Opportunities for palaeoclimate research on Coleoptera in Northwestern Europe

Master thesis
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This thesis deals with the subject of Coleoptera, a subject I've grown fond of the moment I got the opportunity to work on it. Starting with a long forgotten presentation during my Bachelor my interest in Coleoptera started to grow, until I decided to find out whether this somewhat uncommon branch of palaeoecology was worth to study. Therefore, I moved to south Sweden for four months to do my internship on fossil beetles. Under the supervision of Geoffrey Lemdahl I quickly became aware of the great diversity of species and ecology of Coleoptera, the great results that can be produced with Coleoptera as a proxy for climate as well as landscape/vegetation, and the opportunities for more research on Coleoptera that are still waiting to be taken on. Being such exciting organisms, it was important to me to find out if there are still opportunities for valuable palaeoclimate research on Coleoptera in northwestern Europe, to quantify and qualify these optional studies. This will be the main goal of this thesis. Chapter one introduces Coleoptera and shows the special properties of this family of insects, which make them very suitable for (palaeo)climate research. Chapter two gives an overview of research done on Coleoptera in the past. Chapter three shows research opportunities on Coleoptera in Weichselian and subsequently, older deposits. In chapter four the potential sites for new research on Coleoptera are identified, which were found in this study. Finally, in chapter five all the findings will be summarized and conclusions can be drawn.

Although it was hard to write this thesis in a restricted time frame, I had a lot of fun putting my ideas and findings down on paper. Ever since I started to explore a possible career in beetles, I've had nothing but fun. Geoffrey Lemdahl has been a great teacher and his passion for beetles greatly enlarged my own enthusiasm. Now that my studies are almost at their end I can only hope to find a job as a palaeoentomologist. As with all things, time will tell.

Chapter 1   On the topic of Coleoptera

1.1   The diversity of Coleoptera

Coleoptera, or beetles, form one of the largest groups of organisms at the order level (Crowson, 1981). With their characteristic shape they form a unique insect family with also great variety in size and shapes into many extremities (Figure 1). Already back in ancient time people showed great interest in beetles (Kitchen, 2008) and this continued through time: some species were worshiped as godlike creatures, others were admired for their beauty and more others were and still are useful as pest controls and food source. What makes many people admire beetles in general is the sturdiness of this group of animals, being able to survive almost every environment. They occupy the earth from the deserts to the tropics, dominate lakes and streams and are only restricted from the coldest places on earth (Mani, 1968), being cold blooded. Some species are even found living in brackish water and hot springs (Schwartz, 1914). By the development of impermeable exoskeletons and the excretion of thick waxy layers Coleoptera have become able to maintain in the harshest deserts (Koch, 1962; Hadley, 1979), while in the arctic and alpine regions species have adapted themselves by altering their metabolic processes (Danks, 1978).

Figure 1. A collection of beetles in all shapes and sizes.
Picture from independent.co.uk

1.2   The exoskeleton of Coleoptera

Like all insects Coleoptera have an exoskeleton, covering the outside of their body parts. This exoskeleton consists of a waxy outer epicuticle, and a thicker procuticle just beneath (Figure 2). The procuticle contains an extremely durable substance called sclerotin (Vincent & Wegst, 2004), which forms during the initial hardening of the exoskeleton of an emerging adult. While in all insect cuticles the procuticles main substance is chitin, which is also not very easily broken down (Tomihata & Ikada, 1997), the extreme amounts of sclerotin in the exocuticle of beetles explains why they are always well preserved and often the dominant group in the fossil record. The exoskeleton of beetles can have some typical shapes
and even extremities in the shape of the heads are not uncommon, especially in the family of Scarabideae with genera of rhinoceros and elephant beetles (CEE, 2011). Also pronotum and elytra can be exceptionally distinguishable and can be considered truly beautiful, in shape and color. Apart from color there are a number of features to distinguish species from one another. Striae, carinae, grooves, tubercles, punctures (with or without seta), scales and different types of teeth are found in wide variations in shape and size. Many beetle families have some clear general features and species of beetles can often directly be assigned to a certain family.
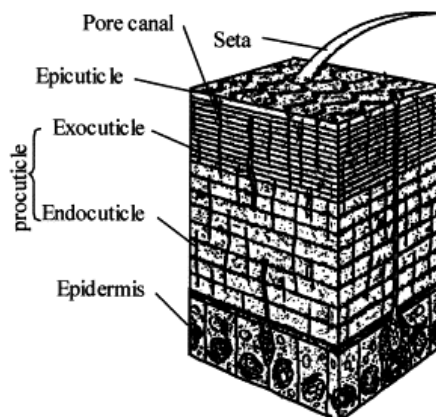
Figure 2. Cross section of an insect cuticle, showing its different layers (by Chen *et al*., 2002).

4

1.3   Microsculpture

Furthermore, many parts of the exoskeleton are covered in microsculpture. This microsculpture often reflects the pattern of the underlying hypodermic cells and may not only be present on the sclerites below the waxy layer but also on the connecting membranes (Crowson, 1981). The microsculpture is so typical for each species that beetles can often be determined to species level just by examining their microsculpture. There are different types of microsculpture, from which micropunctures and meshes are the most common. These meshes can have various shapes, from rounded to isodametric to very stretched (Figure 3a), giving each beetle species a different appearance. Also close parallel lines of teeth occur (Figure 3b), giving its bearer an iridescent appearance. In extreme cases, if the microsculpture of a genus is almost similar between different species, one could also look at the male gonads (aedagus) of individuals. The gonads are also heavily scelotized and clearly distinguishable between species. Some genera of beetles can only be determined onto species level by comparing their aedagus (Lemdahl, pers. comm.).
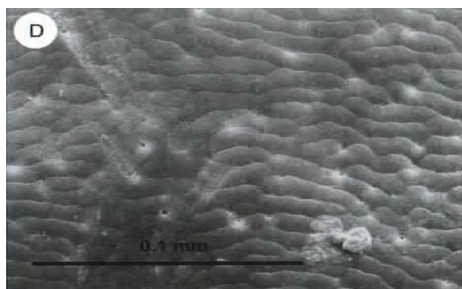

Figure 3a. Horizontally stretched meshes on the rove beetle *Tachinus brevipennis*. Photo adapted from Elias (2010).
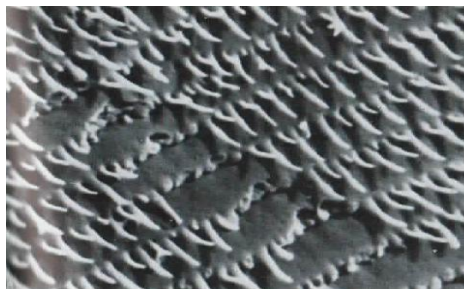

Figure 3b. An array of microtrichia on the elytron of *Sericestis micans*. Photo adapted from Crowson (1981).

1.4   Preservation of the exoskeleton

Because the exoskeleton of beetles contains sclerotin it preserves extremely well, especially under anoxic conditions. The head capsule, the pronotum (abdominal dorsal shield) and the wing covers (elytra) are the main parts that preserve in sediments. The special features of these skeletal parts, like rows of punctures or striae, and even de microsculpture on these plates do not alter in time and are preserved as long as the skeletal plates themselves are preserved (Elias, 2010). Insect exoskeletons are mainly found in anoxic sediments which contain organic detritus. Sediments which (have been) waterlogged are best in this category, since the water also concentrates the insect remains (Elias, 2010). Fossil insect remains can be found where the plant material has accumulated in these water bodies, like the shores or the place where a stream enters a body of stagnant water. Also fluvial sediments accumulate organic detritus, especially in parts of the stream where the water flows more slowly (Coleman, 1964). Most organic rich are bogs or fens, filling a previous stagnant body of water, having accumulated meters of organic sediment in a moist environment over sometimes thousands of years (Olsson & Lemdahl, 2009). While a corer is required to collect a column of sediment from bogs and lacustrine sediments (e.g. Berglund & Digerfeldt, 1970) old stream-beds of rivers provide thick columns of organic-rich sediment of which the stratigraphic layers can readily be found by correlating horizons (Elias *et al.*, 1991). However, this type of deposit requires large quantities of sediment in order to yield enough insect remains. Different other interesting places to search for insect remains, ways of processing organic rich sediment, and the isolation of insect remains from the detritus are extensively described in chapter 2 of the recent book of Elias (2010).

1.5   Migration due to climate shifts

As mentioned earlier in this chapter, the diversity in habitats and ecological niches of beetles in enormous. One feature they share with many other classes of insects is the rapid migration due to variation in habitat. Instead of adapting to local climate insect species invest enormous amounts of energy in dispersal and migration (e.g. Dantharanayana, 1970). Studies have shown that beetle populations respond even to changes in microclimate (Howden & Scholtz, 1986). Climate shifts within such short time frames are often not recorded in the vegetational record, which often has a lag in response to climatic change (e.g. Cole, 1985). Using fossil insects as a proxy should avoid this issue. Not only is the migration of certain beetle species due to climatic shifts clearly noticeable, as for example by the presence of the rove beetle *Tachinus*

caelatus in deposits from the last glaciation in Britain (Taylor and Coope, 1985), while it is at present endemic to Mongolia. Being not altered in appearance and ecology through time, and quickly migrating along with climatic changes, beetles make an excellent proxy for climate change. This will be more extensively discussed in Chapter 2, which handles palaeoclimate research on Coleoptera.

Since Coleoptera are such a valuable proxy for short-term climatic change and variation and can contribute to the development of an ecological overview of an area in addition to more mainstream proxies like pollen grains, it is worth to explore which areas and time zones have still (partly) unknown climatic, ecological and landscape evolution to which data from Coleoptera could contribute. In the following chapters 3 and 4 this will be explored.

Chapter 2   The history of palaeoclimate research on Coleoptera

2.1   Species longitivity

When the first studies on fossil Coleoptera emerged in the second half of the 19th century (Scudder, 1877) it was presumed that all excavated samples were of extinct species. Early workers on Quaternary beetles came up with names for their discoveries like *Helophorus pleistocenicus* (Lomnicki, 1894) and *Platynus exterminatus* (Scudder, 1900). Until halfway through the 20th century it was assumed that a great part of all fossil beetles from Pleistocene deposits were extinct species. Particularly Carl Lindroth (1905-1979) played an important role in establishing the modern aspects in Quaternary entomology, namely that all species from Quaternary deposits belong to extant species. His revisions of various previous Swedish studies concluded that all fossils described as extinct species were in fact from extant species (Lindroth, 1948). Lindroth concluded that the most useful taxonomic features of fossil beetle sclerities are in their microsculpture. Ever since, the microsculpture of fossil Coleoptera has contributed greatly in their identification. Other extensive work on the development of Quaternary entomology has been performed by Russell Coope (1930-2011). Coope didn't cease to look for modern counterparts to British Pleistocene fossils which couldn't be related to an extant species. For instance, after years of searching Coope found modern specimens from a species which are living today only on the Tibetan Plateau (Coope, 1973). Mainly by the work of Coope it was finally accepted by the community that most species of Coleoptera we find today have been extant since the beginning of the Pleistocene. In a recent study, Elias *et al.* (2006) summarized all available fossil data from northern Siberia, arctic North America and Greenland, of which a large part are early Pleistocene sites. Approximately 5% of all beetle species were known to have become extinct.

Another striking feature of Coope's interpretation of Pleistocene beetle remains is that in all known studies during the time of publication (Coope, 1970), there was not a single fossil known with intermediate features between two known species. Therefore, Coope concluded, later on seconded by Matthews (1976a,b) that the fossil beetle record of the Middle and Late Pleistocene provides no evidence of speciation. Recently some examples of intermediate features were found (Elias, 2007), but these are infrequent occurences.

While many species have been persisting for millions of years, their appearance in the fossil record is very constant as well. In well studied regions such as Britain, assemblages of nearly identical composition were found in series of glacial, interglacial and interstadial climate episodes. Not only was the beetle community of a region consistent of the same species in each warmer time period, this was also the case in colder time periods. Nearly all found fossil beetle species assemblages correspond to a fairly narrow climatic envelope in which all the species are found living. If there would have been evolution among species climate preference, for instance, then the referred species would be incompatible with the fauna as a whole.

2.2   Climate preferences and consistency

More research on long-term species constancy of beetles has been worked out by Angus (1983). The aquatic scavenger beetle *Helophorus lapponicus* was in the last cold phases of the last glaciations very common throughout Western Europe but after the glaciations retreated to the remaining cold regions, including northern Scandinavia and mountain regions in central Spain. Angus successfully interbred two populations from Sweden and Spain, even though these two populations had been isolated from each other for the last 10,000 years. Also other studies, aiming on the evolution of beetles during geographic isolation, also reported non or very slow speciation of the species that were present (Basilewsky, 1970; Thiele, 1977). Thiele (1977) also studied the thermal preferences of ground beetles (Carabidae), using environments with controlled temperatures. With a determined preferred temperature (PT), Thiele concluded that the PT was identical for every measured population within the species. In additional experiments, it was determined that the PT of every species corresponded with that species' optimal metabolisms. These results are supported by recent modeling of beetle distribution in France (Lobo *et al.*, 2002), concluding the distribution of the species to be mainly influenced by temperature and the "failure of many species to go beyond determined temperature range limits".

2.3 Coleoptera as proxy for quantitative temperatures

The first researchers which used fossil beetle remains as a proxy for climate reconstruction, starting with Coope (1959), still used fairly primitive methods to estimate past temperatures. While studying the fossil beetle assemblage they were interested in, they tried to find areas where the different species from the assemblage were living together at present. Although at present many species don't share the same geographic range any more this method, called the Range Overlap Method, generally came up with good results. It must have been for the experience of the researchers that good together fitting species were emphasized in these studies (e.g. Osborne, 1980), as well as finding the climatically sensitive species.

In 1982, the Mutual Climatic Range (MCR) method was created. It works by establishing the present climatic envelope for each separate species found in a fossil assemblage and after that overlapping these climatic envelopes to find a climatic envelope suitable for all present species (Atkinson et al., 1986). In this way, two species with overlapping climatic envelopes can be compared to one another, even if they don't occupy the same areas but are even present on different continents. Most important, since the whole geographic ranges of different species are documented and not single locations where species are spotted together, the whole temperature range of areas where species are living is documented and true quantitative measurements of the temperature can be given. Only predators and scavenger species are used for the MCR method, since phytophagous species might be tied to a host plant and therefore restricted to a certain area by far more factors than temperature alone.

By far the most used variables in MCR are mean temperature of the warmest month of the year (T_{max}) and the temperature range between the warmest and coldest month (T_{range}). This last factor serves as a degree of seasonality. Almost the entire range of (micro)climates in Europe and North America is found to be determined by these two factors (Atkinson *et al.*, 1987). Figure 4 shows an MCR temperature reconstruction for two North American species. As mentioned, an MCR plot can be made for an endless amount of species together and of course from different parts of the world.
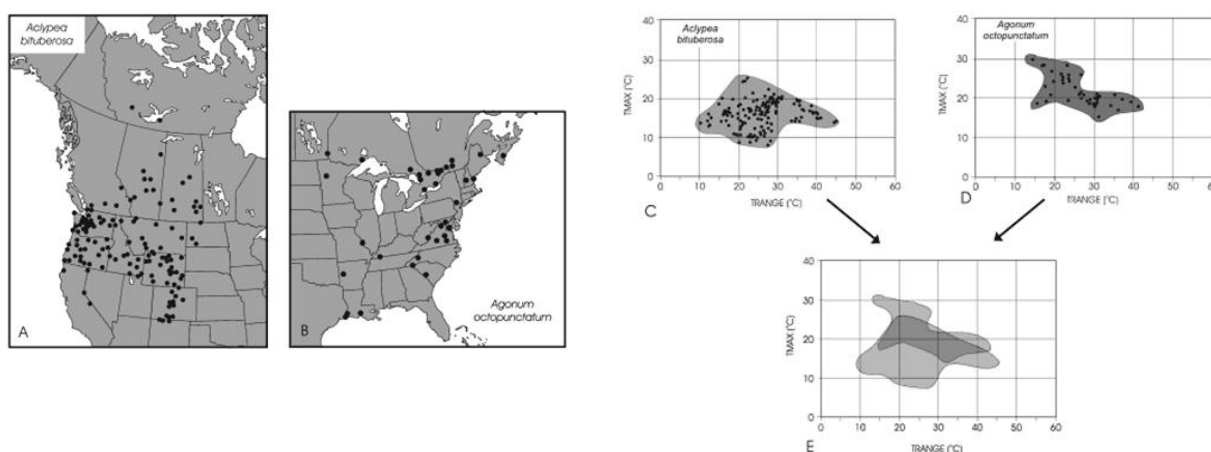

Figure 4. Modern distribution maps for the carrion beetle *Aclypea bibuterosa* (A) and the ground beetle *Agonum octopunctatum* (B). The corresponding T_{max} and T_{range} are plotted, showing the climatic envelope of both species (C & D). By overlapping these two envelopes the mutual climatic range of the two species is clarified (E) (Adapted from Elias, 2010).

One of the true criticisms of MCR is that the difference in abundance of a species within its geographic range are not recorded (Huppert & Solow, 2004) By using a technique called ubiquity analysis (Bray *et al.*, 2006) these problems might be overcome, but the technique is still in development.

2.4 Other studies on fossil insects

Finally, it is worth noting that ongoing studies in dating isotopes of chitin layers of insects are advancing (Walker *et al.*, 2001; Van Hardenbroeck *et al.*, 2012), but no solid methods for dating insect sclerities or stable isotope studies have been developed yet. Also, with DNA analysis it is attempted to gain insight in the history of insect populations and the past geographical dispersal of beetle species (e.g. Reiss *et al.,* 1999). These relatively new fields of research will continue to develop, just like palaeoclimate studies with Coleoptera.

Chapter 3   Coleoptera from Weichselian and older deposits

3.1   Glacials and interglacials

In climatic research, people are mostly interested in trying to predict our future climate. Vast discussions about the future of our climate and the anthropogenic role in it (Charlson *et al.*, 1992; Mann, 2002; Walther *et al.*, 2002) have enhanced the interest in (palaeo)climate research and is expected that this interest will not diminish for the upcoming decades. The Holocene period, which is the present time period, is in fact an Interglacial between two Glacials and can readily be compared to the other interglacials of the Pleistocene (Figure 5). While the glacial-interglacial pattern of the Pleistocene is a pattern of Milankovic cycles (Imbrie, 1984; Grootes & Stuiver, 1997) it is expected that a new Glacial will turn up sooner or later.
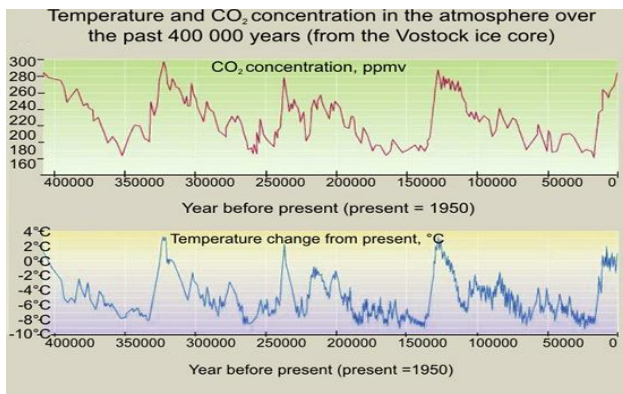

Figure 5. Measured CO_2 concentrations and derived temperatures from the Vostok ice core from the past 400,000 years showing five interglacials, noticeable by peaks in CO_2, including the Holocene at present (from sahfos.ac.uk, adapted from Petit *et al.*, 1999).

The Late Glacial (the last part of the Weichselian) and the Holocene, the present interglacial, are mostly studied since this period is ideal for studying the termination of a glacial period and the response and development of climate and landscape (Monnin *et al.*, 2001; Demske *et al.*, 2005). Since this transition from glacial to interglacial condition is the most recent one the different proxies from the fossil record are often well preserved. Although sections could have undergone compaction and erision just like older deposits, they haven't suffered from great erosion due to younger ice advances. Because of this, and because of the fact that young enough deposits can be readily carbon-dated, age of the deposits can be determined relatively easy. Furthermore, the chance that a certain taxon has changed its environmental preferences compared to the present is the smallest (e.g. Knies *et al.*, 2006; Rogers *et al.*, 2011).

        Mainland Nortwestern Europe (northern France, Belgium, The Netherlands, Western Germany) is a unique area to study the onset and termination of past glaciations, and the climate of the interglacials. During the last glacial maximum this area was close to the edge of the Fennoscandian ice sheet (Clark & Mix, 2001) while during earlier glacial maximums covered underneath and one of the first regions to become ice free after a glaciations (Ehlers & Gibbard, 2004). As being mostly lowland and rich in rivers and streams which transported great amounts of sediment (Gibbard *et al.*, 1988), many areas are yet to be explored for their fossil contents. While the small lakes in mountainous areas, which serve as sediment traps, have already been widely explored there are still many research opportunities in the European lowland.

3.2   Chronology

In order to refer easily to different time periods, and to readily compare different periods to each other, associated Marine Isotope Stages (MIS) are used. These stages are based on the shifts in $\delta^{18}O$ in the shells of benthic foraminifera (Imbrie *et al.*, 1984), which have developed in stages (oxygen isotope stages). By correlation with subchrons (Raymo *et al.*, 1989) a very reliable dating method was acquired and has been used ever since. The Holocene is correlated to MIS 1, while each older oxygen isotope stage receives a

higher number. For instance, the Eemian interglacial corresponds to MIS 5e. Figure 6 displays a MIS schedule for the last ~900 ky for European mainland sections. As can be seen, MIS stages have different names in different regions of the world. Furthermore, not every stage contains the same amount of sub stages in every region.
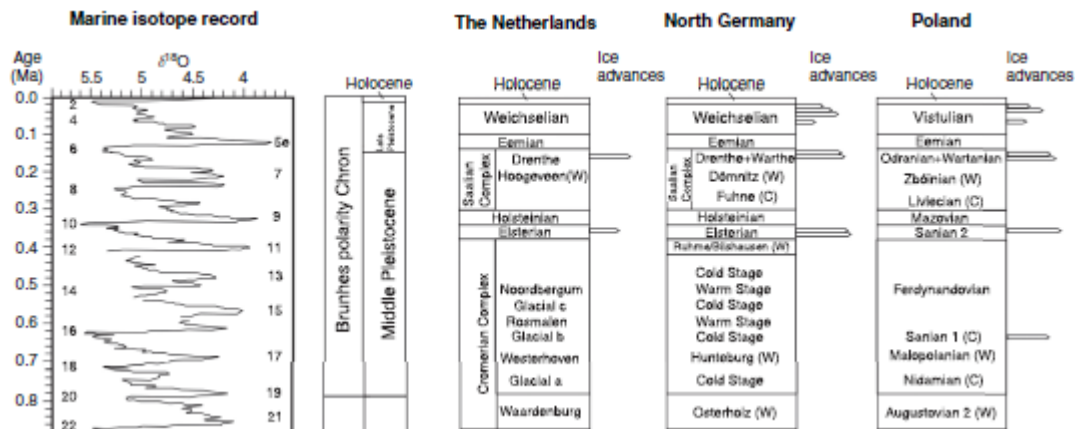
Figure 7. Chronostratigraphical correlation table of the Middle and Upper Pleistocene in north-central Europe (From Litt 2007; compiled after Zagwijn, 1989; Gibbard and van Kolfschoten, 2004; Lindner et al., 2004; Litt *et al*., 2005). (C) – cold stage, (W) – warm stage.

3.3   Weichselian deposits

First, the focus further on in this chapter will be on studies with Coleoptera as proxy. Then, studies using other proxies will be briefly considered. In this way an effort will be made to show areas in which climate studies using Coleoptera as proxy will improve the knowledge of past climate. For this goal, northwestern Europe is divided into three regions: northern France, the Benelux, and western Germany (Figure 7).

Figure 7. Map of western Europe (Google Maps), showing the Weichselian-Holocene sites with studied insect remains, mentioned in Chapter 3. Depicted are Houdancourt (1), Conty (2), St-Momelin (3), High Ardenne (4), Usselo (5), Mark valley (6), Peelo (7), Voorthuizen (8), Orvelte (9) and Tilligte (10). The long record sites La Grande Pile and Oerel are depicted with a star, with La Grande Pile in the south and Oerel in the north.

3.3.1 Northern France

In northern France, a few Weichselian-Holocene studies on Coleoptera were executed. A study by Ponel *et al.* (2005) extensively describes the vegetation and entomological records of two sites; Houdancourt in the Oise valley (**1**) and Conty in the Selle valley (**2**), which were chiefly used in previous studies concerning the human occupation of these areas (Antoine *et al.*, 2003). The sites yielded sufficient fossil insect remains from the Bølling and Allerød periods to determine that temperatures during these times were similar to one another and nearly as warm as today, according to MCR reconstruction. A different study by Ponel *et al.*(2007) handles a site at St-Momelin (**3**), where the long record includes organic rich sediments from the Younger Dryas. Although the area is situated close enough to the coast to have been subdued under several transgressions through time, enough fossil Coleoptera remains were identified to give sufficient information on the environment of the region through time and give quantative temperature estimations for each determined faunal unit. For instance, the well known sudden shift of temperature between the Younger Dryas and the Holocene (Atkinson *et al.*, 1987; Berglund *et al.*, 1994; Lang *et al.*, 2010) is well documented in this study. A study by Damblon *et al.* (1977) on peat bogs in the High Ardennes (**4**) uses, besides plant macro- and microfossils, subfossil beetle remains to investigate the ecological evolution of these bogs. Unfortunately these records go back only a few thousand years and the focus of the study lies on the evolution of the bogs and not the local climate. The site La Grande Pile (Vosges mountains, depicted with a star in Figure 7) is located just outside the area of interest. This site holds a long climatic record of the last 140,000 years (Woillard, 1978; De Beaulieu & Reille, 1992) and is providing an indispensible site for other studies to be compared with. Only for periods prior to the Late Glacial, climate studies on Coleoptera have been performed for this site. The study by Ponel (1995) shows MCR temperature reconstructions from the early Weichselian to the Late Glacial.

There are many Weichselian – early Holocene climate reconstructions based on other proxies in northern France. For instance, the site at St-Momelin also yielded studies on pollen grains (Gandouin *et al.*, 2009) and chironomids (Gandouin *et al.*, 2007b). Other climate reconstructions include old studies on peat deposits (Dubois, 1948), which have largely not been digitalized but are used in later studies (e.g. Guiter *et al.*, 2003).

3.3.2 Benelux

In the Benelux, Weichselian-Holocene climate research with Coleoptera as proxy has been concentrated in The Netherlands. Two Late Glacial sequences exist: Usselo (**5**), near Enschede (Van Geel, Coope & Van der Hammen, 1989) and the Mark valley (**6**) near Notsel in the southern Netherlands (Bohncke *et al.*, 1987).

The Usselo section, with its base dated 12,930 ± 210 ^{14}C yrs BP, contains Oldest Dryas to early Holocene sediments. The ecology and climate of the area is quite detailed recorded; with sparse vegetation and cold conditions (for instance by the presence of chironomid species *Corynocera ambigua*) during the Oldest Dryas, a maximum summer temperature of 15-20˚C during the Bølling and a somewhat colder Allerød (13-16˚C), while the Older Dryas in between is calculated to have had warmer or equal temperatures (14-16˚C) than the Allerød. Finally, the Younger Dryas is recorded to have significantly lower temperatures than the previous periods (10-11˚C). While the beetle assemblages from this record were suitable for MCR temperature reconstructions, they also contributed greatly to the reconstruction of the landscape through time. The Mark valley section was dated 12,600 ± 60 – 10,970 ± 50 ^{14}C yrs BP and comprises the Bølling up to and including the beginning of the Younger Dryas. This section shows in detail the transition to colder climate during the Younger Dryas.

Studies from The Netherlands also contributed greatly to our knowledge on Weichselian interstadials. For a long time, climatic reconstructions of the early Weichselian were mainly based on Dutch palaeobotanical records from Zagwijn (1957, 1963). Four studies describing Coleoptera from late Pleniglacial sites are known, from Peelo (**7**), Voorthuizen (**8**), Orvelte (**9**) and Tilligte (**10**). The section from Peelo (Coope, 1969) was a single lens of peat, radiocarbon dated 33,000 BP. *The fossil* beetle assemblage consists of many tundra species, at present living in colder regions. Holding hardly any phytophagous species, the assemblage is indicative of sparse vegetation. The presence of flightless species indicates that this landscape had been in existence for a longer period of time in this region. The Peelo fauna resembles to great extent Mid Weichselian insect faunas from the English Midlands, with an tundra fauna suggesting a "severe climatic regime". It is generally accepted that in order for a treeless landscape to persist, July temperatures would not have exceeded 10 ˚C (Koppen, 1936). The sections from Voorthuizen (Angus,

1975), Orvelte (Cappers *et al.*, 1993) and Tilligte (Brinkkemper *et al.*, 1987) all confirm a severe climate during the pleniglacial, some with slightly warmer intervals.

In The Netherlands, many geological and palaeoclimatological studies have been performed throughout the country (e.g. Van Geel *et al.,* 1980; Van Leeuwaarden & Janssen, 1987; Van der Molen & Van Dijk, 2000; Bos et al., 2005). Special attention should be drawn to the article about Hijkermeer (Heiri *et al.*, 2007), which describes a continuous record of chironomids from the Older Dryas to the Early Holocene, indicating sudden temperature shifts between the different time periods. While the chironomid record probably shows temperature shifts very accurate and could be an alternative to oxygen isotope records, as the authors state, the quantitative temperature record is somewhat deviating from other proxies. If good calibration is possible to overcome the bias between lake water temperatures and actual air temperatures (e.g. Olander *et al.*, 1999) then chironomids might add as much to quantitative climate reconstruction as Coleoptera. There might not be as extensive knowledge on all separate chironomid species as with Coleoptera, which might prove to be a complicating factor.

Few articles on palynological sites and other sites with biological fossils are available from Belgium in the general libraries. In Belgium, this mostly is caused by the lack of development of suitable sites during the Late Glacial and early Holocene (Verbruggen, 1999). A single article by Guiot & Couteaux (1992) gives a quantitative climate reconstruction of the region of Luxembourg since 15,000 yr BP. It might be that studies in Belgium and Luxemburg have been focusing more on the history of Paleolithic settlements (Naton *et al.*, 2009; Derese *et al.*, 2009; Crombé *et al.*, 2011) and less on the overall climate of the region.

3.3.3   Western Germany

No Late Glacial-Holocene studies describing Coleoptera are present in the general libraries. The site Oerel, depicted with a star symbol, dates from the Warthe/Drenthe stadial (MIS 6) to the Holocene and has contributed greatly to the correlation and dating of the different stadials of the early Weichselian (Behre & Van der Plicht, 1992). The study by Behre *et al.* (2005) on Coleopteran remains from this section includes only to MIS 4 and gives detailed temperature reconstructions of different stadials and interstadials.

Western Germany is in several aspects a special area during the Weichselian as it was the region of volcanic eruptions at least since the Eocene (Mingram, 1998), including the Pleniglacial and Late Glacial (Van den Boogaard & Schminke, 1984; Schminke *et al.*, 1999). A summary of these volcanic events in the whole region of western Germany is given by Litt *et al.* (2003). From this article it becomes apparent that many fossil proxies have been studied to great extent, and that exact timing of climatic events could be correlated between different regions by the correlation of varved lakes from old volcanic craters called maar lakes. Many of these lakes, like Meerfelder Maar (Lücke & Brauer, 2004) and lake Holzmaar (e.g. Litt *et al.*, 2009) are annually laminated and provide valuable information about timing and transition between different climate periods. Not only in the Eiffel region but also further north, many Weichselian sites exist (e.g. Merkt & Müller, 1999). Meyrick (2001) studied the mollusk fauna in northwestern Germany. Mollusk fauna is a good indicator for different types of landscape and landscape reconstructions can be readily made from mollusk assemblages. Although cold-adapted assemblages can be distinguished, quantitative temperature reconstructions have not been made with mollusk assemblages as proxy.

3.3.4   Discussion

By showing summarized conclusions from different existing papers on climate reconstruction with Coleoptera as proxy, it was shown to what extent studies on fossil Coleoptera can contribute in practice. For instance, quantitative temperature reconstructions make it easy to compare with present day conditions and presence/absence of indicator species for trees have greatly supported the assumption of temperate but treeless landscapes at certain times. Many other proxies have been used in various studies, among which pollen grains, plant macro remains, chironomids, mollusks and diatoms. Where all proxies have the advantage over Coleoptera that they are generally found in more types of deposits (and in many cases more numerous, which saves time) Coleoptera seem to be the only of these proxies which could directly indicate quantitative air temperatures and landscape indications as well, apart from pollen grains. However, pollen grains only can give good climate and landscape indications in larger temporal and distal frames and Coleopteran fossils have proven a great addition to pollen records. Furthermore, in contrast to pollen Coleoptera fossils can also provide quantitative minimum temperatures of a region in a certain time frame.

Research on Weichselian, Late Glacial, and early Holocene climate dynamics has been continuing since the beginning of the last century. With large amounts of information and dating methods that have been growing in reliability, many syntheses of Weichselian to Holocene climate history have been made for many parts of the world including (and especially) Northwestern Europe. The synthesis from Walker *et al* (1994) of Late Glacial West European data from vegetation and Coleopteran data actually compares all areas in and around Western Europe with each other, from Ireland to Germany. Important features in Walker's conclusions about the synthesis (1995) are a) a lag in vegetational response to climate of about 1000 years,

b) a delayed Late Glacial thermal maximum in northern Germany, dated around 12.5-12 ka BP, and c) the lack of data for (Northern) Belgium. Reconstructions of early and middle Weichselian climate are fewer, but Huijzer and Vandenberghe (1998) give a good overview of temperatures in North-West Europe during the Pleniglacial (72-13 ka, MIS 4-2), combining 720 climate records from 268 sites. These studies focus on MIS 3-2, since MIS 4 is not well preserved in Europe, left hardly any fossils and its stratigraphy is still under construction (Abbott *et al.*, 2011). More recently, many Late Glacial-Holocene climate modeling studies have been published (e.g. Isarin *et al.*, 1998; Renssen & Isarin, 2001; Simonis *et al.*, 2012) and even for older MIS stages (Huntley *et al*., 2003). From the synthesized data it became apparent that insufficient data from (Northern) Belgium is available for temperature reconstruction. A summary of articles by Verbruggen *et al.* (1996) contains solely data from pollen records and could only give estimations on qualitative climate change in Belgium. However, in another article concerning Coleoptera data in Europe (Witte et al., 1998) three Belgian sites are named which contained remains from Coleoptera. One of these sites, Snellegem near Brugge, contained few determinable insect remains and was therefore not published (Lemdahl, pers. comm.). Unfortunately many articles were not readily accessible. For example the article by Walkling on the site Gross Todshorn in 1997 (in Behre *et al*., 2005). While these articles would eventually be obtained by contacting the authors, it was not possible to include these data in the given time to write this thesis. Articles published in the magazine of national geological societies, like *Schriftenreihe der Deutschen Geologischen Gesellschaft* (Germany), are often only available in the concerning country.

Furthermore, after assessing the different articles a few questions remain. Results from Northern France by Ponel (2005, 2007) show some discrepancy with other regions, with respect to the Bølling-Allerød. According to Coope & Lemdahl (1995) temperatures in northern Europe were lower in the Allerød than in the Bølling, while the data from northern France suggests a temperature rise at the end of the Allerød. As it seems these articles by Ponel are the only quantitative climate reconstructions of the Late Glacial in Northern France and thus it might be useful to perform an extra study to confirm the present data. Other uncertainties remain about temperatures during MIS 3. Huntley *et al.* (2003) state that the model in their study simulates higher temperatures than were inferred from the pollen records. In this case it would aid greatly to add data from Coleoptera, like Coope (2006) did for Britain. If the discrepancy between pollen and Coleoptera would be solved for this period, only a few sections with Coleoptera data would solve many issues. Since the main obstacle in this matter is the uncertain chronology of MIS 3 Northwestern Europe, it would be useful to perform studies on Coleoptera from the long records in Southern Europe which were used in the study by Huntley *et al*. (2003). However, MCR constructions cannot be made in many cases for Southern European beetle species due to lack of data.

3.4   Older deposits

This section will discuss the periods older than the Weichselian. Its focus will be on warmer prolonged stages, as very little is known about short climate events. At least, if there are any recorded short events these are quite different per region (see figure 6). The interglacial/interstadial periods handled with are the Eemian (MIS 5e), the somewhat elusive interglacial periods MIS 7 and MIS 9, and the distinct interglacial MIS 11, which was termed the Holsteinian. Although older interglacials are known, little has been studied on these interglacials in Europe, apart from Britain (Rose, 2009). Even Coleoptera from older deposits were described (Coope, 2006), where they were used for biostratification with other sites. Apart from a few articles giving a stratification of the sediments of mainland Europe (e.g. Zagwijn, 1992) no other studies were found and therefore this study will not go further back in time than MIS 11.

3.4.1 Challenges with older deposits

The development and termination of the Eemian are quite well recorded, but the scale and correlation of events during the Eemian are still widely discussed (Turner, 2000). While the Eemian and Holsteinian are distinct interglacial periods, MIS 7 and 9 were found at less locations in Europe (Turner, 1998). Further-more, the palynological characteristics of MIS 7 and 9 are less clear than from the Eemian and the Holsteinian. With the correlations of maar lakes in southern Europe (e.g. De Beaulieu & Reille, 1995) to other sections, at least it was concluded that MIS 7 and 9 represent distinct warmer periods and are not part part of a 'Holsteinian complex'. Another challenge occurs when addressing the Eemian and Holsteinian interglacials. Since quite some time there have been discussions on which interglacial resembles the Holocene the most, to decide which one would be more important to study. While it was attempted to compare the different interglacials in terms of vegetation (e.g. Cheddadi *et al*., 2005), it was concluded that none of the interglacials of the last 500 ka resembles the Holocene. If solely earths orbital positions and greenhouse gasses derived from ice cores are considered (De Abreu *et al*., 2005; Ruddiman, 2005; Voelker *et al.,* 2009) then MIS 11 looks in several aspects more like the Holocene than MIS 5. Finally, increasing evidence shows that the typical Holsteinian sites in Germany are correlated to MIS 9 instead of MIS 11 (e.g. Geyh & Müller, 2005). Since, in this light, not many localities for MIS 11 remain in Northwestern Europe, new queries for MIS 11 sites should be undertaken.

Figure 8. Map of western Europe (Google Maps), showing sites mentioned in chapter 4. Round symbol are Eemian-early Weichselian sites of which insect remains were studied, and square symbol are sites dated MIS 7. Depicted are Normandy (11), La Grande Pile (12), Dingé (13) and Oerel (14).

3.4.2 Northern France

Eemian sites with research on Coleoptera are absent in the area of interest. A study on Eemian deposits from the Seine region (Antoine *et al*., 2007) mentions Eemian deposits, but shows that older deposits in this region consist of calcareous tufa. Two studies were found from other parts in France; the studies on sites in Normandy by Coope (1987) and the study on Coleoptera from the site La Grande Pile by Ponel (1995). While the sections from Normandy **(Figure 8: 11)** present ample results from Coleoptera about the climate, thus far the dating of the sections remains problematic and it was not possible to correlate these coastal sections to other sections. La Grande Pile **(Figure 8: 12)** shows in how much detail a environment reconstruction can be made solely from Coleopteran assemblages and from these assemblages quantitative temperature recon- structions could be made for several phases of the Eemian.

France contains several long records which include the Eemian. The sections from Les Echets (De Beaulieu & Reille, 1989) record the end of the Eemian, while the many maar lakes at the Velay region (e.g.

14

Reille *et al.*, 1998, 2000) cover the period from MIS 11 to the present. Together these sections make up a framework for the stratigraphy of Western Europe of the last 400,000 years. Apart from chironomids (Gandouin *et al.*, 2007a) every climate study from these cores is on pollen.

With the area of northernmost France quite sparse of older organic deposits, it becomes unfavorable to search this area for new sites. Two other studies were found on the topic of Coleoptera. One in Brittany, not far from the area of interest (Andrieu *et al.*, 1997) and the other one quite far away in the Alps (Field *et al.,* 2000). The core from Dingé **(Figure 8: 13)** in Brittany has been difficult to date but it was concluded that the record must be older than the Eemian but younger than the Holsteinian and thus should be attributed to MIS 7 or MIS 9. The record from the Alps was correlated with MIS stage 11. Both cores yielded more than a few insect remains.

3.4.3 Benelux

The Netherlands is rich in Eemian sites. From the famous boreholes with shallow marine sediments, Amersfoort and Amsterdam-Terminal (Cleveringa *et al.*, 2000; Van Leeuwen *et al.*, 2000), to fluvial deposits (e.g. Van der Ham, 2008) to lacustrine deposits in the east (e.g. Denekamp; Van Geel *et al.*, 1986) and the south of the country (e.g. Boxtel; Schokker *et al.*, 2004). However, none of these studies has included insects. This leaves a literal hiatus in knowledge between sites La Grance Pile and Oerel. Unfortunately, no organic deposits describing climate from Belgium or Luxembourg were found from the Eemian or older periods.

The type location of MIS 7 in The Netherlands, Maastricht-Belvédère (Roebroeks *et al.*, 1993), has been the subject of climatic studies but only pollen and fossils from large animals have been retrieved from this site. This has quite possibly to do with the type of sediments of the site. Other studies on the period between the Holsteinian and Eemian focus on the geology of The Netherlands during the Saalian. With very interesting results, since it was concluded that sea levels during MIS 7 were at least as high as during the Eemian and that on top of that the stratigraphy of The Netherlands might need to be reviewed for this period (Meijer & Cleveringa, 2009). Finally, it has been found that the core from Boxtel contains organic sediments from MIS 9/11 as well (Schokker *et al.*, 2005).

After contacting the Dutch Center of Geosciences a site which records MIS 11 was suggested, called Kornwerderzand (Bunnik, 2010). This site has been used to determine if the Holsteinian should be correlated to MIS 9 or MIS 11 and contains organic rich layers.

3.4.4 Western Germany

The only Eemian site in Western Germany from which insect remains have been investigated is the Oerel site (Behre *et al.*, 2005)**(Figure 8: 14)**. Many of the sites which were used for Eemian climate reconstruction lie outside the area of interest. Sites inside the area of interest are firstly maar lakes from the Eiffel region (Sirocko *et al.*, 2005). Other sites, like Bispingen (in Field *et al.*, 1994), Quakenbrück (in Müller *et al.*, 2003) Odderade and Rederstall (in Grüger, 1989) are not readily accessible in the literature and could not be considered as potential sites.

No research on Coleoptera has been found from MIS 7 or 9. After many queries, three sites dating MIS 7-9 appear to be in the area of interest. The Nachtigall clay pit, the Schöningen lignite mine and Leck.
The Nachtigall section, near Holzminden, shows several peat, silt and silty mud horizons, together more than 7 meters thick (Kleinmann *et al.*, 2011). These were ^{230}Th/U dated to be between ~227 to ~201 ka and, correlated with the Velay section, to have been deposited during MIS 7c (Waas *et al.*, 2011; Kleinmann *et al.*, 2011). During this long time period a fen or shallow lake continued to exist at this location, due to continuous subsidence of the basin.
The Schöningen lignite mine has been studied since the 1980's and the section consists of consecutive lacustrine deposits (Urban, 2007). These old lakes, of which the ones considered to have originated in warmer periods contain peat and limnic telmatic deposits, are correlated to date from the Holsteinian to the Holocene. After ^{230}Th/U dating of these layers the Holsteinian layer of peat and limnic sediments was correlated to be from MIS 9. The site Leck, in the very north of Germany near Denmark, was mentioned together with the Schöningen site in subsequent studies (Urban *et al.*, 2011). The Leck formation consists of almost 10 meters of silty gyttja and fine sand with organic striae. Unfortunately dating points from the core from Leck were found to be unreliable. Additionally the Leck formation was correlated to among others the

Nachtigall formation and it was tentatively proposed that the Leck formation should be correlated to MIS 7.

Holsteinian deposits in Germany are not rare, and many mentioned key sites are situated in Western Germany. As the titles of the corresponding articles show (e.g. Hallik, 1960; Müller, 1974) these sections consist mainly of diatomite and only pollen and diatoms were studied from these sites. Recently, two sites were investigated containing other sediments than diatomite. The core from Bilshausen (Kühl & Gobet, 2010) contains thick layers of organic rich clay, while the Döttingen dry maar contains lake sediments (Diehl & Sirocko, 2007). However, it was stated that the Döttingen dry maar lake corresponds to the classical Holsteinian sites from western Germany and these sediments thus might sooner correspond to MIS 9.

3.4.5   Discussion

The past decades, a lot of work has been dedicated to reconstruct the climate of the Eemian. Fine reconstructions exist for the early part of the Eemian in southern Britain with Coleoptera (Coope, 2000) and reconstructions by pollen and plant macro remains for the first part of the Eemian in western Europe were published by Zagwijn (1996) and the whole of the Eemian and further stages of MIS 5 by Aalbersberg & Litt (1998). The article by Aalbersberg & Litt shows that many estimates could be made and that low-quality sites could fill in the gaps between high-quality sites. It also shows the lack of data on Coleoptera from mainland Europe, although the authors clearly use these data for verifying the botanical data. While new studies on the Eemian are still performed, recently most of the attention was aimed at MIS 7, 9 and 11.

Other than the Eemian, no stratigraphic framework exists for MIS 7, 9 and 11. Research has developed more rapidly after the discovery of the long records in France and the correlation with long cores from southern Europe, like in Italy (e.g. Pini *et al.*, 2009), but correlation between cores in northwestern Europe still happens by comparing pollen zones. Until a framework has been created for these older interglacials and interstadials, each new research will contribute to our knowledge of these periods. As Coope (1987) put into practice while dating shore deposits in Normandy, Coleoptera could contribute to the stratigraphy of sections. It remains a question if this can be applied to older time periods than the Eemian.

Chapter 4   Potential NW European sites for palaeoclimate research on Coleoptera

For different time periods, the amount of knowledge we have on climate from that period differs per region. In this chapter, it will be considered for each period if there remain hiatuses on our knowledge on climate in certain regions and subsequently potential sites for new research on Coleoptera in this regions will be suggested. In many cases these sites were already mentioned in the previous chapters and more information on these sites should also be found in chapter 3 and 4. To conclude this chapter, a map of northwestern Europe (Figure 10) will depict the potential sites found in this study.

4.1   Late Glacial - Holocene

While climate has been extensively reconstructed for the Late Glacial in northwestern Europe, it became apparent that no complete record from Belgium could be made. Unfortunately no suitable sites containing long-term climate records were found during this study. Secondly, there appears to be a discrepancy between the record from northern France and northern European sites, concerning Coleopteran MCR calculated temperatures during the Bølling and Allerød. Northern France contains many (palaeo) streambeds which could be used as site for a new study to add to the studies by Ponel (2005, 2007). It proved to be difficult to find articles describing peat deposits containing sediment from Bølling and Allerød age as many Holocene sites did not extend that far back (e.g. Bakels, 1995) and no potential sites were found in this study, although it is without question that more suitable sites exist in northern France. It should be attempted to explore sites containing peat lenses as in the study by Frouin *et al.* (2006), instead of obtaining bulk material from river banks.

4.2   Pleniglacial

Although many uncertainties about climate in MIS 3 could be overcome by assuming that discrepancies are due to differences in the timing of interstadials throughout northwestern Europe, opportunities still lie ahead in identifying Coleopteran remains in existing cores from MIS 3 from The Netherlands. Kolstrup & Wijmstra (1977) describe four sites containing peat layers, of which only the site at Voorthuizen has been investigated on beetle remains (Angus, 1975). Unfortunately no site was dated 43,000-40,000 and direct comparison to temperatures in Britain during this time period (Coope, 2006) would be unable to execute, but there are still discrepancies found between Britain and mainland Europe which would be valuable to investigate. These sections (Eerbeek, Voorthuizen, Bussloo, Laarhuis) all lie in the eastern part of The Netherlands and it is expected that more potential sites lie in this region.

4.3   The Eemian

While data from Britain is plentiful and long records from the sites La Grande Pile (Ponel, 1995) and Oerel (Behre *et al.*,2005) provide evidence from France and Germany, no Eemian studies concerning Coleoptera from The Netherlands have been published. This leaves a gap in the European map considering other proxies than pollen grains and vegetation macro remains. The limitations of vegetation as a quantitative temperature proxy for the Eemian (Aalbersberg & Litt, 1998) leaves a wanting for data from Coleoptera in The Netherlands, especially since the Oerel section in Germany lacks the latest part of the Eemian.

    Not a few Eemian sites have been described from The Netherlands, as the area is extremely well described (see figure 9). The well-known boreholes Amersfoort and Amsterdam-Terminal are not suitable for retrieving insect remains as these are marine sections. However, the top of the Amersfoort section exists of wood peat and most probably records the end of the Eemian perfectly (Cleveringa *et al.*, 2000). Besides sediments from fluvial deposits (Van der Ham, 2008) several Eemian sites from palaeolakes and depressions containing organic material have been recorded, like the Drentse Aa valley (De Gans, 1981), Denekamp (Van Geel *et al.*, 1986) and Vollenhove (Van der Vlerk & Florschütz, 1953). The Vollenhove site is said to contain a layer of peat on or very near the surface. It seems that knowledge of this site has become lost through time and it might be worthwhile to rediscover this site. Recent studies took place near Boxtel (Schokker *et al.*, 2004), where a continuous record of peat and loam of almost 2 meters was dated by OSL dating to be of

Eemian age. These sediments are with 4-6 meters below surface very shallow compared to cores further north in The Netherlands, and all these properties make this the best known potential site for climate research on the Eemian in The Netherlands.

Just over the Dutch border, in Belgium, near Antwerp, Eemian sediments were discovered by accident (Vanhoorne & Ferguson, 1997). Thus, Northern Belgium could be searched for additional sites as well.
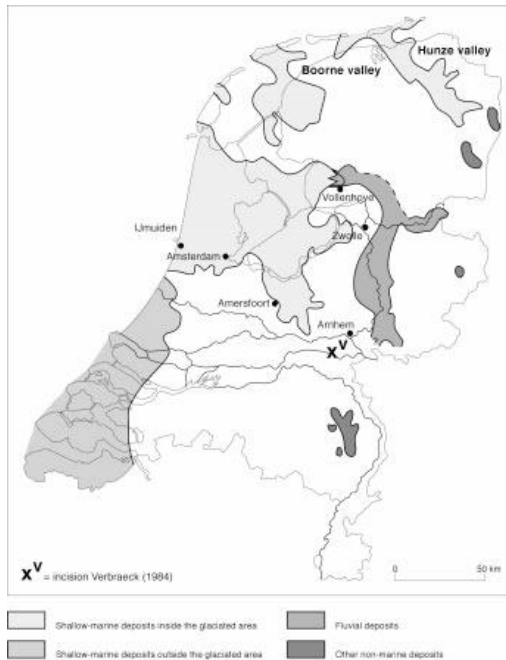

Figure 9. Distribution of Eemian deposits in The Netherlands.
From lighter color to darkest color are depicted: Shallow
Marine deposits; Marine deposits outside the glaciated area;
Fluvial deposits; Other non-marine deposits. (from Bosch *et al.*, 2000).

Almost no data had been available from Western France and Southwestern Germany for a long time (Zagwijn, 1996). With the research on many maar lakes in the region of Southwestern Germany, the majority of which was present during the Eemian (Sirocko *et al.*, 2005), further possibilities emerge for climate studies on Coleoptera. The ELSA project (Eiffel laminated sediment archive) stores sediment cores from 30 dry maar lakes (Rein *et al.*, 2007) and suitable sites could be yielded from their records. A possible challenge would be to collect enough beetle remains from such a lake, since the relatively large size and depth of the lakes might have impeded the capture of insects. A different option is to retrieve material from one of the many lakes in Northwestern Germany that formed after the retreat of the Saalian ice sheet (Caspers *et al.,* 2001). In Western France, the study at Dingué (Andrieu *et* al., 1997) provides extensive data on Coleoptera but was tentatively dated between MIS 5e and MIS 11. Nevertheless, the existence of this site proves that older deposits in Northern France could be accessed. In corporation with French geologists it should be possible to obtain Eemian sites in Western France for research on Coleoptera.

4.4   MIS 7 and MIS 9
With the French framework of long records from La Grande Pile, Les Echets and the Velay region (see chapter 3 for references) there is no urgent request for new climate records from France. If the site at Dingué (Andrieu *et al.*, 1997) could be better dated or correlated, even a record with Coleoptera from the north of France would be present for MIS 7 or MIS 9.

The key site on MIS 7 from the Netherlands, Maastricht-Belvedere (Vandenberghe, 1993), consists mainly of gravel, loess and calcareous tufa. Therefore it is questionable if enough insect remains could be yielded from this section. In a subsequent study on the core from Boxtel (Schokker *et al.*, 2005) it was found

that a lower horizon of peat dates from MIS 9 or 11. Thus, apart from the Eemian, this section could be used for studies on MIS 9/11 as well. In this light, the Boxtel section might contribute to the stratigraphic framework of Western Europe, mainly made up by the French sections and the Oerel section in Germany.

The sites that were found in Western Germany in this study, the Schöningen lignite mine (Urban, 2007) and the Nachtigall clay pit (Waas *et al.*, 2011; Kleinmann *et al.*, 2011) are also good potential sites for climate studies on Coleoptera. Quite recently these sites were re-dated by performing [230]Th/U dating and this technique holds promises for re-dating or correctly dating other middle Pleistocene sites. The site of Leck (Urban *et al.*, 2011) could not be dated and was tentatively dated to be from MIS 7. Apart from the lack of an exact age it also became apparent that the Leck formation has been inundated by seawater for a longer period of time. This indicates that the Leck formation might not be very suitable for new studies in insect remains. While the Schöningen site lies just outside the area of interest it is the only found site in western Germany dating from MIS 9.

4.5   MIS 11
No potential sites for new research on MIS 11 in Northern France were found in this study, as it was concluded by Antoine *et al*. (2007) that the fluvial terraces of the Seine, Somme and Yonne in northern France contain sediments from MIS11, but that these are all calcareous tufa.

From The Netherlands, a new site was recommended by the TNO (Dutch center for geosciences): the site Kornwerderzand, located in the north of The Netherlands, has almost certainly sediments from MIS 11. The bottom of the core taken from this site was interpreted to be dating form MIS 11 and contains a 20 cm peat layer (Bunnik, 2010). This core is stored at TNO and easily accessible.

Western Germany has many sites which were determined as MIS 11 or Holsteinian, most of which are situated very deep and seem only useful for analysis of microfossils. The site at Bilshausen (Kühl & Gobet, 2011) might be the best known option for studies on Coleoptera, although the chances of finding enough macro remains are still low for this site. Also, the Eiffel area contains maar lakes dating from the Holsteinian.

4.6   Summary
Figure 10 and Table 1 summarize the discussed sites in this chapter.

Figure 10. Potential sites for research on fossil Coleoptera in northwestern Europe. Table 1 gives a description of the different sites.

Table 1. Sites from figure 11, with associated age, site type and their reference.

	Site	Age	Deposit	Reference
1	Seine estuary	Late Glacial	Peat marsh	Frouin *et al.*, 2006
2	Eerbeek	MIS 3	Peat lens	Kolstrup & Wijmstra, 1977
3	Bussloo	MIS 3	Peat deposits	Kolstrup & Wijmstra, 1977
4	Laarhuis	MIS 3	Peat deposits	Kolstrup & Wijmstra, 1977
5	Amersfoort borehole	Eemian	Lacustrine	Cleveringa *et al.*, 2000
6	Drentse Aa valley	Eemian	Fluviatile	De Gans, 1981
7	Denekamp	Eemian	Lacustrine- peat	Van Geel *et al.*, 1986
8	Raalte	Eemian	Fluviatile	Van der Ham, 2008
9	Vollenhove	Eemian	Peat deposit	Van der Vlerk & Florschütz, 1953
10	Boxtel	Eemian-Holsteinian	Fluviatile and lacustrine	Schokker*et al.*, 2004; Schokker *et al.*, 2005
11	Liefkenshoek	Eemian	Fluviatile	Vanhoorne & Ferguson, 1997
12	Eiffel maar lakes	Eemian-MIS 11	Maar lakes	Sirocko *et al.*, 2005
13	NW Germany lakes	Eemian	Lacustrine	Caspers *et al.,*2001
14	Dingé	MIS 7-9	Peat deposits	Andrieu *et* al., 1997
15	Belvédère	MIS 7	Fluviatile	Vandenberghe, 1993
16	Schöningen mine	MIS 7-9	Lacustrine- peat	Urban, 2007
17	Nachtigall clay pit	MIS 7	Lacustrine- peat	Waas *et al.*, 2011
18	Leck	MIS 7	Lacustrine	Urban *et al.*, 2011
19	Kornwerderzand	MIS 9-11	Lacustrine- peat	Bunnik, 2010
20	Bilshausen	MIS 11	Maar lake	Kühl & Gobet, 2011

Chapter 5 Conclusion

During this study it became apparent that the Weichselian and onset of the Holocene have been recorded into detail throughout Europe. The last few decades, the climate of the Eemian has been largely clarified and only the scale and correlation of events should receive extensive studying. As the focus of attention in northwestern Europe has shifted to MIS 7, 9 and 11, more knowledge on these periods have become available. For instance, it is now believed that MIS 11 is the best analog to the Holocene. Furthermore it has been stated that many classical Holsteinian sites should be attributed to MIS 9. While many studies prove that much is already known of the older interglacials, by giving syntheses and by modeling temperatures and other environmental variables for these periods, in several of these articles it has been clearified directly or indirectly that there is need of extra proxies to verify the data. Model outputs show deviating results from the fossil records (Huntley *et al*., 2003) and syntheses of data rely heavily on data from fossil Coleoptera apart from pollen records, even though data from Coleoptera are rare outside Britain (Aalbersberg & Litt, 1998). My study might aid in this need by pointing out potential sites for research on fossil Coleoptera. Still, at present the question has arisen if research on fossil Coleoptera still deserves financing, as other proxies for temperature and other environmental variables have been (further) developed. Among the studies on Coleoptera in Northwestern Europe, the most recent one dates from 1997 (Andrieu *et al*., 1997). This is a missed opportunity, since Coleoptera fossils might be one of the few proxies which could give quantitative temperature reconstructions as well as reconstruction of the landscape during that time., as well as quantitative winter temperatures. Quite recently, many new long records were discovered in southern Europe (e.g. Pini *et al*., 2009). If temperature ranges would be determined for southern European beetle species as well, these cores might provide additional studies on quantitative MCR-derived temperatures for southern Europe as well.

Extensive knowledge of the geological history of the region is required to discover potential sites; in many cases it remained elusive if any organic deposits were located in a region. While sites from The Netherlands could be pointed out in many occasions and even extensive data from the cores itself was available, information from Belgium, France and Germany was frequently limited to the finding of a suitable region. In order to find potential sites in these regions it would be necessary to get in contact with the local geologists, and gain access to the national or regional geosciences magazines. For instance, the discovery of the potential Dutch sites Boxtel and Kornwerderzand would not have happened without the aid of people from the Dutch center of geosciences (TNO).

Still, more than a few potential sites were identified during this study. Northern France might have more sites from the Eemian and older periods, but without contacting the local geologists it would prove impossible to find these sites. The finding of an Eemian organic deposit in northern France would prove very worthwhile, as there were no published sites found. Many more sites were discovered in Germany. These sites, like the Schöningen lignite mine and the Nachtigall clay pit, show that countless organic deposits from MIS 7-11 are available through western Germany. If the local scientists could be convinced of the value of new studies on fossil Coleoptera then western Germany proves an excellent area for these studies. The soils of The Netherlands are extremely well mapped and many sites are known and available. Since so much information is available, it is truly a waste that no studies on Coleoptera have taken place since the early 1990's. For instance, the cores from Boxtel could greatly contribute to our knowledge on Eemian climate and earlier and would bridge a gap between the records from Oerel and La Grande Pile, especially since the Oerel section has a hiatus at the latest part of the Eemian (Behre *et al*., 2005). When the value of new research on fossil Coleoptera is again recognized, The Netherlands will prove an excellent area for starting this research, for instance with the section from Boxtel.

References

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Aalbersberg, G. and Litt, T., 1998. Multiproxy climate reconstructions for the Eemian and Early Weichselian. *Journal of Quaternary Science* **13**(5): 367-390.

Abbott, P.M., Davies, S.M., Austin, W.E.N., Pearce, N.J.G. and Hibbert, F.D., 2011. Identification of cryptotephra horizons in a North East Atlantic marine record spanning marine isotope stages 4 and 5a (-60,000-82,000 a b2k). *Quaternary International* **246**(1-2): 177-189.

Andrieu, V., Field, M.H., Ponel, P., Guiot, J., Guenet, P., De Beaulieu, J.-L., Reille, M. and Morzadec-Kerfourn, M.-T., 1997. Middle Pleistocene temperate deposits at Dingé, Ille-et-Vilaine, northwest France: Pollen, plant and insect macrofossil analysis. *Journal of Quaternary Science* **12**(4): 309-331.

Angus, R.B., 1975. Fossil Coleoptera from Weichselian deposits at Voorthuizen, The Netherlands. *Geologie en Mijnbouw* **54**(3-4): 146-147.

Angus, R.B., 1983. Evolutionary stability since the Pleistocene illustrated by reproductive compatibility between Swedish and Spanish *Helophorus lapponicus* Thompson (Coleoptera:Hydrophilidae). *Biological Journal of the Linnean Society of London* **19**: 17-25.

Antoine, P, Limondin-Lozouet, N., Auguste, P., Lamotte, A., Bahain, J.-J., Falguères, C., Laurent, M., Coudret, P., Locht, J.-L., Depaepe, P., Fagnart, J.-P., Fontugne, M., Hatté, C., Mercier, N., Frechen, M., Moigne, A.-M., Munaut, A.-V., Ponel, P. and Rousseau, P.-P., 2003. Paléoenvironments pléistocènes et peuplements paléolithiques dans le bassin de la Somme (nord de la France). *Bulletin de la Société préhistorique Française* **100**(1): 5-28.

Antoine, P., Limondin Lozouet, N., Chaussé, C., Lautridou, J.-P., Pastre, J.-F., Auguste, P., Bahain, J.-J., Falguères, C. and Galehb, B., 2007. Pleistocene fluvial terraces from northern France (Seine, Yonne, Somme): synthesis, and new results from interglacial deposits. *Quaternary Science Reviews* **26**(22-24): 2701-2723.

Atkinson, T.C., Briffa, K.R., Coope, G.R., Joachim, M. and Perry, D.W., 1986. Climatic calibration of Coleopteran data. *In*: Berglund, B. (Ed), Handbook of Holocene palaeoecology and palaeohydrology. New York, Wiley, 851-858.

Atkinson, T.C., Briffa, K.R. and Coope, G.R., 1987. Seasonal temperatures in Britain during the last 22,000 years, reconstructed using beetle remains. *Nature* **325**: 586-592.

Bakels, C., 1995. Late Glacial and Holocene pollen records from the Aisne and Vesle valleys, Northern France: the pollen diagrams Maizy-Cuiry and Bazoches . *Mede. Rijks Geol. Dienst* **52**: 221-234

Basilewsky, P., 1970. Les Coléopteres Carabidae de L'Ille d'Aldabra (Océan Indien). *Bulletin Annuel de la Société Royale Entomologique de Belgique* **106** : 221-222 [In French].

Behre, K.-E. and Van der Plicht, J., 1992. Towards an absolute chronology for the last glacial period in Europe: radiocarbon dates from Oerel, northern Germany. *Vegetation History and Archaeobotany* **1**(2): 111-117.

Behre, K.-E., Hölzer, A. and Lemdahl, G., 2005. Botanical macro-remains and insects from the Eemian and Weichselian site of Oerel (northwest Germany) and their evidence for the history of climate. *Vegetation History and Archaeobotany* **14**(1): 31-53.

Berglund, B.E. and Digerfeldt, G., 1970. A palaeoecological study of the Late-Glacial lake at Torreberga, Scania, South Sweden. *OIKOS* **21**: 98-128.

Berglund, B.E., Bjorck, S., Lemdahl, G., Bergsten, H., Nordberg, K. and Kolstrup, E., 1994. Late Weichselian environmental change in southern Sweden and Denmark. *Journal of Quaternary Science* **9**(2): 127-132.

Bohnke, S., Vandenberghe, J., Coope, G. and Reiling, 1987. Geomorphology and papaeoecology of the Mark valley (southern Netherlands): palaeoecology, palaeohydrology and climate during the Weichselian Late Glacial. *Boreas* **16**: 69-85.

Bos, J.A.A., Huisman, D.J., Kiden, P., Hoek, W.Z. and van Geel, B. 2005. Early Holocene environmental change in the Kreekrak area (Zeeland, SW-Netherlands): A multi-proxy analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* **227**(4): 259-289.

Brauer, A., Allen, J.R.M., Mingram, J., Dulski, P., Wulf, S. and Huntley, B. 2007. Evidence for last interglacial chronology and environmental change from Southern Europe. P*roceedings of the National Academy of Sciences of the United States of America* **104**(2): 450-455.

Bray, P.J., Blockley, S.P.E., Coope, G.R., Dadswell, L.F., Elias, S.A., Lowe, J.J. and Pollard, A.M., 2006. Refining mutual climatic range (MCR) quantitative estimates of palaeotemperature using ubiquity analysis. *Quaternary Science Reviews* **25**: 1865-1876.

Brinkkemper, O., van Geel, B. and Wiegers, J., 1987. Palaeoecological study of a Middle-Pleniglacial deposit from Tilligte, The Netherlands. *Review of palaeobotany and palynology* **51(**4): 235-269.

Bunnik, F.P.M., 2010. Pollenanalyses van boring Kornwerderzand (B10A0154). TNO report TNO-034-UT-2010-01726/B
[In Dutch].

Cappers, R.T.J., Bosch, J.H.A., Bottema, S., Coope, G.R., van Geel, B., Mook-Kamps, E. and Woldring, H., 1993. De reconstructive van het landschap. *In*: Van der Sanden, W.A.B., Cappers, R.T.J., Beuker, J.R., Mol, D. (Eds), Mens en mammoet. De mammoeten van Orvelte en de vroegste van Noord-nederland. Drents, The Netherlands, Drents Museum, 27-41. [In Dutch].

Caspers, G., Merkt, J., Müller, H. and Freund, H., 2002. The Eemian interglaciation in northwestern Germany. *Quaternary Research* **58**(1): 49-52.

CEE: Scarab beetle. *Columbia Electronic Encyclopedia*, 6th Edition, 11/1/2011

Charlson, R.J., Schwartz, S.E., Hales, J.M., Cess, R.D., Coakly, Jr, J.A., Hansen, J.E. and Hofman, J.D., 1992. Climate forcing by anthropogenic aerosols. *Science* **255**(5043): 423-430.

Cheddadi, R., De Beaulieu, J.-L., Jouzel, J., Andrieu-Ponel, V., Laurent, J.-M., Reille, M., Raynaud, D. and Bar-Hen, A., 2005. Similarity of vegetation dynamics during interglacial periods. *Proceedings of the National Academy of Sciences of the United States of America* **102**(39): 13939-13943.

Chen, B., Peng, X., Wang, W., Zhang, J. and Zhang, R., 2002. Research on the microstructure of insect cuticle and the strength of a biomimetic preformed hole composite. *Micron* **33**(6): 571-574.

Clark, P.U. and Mix, A.C., 2001. Ice sheets and sea level of the Last Glacial Maximum. *Quaternary Science Reviews* **21**(1-3): 1-7.

Cleveringa, P., Meijer, T., Van Leeuwen, R.J.W., De Wolf, H., Pouwer, R., Lissenberg, T. and Burger, A.W., 2000. The Eemian stratotype locality at Amersfoort in the central Netherlands: A re-evaluation of old and new data. *Netherlands Journal of Geosciences* **79**(2-3): 197-216.

Coleman, J.M., 1964. *Cyclic sedimentation in the Mississippi River deltaic plain*; [transactions of the Gulf Coast Association of Geological Societies , 14^(th) annual convention. Baton Rouge, Louisiana State University.

Coope, G.R., 1959. A late Pleistocene insect fauna from Chelford, Cheshire. *Proceedings of the Royal Society of London,* Series B 151: 70-86.

Coope, G.R., 1969. Insect remains from Mid Weichselian deposits at Peelo, The Netherlands. *Med. Rijks Geol. Dienst*, N.S., **20**: 79-83.

Coope, G.R., 1970. Interpretations of Quaternary insect fossils. *Annual Review of Entomology* **15**: 97-120.

Coope, G.R., 1973. Tibetan species of dung beetle from Late Pleistocene deposits in England. *Nature* **245**, 335-336.

Coope, G.R. 2000, "The climatic significance of coleopteran assemblages from the Eemian deposits in southern England", Geologie en Mijnbouw/Netherlands Journal of Geosciences, vol. 79, no. 2-3, pp. 257-267.

Coope, G.R., 2006. Insect faunas associated with palaeolithic industries from five sites of pre-Anglian age in central England. *Quaternary Science Reviews* **25**(15-16): 1738-1754.

Coope, G.R., Dickson, J.H., Jones, R.L. and Keen, D.H., 1987. The flora and fauna of late Pleistocene deposits of the Cotentin Peninsula, Normandy. *Philosophical Transactions of the Royal Society of London, series B* **315**: 231-265.

Coope, G.R. and Lemdahl, G., 1995. Regional differences in the lateglacial climate of northern Europe based on coleopteran analysis. *Journal of Quaternary Science* **10**(4): 391-395.

Crombé, P., Sergant, J., Robinson, E. and De Reu, J., 2011. Hunter-gatherer responses to environmental change during the Pleistocene-Holocene transition in the southern North Sea basin: Final Palaeolithic-Final Mesolithic land use in northwest Belgium. *Journal of Anthropological Archaeology* **30**(3): 454-471.

Crowson, R.A., 1981. *The biology of the Coleoptera.* Academic Press Inc. (London).

Damblon, F., Coope, G.R. and Osborne, P.J., 1977. Palaeoecological studies of peat bogs in the High Ardenne. *Proceedings of the X INQUA Congress, Birmingham.* Geobooks, Norwich, 101.

Danks, H.V., 1978. Modes of seasonal adaptation. 1. Winter survival. *Canadian Entomologist* **110**: 1167-1205

Dantharanayana, W., 1970. Studies on the dispersal and migration of *Sitona regensteinensis* (Coleoptera: Curculionidae). *Entomologia experimentalis et applicata* **13**(3): 236-246

de Abreu, L., Abrantes, F.F., Shackleton, N.J., Tzedakis, P.C., McManus, J.F., Oppo, D.W. and Hall, M.A. 2005. Ocean climate variability in the eastern North Atlantic during interglacial marine isotope stage 11: A partial analogue to the Holocene? *Paleoceanography* **20**(3): 1-15.

de Beaulieu, J.-L. and Reille, M., 1989. The transition from temperate phases to stadials in the long upper Pleistocene sequence from Les Echets (France). *Palaeogeography, Palaeoclimatology, Palaeoecology* **72**(C): 147-159.

de Beaulieu, J.-L. and Reille, M., 1992. The last climatic cycle at La Grande Pile (Vosges, France) a new pollen profile. *Quaternary Science Reviews* **11**(4): 431-438.

de Beaulieu, J.-L. and Reille, M., 1995. Pollen records from the Velay craters: a review and correlation of the Holsteinian interglacial with isotopic stage 11. *Dutch Journal of Geosciences* **52**: 59-70.

De Gans, W., 1981. Stratigraphy, palynology and radio carbon data of Eemian and early Weichselian fluvial deposits in the Drentse Aa vally system (Drente, The Netherlands). *Geologie & mijnbouw* **60**(2): 193-202.

Demske, D., Heumann, G., Granoszewski, W., Nita, M., Mamakowa, K., Tarasov, P.E. and Oberhänsli, H., 2005. Late glacial and Holocene vegetation and regional climate variability evidenced in high-resolution pollen records from Lake Baikal. *Global and Planetary Change* **46** (1-4 Spec. Iss.): 255-279.

Derese, C., Vandenberghe, D., Paulissen, E. and van den Haute, P., 2009. Revisiting a type locality for Late Glacial aeolian sand deposition in NW Europe: Optical dating of the dune complex at Opgrimbie (NE Belgium). *Geomorphology* **109**(1-2): 27-35.

Diehl, M. and Sirocko, F., 2007. 27. A new holsteinian pollen record from the dry maar at Döttingen (Eifel). *In*: Sirocko, F., Claussen, M., Sánchez Goñi, M.F. and Litt, T. (Eds), Developments in Quaternary science 7, pp 397-416. Elsevier, Amsterdam.

Dubois, G., 1948. Pollen analysis of post glacial peats and deposits in France for the period 1939-1946. *Vegetatio* **1**(1): 43-50.

Ehlers, J., Gibbard, P.L., 2004. *Quaternary Glaciations - Extent and Chronology Part I: Europe*. Elsevier, Amsterdam.

Elias, S.A., 2007. Beetle records: Late Tertiary and Early Quaternary. *In*: Elias, S.A. (Ed), Encyclopedia of Quaternary Science. Amsterdam, Elsevier, 163-172.

Elias, S.A., 2010. *Advances in Quaternary Entomology*. Elsevier, Amsterdam.

Elias, S.A., Carrara, P.E., Toolin, L.J. and Jull, A.J.T., 1991. Revised age of deglaciation of Lake Emma based on new radiocarbon and macrofossil analyses. *Quaternary Research* **36**: 307-321.

Field, M.H., Huntley, B. and Müller, H., 1994. Eemian climate fluctuations observed in a European pollen record. *Nature* **371**(6500): 779-783.

Field, M.H., De Beaulieu, J.-L., Guiot, J. and Ponel, P. 2000. Middle Pleistocene deposits at La Cote, Val-de-Lans, Isere department, France: Plant macrofossil, palynological and fossil insect investigations. *Palaeogeography, Palaeoclimatology, Palaeoecology* **159**(1-2): 53-83.

Frouin, M., Sebag, D., Laignel, B., Ogier, S., Verrecchia, E.P. and Durand, A., 2006. Tidal rhythmites of the Marais Vernier Seine estuary, France and their implications for relative sea-level. *Marine Geology* **235**(1-4 SPEC. ISS): 165-175.

Gandouin, E., Ponel, P., Andrieu-Ponel, V., Franquet, E., de Beaulieu, J.-L., Reille, M., Guiter, F., Brulhet, J., Lallier-Vergès, E., Keravis, D., von Grafenstein, U. and Veres, D., 2007a. Past environment and climate changes at the last Interglacial/Glacial transition (Les Échets, France) inferred from subfossil chironomids (Insecta). *Comptes Rendus – Geoscience* **339**(5): 337-346.

Gandouin, E., Ponel, P., Franquet, E., Van Vliet Lanoë, B., Andrieu-Ponel, V., Keen, D.H., Brulhet, J. and Brocandel, M., 2007b. Chrironomid responses (Insect: Diptera) to Younger Dryas and Holocene environmental changes in a river floodplain from northern France (St-Momelin, St-Omer basin). *The Holocene* **17**(3): 331-347.

Gandouin, E., Ponel, P., Andrieu-Ponel, V., Guiter, F., De Beaulieu, J.-L., Djamali, M., Franquet, E., Van Vliet-Lanoë, B., Alvitre, M., Meurisse, M., Brocandel, M., Brulhet, J., 2009. 10,000 years of vegetation history of the Aa palaeoestuary, St-Omer basin, northern France. *Reviewof Palaeobotany and Palynology* **156**: 307-318.

Geyh, M.A. and Müller, H., 2005. Numerical 230Th/U dating and a palynological review of the Holsteinian/Hoxnian Interglacial. *Quaternary Science Reviews* **24**(16–17): 1861-1872

Gibbard, P.L., Rose, J. and Bridgland, D.R., 1988. The history of great Northwest European rivers during the past three million years [and discussion]. *Philosophical transactions of the Royal Society of London, Ser. B, biological sciences*, **318**(1191): 559-602.

Grootes, P.M. and Stuiver, M., 1997. Oxygen 18/16 variability in Greenland snow and ice with 10^{-3} to 10^{-5}- year time resolution. *Journal of Geophysical Research* **102**(C12): 26455-26470.

Grüger, E., 1989. Palynostratigraphy of the last interglacial/glacial cycle in Germany. *Quaternary International* **3-4**(C): 69-79.

Guiot, J. and Couteaux, M., 1992. Quantitative climate reconstruction from pollen data in the Grand Duchy of Luxembourg, since 15 000 yr BP. *Journal of Quaternary Science* **7**(4): 303-309.

Guiter, F., Andrieu-Ponel, V., De Beaulieu, J.-L., Cheddadi, R., Calvez, M., Ponel, P., Reille, M., Keller, T. and Goeury, C., 2003. The last climatic cycles in Western Europe : a comparison between long continuous lacustrine sequences from France and other terrestrial records. *Quaternary International* **111**: 59-74.

Hadley, N.F., 1979: Wax secretion and color phases of the desert tenebrionid beetle *Cryptoglossa verrucosa* (Leconte). *Science* **203**, 367-369.

Hallik, R., 1960. Die Vegetationsentwicklung der Holstein-Warmzeit in Nordwestdeutschland und die Altersstellung der Kieselgurlager der südlichen Lüneburger Heide. *Zeitschrift deutsche geologische Gesellschaft* **112**: 326-333.

Howden, H.F. and Scholtz, C.H., 1986. Changes in a Texas dung beetle community between 1975 and 1985 (Coleoptera: Scarabeidae, Scarabeinae). *Coleopterists Bulletin* **40**, 313-316.

Huijzer, B. and Vandenberghe, J., 1998. Climatic reconstruction of the Weichselian Pleniglacial in northwestern and central Europe. *Journal of Quaternary Science* **13**(5): 391-417.

Huntley, B., Alfano, M.J., Allen, J.R.M., Pollard, D., Tzedakis, P.C., de Beaulieu, J.-L., Grüger, E. and Watts, B., 2003. European vegetation during marine oxygen isotope stage-3. *Quaternary Research* **59**(2): 195-212.

Huppert, A. and Solow, A.R., 2004. A method for reconstructing climate from fossil beetle assemblages. *Proceedings of the Royal Society of London* Series B271: 1125-1128.

Imbrie, J., Hays, J.D., Martinson, D.G., McIntyre, A., Mix, A.C., Morley, J.J., Pisias, N.G., Prell, W.L. and Shackleton, N.J., 1984. The orbital theory of Pleistocene climate: support from a revised chronology of the marine δ^{18}O record. *In:* A. Berger (Ed): Milankovitch and climate, Part 1 (pp 269-305), Hingham MA.

Isarin, R.F.B., Renssen, H. and Vandenberghe, J. 1998. The impact of the North Atlantic Ocean on the Younger Dryas climate in northwestern and central Europe. *Journal of Quaternary Science* **13**(5): 447-453.

Kitchen, K. A. (2008). Scarabs, Chronology, and Interconnections: Egypt and Palestine in the Second Intermediate Period. *Journal For The Study Of The Old Testament*, **32**(5), 185.

Kleinmann, A., Müller, H., Lepper, J. and Waas, D., 2011. Nachtigall: A continental sediment and pollen sequence of the Saalian Complex in NW-Germany and its relationship to the MIS-framework. *Quaternary International* **241**(1-2): 97-110.

Knies, J.L., Izem, R., Supler, K.L., Kingsolver, J.G., Burch, C.L. and Noor. M., 2006. The Genetic Basis of Thermal Reaction Norm Evolution in Lab and Natural Phage Populations. *PloS biology* **4**(7): e201.

Koch, C., 1962. The Tenebrionidae of southern Africa XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum* **24**, 61-103.

Kolstrup, E. and Wijmstra, T.A., 1977. A palynological investigation of the Moershoofd, Hengelo, and Denekamp interstadials in The Netherlands. *Geologie en Mijnbouw* **56**(2): 85-102.

Koppen, W., 1936. Das geographische System der Klimate. *In*: Koppen, W. and Geiger, G. (Eds): Handbuch der Klimatologie. 1.C. Gebr, Borntraeger, 1-44.

Kühl, N. and Litt, T., 2003. Quantitative time series reconstruction of Eemian temperature at three European sites using pollen data. *Vegetation History and Archaeobotany* **12**(4): 205-214.

Kühl, N. and Gobet, E., 2010. Climatic evolution during the Middle Pleistocene warm period of Bilshausen, Germany, compared to the Holocene. *Quaternary Science Reviews* **15**: 1-14.

Lang, B., Bedford, A., Brooks, S.J., Jones, R.T., Richardson, N., Birks, H.J.B. and Marshall, J.D., 2010. Early-Holocene temperature variability inferred from chironomid assemblages at Hawes Water, northwest England. *Holocene* **20**(6): 943-954.

Lindroth, C. H., 1948. Interglacial insect fossils from Sweden. *Arsbok Sveriges Geologiska Undersökn*, Series C 42: 1-29.

Litt, T., 2007. 23. Introduction: Climate, Vegetation and Mammalian Faunas in Europe during Middle Pleistocene Interglacials (MIS 7, 9, 11). *In*: Sirocko, F., Claussen, M., Sánchez Goñi, M.F. and Litt, T. (Eds): The climate of past interglacials, pp 351-357. Elsevier, Amsterdam.

Litt, T., Schminke, H.-U. and Kromer, B., 2003. Environmental response to climatic and volcanic events in central Europe during the Weichselian Lateglacial. *Quaternary Science Reviews* **22**: 7-32.

Litt, T., Schölzel, C., Kühl, N. and Brauer, A., 2009. Vegetation and climate history in the Westeifel Volcanic Field (Germany) during the past 11 000 years based on annually laminated lacustrine maar sediments. *Boreas* **38**(4): 679-690.

Lobo, J.M., Lumaret, J.-P and Jay-Robert, P., 2002. Modeling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. *Global Ecology and Biogeography* **11**: 265-277.

Lomnicki, A.M., 1894. Pleistocienskie owady z Borislawia. (Fauna PLeistocenica insectorum Boryslaviensum). *Wydawnictwa Muzeum imienia Dzieduszyckich* **4**: 1-116. [In Polish].

Lücke, A. and Brauer, A., 2004. Biogeochemical and micro-facial fingerprints of ecosystem response to rapid Late Glacial climatic changes in varved sediments of MeerfelderMaar (Germany).
Palaeogeography, Palaeoclimatology, Palaeoecology **211**(1-2): 139-155.

Mani, M.S. , 1968. *Ecology and biogeography of high altitude insecs*. The Hague, The Netherlands, Junk.

Mann, M.E., 2002. The value of multiple proxies. *Science* **297**(5586): 1481-1482.

Matthews, Jr, J.V., 1976a. Evolution of the subgenus *Cyphelophorus* (Genus *Helophorus*, Hydrophilidae): description of two new fossil species and discussion of *Helophorus tuberculatus* Gyll. *Canadian Journal of Zoology* **54**: 653-673.

Matthews, Jr, J.V., 1976b. Insect fossils from the Beaufort Formation: geological and biological significance. *Geological Survey of Canada Papers* 76-1B: 217-227.

Meijer, T. and Cleveringa, P., 2009. Aminostratigraphy of Middle and Late Pleistocene deposits in The Netherlands and the southern part of the North Sea Basin. *Global and Planetary Change* **68**(4): 326-345.

Merkt, J. and Müller, H., 1999. Varve chronology and palynology of the Lateglacial in Northwest Germany from lacustrine sediments of Hamelsee in Lower Saxony. *Quaternary International* **61**: 41-59.

Meyrick, R.A., 2001. The development of terrestrial mollusc faunas in the 'Rheinland region' (western Germany and Luxembourg) during the Lateglacial and Holocene. *Quaternary Science Reviews* **20** (16-17): 1667-1675.

Mingram, J., 1998. Laminated Eocene maar-lake sediments from Eckfeld (Eifel region, Germany) and their short-term periodicities. *Palaeogeography, Palaeoclimatology, Palaeoecology* **140**(1-4): 289-305.

Moine, O., Antoine, P., Deschodt, L. and Sellier-Segard, N., 2011. High resolution molluscan records in upper weichselian loess and tundra gleys: First examples from northern france. *Quaternaire* **22**(4): 307-325.

Monnin, E., Indermühle, A., Dällenbach, A., Flückinger, J., Stauffer, B., Stocker, T.F., Raynaud, D. and Barnola, J.-M., 2001. Atmospheric CO_2 concentrations over the last glacial termination. *Science* **291**(5501): 112-113.

Müller, H., 1974. Pollenanalytische Untersuchungen und Jahresschichtenzählungen an der holsteinzeitlichen Kieselgur von Munster-Breloh. *Geologisches Jahrbuch A* **21**: 107-140.

Müller, U.C., Pross, J. and Bibus, E., 2003. Vegetation response to rapid climate change in Central Europe during the past 140,000 yr based on evidence from the Füramoos pollen record. *Quaternary Research* **59**(2): 235-245.

Naton, H.-G., Cordier, S., Brou, L., Damblon, F., Frechen, M., Hauzeur, A., Le Brun-Ricalens, F., Valotteau, F., Baes, R., Dövener, F. and Krier, J. 2009. Fluvial evolution of the moselle valley in luxembourg during late pleistocene and holocene: palaeoenvironment and human occupation. *Quaternaire* **20**(1): 81-92.

Olander, H., Birks, H.J.B., Korhola, A. and Blom, T., 1999. An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *Holocene* **9**(3): 279-294.

Olsson, F. and Lemdahl, G., 2009. A continuous Holocene beetle record from the site Stavsåkra, southern Sweden: implications for the last 10,600 years of forest and land use history. *Journal of Quaternary Science* 24(6):612-626.

Osborne, P.J., 1980. The insect fauna of the organic deposit at Sugworth and its environmental and stratigraphic implications. *Philosophical transactions of the Royal Society of London, Ser. B, biological sciences*, **289**(1034): 119-133.

Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davis, M., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V.Y., Lorius, C., Pépin, L., Ritz, C., Saltzman, E. and Stievenard, M., 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**: 429-436.

Pini, R., Ravazzi, C. and Donegana, M., 2009. Pollen stratigraphy, vegetation and climate history of the last 215 ka in the Azzano Decimo core (plain of Friuli, north-eastern Italy). *Quaternary Science Reviews* **28**(13-14): 1268-1290.

Ponel, P., 1995. Rissian, Eemian and Würmian Coleoptera assemblages from La Grande Pile (Vosges, France). *Palaeogeography, Palaeoclimatology, Palaeoecology* **114**: 1-41.

Ponel. P., Coope, G.R., Antoine, P., Limondin-Lozouet, N., Leroyer, C., Munaut, A.-V., Pastre, J.-F. and Guiter, F., 2005. Lateglacial palaeoenvironments and palaeoclimates from Conty and Houdancourt, northern France, reconstructed from Beetle remains. *Quaternary Science Reviews* **24**: 2449-2465.

Ponel, P., Gandouin, E., Coope, G.R., Andrieu-Ponel, V., Guiter, F., Van Vliet-Lanoë, B., Franquet, E., Brocandel, M. and Brulhet, J., 2007. Insect evidence for environmental and climate changes from Younger Dryas to Sub-Boreal in a river floodplain at St-Momelin (St-Omer basin, northern France), Coleoptera and Trichoptera. *Palaeogeography, Palaeoclimatology, Palaeoecology* **245**:483-504.

Raymo, M.E., W.F. Ruddiman, J. Backman, B.M. Clement, and D.G. Martinson, 1989. Late Pliocene variation in Northern Hemisphere ice sheets and North Atlantic deep circulation. *Paleoceanography* **4**: 413-446.

Reille, M., Andrieu, V., De Beaulieu, J.-L., Guenet, P. and Goeury, C. 1998. A long pollen record from Lac du Bouchet, Massif Central, France: For the period ca. 325 to 100 ka BP (OIS 9c to OIS 5e). *Quaternary Science Reviews* **17**(12): 1107-1123.

Reille, M., De Beaulieu, J.-L., Svobodova, H., Andrieu-Ponel, V. and Goeury, C., 2000. Pollen analytical biostratigraphy of the last five climatic cycles from a long continental sequence from the Velay region (Massif Central, France). *Journal of Quaternary Science* **15**(7): 665-685.

Rein, B., Jäger, K., Kocot, Y., Grimm, K. and Sirocko, F., 2007. 10. Holocene and Eemian varve types of Eifel maar lake sediments. *In*: Sirocko, F., Claussen, M., Sánchez Goñi, M. F. and Litt, T. (Eds), The Climate of Past Interglacials, pp 141-156. Elsevier, Amsterdam.

Reiss, R.A., Ashwordt, A.C. and Schwert, D.P., 1999. Molecular genetic evidence of post-Pleistocene population divergence of the arctic/alpine ground beetle *Amara alpina* (Paykull) (Coleoptera: Carabidae). *Journal of Biogeography* **26**:785-794.

Renssen, H. and Isarin, R.F.B., 2001. The two major warming phases of the last deglaciation at ~14.7 and ~11.5 ka cal BP in Europe: Climate reconstructions and AGCM experiments. *Global and Planetary Change* **30**(1-4): 117-153.

Roebroeks, van Kolfschoten and Vandenberghe, 1993. The Belvédère project: Introduction. *Dutch Journal of Geosciences* **47**: 5-6.

Rogers, S. Barrett, R., Paccard, A., Healy, T., Bergek, S., Schulte, P. and Schluter, D., 2011. Rapid evolution of cold tolerance in stickleback. *Proceedings of the Royal Society of London. Biological Sciences*. **278**(1703): 233-238.

Rose, J., 2009. Early and Middle Pleistocene landscapes of eastern England. *Proceedings of the Geologists' Association* **120**(1): 3-33.

Ruddiman, W.F., 2005. Cold climate during the closest Stage 11 analog to recent Millennia. *Quaternary Science Reviews* **24**(10-11): 1111-1121.

Schminke, H.-U., Park., C., and Harms, E., 1999. Evolution and environmental impacts of the eruption of LaacherSee Volcano (Germany) 12,900 a BP. *Quaternary International* **61**(1): 61-72.

Schokker, J., Cleveringa, P. and Murray, A.S., 2004. Palaeoenvironmental reconstruction and OSL dating of terrestrial Eemian deposits in the southeastern Netherlands. *Journal of Quaternary Science* **19**(2): 193-202.

Schokker, J., Cleveringa, P., Murray, A.S., Wallinga, J. and Westerhoff, W.E., 2005. An OSL dated Middle and Late Quaternary sedimentary record in the Roer Valley Graben (southeastern Netherlands). *Quaternary Science Reviews* **24** (20-21): 2243-2264.

Schwartz, E.A., 1914. Aquatic beetles, especially *Hydroscapha*, in hot springs in Arizona. Proc. Ent. Soc. Wash. **16**, 163-168.

Scudder, S.H., 1877. Description of two new species of Carabidae found in the interglacial deposits at Scarborough Hts., in Toronto, Canada. *United States Geological Survey of the Territories* (Hayden) B3: 763- 764.

Scudder, S.H., 1900. Canadian fossil insects. Geological Survey of Canada, Publication No. 710, *Contributions to Canadian Palaeontology* **2**(2): 67-92.

Simonis, D., Hense, A. and Litt, T., 2012. Reconstruction of late Glacial and Early Holocene near surface temperature anomalies in Europe and their statistical interpretation. *Quaternary International* (in press), doi:10.1016 .

Sirocko, F., Seelos, K., Schaber, K., Rein, B., Dreher, F., Diehl, M., Lehne, R., Jäger, K., Krbetschek, M. and Degering, D., 2005. A late Eemian aridity pulse in central Europe during the last glacial inception. *Nature* **436**(7052): 833-836.

Taylor, B.J. and Coope, G.R., 1985. Arthropods in the Quaternary of East Anglica – their role as indices of local paleoenvironments and regional paleoclimates. *Modern Geology* **9**: 159-185.

Thiele, H.U., 1977. *Carabid beetles in their environments*. Springer, Berlin/New York.

Tomihata, K. and Ikada, Y., 1997. In vitro and in vivo degradation of films of chitin and its deacetylated derivatives. *Biomaterials* **18**(7): 567-575.

Turner, C., 1998. Volcanic maars, long quaternary sequences and the work of the INQUA subcommission on European quaternary stratigraphy. *Quaternary International* **47-48**: 41-49.

Turner, C., 2000. The Eemian interglacial in the North European plain and adjacent areas. *Netherlands Journal of Geosciences* **79**(2-3): 217-231.

Urban, B., 2007. 28. Interglacial pollen records from schöningen, North Germany. *In*: Sirocko, F., Claussen, M., Sánchez Goñi, M.F. and Litt, T., (Eds): The climate of past interglacials, pp 417-444. Elsevier, Amsterdam.

Urban, B., Sierralta, M. and Frechen, M., 2011. New evidence for vegetation development and timing of Upper Middle Pleistocene interglacials in Northern Germany and tentative correlations. *Quaternary International* **241**(1-2): 125-142.

Vandenberghe, J., 1993. River terrace development and its relation to climate: the Saalian Caberg terrace of the Maas River near Maastricht (the Netherlands). *Netherlands Journal of Geosciences* **47**:19-24.

van den Boogaard, P. and Schminke, H.-U., 1984. The eruptive center of the late quaternary Laacher see tephra. *Geologische Rundschau* **73**(3): 933-980.

van der Ham, R.W.J.M., Kuijper, W.J., Kortselius, M.J.H., Van Der Burgh, J., Stone, G.N. and Brewer, J.G., 2008. Plant remains from the Kreftenheye Formation (Eemian) at Raalte, The Netherlands. *Vegetation History and Archaeobotany* **17**(1): 127-144.

van der Molen, J. and Van Dijck, B. 2000. The evolution of the Dutch and Belgian coasts and the role of sand supply from the North Sea. *Global and Planetary Change* **27**(1-4): 223-244.

van der Vlerk, I.M. and Florschütz, F., 1953. The palaeontological base of the subdivision of the Pleistocene in The Netherlands. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen. [Afdeling Natuurkunde]*, *reeks 1*, dl XX: No. 2.

van Geel, B., Bohncke, S.J.P. and Dee, H. 1980. A palaeoecological study of an upper late glacial and holocene sequence from "de borchert", The Netherlands. *Review of palaeobotany and palynology* **31**(C): 367-392,397-448.

van Geel, B., Klink, A.G., Pals, J.P. and Wiegers, J.,1986. An Upper Eemian lake deposit from Twente, eastern Netherlands. Review of palaeobotany and palynology **47**(1-2): 31-37,40,43,45,47,49,51-61.

van Geel, B., Coope, G.R. and van Der Hammen, T., 1989. Palaeoecology and stratigraphy of the lateglacial type section at Usselo (the Netherlands). *Review of palaeobotany and palynology* **60**(1-2): 25-38,41-42,45-46,48-49,51-60,63-64,67-68,75-129.

van Hardenbroeck, M.R., Lotter, A.F., Bastviken, D., Duc, N.T. and Heiri, O., 2012. Relationship of δ^{13}C of chironomid remains and methane flux in Swedish lakes. *Freshwater Biology* **57**(1): 166-177.

Vanhoorne, R. and Ferguson, D.K., 1997. A palaeoecological interpretation of an eemian floral assemblage in the Scheldt Valley at liefkenshoek near Antwerp (Belgium). *Review of palaeobotany and palynology* **97**(1-2): 97-107.

van Leeuwaarden, W. and Janssen, C.R. 1987. Differences between valley and upland vegetation development in eastern Noord-Brabant, The Netherlands, during the Late Glacial and early Holocene. *Review of palaeobotany and palynology* **52**(2-3): 179-204.

van Leeuwen, R.J.W., Beets, D.J., Bosch, J.H.A., Burger, A.W., Cleveringa, P., Van Harten, D., Herngreen, G.F.W., Kruk, R.W., Langereis, C.G., Meijer, T., Pouwer, R. and de Wolf, H., 2000. Stratigraphy and integrated facies analysis of the Saalian and Eemian sediments in the Amsterdam-Terminal borehole, the Netherlands. *Netherlands Journal of Geosciences* **79**(2-3): 161-196.

Verbruggen, C., 1999. Quaternary palaeobotanical evolution of northern Belgium. *Geologica Belgica* **2/3-4**: 99-110.

Verbruggen, C., Denys, L., and Kiden, P., 1996. Belgium. *In:* Berglund, B.E., Birks, H.J.B., Ralska-jasiewiczowa, M. and Wright, H.E. (Eds), Palaeoecolological events during the last 15,000 years, pp 553-574. Wiley and Sons, Chichester.

Vincent, J.F.V. and Wegst, U.G.K., 2004. Design and mechanical properties of insect cuticle. *Arthropod Structure and Development* **33**(3): 187-199.

Voelker, A.H.L., Rodrigues, T., Stein, R., Hefter, J., Billups, K., Oppo, D., Mcmanus, J. and Grimalt, J.O., 2009. Variations in mid-latitude North Atlantic surface water properties during the mid-Brunhes: Does Marine Isotope Stage 11 stand out? *Climate of the Past Discussions* **5**(3): 1553-1607.

Waas, D., Kleinmann, A. and Lepper, J., 2011. Uranium-series dating of fen peat horizons from pit Nachtigall in northern Germany. *Quaternary International* **241**(1-2): 111-124.

Walker, M.J.C., 1995. Climatic changes in Europe during the last glacial/interglacial transition. *Quaternary International* **28**: 63-76.

Walker, M.J.C., Bohncke, S.J.P., Coope, G.R., O'Connell, M., Usinger, H. and Verbruggen, C., 1994. The Devensian/ Weichselian late-glacial in northwest Europe (Ireland, Britain, north Belgium, The Netherlands, northwest Germany). *Journal of Quaternary Science* **9**(2): 109-118.

Walker, M.J.C., Coope, G.R., Harkness, D.D., Lowe, J.J. and Scott, E.M., 2001. Towards a radiocarbon chronology of the Late-Glacial: sample selection strategies. *Radiocarbon* **43**: 1007-1019.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. and Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* **416**(6879): 389-395.

Witte, H.J.L., Coope, G.R., Lemdahl, G. and Lowe, J.J., 1998. Regression coefficients of thermal gradients in northwestern Europe during the last glacial-Holocene transition using beetle MCR data. *Journal of Quaternary Science* **13**(5): 435-445.

Woillard, G.M., 1978. Grande Pile peat bog: A continuous pollen record for the last 140,000 years. *Quaternary Research* **9**(1): 1-21.

Zagwijn, W.H., 1957. Vegetation, climate and tine-correlations in the early Pleistocene of Europe. *Geologie en Mijnbouw* **19**: 233-244.

Zagwijn, W.H., 1963. Pleistocene stratigraphy in The Netherlands, based on changes in vegetation and climate. *Kon. Ned. Geol. Mijnb. Gen.*, Geol. Serie 21-2: 173-196.

Zagwijn, W.H., 1992. The beginning of the Ice Age in Europe and its major subdivisions. *Quaternary Science Reviews* **11** (5): 583-591.

Zagwijn, W.H., 1996. An analysis of Eemian climate in western and central Europe. *Quaternary Science Reviews* **15** (5-6): 451-469.