should be added, which is indicative of interglacial environments.

4.6. Eurogeul (North Sea, the Netherlands)

Eurogeul is a channel in the southern North Sea, which gives ships access to the Port of Rotterdam. In 2000 started 'the North Sea project', which aims to tell the story of the region in Pleistocene, according to faunal and floral elements (Mol *et al.*, 2006).

4.6.1. Biostratigraphy

The Eurogeul has not been well studied until now and there are many complications that still need to be solved yet. Although, the available stratigraphic data can be seen in **Figure 9**. The fossils were found in the Kreftenheye Formation (Eemian-L. Weichselian), which is divided in three layers: sands with marine molluscs at the lower part (Eemian), fluvial sands with no marine indication and fine-grained fluvial sands at the upper part.



4.6.2. The fauna

An updated faunal list of the terrestrial mammals that were found in Eurogeul is given in **Table 11**.

Table 11. Updated faunal list of the Eurogeul fossiliferous locality (according to own observations from the Natuurhistorisch Museum Rotterdam collection (**Table 3**) and Mol et al., 2006 – authors that have discussed this faunal assemblage).

<i>Eurogeul Faunal Assemblage</i>	
Carnivora:	
<i>Ursus cf. arctos</i>	<i>Panthera spelaea</i>
<i>Crocuta crocuta spelaea</i>	<i>Canis sp.</i>
Perissodactyla:	
<i>Equus caballus</i>	<i>Coelodonta antiquitatis</i>
<i>Equus sp.</i>	<i>Stephanorhinus kirchbergensis</i>
Artiodactyla:	
<i>Bison priscus</i>	<i>Megaloceros giganteus</i>
<i>Ovibos moschatus</i>	<i>Alces alces</i>
<i>Rangifer tarandus</i>	<i>Cervus elaphus</i>
Proboscidea:	
<i>Mammuthus primigenius</i>	<i>Elephas antiquus</i>
Rodentia:	
<i>Castor fiber</i>	
Soricomorpha:	
<i>Desmana cf. moschata</i>	

The only inaccuracies or misinterpretations of the Eurogeul faunal assemblage had to do with *Panthera spelaea*. For this case, the cave lion sometimes is referred as a subspecies of *Panthera leo*, *Panthera leo spelaea*. Although, a recent study has shown that the cave lion is a distinct species from *Panthera leo* (Sotnikova & Nikolskiy, 2006).

4.6.3. Age of the fauna

The faunal assemblage of Eurogeul has an estimated age of 44.1-28.0 Ka (L. Pleistocene) according to radiocarbon dating (Mol et al., 2006; Natuurhistorisch Museum Rotterdam).



4.6.4. Palaeoenvironment

The Eurogeul faunal assemblage is indicative of the *Mammuthus* – *Coelodonta* Faunal Complex, which is comprised of cold-adapted faunal elements (Mol *et al.*, 2006; Kahlke & Lacombat, 2008). Specifically, it represents a cold stage, shortly before the Last Glacial Maximum (Mol *et al.*, 2006). Furthermore, the palaeohabitat shows Mammoth steppe characteristics, which is also confirmed by palynological evidence. The region must have been part of the Rhine-Meuse delta system, two rivers that were drained in the shallow North Sea and formed a large estuary (Mol *et al.*, 2006).

The taxa that belong to the *Mammuthus* – *Coelodonta* Faunal Complex (apart from *Mammuthus primigenius* and *Coelodonta antiquitatis*) are *Rangifer tarandus*, *Ovibos moschatus* and *Bison priscus*. *Elephas antiquus* and *Stephanorhinus kirchbergensis* which are indicative of an interglacial stage can be considered as a contamination of the assemblage. Although, they could have been the last or first members of the beginning or termination of an interglacial stage. *Desmana cf. moschata* and *Castor fiber* show a more humid environment. All those point to a cold open environment with forested patches, which was part of the Rhine-Meuse delta system.

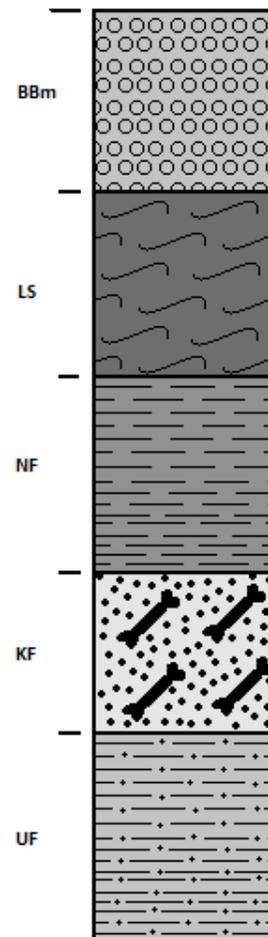


Figure 9. Synopsis of the stratigraphy of the Eurogeul locality; layers are indicated from the top (the bottom of the sea) downwards (BBm: Blight Bank member of the Southern Bight Formation (M. Holocene-Recent), LS: Lagoonal sediments (E. Holocene), NF: Naaldwijk Formation (L. Weichselian-E. Holocene grey clay), KF: Fossiliferous Kreftenheye Formation (Eemian-L. Weichselian), UF: Urk Formation (L. Saalian fluvatile deposits)) (Mol *et al.*, 2006). *Note that Urk Formation is not exposed in Eurogeul.

4.7. Maasvlakte-2 (South Holland, the Netherlands)

Maasvlakte-2 is an artificial peninsula, the construction of which is based on sand suppletion, which is aiming to the extension of the port of Rotterdam. The sand that is used for the construction of Maasvlakte-2 is dredged from a nearby area and then it is



sprayed in the sea again. L. Pleistocene fossils have been retrieved from the sediments of this locality by sand dredging and fishing vessels.

4.7.1. Biostratigraphy

The extension of the Maasvlakte (Maasvlakte-2) at the Port of Rotterdam is done by land retrieval from the North Sea. The sand that is used for the construction of Maasvlakte-2 is retrieved from an area 15 Km west of it (Reumer *et al.*, 2010; Mol *et al.*, 2006). Those sands were originally taken from a depth of ca. 22-23 m (now the sea-floor of the area is ca. 40m) (Reumer *et al.*, 2010). As a result it is not possible to derive any information concerning the biostratigraphy of this locality. At least not until more research will be conducted concerning this topic.

4.7.2. The fauna

A list of the faunal elements that have been identified is given in **Table 12**.

Table 12. Updated faunal list of the Maasvlakte-2 fossiliferous locality (according to own observations from the Natuurhistorisch Museum Rotterdam collection (**Table 4**) and Reumer *et al.*, 2010 – authors that have discussed this faunal assemblage).

Maasvlakte-2 Faunal Assemblage	
Carnivora:	
<i>Lutra lutra</i>	<i>Panthera spelaea</i>
<i>Ursus cf. arctos</i>	<i>Crocuta crocuta spelaea</i>
<i>Canis sp.</i>	
Perissodactyla:	
<i>Coelodonta antiqutatis</i>	<i>Equus caballus</i>
Artiodactyla:	
<i>Bison priscus</i>	<i>Megaloceros giganteus</i>
<i>Cervidae sp.</i>	<i>Rangifer tarandus</i>
<i>Cervus (cf.) elaphus</i>	<i>Bos primigenius</i>
<i>Bos sp.</i>	
Proboscidea:	
<i>Mammuthus primigenius</i>	
Primates:	
<i>Homo sapiens</i>	
Rodentia:	
<i>Castor fiber</i>	<i>Arvicola cantiana</i>
<i>Arvicola sp.</i>	<i>Mimomys savini</i>
<i>Microtus agrestis</i>	<i>Microtus sp.</i>



The inaccuracies of this faunal assemblage are not significant, too. Apart from some specimens that have been identified up to the genus level, the most interesting discussion is erected from the relationship between *Crocota crocuta* and *Crocota crocuta spelaea*, which has been recently questioned (Rohland *et al.*, 2005). For the purpose of this research they will be considered the same species, due to the many similar morphological characteristics that they share. Future research based on DNA analysis could resolve this matter.

4.7.3. Age of the fauna

The age of the Maasvlakte-2 faunal assemblage is of L. Pleistocene and more specific ca. 40 Ka (Reumer *et al.*, 2010 and pers. comm.; Natuurhistorisch Museum Rotterdam).

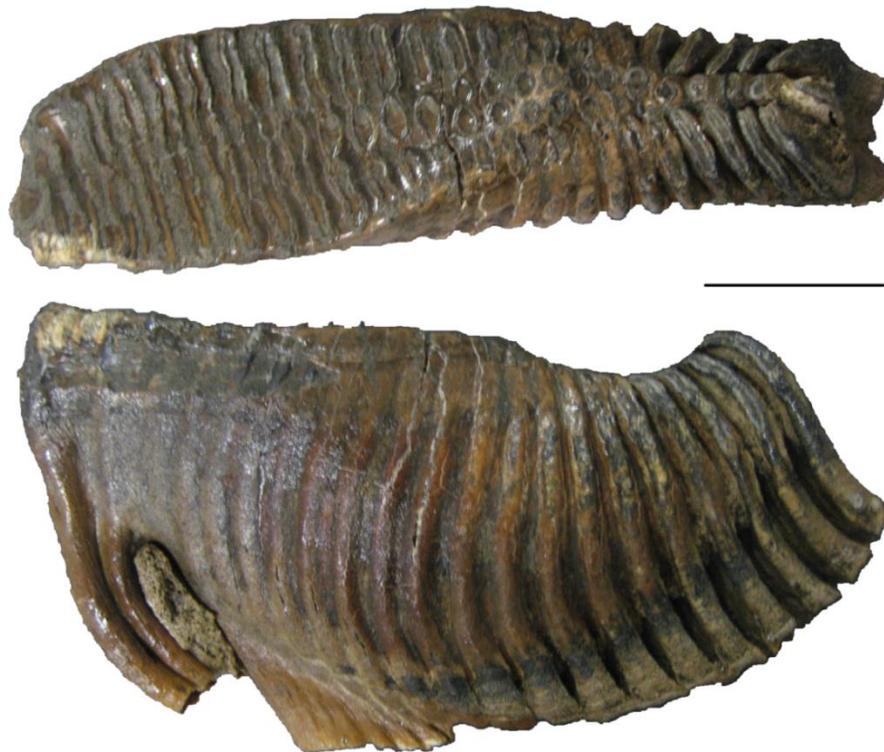


Figure 10. *Mammuthus primigenius molar*. Scale = 5 cm.

4.7.4. Palaeoenvironment

The Maasvlakte-2 faunal assemblage is representative of the *Mammuthus* – *Coelodonta* Faunal Complex (**Figure 10**), a faunal complex distinguished by cold-adapted faunal elements (Kahlke & Lacomat, 2008; Reumer *et al.*, 2010).



The fossiliferous locality of Maasvlakte-2 has similar palaeoenvironmental indications to that of Eurogeul. As a result the fauna shows characteristics of an open cold environment with forested patches, which must have been part of the Rhine-Meuse delta system, too.

4.8. Faunal Similarity

In order to further investigate the studied faunae, it was chosen to compare them aiming to the better understanding of the reasons that govern their composition. For that purpose each fauna was compared to all the others both for macro- and micromammals. The derived results of that comparison can be seen in **Table 13** and **14**.

Table 13. Comparison of the macromammals from the studied localities between them.

<i>Chilhac - Oosterschelde</i>	<i>Chilhac - Tegelen</i>	<i>Chilhac - Untermassfeld</i>
species in common: 5	species in common: 5	species in common: 1
genus in common: 3	genus in common: 2	genus in common: 6
total taxa in common: 8	total taxa in common: 7	total taxa in common: 7
<i>Chilhac - Het Gat</i>	<i>Chilhac - Eurogeul</i>	<i>Chilhac - Maasvlakte-2</i>
species in common: 3	species in common: 0	species in common: 0
genus in common: 4	genus in common: 3	genus in common: 5
total taxa in common: 7	total taxa in common: 3	total taxa in common: 5
<i>Oosterschelde - Tegelen</i>	<i>Oosterschelde - Untermassfeld</i>	<i>Oosterschelde - Het Gat</i>
species in common: 8	species in common: 0	species in common: 5
genus in common: 4	genus in common: 11	genus in common: 6
total taxa in common: 12	total taxa in common: 11	total taxa in common: 11
<i>Oosterschelde - Eurogeul</i>	<i>Oosterschelde - Maasvlakte-2</i>	<i>Tegelen - Untermassfeld</i>
species in common: 4	species in common: 8	species in common: 2
genus in common: 8	genus in common: 6	genus in common: 6
total taxa in common: 12	total taxa in common: 14	total taxa in common: 8
<i>Tegelen - Het Gat</i>	<i>Tegelen - Eurogeul</i>	<i>Tegelen - Maasvlakte-2</i>
species in common: 5	species in common: 0	species in common: 1
genus in common: 1	genus in common: 5	genus in common: 5
total taxa in common: 6	total taxa in common: 5	total taxa in common: 6
<i>Untermassfeld - Het Gat</i>	<i>Untermassfeld - Eurogeul</i>	<i>Untermassfeld - Maasvlakte-2</i>
species in common: 3	species in common: 0	species in common: 1
genus in common: 6	genus in common: 8	genus in common: 8
total taxa in common: 9	total taxa in common: 8	total taxa in common: 6
<i>Het Gat - Eurogeul</i>	<i>Het Gat - Maasvlakte-2</i>	<i>Eurogeul - Maasvlakte-2</i>
species in common: 0	species in common: 1	species in common: 8
genus in common: 7	genus in common: 7	genus in common: 4
total taxa in common: 7	total taxa in common: 8	total taxa in common: 12



Table 14. Comparison of the micromammals from the studied localities between them.

<i>Chilhac - Oosterschelde</i>	<i>Chilhac - Tegelen</i>	<i>Chilhac - Untermassfeld</i>
species in common: 0	species in common: 0	species in common: 0
genus in common: 1	genus in common: 2	genus in common: 2
total taxa in common: 1	total taxa in common: 2	total taxa in common: 2
<i>Chilhac - Eurogeul</i>	<i>Chilhac - Maasvlakte-2</i>	<i>Oosterschelde - Tegelen</i>
species in common: 0	species in common: 0	species in common: 8
genus in common: 1	genus in common: 1	genus in common: 1
total taxa in common: 1	total taxa in common: 1	total taxa in common: 9
<i>Oosterschelde - Untermassfeld</i>	<i>Oosterschelde - Eurogeul</i>	<i>Oosterschelde - Maasvlakte-2</i>
species in common: 3	species in common: 1	species in common: 1
genus in common: 1	genus in common: 0	genus in common: 1
total taxa in common: 4	total taxa in common: 1	total taxa in common: 2
<i>Tegelen - Untermassfeld</i>	<i>Tegelen - Eurogeul</i>	<i>Tegelen - Maasvlakte-2</i>
species in common: 5	species in common: 1	species in common: 1
genus in common: 7	genus in common: 1	genus in common: 1
total taxa in common: 12	total taxa in common: 2	total taxa in common: 2
<i>Untermassfeld - Eurogeul</i>	<i>Untermassfeld - Maasvlakte-2</i>	<i>Eurogeul - Maasvlakte-2</i>
species in common: 1	species in common: 1	species in common: 1
genus in common: 0	genus in common: 2	genus in common: 0
total taxa in common: 1	total taxa in common: 3	total taxa in common: 1

From the tables above it is apparent that the best correlation is between Oosterschelde, Tegelen and Untermassfeld for both macro- and micromammals. The aforementioned are well correlated with Het Gat as well (in terms of macromammals only). Moreover, Chilhac shows a relatively good resemblance with all the aforementioned localities. Eurogeul and Maasvlakte-2 are sharing many common faunal elements, too.

4.9. Great Britain – The Netherlands

Another topic that has undergone a lot of research the past decades is the stratigraphic correlation of the eastern part of Great Britain with the Netherlands. Both areas show many similarities in terms of stratigraphy, vertebrate and invertebrate palaeontology, etc. Gibbard *et al.* (1991) showed that the different stages between the two regions correlate well. This correlation can be seen in **Figure 11**.

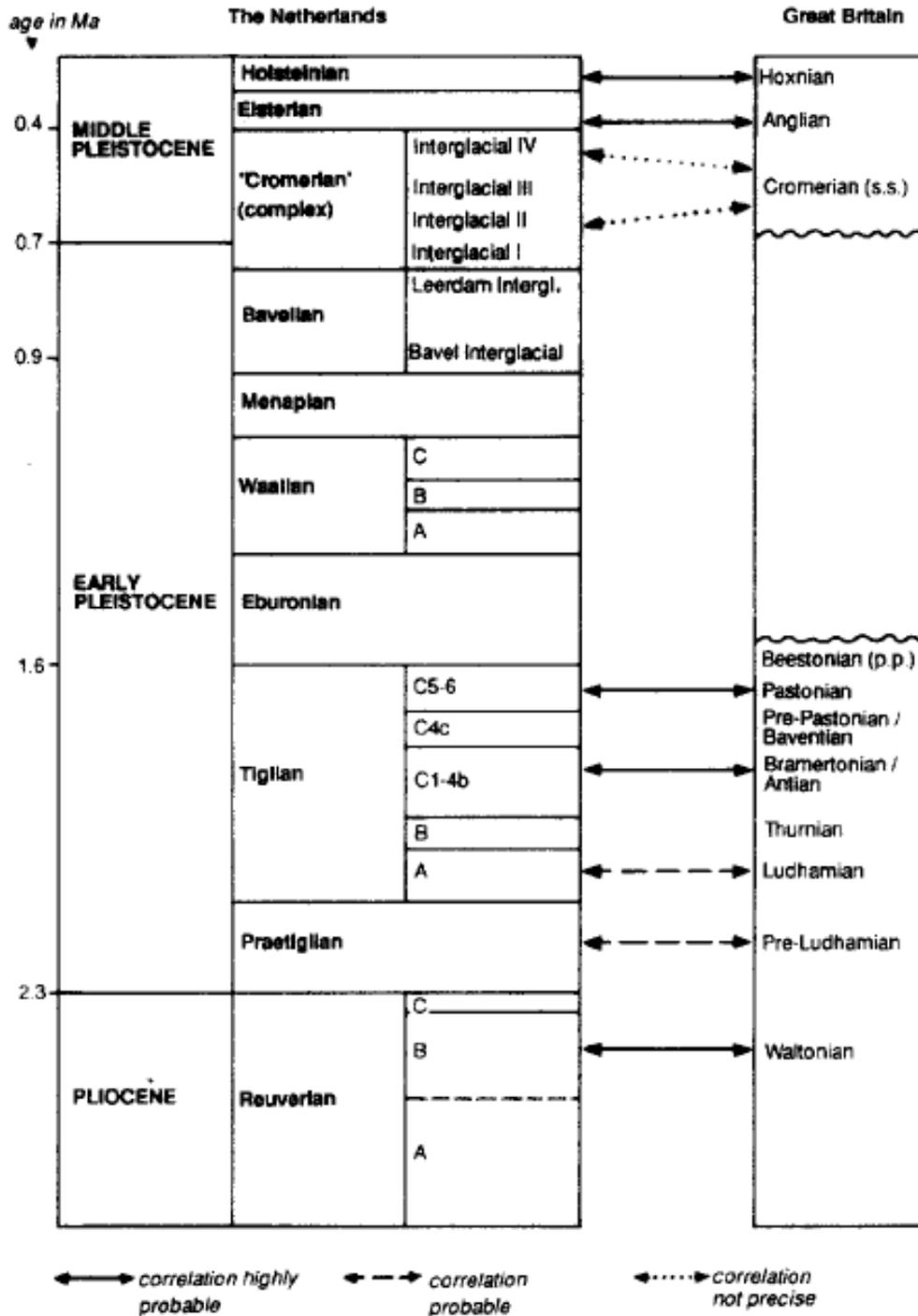


Figure 11. Correlation of Pliocene-Recent beds in East Great Britain and the Netherlands (Gibbard et al., 1991). *Note that the limits of the different stages are not equivalent to the ones used for this project.



5. Discussion

As was stated before, the so-called ‘Wolf Event’ is a good starting point for this chapter. As long as carnivores are not usually specialists, their reaction to climate changes is slower than that of herbivores, which are more easily affected by such changes. Therefore the carnivores react (almost) only when the climatic changes are modifying the vegetational cover which deeply affects the herbivore guild in terms of evolution and/or migration (Palombo *et al.*, 2008). The ‘true wolves’ first appear in the European record only during E. Pleistocene. This (almost) coincides with a shift in Milanković cyclicity in Earth’s climate towards more pronounced changes (3 Ma). The effects of the orbital cycles were not so pronounced only until 2.6 Ma (Kahlke *et al.*, 2011), when the obliquity starts to be the controlling factor of the climate. Northern Africa’s climate gradually starts to be affected mainly through the change of the monsoonal system, which in turn affects the vegetational cover and causes the herbivores to migrate. Although, those changes that are becoming even more pronounced trigger even more substantial changes to the faunae and result in the migration of the carnivores as well, which follow their prey. As a result, the arrival of wolves in Europe occurs during E. Pleistocene, some 0.8 Ma since the beginning of the climate change. Nevertheless, as it was already stated, carnivores reacted to the climate change slower than the herbivores and the turnover lagged behind the herbivore renewal (Palombo *et al.*, 2008).

Turnover/migration events (like the ‘Wolf Event’) are not something new for the mammals though. In the recent geological history (Pleistocene-Recent) other events (**Figure 12**) that are of great significance, too, have occurred. Those are the ‘Elephant-Equus Event’ which occurred at ca. 2.6 Ma (at the

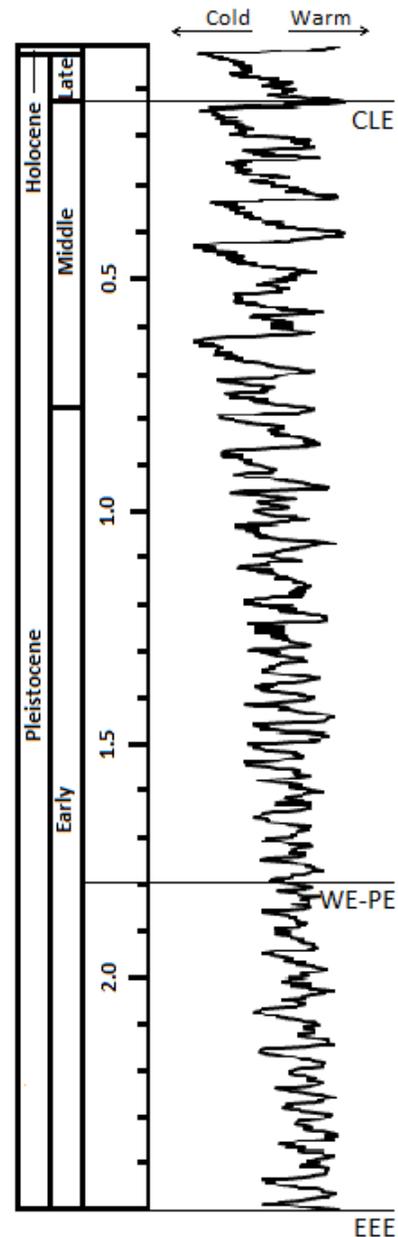


Figure 12. Major mammalian events during E. Pleistocene-Recent (EEE: Elephant-Equus Event, WE: Wolf Event, PE: Pachycrocuta Event, CLE: Crocuta “lion”-Leopard Event) together with the $\delta^{18}\text{O}$ record for the last 2.5 Ma (after Lisiecki & Raymo, 2005).



Plio/Pleistocene boundary (or the Gauss/Matuyama boundary)) (Azzaroli, 1995), the ‘*Pachyrocuta* Event’ that is dated during the former Plio/Pleistocene boundary (Palombo *et al.*, 2008) and the ‘*Crocota* “lion”-Leopard Event’ of the end of M. Pleistocene (Palombo *et al.*, 2008). All those events have to do with massive migrations from Africa and new arrivals in Europe, which are linked to renewals and/or replacements of the pre-existing faunae.

In other words, those mammalian events can be linked to climate change and more specific to Milanković oscillations (**Figure 12**). The Elephant-*Equus* Event coincides with the establishment of the new climatic conditions, the ‘*Wolf Event*’ and the ‘*Pachyrocuta* Event’ are a consequence of those changes and the ‘*Crocota* “lion”-leopard Event’ occurs at the time of a dramatic change from a glacial to an interglacial cycle.

A closer investigation of the $\delta^{18}\text{O}$ record (**Figure 13**) shows that until ca. 1.2 Ma the dominant oscillation that regulated the climate was obliquity. Between ca. 1.2-0.9 Ma the situation changes and the effect of eccentricity becomes stronger. During this period it is not clear, which is the major orbital parameter that influences the Earth’s climate. This trend progresses until after 0.9 Ma the main orbital parameter is the 100 Ka cycle of eccentricity, which continues until recent. The Pleistocene experiences a steady decrease of the temperature. Moreover, later into the Pleistocene when eccentricity is the controlling factor the differences between extreme warm/cold climatic oscillations are more pronounced than they were before.

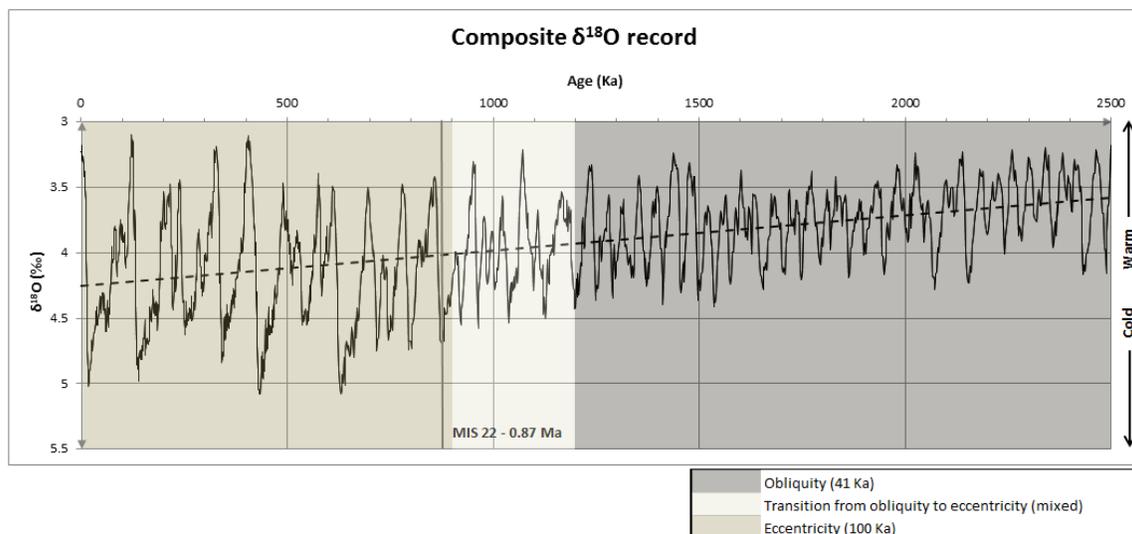


Figure 13. Composite $\delta^{18}\text{O}$ record for the last 2.5 Ma (data were taken from Lisiecki & Raymo, 2005). The dashed line represents an overall linear decrease of the $\delta^{18}\text{O}$. The grey line indicates the Marine Isotope Stage (MIS) 22, which occurs at 0.87 Ma.



Pronounced (inter-)glacial cyclicity started at ca. 3 Ma and it continues till recent (Raymo *et al.*, 2006). Glaciations are due to the amount of insolation that arrives on the surface of the Earth, which affects the temperature and enhances or lessens the development of ice sheets, which in turn alter the sea-level (more ice cover leads to sea-level drop and vice versa) and furthermore alter the geography and topography of the Earth. The Northern Hemisphere has been significantly affected by those (inter-)glacial cycles and especially Europe. The ice-sheets during Pleistocene were controlled by the orbital parameters that were described before.

The onset of the especially cold Marine Isotope Stage 22, at ca. 0.87 Ma (**Figure 13**), seems to form the inception of the eccentricity dominated period (Muttoni *et al.*, 2003). This correlates very well with a faunal turnover that is observed during E.-M. Pleistocene, where many species/taxa are becoming extinct at the end of the E. Pleistocene (end-Villafranchian) and new ones are taking over at the beginning of the M. Pleistocene (**Figure 14**). At some occasions it is observed that there is a time lag concerning an extinction/appearance, which can be postulated by a slower adaptation to new environmental conditions by a specific taxon.

Moreover, in **Figure 14** is observed that in several cases (e.g. Oosterschelde) the faunal assemblage contains taxa that are younger than the age of the locality and are unlikely to be found. There are several explanations for this occasion. First of all, all the studied localities were rivers or estuaries. This implies that the fossils are (almost) never found in situ, but they were carried by rivers, landslides, etc. It is also highly probable that the dating of those localities has to be reconsidered. Another problem that can lead to inaccuracies is contamination of an in situ fauna. This means that some other elements, which time range is out of the age of the locality, were brought and mixed with the other ones. An example of this is *Eucladoceros ctenoides* from Het Gat.

Coming back to the “*Wolf Event*’ topic again, it is clear that the story of the *Canis* lineage in Europe is complicated. Because the occurrences of *Canis “cipio”* from L. Miocene (Teruel, Spain) and *Canis* sp. from the 3.1 Ma site of Vialette (France) are unconfirmed, the most probable hypothesis would be the origination of this genus in N. America at ca. 4 Ma. The first Asian (East China) *Canis* that is dated at ca. 3.4 Ma shows that *Canis* dispersed in the whole Eurasia gradually and not instantaneously. This leads us to rethink the ‘*Wolf Event*’. The initial idea this hypothesis was that the dispersal of *Canis* in Europe was accomplished in a short interval. On the other hand, following the suggestion of Rook & Martínez-Navarro (2010) and Sotnikova & Rook (2010), this dispersal lasted longer and it must have been a diachronous event.

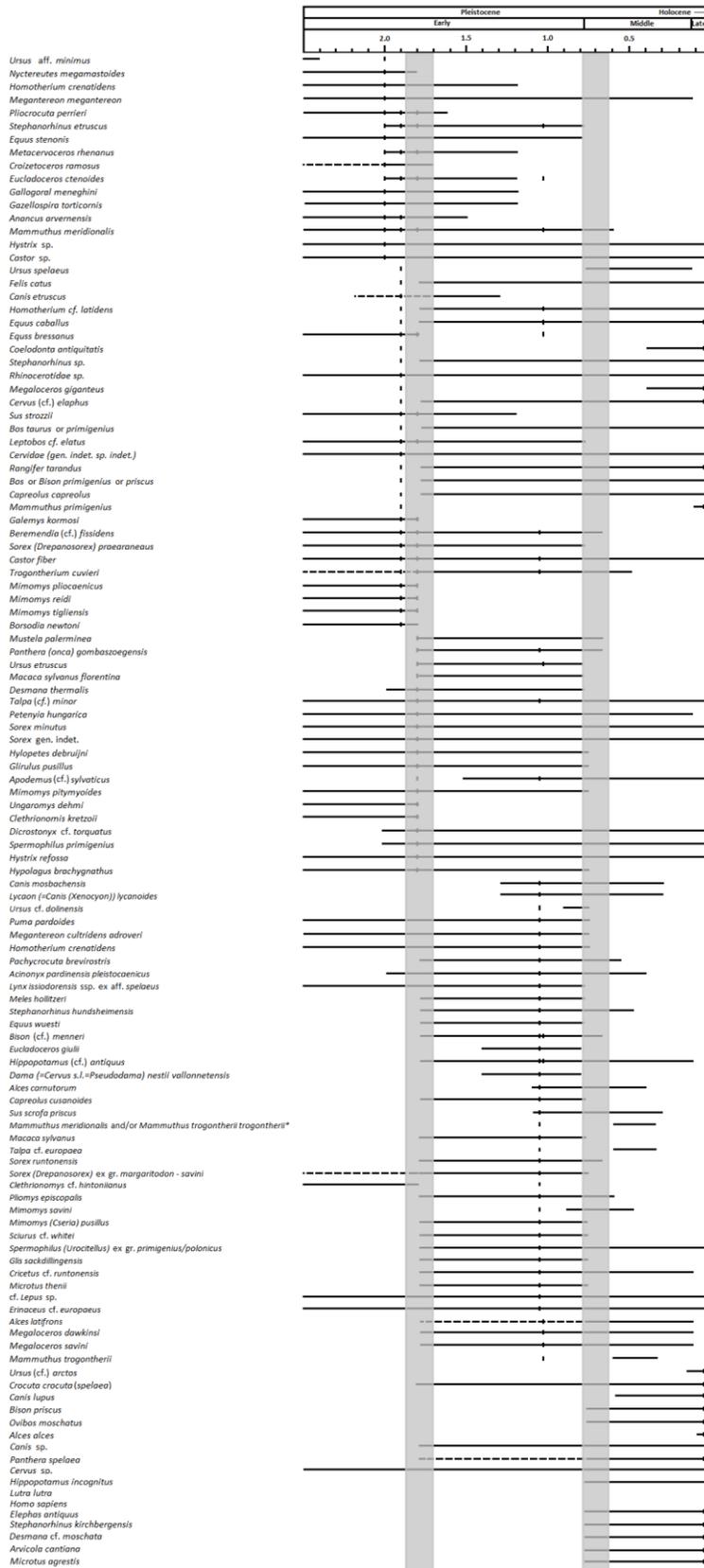


Figure 14. Biochronological distribution chart of all the taxa that were found at the localities that were studied for this project including their stratigraphic distribution (from the left to the right: Chiljac, Oosterschelde, Tegelen, Untermassfeld, Het Gat, Eurogeul, Maasvlakte-2). The grey stripes show the major turnover events of the Pleistocene as it derives from the studied faunal assemblages. *For the biostratigraphic distribution of all the taxa see **Table A4** and **A5**.



It is also worth to note that the Oosterschelde find results in the expansion of the geographical range of *Canis etruscus* up to North-Northwestern Europe, as the record until now spanned only up to Central Europe (Brugal & Boudadi-Maligne, 2011), showing that the dispersal of Canini was greater than currently believed.

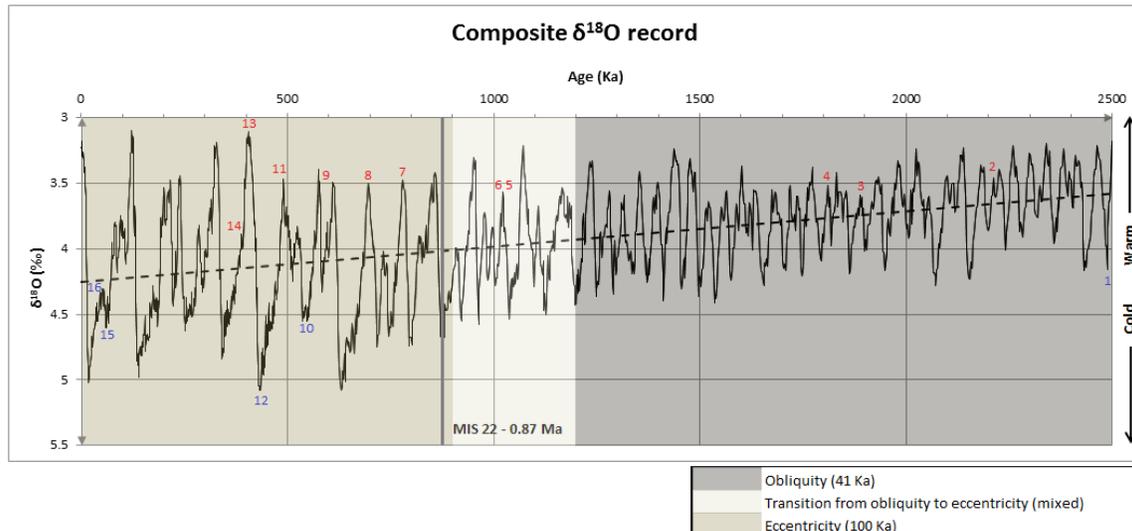


Figure 15. Composite $\delta^{18}\text{O}$ record for the last 2.5 Ma with faunae from Southern North Sea basin, Western, Northwestern and Central Europe ($\delta^{18}\text{O}$ data were taken from Lisiecki & Raymo, 2005). The dashed line represents an overall linear decrease of the $\delta^{18}\text{O}$. The grey line indicates the Marine Isotope Stage (MIS) 22, which occurs at 0.87 Ma. Numbers with blue colour indicate cold-adapted faunae and with red, warm-adapted faunae (1: Red Crag; 2: Chilhac; 3: Oosterschelde; 4: Tegelen, Cromer Forest-bed Formation; 5: Untermassfeld; 6: Het Gat; 7: Dorn-Drückheim 3; 8: Voigtstedt; 9: Mauer; 10: Ensemble I; 11: Ensemble II; 12: Ensemble III, Bad Frankenhausen; 13: Hoxne, Swancombe, Clacton, Neede, Steinheim/Murr, Heppenloch cave; 14: Terra Amata, Lunel-Viel; 15: Eurogeul; 16: Maasvlakte-2). Information for the faunae that were not described before were obtained by Kahlke et al. (2011).

By observing **Figure 15** it is evident that the terrestrial mammals of Europe are indirectly corresponding to the Milanković cyclicity. This means that during glacial ages, mainland Europe was inhabited by cold-adapted mammals and during interglacial stages by warm-adapted mammals. This can be easily seen at ca. 0.5 Ma, where the fossil record is richer and well dated. The Mauer faunal assemblage contains many taxa which are indicative of forested environment (*Capreolus capreolus priscus*, *Sus scrofa priscus*, *Stephanorhinus kirchbergensis*), a hippopotamus which indicates high temperatures in combination with humid environment and several other generalists. In total it represents an interglacial stage. This warm-adapted fauna is followed by a cold-adapted one, the Ensemble I faunal assemblage, with the occurrence of *Hemitragus bonali*, *Ovis ammon antiqua*, *Rangifer tarandus*, *Stephanorhinus hemiteochus*, *Equus mosbachensis*



and *Praeovibos priscus*. Ensemble II with *Dama clactoniana* and *Cervus elaphus* represents the following interglacial stage. The next glacial stage is apparent from the faunal assemblages of Ensemble III and Bad Frankenhausen with the latter being the earliest site of the *Mammuthus – Coelodonta* Faunal Complex and several other cold-adapted taxa in both localities (e.g. *Bison priscus*, *Rangifer tarandus*, etc.). Later on, a well-developed interglacial is following as it is seen in the faunal assemblages of Hoxne, Swancombe, Clanton, Neede, Steinheim/Murr and Heppenloch cave. The taxa found at those localities include *Dama clactoniana*, *Bos primigenius*, *Megaloceros giganteus*, *Capreolus capreolus*, *Cervus elaphus*, *Sus scrofa*, *Stephanorhinus kirchbergensis*, etc., all indicative of the warm conditions that dominated Europe at that time (ca. 0.4 Ma).

The comparison of the studied faunae revealed many interesting clues. Faunae which are close in terms of their age and geographical position were expected to be more closely related. This point of view was confirmed by the observation that Oosterschelde and Tegelen share many common faunal elements. This conclusion fits well with the criteria that were established. Although, sometimes similarities were observed between two localities that at least one or even both of the criteria were fulfilled (e.g. Chilhac-Het Gat). This can be explained concerning several factors. Firstly, the geographical range might not be a key factor for species distribution, as during those times of the intense climatic changes, migration and/or adaptation of species, was something common. Moreover, it was shown before (see **Figure 14**) that several species inhabited Europe for long time spans, which allows them to be found in several localities throughout Europe. This means, the (dis)similarity method needs closer consideration before giving any definite results.

For the case of this project it would be more accurate to say that Oosterschelde and Untermassfeld are correlated very well with Tegelen and Het Gat, respectively and they represent similar environments. In addition, there is a good resemblance between the two groups (one middle E. Pleistocene group and one late E. Pleistocene group). This is a basic characteristic of the Villafranchian faunae. More specific, those faunal units are all indicators of the L. Villafranchian biochronological unit. Villafranchian was divided in three stages (Early, Middle and Late) according to dispersal events (and evolutionary stages) of mammals that occurred during this period (Rook & Martínez-Navarro, 2010). As a result, during each stage of the Villafranchian is observed homogeneity of the faunae throughout most of the European continent (Rook & Martínez-Navarro, 2010). Chilhac shows a good resemblance with most of the faunae (Oosterschelde, Tegelen, Untermassfeld, Het Gat). This shows that this locality should have been part of the L. Villafranchian, too. On the other hand, Eurogeul and Maasvlakte-2 correlate well only between themselves, which are representatives of the *Mammuthus – Coelodonta*



Faunal Complex. Apart from this, the chronological difference with the rest of the faunae is minimum ca. 1 Ma. As a result, it is expected nothing more than a good correlation between them. It is observed though that Oosterschelde has a strong correlation with Eurogeul and Maasvlakte-2, too. This is due to the fact that the Oosterschelde faunal assemblage is a faunal mix, containing taxa of a later age as it has already been described (see **Section 4.2.2.**).

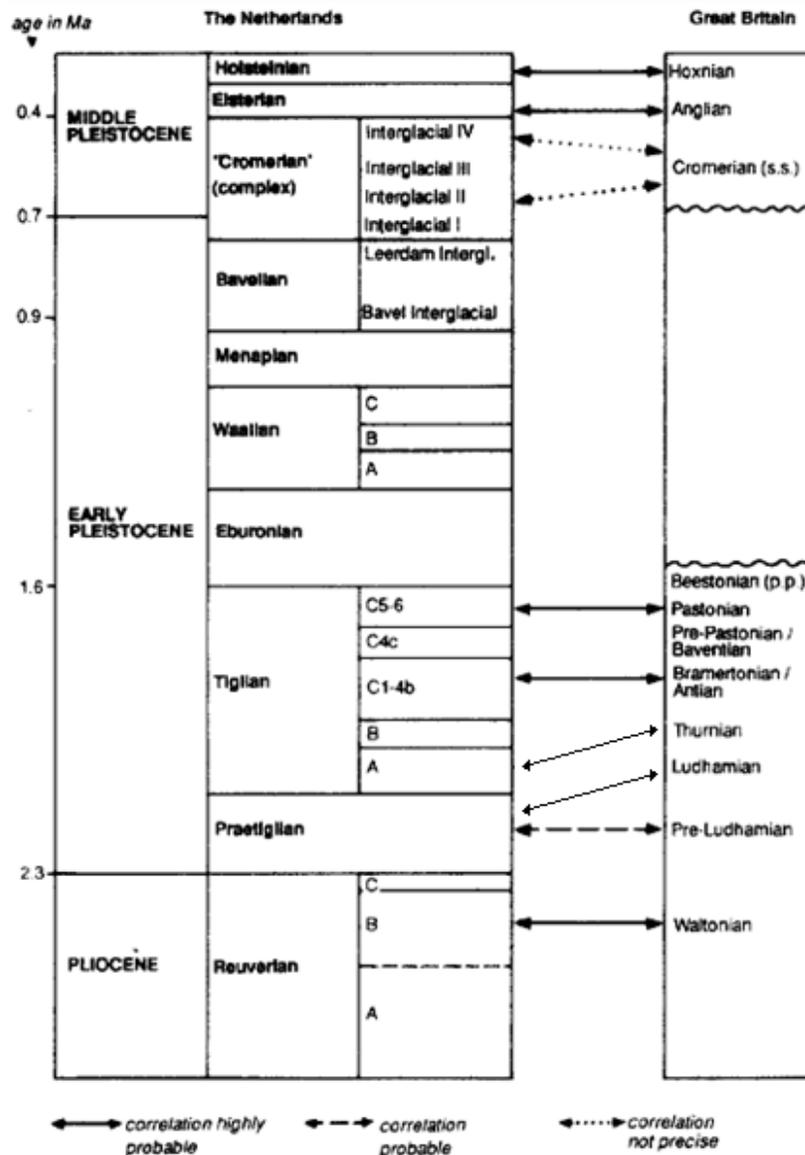


Figure 16. Correlation of Pleistocene-Recent beds in East Great Britain and the Netherlands (Gibbard et al., 1991), with the corrections (thin arrows) that were added by Kuhlmann et al. (2006) for Thurnian and Ludhamian. *Note that the limits of the different stages are not equivalent to the ones used for this project.

Concerning *Anancus arvernensis*, Kahlke et al. (2011), states that the last occurrence of this species is at Chilhac at ca. 2.0 Ma. In contrast, the same species occurs at Tegelen-Maalbeek, too. This locality is slightly older than Tegelen (van den Hoek Ostende & de Vos, 2006) and approximately of the same age with Oosterschelde. As a result, by taking this into account in addition to the results produced from this research, it is apparent that the last occurrence of *Anancus arvernensis* slightly postdates the suggestion of Kahlke et al. (2011) and places it at 1.9 Ma.

Concerning the biostratigraphic correlation between the



eastern part of Great Britain and the Netherlands, it was shown before (**Figure 11**) that both regions share many similar characteristics. Kuhlmann *et al.* (2006) worked on that topic and showed that the suggestion of Gibbard *et al.* (1991) is strong enough. The only inaccuracies that were observed are that the Ludhamian is a short warm interval that corresponds to the Pretiglian stage and the Thurnian to the Tiglian A (**Figure 16**). Also the limits of the different stages are not equivalent to the ones used for this project.



6. Conclusions

The recent find of a *Canis etruscus* mandible at Oosterschelde (Zeeland, the Netherlands) shows that the *Canis* group was dispersed up to Northwestern Europe at ca. 1.9 Ma, expanding its previous geographical range. However, the famous 'Wolf Event' seems to never have existed, as the dispersal of Canini was diachronous. The faunal assemblages of Chilhac (Auvergne, France), Oosterschelde (Zeeland, the Netherlands), Tegelen (Limburg, the Netherlands), Untermassfeld (Thuringia, Germany), Het Gat (North Sea, the Netherlands), Eurogeul (North Sea, the Netherlands) and Maasvlakte-2 (South Holland, the Netherlands) were updated and several of their characteristics (age, palaeoenvironment, resemblance) were redefined. Moreover, it was shown that *Anancus arvernensis* last appearance is at Tegelen-Maalbeek at ca. 1.9 Ma and not at Chilhac (2.0 Ma), which places it 0.1 Ma later than it was believed.

The faunae of Chilhac, Oosterschelde, Tegelen, Untermassfeld and Het Gat correlate well with each other in terms of their ecological niches. On the other hand, Eurogeul and Maasvlakte-2 share many common characteristics only between themselves. Those correlations prove the homogeneity that has been observed on the Villafranchian faunae. To continue, the correlation between the Netherlands and the East coast of Great Britain is further confirmed according to palaeontological, palynological, (bio)stratigraphical and lithological criteria and some inaccuracies that occurred during the past years were resolved.

In general, the study of the different faunal assemblages shows that Milanković cycles and the related sea-level fluctuations have caused mammalian events and more specific massive migrations and/or extinctions. This is evident from the patterns that occur concerning their composition. Nevertheless, it is certain that more research on this topic would give us a better insight. Hopefully, new finds will also help us fill the gaps that arise complications and will allow palaeontologists to reconstruct the history of the Quaternary mammals.



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Appendix

Table A1. Ramus measurements from the collection of the Laboratory of Paleontology (Department of Geology, Aristotle University of Thessaloniki) (W1: Width under P₁, H1: Height under P₁, W2: Width under P₂, H2: Height under P₂, L: Length, W: Width).

	Ramus				
	W1 (mm)	H1 (mm)	W2 (mm)	H2 (mm)	Diastema (mm)
<i>C. etruscus</i>	-	-	9.6	-	-
	12.2	20.6	12.2	23.5	-
<i>C. arnensis</i>	-	-	10.9	20.2	-
	10.8	17.6	10.2	19.7	3.4
	10.6	16.3	9.6	17.3	0.0
<i>C. apolloniensis</i>	10.7	18.3	9.7	19.1	4.8
	10.5	17.6	9.7	19.4	4.1
	10.2	15.9	9.6	19.1	2.7
	-	-	-	19.2	-
<i>C. (Xenocyon) sp.</i>	8.7	-	9.1	-	6.5
	9.7	16.9	8.7	19.6	5.4

Table A2. Teeth measurements from the collection of the Laboratory of Paleontology (Department of Geology, Aristotle University of Thessaloniki).

	P ₁		P ₂		C	
	L (mm)	W (mm)	L (mm)	W (mm)	L (mm)	W (mm)
<i>C. etruscus</i>	4.3	3.2	11.4	5.4	-	-
	-	-	11.0	5.0	-	-
<i>C. arnensis</i>	4.9	3.8	10.8	5.3	9.1	7.8
	4.5	3.8	10.3	5.0	9.1	6.4
<i>C. apolloniensis</i>	5.1	3.4	10.7	4.6	9.4	7.5
	5.2	3.6	10.3	4.6	9.2	6.9
	5.6	3.3	9.9	7.2	9.2	7.2
	-	-	9.4	4.4	-	-
<i>C. (Xenocyon) sp.</i>	5.6	3.9	11.1	4.6	9.4	6.2
	5.9	4.1	11.6	4.5	9.6	5.9

Table A3. Synonyms of the taxa encountered in this project.

In this project	Synonyms
<i>Megantereon megantereon</i>	<i>Megantereon cultridens</i>
<i>Pliocrocuta perrieri</i>	<i>Pachycrocuta perrieri</i>
<i>Stephanorhinus etruscus</i>	<i>Dicerorhinus etruscus</i>



<i>Cervus rhenanus</i>	<i>Cervus philisi</i>
<i>Eucladoceros ctenoides</i>	<i>Eucladoceros tegulensis</i> = <i>Eucladoceros senezensis</i> = <i>Cervus</i> or <i>Eucladoceros falconeri</i>
<i>Equus robustus</i>	<i>Equus major</i> = <i>Equus bressanus</i>
<i>Mammuthus meridionalis</i>	<i>Archidiskodon meridionalis</i>
<i>Panthera (onca) gombaszoegensis</i>	<i>Panthera gombaszoegensis</i>
<i>Macaca sylvanus florentina</i>	<i>Macaca sylvanus</i>
<i>Trogontherium cuvieri</i>	<i>Trogontherium boisvillettii</i>
<i>Hippopotamus antiquus</i>	<i>Hippopotamus amphibious antiquus</i> = <i>Hippopotamus</i> <i>major</i>
<i>Alces latifrons</i>	<i>Cervalces latifrons</i>
<i>Lycaon lycanoides</i>	<i>Canis (Xenocyan) lycanoides</i>
<i>Puma pardoides</i>	<i>Panthera schaubi</i> = <i>Viretailurus schaubi</i>
<i>Ursus dolinensis</i>	<i>Ursus rodei</i>
<i>Dama nestii vallonnetensis</i>	<i>Cervus nestii vallonnetensis</i> = <i>Pseudodama vallonnetensis</i>
<i>Alces</i>	<i>Cervalces</i>

Table A4. Large mammal stratigraphic distribution of the studied faunal assemblages (CHC: Chilhac; OSD: Oosterschelde; TGL: Tegelen; UMF: Untermassfeld; HG: Het Gat; EUG: Eurogeul; MV2: Maasvlakte-2).

Taxa/Localities	CHC	OSD	TGL	UMF	HG	EUG	MV2
<i>Ursus aff. minimus</i>	+						
<i>Nyctereutes megamastoides</i>	+						
<i>Homotherium crenatidens</i>	+						
<i>Megantereon megantereon</i>	+						
<i>Equus stenonis</i>	+						
<i>Croizetoceros ramosus</i>	+						
<i>Gallogoral meneghini</i>	+						
<i>Gazellospira torticornis</i>	+						
<i>Anancus arvernensis</i>	+						
<i>Mammuthus meridionalis</i>	+	+	+		+		
<i>Pliocrocuta perrieri</i>	+	+	+				
<i>Eucladoceros ctenoides</i>	+	+	+		+		
<i>Stephanorhinus etruscus</i>	+	+	+		+		+
<i>Ursus spelaeus</i>		+					
<i>Felis catus</i>		+					
<i>Canis etruscus</i>		+					
<i>Stephanorhinus sp.</i>		+					
<i>Rhinocerotidae sp.</i>		+					
<i>Bos taurus</i>		+					
<i>Alces sp.</i>		+					
<i>Bos taurus</i> or <i>primigenius</i>		+					



<i>Bison</i> sp.	+			
<i>Ovis aries</i> or <i>Capra hircus</i>	+			
<i>Cervidae</i> (gen. indet. sp. indet.)	+			
<i>Capra hircus</i>	+			
<i>Bos</i> or <i>Bison primigenius</i> or <i>priscus</i>	+			
<i>Hippopotamus</i> sp.	+			
<i>Capreolus capreolus</i>	+			
<i>Anancus arvarnensis</i>	+			
<i>Elephantidae</i> gen. indet.	+			
<i>Mammuthus</i> sp.	+			
<i>Homo sapiens</i>	+			+
<i>Homotherium</i> cf. <i>latidens</i>	+		+	
<i>Equus caballus</i>	+			+
<i>Coelodonta antiquitatis</i>	+			+
<i>Megaloceros giganteus</i>	+			+
<i>Cervus</i> (cf.) <i>elaphus</i>	+			+
<i>Rangifer tarandus</i>	+			+
<i>Mammuthus primigenius</i>	+			+
<i>Equus robustus</i>	+	+		+
<i>Sus strozzii</i>	+	+		
<i>Leptobos</i> cf. <i>elatus</i>	+	+		
<i>Enhydriactis ardea</i>			+	
<i>Mustela palerminea</i>			+	
<i>Ursus etruscus</i>			+	
<i>Macaca sylvanus</i>		+	+	
<i>Panthera (onca) gombaszoegensis</i>		+	+	
<i>Canis mosbachensis</i>			+	
<i>Lycaon (=Canis (Xenocyon)) lycanoides</i>			+	
<i>Ursus</i> cf. <i>dolinensis (=U. rodei)</i>			+	
<i>Puma pardoides</i>			+	
<i>Megantereon cultridens adroveri</i>			+	
<i>Homotherium crenatidens</i>			+	
<i>Pachycrocuta brevirostris</i>			+	
<i>Acinonyx pardinensis pleistocaenicus</i>			+	
<i>Lynx issiodorensis</i> ssp. ex aff. <i>spelaeus</i>			+	
<i>Meles hollitzeri</i>			+	
<i>Stephanorhinus hundsheimensis</i>			+	
<i>Equus wuesti</i>			+	
<i>Eucladoceros giulii</i>			+	
<i>Dama (=Cervus s.l. =Pseudodama)</i>			+	



<i>nestii vallonnetensis</i>			
<i>Cervales (=Alces) carnutorum</i>	+		
<i>Capreolus cusanoides</i>	+		
<i>Mammuthus</i> sp. (advanced <i>M. meridionalis</i> and/or <i>M. trogontherii trogontherii</i>)	+		
<i>Sus scrofa (priscus)</i>	+		+
<i>Bison (cf.) menneri</i>	+	+	
<i>Hippopotamus (cf.) antiquus</i>	+	+	
<i>Cervalces (=Alces) latifrons</i>		+	
<i>Megaloceros dawkinsi</i>		+	
<i>Megaloceros savini</i>		+	
<i>Mammuthus trogontherii</i>		+	
<i>Canis lupus</i>			+
<i>Ovibos moschatus</i>			+
<i>Stephanorhinus kirchbergensis</i>			+
<i>Elaphas antiquus</i>			+
<i>Alces alces</i>			+
<i>Crocota crocuta (spelaea)</i>			+
<i>Ursus (cf.) arctos</i>			+
<i>Panthera leo spelaea</i>			+
<i>Bison priscus</i>			+
<i>Canis</i> sp.			+
<i>Equus</i> sp.			+
<i>Lutra lutra</i>			+
<i>Cervus</i> sp.			+
<i>Hippopotamus incognitus</i>			+
<i>Bos primigenius</i>			+
<i>Bos</i> sp.			+

Table A5. Micromammal stratigraphic distribution of the studied faunal assemblages (CHC: Chilhac; OSD: Oosterschelde; TGL: Tegelen; UMF: Untermassfeld; HG: Het Gat; EUG: Eurogeul; MV2: Maasvlakte-2; n/a: no available data).

Taxa/Localities	CHC	OSD	TGL	UMF	HG	EUG	MV2
<i>Castor</i> sp.	+				n/a		
<i>Hystrix</i> sp.	+			+	n/a		
<i>Borsodia newtoni</i>		+			n/a		
<i>Galemys kormosi</i>		+	+		n/a		
<i>Sorex (Drepanosorex) praeearaneus</i>		+	+		n/a		
<i>Mimomys pliocaenicus</i>		+	+		n/a		
<i>Mimomys reidi</i>		+	+		n/a		



<i>Mimomys tigliensis</i>	+	+		n/a		
<i>Beremedia (cf.) fissidens</i>	+	+	+	n/a		
<i>Trogontherium cuvieri</i>	+	+	+	n/a		
<i>Castor fiber</i>	+	+	+	n/a	+	+
<i>Desmana thermalis</i>			+	n/a		
<i>Petenya hungarica</i>			+	n/a		
<i>Sorex minutus</i>			+	n/a		
<i>Sorex gen. indet.</i>			+	n/a		
<i>Hylopetes magistri</i>			+	n/a		
<i>Muscardinus pliocaenicus</i>			+	n/a		
<i>Glirulus pusillus</i>			+	n/a		
<i>Micromys sp.</i>			+	n/a		
<i>Mimomys pitymyoides</i>			+	n/a		
<i>Ungaromys dehmi</i>			+	n/a		
<i>Clethrionomys kretzoi</i>			+	n/a		
<i>Dicrostonyx cf. torquatus</i>			+	n/a		
<i>Spermophilus primigenius</i>			+	n/a		
<i>Sciurus sp.</i>			+	n/a		
<i>Hystrix refossa</i>			+	n/a		
<i>Hypolagus brachygnathus</i>			+	n/a		
<i>Chiroptera sp.</i>			+	n/a		
<i>Apodemus (cf.) sylvaticus</i>			+	+	n/a	
<i>Talpa (cf.) minor</i>			+	+	n/a	
<i>Talpa cf. europaea</i>				+	n/a	
<i>Sorex runtonensis</i>				+	n/a	
<i>Sorex (Drepanosorex) ex gr. margaritodon - savini</i>				+	n/a	
<i>Clethrionomys cf. hintoniiianus</i>				+	n/a	
<i>Pliomys episcopalis</i>				+	n/a	
<i>Mimomys (Cseria) pusillus</i>				+	n/a	
<i>Sciurus cf. whitei</i>				+	n/a	
<i>Spermophilus (Uroditellus) ex gr. primigenius/polonicus</i>				+	n/a	
<i>Glis sackdillingensis</i>				+	n/a	
<i>Cricetus cf. runtonensis</i>				+	n/a	
<i>Microtus thenii</i>				+	n/a	
cf. <i>Lepus sp.</i>				+	n/a	
<i>Erinaceus cf. europaeus</i>				+	n/a	
<i>Mimomys savini</i>				+	n/a	+
<i>Desmana moschata</i>				n/a	+	
<i>Arvicola cantiana</i>				n/a		+



<i>Arvicola</i> sp.	n/a	+
<i>Mimomys</i> sp.	n/a	+
<i>Microtus agrestis</i>	n/a	+
<i>Microtus</i> sp.	n/a	+