Holocene palaeoenvironmental reconstruction based on fossil beetle faunas from the Altai-Xinjiang region, China

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By

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Declaration of Authorship

I Tianshu Zhang hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated.

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Date: 25/02/2018

Abstract

This project presents the results of the analysis of fossil beetle assemblages extracted from 71 samples from two peat profiles from the Halashazi Wetland in the southern Altai region of northwest China. The fossil assemblages allowed the reconstruction of local environments of the early (10,424 to 9500 cal. yr BP) and middle Holocene (6374 to 4378 cal. yr BP). In total, 54 Coleoptera taxa representing 44 genera and 14 families have been found, and 37 species have been identified, including a new species, *Helophorus sinoglacialis*. The majority of the fossil beetle species identified are today part of the Siberian fauna, and indicate cold steppe or tundra ecosystems. Based on the biogeographic affinities of the fossil faunas, it appears that the Altai Mountains served as dispersal corridor for cold-adapted (northern) beetle species during the Holocene.

Quantified temperature estimates were made using the Mutual Climate Range (MCR) method. In addition, indicator beetle species (cold adapted species and bark beetles) have helped to identify both cold and warm intervals, and moisture conditions have been estimated on the basis of water associated species. Generally, the fossil beetle record indicates a cold and wet early Holocene (from ~10,424 to ~ 9500 cal. yr BP) and a relativly cold and dry middle Holocene (from ~6374 to ~ 4378 cal. yr BP) at the Halashazi Wetland.

The appearance of bark beetle fossils (*Phloeotribus spinulosus* and *Trypodendron sp.*) clearly demonstrate the presence of trees at or very near the site around 9665, 9570 and 5451 cal. yr BP, whereas the spruce pollen values at the site never exceeded five percent, and there were no spruce macrofossils found in the palaeobotanical study.

Using Quaternary beetles to reconstruct palaeoenvironments is a new research method for this region, and has never before been done in China. The project provides new evidence concerning the environmental history of the study area. This study has helped establish Quaternary beetle research in China, and has contributed to beetle faunal research in Eurasia.

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Chapter 1. Introduction

1.1 Research Aims and Objectives

The principle aim of the project is to produce a high-precision palaeoclimatic record for the southern Altai Mountains based on fossil beetle assemblages. To achieve this aim, this project intends to meet the following objectives:

1) To identify the beetle species found in Holocene sediment sequences in the Altai region.
2) To produce a beetle species list for each sample recovered from the Altai mountain sequence.
3) To use BUGS program to generate Tmin and Tmax MCR estimates for each sample.
4) To reconstruct a history of local hydrology based on the water beetle record from this site.
5) To use the stratigraphy of the site to generate an independent record of changing temperature and local moisture condition through the sequence
6) To use radiocarbon dating to produce an age model for the peat profiles.

1.2 Research Significance

1) This research will use Quaternary beetles to reconstruct palaeoenvironments in the southern Altai region of northwest China. This is a new research method for this region, and has never before been done in China.

2) The MCR method will be used to reconstruct the palaeotemperatures, providing reliable temperature estimates for this poorly-studied region

3) The study of the fossil beetles will help to establish Quaternary beetle research in China, and contribute to the beetle faunal research in Eurasia.

4) The study sites’ proximity to the Altai Mountains makes this site useful for biogeographic study.

Chapter 2. Literture review

2.1 The development of Quaternary insect studies

The study of Quaternary insect essentially started in the mid-19th century. In 1864, Strobel and Pigorni (1864) made a first attempt on palaeoenvironmental reconstruction through fossil insects in Italy. Other studies mostly were focused strictly on palaeontology, such as in Britain (Bolton, 1862; Wollaston, 1863), SwitzerlanAd (Heer, 1865), France (Fliche, 1875; 1876), Germany (Flach, 1884; Schaff, 1892; Kolbe, 1894), Denmark (Wesenberg-Lund, 1896), Finland (Andersson, 1898), eastern United States (Horn, 1876; Ami, 1894; Scudder, 1898), and Canada (Scudder, 1877, 1900). However, all of these early studies named the fossil specimens as extinct species, which more recent studies have shown was incorrect. Fordyce Grinnell was one of the first scientists who did not make the mistake of naming Pleistocene fossils as representing extinct species (Ashworth, 1979). In 1908, Grinnell started his fossil insect work at the Rosemary site, near Los Angeles (Miller, 1983), and matched many fossil remains with modern species (Ashworth, 1979). Pierce (1948, 1949) had named many fossil insects from the La Brea and McKittrick sites as extinct Pleistocene species, but Miller (1983) re-examined Pierce's collections, and found that his specimens matched modern species.

Scudder's 19th century work on fossils from eastern North America has also been reexamined by taxonomists in later studies, who found that the specimens represent extant species (Darlington, 1938; Goulet, 1983). In 1877, Scudder published his first paper on the study of fossil insects from the Late Quaternary deposits at Scarborough, Ontario. During his work on fossil insects, he described 1,144 insect specimens, including 54 species of Pleistocene beetles, and most of the others are Tertiary specimens. All but two of the fossil beetles were described as extinct species. Unfortunately, much of these fossil materials have since been lost. Even so, as the first step for North American studies, Scudder's work made a great contribution to palaeoentomology (Cockerell, 1911).

After World War II, the reexamination of "extinct" species in early studies contributed to the development of Quaternary entomology. Carl Lindroth (1948) revised the early studies of interglacial insects, especially fossil ground beetles (Carabidae) from the northern Swedish sites of Frösön, Härnön, Hälsingland, Pilgrimstad, and Angermanland. Especially in Härnön, Eric Mjöberg (1904, 1905, 1915, 1916) named a set of fossil beetle fragments as representing extinct species, while Lindroth (1948) found that these ‘extinct’ fossil beetles actually represent extant species, and he also pointed out that some species had been misidentified by being placed in the wrong genera. By the study of the interglacial insect assemblages, Lindroth made several significant advances. He suggested that the cuticular microsculpture is the most useful taxonomic characters in fossil material observation, especially for beetles, and this concept has been employed ever since (Coope, 1970, 1989). Lindroth also identified 42 species of Hemiptera and Coleoptera, and used their modern distributions and environmental requirements to reconstruct palaeoenvironments (Lindroth, 1948).

In 1973, Angus published a paper about the revision of *Helophorus* (Hydrophilidae) fossils from Pleistocene deposits in the Ukraine. These *Helophorus* fossils had been described as extinct species by Lomnicki (1894) in his early study. However, through the detailed reexamination of these fossils, even including the male genitalia, Angus (1973) successfully matched them with four extant species.

Another remarkable Quaternary entomologist was Russell Coope, who started his Quaternary insect fossil studies in 1955, at the Upton Warren site, near Birmingham (Coope et al., 1961). This site yielded fossil beetle assemblages that Coope came to recognize as representing an interstadial interval during the last glaciation. Coope insistently refused to accept that all fossil specimens represented extinct species. He compared the Upton Warren insect fossils with the modern species in the Natural History collection of the Birmingham Museum, and the Natural History Museum (London), and found that nearly all of the fossils represent extant species (Coope et al., 1961). Coope came to believe that all the fossil material could eventually be matched with modern species. Coope focused his studies on British Isles and Western Europe, and published more than 200 papers on Quaternary palaeontology, establishing most of the important principles in the field (Elias, 2010). Some of his most influential publications include an overview of Quaternary entomology published in Annual Review of Entomology (Coope, 1970), the discovery of the Tibetan species of dung beetle in British Pleistocene deposits (Coope, 1973), a review of the fossil beetle record of Britain during the Devensian glaciation (Coope, 1977), a discussion of the constancy of insect species versus the inconstancy of Quaternary environments (Coope, 1978), and a study of British interglacial insect assemblages

(Coope, 2010). Furthermore, Coope's outstanding eloquence and training skill "brought the field of Quaternary entomology out of obscurity and into the limelight" (Elias, 2010, page 7).

From the 1970s, some of the students trained by Russell Coope and his colleague Peter Osborne established their own laboratories and research programmes in various regions. Coope's interests mostly focused on Pleistocene-age fossil assemblages. Osborne dealt mainly with Holocene-age sites, especially in archaeological settings. His work includes studies of an insect from a Bronze-Age sites at Wilsford, Wiltshire (Osborne, 1969), and along the River Avon in Warwickshire (Osborne, 1988). But he also worked on purely palaeontological projects, such as insect fossils from the Pleistocene-Holocene transition at West Bromwich, Staffordshire (Osborne, 1980) and an early Holocene fauna from Lea Marston, Warwickshire (Osborne, 1974).

Also,A in the UK, Harry Kenward developed an environmental archaeology laboratory at York University, as did David Smith in Birmingham University, and Paul Buckland at first the University of Sheffield and then at the University of Bournemouth. These three scientists and their colleagues developed some useful new approaches to the interpretation of archaeological assemblages (e.g., Buckland, 1976, Buckland et al., 1991; Hall and Kenward, 2003; Kenward, H., and Carrott, J., 2006; Smith, 1998, Smith, 2000), and for distinguishing subtle differences between adjacent environments (e.g., Kenward, 2006; Smith and Whitehouse, 2005; Smith et al., 2010)

Buckland's students have also established palaeoentomology research centres in Britain. Eva Panagiotakopulu works on insects from archaeological sites at the University of Edinburgh and Nicki Whitehouse is at University of Plymouth. Panagiotakopulu has made important contributions to the study of insect fossils from archaeological sites in the Mediterranean region, especially in Egypt and Greece (Panagiotakopulu, 2001, 2004, Panagiotakopulu and Buckland, 1991; Panagiotakopulu et al., 1997).

Whitehouse has worked both on strictly palaeontological sites as well as archaeological sites. Her work includes studies of Holocene insect fossils from Thorne Moor and Hatfield Moor in northeast England (Whitehouse, 2000, 2004). She has done extensive work on the reconstruction of postglacial forest history in England and Ireland (Whitehouse, 2006) and also in collaboration with David Smith (e.g., Whitehouse and Smith, 2010).

Coope's European students including Philippe Ponel who studies Late Pleistocene and Holocene insect fossils at the University of St. Jérôme in Marseille, France; Geoffrey Lemdahl, who works at Kalmar University in Sweden, where he studies Late Pleistocene and Holocene insect assemblages from a variety of sites in Europe.

Ponel's work includes purely palaeontological studies, such as his contribution to the study of the Grande Pile interglacial site in France (Ponel, 1994, 1995), as well as environmental archaeological research in France (Ponel et al., 2000; Andrieu-Ponel, V. and Ponel, P., 1999).

Lemdahl has worked on a number of Late Pleistocene and Holocene insect assemblages from Sweden, Norway, Poland, Denmark and Switzerland (Lemdahl 1985, 1991a, 1991b, 1997, 2000; Birks et al., 1993; Birks et al., 1996). His work with Coope on MCR results from across Europe documented regional variations in the pace and intensity of climatic change during the MIS 2 -MIS 1 transition (Coope and Lemdahl, 1995; Coope et al., 1998).

Some of the students trained by Russell Coope are now working in North America. Allan Ashworth has recently retired from North Dakota State University, in Fargo. He has contributed to our knowledge of late Pleistocene environments of the upper Midwest region of the United States (Ashworth and Brophy, 1972; Ashworth et al., 1972; Ashworth, 1980; Ashworth et al., 1981). He also almost single-handedly developed the study of Quaternary insect fossils from sites in southern South America (Ashworth et al., 1989; Ashworth and Markgraf, 1989). He also pioneered work on Tertiary insect fossils from Antarctica (Ashworth et al., 1994; Ashworth, 1996; Ashworth and Kuschel, 2003). He has found faunal connections between pre-glaciated Antarctica and southern South America during the Tertiary.

Alan and Anne Morgan worked at the University of Waterloo, Canada, and have been researching Pleistocene insect fossils from a variety of sites during last 30 years. Following their research on Late Pleistocene insects from the British Midlands (Morgan, 1973), they went on to investigate Late Pleistocene faunas from northeastern North America (Morgan and Morgan, 1979; Morgan et al., 1985; Morgan, 1987). Their work documented tundra environments just south of the Laurentide Ice Sheet, where summer temperatures were depressed to about 10°C during the last glaciation.

Scott Elias is another of Coope's students. Most of his work has been in North America, including studies in arctic Canada (Elias, 1982a and 1982b) the Rocky Mountain region (Elias, 1983, 1985, 1988, 1991a, 1996, 2015), the Chihuahuan and Great Basin deserts (Elias, 1990; 1992a, 1997; Elias and Van Devender, 1990; Elias and Van Devender, 1992; Elias et al., 1995), and in Alaska (Elias, 1991b, 1992b, 2000, 2001; Elias et al., 1996a; Elias et al, 1999a; Elias et al., 1999b; Elias et al., 2000; Elias and Matthews, 2002).

Elias' Rocky Mountain research has mainly focused on Late Glacial and Holocene insect assemblages from high elevations in Montana and Colorado. One of the most significant findings from this line of research has been that regional insect faunas responded very quickly to postglacial warming in the Rockies, whereas altitudinal treeline did not reach modern elevations until at least a thousand years after the beetle faunas became established. His study of MIS stage 5 assemblages from the high altitude Ziegler Reservoir site (Elias, 2014) was the first study of an interglacial insect fauna from the Rocky Mountains, and it revealed that Pacific Northwestern beetle species inhabited the central Rockies during the last interglacial period.

Elias' studies of packrat middens from the Chihuahuan and Great Basin deserts revealed some interesting palaeoclimate and zoogeographic patterns in these regions, from the Late Pleistocene through the Holocene. For instance, some of the Late Pleistocene beetle faunas of the Chihuahuan Desert contained species that are now found today in a wide variety of other regions, from central Mexico to the American Great Plains and the Sonoran Desert. His study of Great Basin Pleistocene insects (Elias, 1997) showed that the fauna living there in the Last glaciation includes moisture-loving species now found in the Sierra Nevada Mountains and the Pacific Northwest region.

Elias' work in Alaska includes studies of assemblages ranging from MIS 5 to recent, and includes MCR temperature reconstructions that strongly suggest a short climatic reversal during the Younger Dryas chronozone in Arctic Alaska, followed by rapid warming to mean summer temperatures greater than modern before 9000 cal yr BP. His work with Susan Short and others on sediment cores taken from the Bering and Chukchi Sea floors documented Late Pleistocene environments at the center of the Bering Land Bridge (Elias et al., 1996a).

John Matthews is self-taught palaeoentomologist in Canada, who started his fossil insect work in 1968 and worked throughout his career at the Geological Survey of Canada at Ottawa, and has retired. He made significant contributions in the areas of Pleistocene insect faunas from Eastern Beringia (unglaciated Alaska and the Yukon) from the late 1960s through the 1990s, starting with his dissertation project from the Fairbanks region of Alaska (Matthews, 1968), followed by work on the origins of the tundra ecosystem, based on early Pleistocene fossil assemblages from Cape Deceit in western Alaska (Matthews, 1974). He collaborated with palynologist Charles Schweger on several important studies, one concerning middle Wisconsin environments of the Yukon (Matthews et al., 1990a) another concerning MIS 5 environments at Ch'ijee's Bluff, Bluefish Basin, Yukon (Matthews et al., 1990b), and a third concerning interglacial deposits at the Ky-11 site in north-central Alaska (Schweger and Matthews, 1985). Matthews pushed the frontiers of arctic insect fossil study back to the Late Tertiary with his research from numerous sites in the Canadian High Arctic, summarized in Matthews 1977. His research extended north to Ellesmere Island, the northernmost island in Canada (Matthews and Fyles, 2000). The major discoveries of these studies were that the high arctic had a boreal or even temperate climate in parts of the Late Miocene and Pliocene.

The studies in Russia have mainly focused on the arctic and subarctic fossil faunas of Siberia. Russian scientists were relatively isolated from their western colleagues until the 1990s. Since the 1970s, Sergei Kiselyov started research on insect fossils from Quaternary deposits from the Kolyma lowland in northeastern Siberia, and in along other regional river basins (Kiselyov, 1981; Kiselvoy et al., 1985). He discovered evidence for steppe-adapted beetles living in what was then Western Beringia during the last glaciation. These are a key element in the steppe-tundra ecosystem. This line of research was continued by Svetlana Kuzmina from Moscow. She studied Holocene and Pleistocene insect remains from northeastern Siberia (Kuzmina and Sher, 2006; Sher et al., 2005) and from west-central Chukotka (Kuzmina et al., 2011). Kuzmina’s work has documented the persistence of steppe-tundra environments in Western Beringia, even through interstadial periods of the last glaciation in some localities.

Evgenij Zinovjev in Ekaterinburg, Russia has been studying Late Pleistocene insect fossils from the Western Siberian region (Zinovjev, 2006). He has focused some of his work on the history of ground beetle species (Carabidae) in Western Siberia over the past glaciation and into the Holocene (Zinovjey, 2008).

In Japan, Quaternary entomology began in the 1980s. However, Japanese scientists did not realize the previous studies in Europe and North America until 1994. Now the principal Japanese researchers are Masakazu Hayashi at the Natural History Museum in Sanda, Yuichi Mori at Mie University, and Shigehiko Shiyake at the Natural History Museum in Osaka. Their studies have mainly focused on insect assemblages from peat deposits that contain specimens of the leaf beetle subfamily Donaciinae. Their publications cover the evolution of donaciine species in Japan (Hayashi, 1999; Hayashi, 2001; Hayashi and Shiyake, 2002). Mori's work has focused on insect fossils from archaeological sites in Japan, including the Kachigawa site (Mori, 1989).

Nick Porch, who was trained by Scott Elias, is currently the only scientist studying Quaternary insects from Australia, and now is working at Australia National University, Canberra. He began by studying insect fossils from Late Pleistocene deposits from swamp deposits in southeastern Australia (Porch et al., 2009; Porch, 2010). His more recent work has focused on insect fossil assemblages from tropical Pacific Islands, including Hawaii and Tahiti. He has documented sharp declines in native beetle species on these islands, since the mostly accidental introduction of invasive insect species (Liebherr and Porch, 2015).

Maureen Marra, who is working at the University of Waikato, is the only scientist currently studying Quaternary insects in New Zealand. She has worked on a fauna from MIS 5e from New Zealand (Marra, 2003a) and an MIS 6 fauna from Banks Island, off the New Zealand coast Marra, 2003b). She has documented several endemic species of beetles in these ancient faunas that have become extinct since European colonization, largely due to the clearance of native forests.

Most Quaternary insect studies have been carried out in Europe and North America, and nearly all archaeological work is limited to Northern Europe. Until recently, a few studies have been made in Australia, New Zealand, and Japan. Research in South America and Asian areas outside of Japan, has been limited to only a few studies, and most regions on these continents are completely without this study. The only exception to this is the region of northeastern Siberia, where about 50 studies have been made. Therefore, the study of insect fossils needs to spread to new regions, and shows great potential for development.

2.2 Important features for beetles as palaeoenvironmental indicators

2.2.1 Abundant species diversity and wide range of habitats

Coleoptera (beetles) is an order of insects in the class Insecta. It is the most important insect order in the Quaternary fossil record. Compared with other orders, Coleoptera include the highest number of modern species, with more than 300,000 species having been identified (White, 1983) and the number of recognized taxa is still growing by about 1,500 each year (Arnett, 1973). Beetles exist all over the world and are able to survive in almost every kind of habitat and environmental conditions. Some species like dry places (xerophiles) while some favour damp places (hygrophiles), some groups live in sunny places (heliophiles) and some groups live in fresh water (aquatic species) (Bechyne, 1956). They can be found everywhere from arctic polar desert (Danks, 1981) to the subantarctic islands (Crowson, 1981), from 5,600m elevation in the Himalaya (Mani, 1968) to the Namib desert of South West Africa (Cloudsley-Thompson, 1969). Their huge species diversity and the wide variety of habitats make them an important group in the fossil record.

2.2.2 Species constancy in the Quaternary

As discussed above, all of the Quaternary beetles were described as extinct species at the early stage of the research, while later studies matched nearly all Quaternary beetles with the modern species. From the fossil records, the species with greatest longevity is an aquatic leaf beetle, *Plasteumaris nitida*. Fossil specimens have been found as far back as the Early Oligocene-age Florissant shales in Colorado, thereby suggesting that *P. nitida* has persisted more than 30 million years (Askevold, 1990). Based on work in arctic North America, Matthews (1977) believes that the evolution or extinction of beetles may have been very slow during the last million years, as most of the fossils can be matched with extant species morphologically. Even in his earlier study of the Pliocene deposits from Lava Camp Mine, Alaska, he described two "extinct" species, *Micropeplus hoogendorni* and *Micropeplus hopkinsi*. These fossils have been dated at around 5.7 million years old (Matthews, 1970). Much younger specimens of *M. hoogendorni* have been found in later studies (Shotton et al., 1993; Parfitt et al., 2005). Finally, a modern Siberian species *Micropeplus dokuchaevi,* described by Rjabukhin, appears to be the same as *M. hoogendorni* (Elias, 2010). In 2006, Elias et al. reviewed the studies of Late Tertiary and Quaternary fossil insects from Alaska, Canada, Northeastern Siberia and Greenland. In total, they cataloged 251 beetle species of which only 13 are known to have become extinct. Some of the tentatively identified extant species may represent extinct species, but on the other hand, some of the species considered to be extinct may eventually be found living, described by a different name in some other region of the world (such as *M. hoogendorni*) (Elias, 2010)

There have been numerous lines of evidence demonstrating the morphological constancy of beetles over millions of years. But how can we be sure that the environmental tolerances and behaviour patterns of ancient beetles are also as same as their modern counterparts? Firstly, the fossil genitalia (aedeagi) are the same shape and size as modern specimens. The study of fossil genitalia provided plenty of evidence for constancy of many species through most of the Quaternary and beyond (Coope, 1970). Modern beetle taxonomists rely on the morphology of aedeagi to separate difficult and/or large groups of taxa into species, so this is one of the most definitive body parts of beetles. Secondly, the species found together in fossil assemblages are still ecologically compatible today. By analysis of the modern distributions and habitats of the dozens or even hundreds of species from one fossil assemblage, the overlap in the environmental tolerances of the various species represent a fairly narrow climatic range in which all the species are found living. If these species had evolved a new set of physiological tolerances, leading to a change of habitat, then the whole fauna would have become ecologically or climatologically incompatible (Coope, 1978, 1979). Furthermore, in certain well-studied regions, such as British Isles, the thermal regimes associated with warm-adapted faunas found in different interglacial periods may be quite similar, even though the species in the different assemblages vary from one interglacial to the next, and are separated by hundreds of thousands years (Coope, 1978). Therefore, unlike most other palaeontological studies, Quaternary fossil beetles can be matched exactly with specimens of modern species, thus obtaining information about the environmental tolerances, behaviour, and distribution patterns of modern beetles, providing accurate information on past environments (Coope, 1970).

However, tropical species shows speciation. Erwin (1979) hypothesized that the last major impulse of ground beetle evolution in tropical regions resulted from changes in Pleistocene precipitation patterns. In contrast, Coope (1979) argued that environmental stability in a constant geographic location might cause rapid speciation. The remarkable diversity of tropical insect species may be due, at least in part, to a lack of intensity of environmental change over long periods (Elias, 2010).

2.2.3 Specific feeding habits

Based on their food requirements, beetles can be divided into three main groups: herbivores, predators, and scavengers. Figure 1 shows the interrelationships between beetles and their particular foodstuffs. However, some species are strict herbivores or predators, while some species eat both plant and animal foods. The figure below is only a guide based on the main foods of beetles.

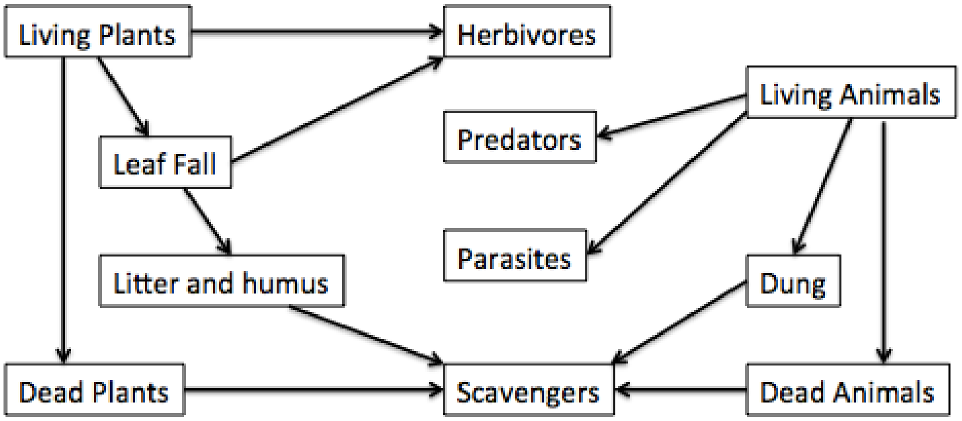


Figure 1. Beetle food group (Evans, 1975)

Most beetles feed on plants or vegetable materials, and beetles eat all sorts of plants, even the lower plants such as algae, mosses, or ferns (Evans, 1975). For instance, an example of a group of moss-feeding beetles include most of the members of the family Byrrhidae (minute moss-feeding beetles). Different phytophagous beetle species have different host plants. They select one or a few species of plant to feed upon, and also they will choose a particular part of plant to consume (flower, bark, timber, root, seed, or associated fungus on trees) (Evans, 1975). Thus, based on their eating habits, fossil remains of plant-feeding beetles provide information on past plant communities, including the composition of plant communities and the health and age class structure of tree stands. For instance, the remains of the bark beetle genus *Pityophthorus* are indicative of young trees with active shoots (Bright, 1976). The remains of the "death watch beetle" *Xestobium rufovillosum* indicate the presence of dead oaks and structural timbers (Fisher, 2008).

Tree-feeding beetles, such as Curculionidae and Scolytidae, have been used to indicate ecological changes in forests, and to estimate the latitude and altitude of tree line. For example, Elias (1982a) indicated the continued presence of spruces at Ennadai Lake, Keewatin, Canada, by using fossil scolytids from Holocene peats, even during times when the pollen record was lacking in spruce pollen.

One ecosystem that has almost disappeared today is the steppe-tundra that dominated the ice-free regions of the northern latitudes during much of the Pleistocene (Lloyd et al., 1994). Fortunately, there is a diagnostic beetle fauna, comprised of modern taxa, that may be used to identify this ecosystem from ancient fossil assemblages. According to fossil beetle studies in Beringia, many beetle assemblages from sites in northwestern North America and northeast Asia indicate the presence of steppe-tundra: a mixture of steppe and tundra herbaceous plants, dominated by grasses and forbs (Sher et al., 2005). The steppe-tundra indicators amongst Beringian insect fossil assemblages include the ground beetles *Harpalus amputatus* and *H. alaskensis*, byrrhid beetles in the genus *Morychus*, abundant presence of dung beetles in the genus *Aphodius*, and weevils in the genera *Stephanocleonus* (Western Beringia) and *Lepidophorus lineaticollis* and *Vitavitus thulius* (Eastern Beringia) (Elias and Berman, 2000).

Predators and scavengers feed on other animals or detritus (Evans, 1975). They are an important component in most fossil assemblages. They are more useful in climatic reconstructions when compared with plant-feeding beetles, since predators and scavengers are not limited by the specific type of vegetation. So, when environments change, they can rapidly move to a new region, and become established along with the first pioneering plant groups (algae, fungi, mosses and herbs). They do not need to wait until a given plant species becomes established, which may take centuries or even millennia to complete. For instance, during the last glaciation, the warm interval of the Upton-Warren interstadial complex (MIS 3) allowed thermophilous predatory beetles in the families Dytiscidae, Carabidae, Staphylinidae, and others, to colonize Britain, while tree species were not able to colonize northwest Europe because the warm period was too brief, and these trees lacked the time to migrate from southern Europe (Coope and Angus, 1975). Likewise, during cold stages (glacial stadials), cold-adapted beetles in these sample predaceous families replaced warm-adapted species almost instantaneously in the fossil record. Examples of these include the Arctic ground beetle *Diacheila polita* (Coope, 1968), the east Palearctic rove beetle *Tachinus jacuticus* (Ullrich and Coope, 1974), and the Tibetan species of dung beetle *Aphodius holdereri* (Coope, 1973). During the most extreme cold periods, it appears that all beetle species were forced out of NW Europe, near the edges of ice sheets (Coope, 1970, 1978).

Dung beetles also provide useful palaeoenvironmental information. Each patch of dung has its own community of animals, including dung feeders, their predators and parasites, and fungus feeders that feed on the fungus growing on the dung (Evans, 1975). Some dung beetles are generalists, while others feed only on the dung of one or two species of vertebrates. For instance, *Aphodius rufipes* reportedly feeds only on the dung of large herbivores; *A. quadrimaculatus* feeds on sheep dung on dry pastures; *A. foetens* is especially found on cow dung (Jessop, 1986). Thus, the presence of certain dung beetles in a fossil assemblage implies the presence of those vertebrate species on the ancient landscape. For example, Osborne (1969) found abundant remains of cow dung-feeding beetles in Late Neolithic Wilsford Shaft deposit, indicating that the well was used for watering cattle.

2.2.4 Sensitivity to environmental change

As an indicator of palaeoenvironment, it is important for a biological proxy group to be sensitive to environmental change. Fortunately, many beetle predators and scavengers are stenotherms, which are adapted only to a narrow temperature range. When the climatic conditions change, stenotherms will depart rapidly, and colonize a new region where they find suitable climatic conditions. This principle has been demonstrated with modern experiments.

For instance, Thiele (1977) tested the thermal preferences of ground beetles by measuring their respiration rates in different thermal conditions. He was able to establish a preferred temperature range for a large number of European species. He found that all populations within one species have same thermal preference, and that modern the geographic distribution of ground beetles is closely associated with their thermal preferences (Thiele, 1977). Following a rapid climate change, other palaeoenvironmental proxies may not respond as rapidly as beetles, which are able to colonize new regions within a few years to decades. As discussed in the literature review (above), vegetation response to climatic amelioration at the beginning of the Holocene lagged behind the beetle response by up to 1,000 years in the Colorado Rockies, and the postglacial invasion of coniferous forest in Alaska took up to 7,000 years to be accomplished (Elias, 2013).

The body temperature of insects is mainly controlled by the temperature of their surroundings. Since the temperature directly affects the rates of insect physiological processes, the variations of weather exert a significant influence on the rates of change of insect numbers (Clark, 1967). Although in the centre of a species' range, biotic factors, such as predation, competition, or parasitism, may affect the insect abundance and diversity, biotic factors such as climate probably limit insect populations toward the edges of their range (Price, 1984). Therefore, the edges of ecosystems are the best place to study the environmental controls on insect populations, rather than the centres of ecosystems. This also holds true for fossil assemblages.

In temperate and high latitude regions, beetles are active mainly in summer months. During the wintertime, beetles use various methods to survive from freezing air temperatures. Some beetles hide themselves in protected environments, such as mud, beneath snow, in piles of leaves, or lay eggs in these protected environments. Some adult beetles have anti-freeze mechanism in their bodies, such as suppression of haemolymph nucleators, or some methods involved with their solutes, to minimize damage to frozen tissues (Danks, 1978). Thus, fossil beetle assemblages provide more tightly constrained, reliable indications of summer temperatures (the time when they are active), but only general indications of winter temperatures (when they are inactive).

2.2.5 High mobility of beetles

High mobility is a very important character that allows beetles to respond rapidly to environmental change. Flight is a helpful adaptation for rapid migration and establishment in new regions. For instance, most species of carabids are fully winged (macropterous) while some have reduced wings (brachypterous). Winged beetles are able to migrate more rapidly at the edges of a species' range than flightless species (Lindroth, 1949). However, long-distance movements have also been documented for flightless species. Some wide-ranging taxa such as species in the ground beetle tribe Carabini, and many species of darkling beetles (Tenebrionidae) are mostly flightless, but their ability to become established in new regions in recent times demonstrates that walking can be almost as effective as flying for dispersal (Crowson, 1981). For instance, Den Boer (1971) demonstrated that dispersal by walking could achieve long-range migration in some species of Carabidae in Holland. Likewise, Roer (1975) made an experiment with the flightless tenebrionid beetle *Onymacris plana* in the Namib Desert of southwest Africa. Roer released marked individuals and then recaptured them. The farthest one was found 20 km from the release point after only 10 days, and several more of them were found more than 10 km from the release point. Moreover, Roer (1975) found that these long-range movements were largely in the same direction.

Natural forces such as flowing water (rivers or floods) and air currents also may help the movements of beetles. For example, Osborne (1980) investigated the insect fauna of the organic flood deposits at Sugworth. He discovered the insect remains were not evenly distributed through the deposit. Instead, their numbers tended to form two distinct peaks. The greatest numbers of these insect species live in rapidly flowing water. Their presence was attributed to periodic flooding.

Numerous modern and fossil studies have shown the astonishing mobility of beetles. For example, Meijer (1974) demonstrated the rapid immigration and settlement of carabids in newly created polders in the Netherlands, where ground beetles became established within 1-2 years after the new land was exposed. Lindroth (1971) studied the beetle invasion of newly created land on the Icelandic island of Surtsey, and showed the rapidity of colonization. In this example, ground beetles arrived on the island and became established within the first decade after the volcanic eruption that created the island (Lindroth et al., 1973). Surtsey emerged from the North Atlantic in 1963. The first vascular plant life became established in 1965 (http://www.vulkaner.no/n/surtsey/ esurtplant.html, accessed February 2018). By 1972, the first ground beetles had become established, namely, *Amara quenseli* (Lindroth et al., 1973).

The migration of beetles in response to climate change is not a deliberate action to move away from unsuitable environments. Rather, most beetles have large numbers of offspring, and most of these offspring move away from their original location, to minimize competition with their species' local population. When climates change, those individuals who happen to migrate in the right direction survive, and their offspring rapidly reproduce to ensure their survival in new environments (Elias, 2015). Elias compared the Late Pleistocene fossil beetle assemblages and fossil mammal assemblages from Rocky Mountain region of North America. Twenty-three percent of the 200 identified beetle species are no longer resident in Rocky Mountains, and none of the 200 species is extinct. This demonstrates the ability of beetles from a variety of different families to become established in new regions in response to climate change, without becoming extinct. On the other hand, only eight percent (six species) of the 73 identified mammal species from Rocky Mountain fossil localities are no longer resident in the Rocky Mountains, and 12 of the 73 species are now extinct. Interestingly, some beetle species that used to live in the Rocky Mountains during the Late Quaternary are now found only in the Pacific Northwest region, suggesting that the Rocky Mountain region was formerly moister than it is today. However, there are no mammals that show this distribution shift, as none of the mammal species found in the Rocky Mountain Late Pleistocene fossil record are found today exclusively in the Pacific Northwest region.

The immigration of beetles also occurred between the continents through Quaternary time. Coope (1973) matched a dung beetle species from British Pleistocene assemblages with the modern species *Aphodius holdereri*, which is only known from the Tibetan Plateau today. The water scavenger beetle *Helophorus mongoliensi*, which lives in Asiatic mountains today has been matched with fossil specimens from 40,000-year-old deposits in England (Angus, 1973). Even a nearly blind, flightless weevil (*Otibazo*), known today from Japan, used to live in Alaska during the Late Tertiary (Matthews et al., 2003).

2.3 The preservation of beetle fossils

The remarkable preservation of beetle fossils in Quaternary sediments is due to their chitinous exoskeletons. Chitin $(C_8H_{13}NO_5)_n$ is a nitrogenous polysaccharide, which is highly resistant to decay. It is insoluble in water, dilute acids, bases, and alcohol (Borror *et al.*, 1981), and cannot broken down even by the digestive enzymes of mammals (Elias and Halfpenny, 1991; Coope, 2007). The exoskeleton of most beetles is particularly reinforced with chitin, causing their remains to be preserved more often than the exoskeletons of most other insect orders (for instance Diptera, Lepidoptera, most Hemiptera, and most Hymenoptera).

In a study on insect taphonomy in lacustrine environments, Martínez-Delclòs and Martinell (1993) found that the decomposition of insect exoskeletons is caused by the activity of bacteria that feed on chitin. However, these bacteria live almost exclusively in oxygenated zones, so once an insect carcass sinks to the bottom of standing water, this kind of decomposition is practically nil. Generally, the best source of insect fossils is sediments deposited in still water. Lakes, ponds and bogs serve as reservoirs that accumulate insect remains, and the sediments accumulated in depositional environments are practically anoxic, retarding bacterial decomposition of insects by covering them rapidly. Further, the authors described two possibilities for the way in which insect carcasses end up in lacustrine sediments. First, aquatic insects (i.e., water beetles) die in the same lacustrine environment in which they lived, and are eventually buried at the bottom of the lake, pond, or wetland. Second, terrestrial and riparian insect carcasses may be transported immediately after death into the lacustrine environment, through the action of gravity, wind, or water movement. The authors also found that the formation of floating algal mats, found on the surface of the water, may lump together and so help in the preservation of insect remains (Martínez-Delclòs and Martinell, 1993). In contrast, insects that die on soil surfaces may decompose rapidly because of long-term exposure to oxygen-loving bacteria. Thus, oxidized sediments do not preserve many fossils.

Lakes, ponds, fluvial sediments, bogs, fens, peats are rich sources of insect fossils (Coope, 1970), as well as locations where a stream enters a lake (deltas), where the flotsam carried by the stream tends to settle out rapidly (Elias, 1985). Organic-rich sediments that accumulate in man-made environments (in castle moats, beneath floorboards of ancient buildings, in wells, in rubbish heaps and latrines) also often produce large numbers of insect remains (Kenward, 1978; Osborne, 1969). It is not uncommon for hundreds or even thousands of insect sclerites (individual body parts) to be recovered from individual samples of organic-rich sediments.

Permanently frozen sediments in the Arctic yield some of the best-preserved insect specimens, and the fossils in this preservation type can extend back to Late Tertiary age (Matthews, 1977). The frozen sediments act as a refrigerator greatly preventing bacterial decomposition, and also locking the specimens in place unless freeze-thaw activity reworks whole layers of sediment (Elias, 1986).

In desert regions, insect fossils can be found in rodent middens. A typical example is the packrat middens from the American southwest (Ashworth, 1976; Elias, 1990). For the reasons of food, curiosity, or protection, packrats accumulate objects in their nests such as edible plants, cactus spines, small pebbles, vertebrate remains, and insect remains, and these become cemented by rat faeces and urine. Then these midden materials dry in rock shelters, preserving a palaeoecological record for thousands of years (Elias, 1987, 1990).

In Egypt, insect fossils have been recovered from the tombs of the pharaohs. When archeologists unwrap the bandages from ancient mummies, numerous carcass beetle remains have been found. These beetles are attracted to dried animal remains, notably the larvae and adults of dermestid beetles, such as *Necrobia violacea* and *Dermestes maculatus* (Panagiotakopulu, 2001). In addition, foodstuffs as offerings in Egyptian tombs have yielded typical species of stored product pests. For example, the grain weevil *Sitophilus granarius* has been found in barley left in a tomb at Saqqarah (Panagiotakopulu and Van der Veen, 1997).

2.4 Palaeoclimatic reconstructions using fossil beetles

2.4.1 The Mutual Climate Range method

In 1959, Coope first applied the geographic overlap method in his research to interpret palaeoenvironments based on a Late Pleistocene insect fauna from Chelford, Cheshire. The organic deposits from which Coope's samples were taken are now though to pre-date the Devensian Glaciation (Worsley, 2015). Coope's initial method of climatic reconstruction is based on the geographic overlap of the modern distributions of the predatory and scavenging species in a fossil assemblage. Once the geographic overlap is determined, the palaeoclimatic reconstruction is based on the modern climatic parameters within that zone of overlap. This method worked reasonably well for many assemblages. For example, Elias (1997) reconstructed the mean July temperatures of late glacial-age at the Aubrey site in north-central Texas with beetle fossil assembles by using both the distributional overlap method and the Mutual Climate Range method (see below). These two methods yielded similar results in one study unit, and only have slightly different in another study unit. However, the geographic overlap method fails for assemblages that contain species that do not have overlaps in their modern distributions, and this method also relies heavily on the presence of indicator species, which are climatically sensitive species (stenotherms). These species receive more weight in palaeoclimatic reconstructions.

During the mid-1980s, Atkinson *et al.* (1986) developed the Mutual Climatic Range (MCR) method. Instead of looking for the overlaps of distribution, this method is focused on the overlaps of the modern climatic conditions associated with the species in the assemblages. Species in an assemblage do not have to have modern ranges that overlap, which perhaps cannot be found. For instance, species that live today in the Alps may be climatically compatible with species that live in the Arctic, even though there is no geographic overlap between their modern ranges.

The first step in the MCR method is determining the modern geographic distribution for each beetle species of interest. Since phytophagous species may reflect the distribution of their host plant more than climatic parameters, only predators and scavengers are used in this method. However, all species of predators and scavengers in assemblage can be used in this method, because it does not rely on indicator species. The modern European distributions of beetle species found in British and some Western European Quaternary fossil assemblages is available through the BUGS CEP database (Buckland and Buckland, 2006; Buckland, 2007)

A species' individual climatic tolerances can then be established by matching their modern distribution with climatic data. In Europe, with the help of a base map showing locations of meteorological stations, the geographic range of each species is converted into a species' climatic envelope. Through computer processing, the climatic envelope for a species is typically shown on a graph with Trange (the temperature difference between the warmest and coldest mouths) and TMAX (the mean temperature of the warmest month of the year) as the x-axis and y-axis respectively. Thus both average summer (TMAX) and winter (TMIN) temperatures can be reconstructed (Atkinson *et al.*, 1987). However, in the North American Arctic there are far fewer meteorological stations, because of the great distances between towns and villages in these remote regions. The climate envelopes have been developed by a 25-km-grid North American climate database (Bartlein *et al.*, 1994). This database uses the geographically nearest grid locations to each collecting site, to estimate the climate parameters of the modern beetle collection sites well away from meteorological stations (Elias et al., 1996b).

Once each species of predator or scavenger found in a fossil assemblage has a species climate envelope developed from modern range records, the overlap of all species' climate envelopes is their Mutual Climatic Range (figure 2). This overlap region of climate space represents a set of climatic parameters in which all species in an assemblage can live (Atkinson *et al.*, 1986).

Furthermore, the MCR method is not limited in palaeotemperature reconstruction. In desert regions, where precipitation may be the driving force behind distributions, mean annual precipitation (MAP) values may be derived from the MCR. For example, Elias (1998) developed a different set of species climate envelopes for beetles found in packrat midden assemblages from the Chihuahuan Desert, the Colorado Plateau, and the Great Basin. In these MCR reconstructions, the species climate envelopes were plotted using TMAX values and MAP values.

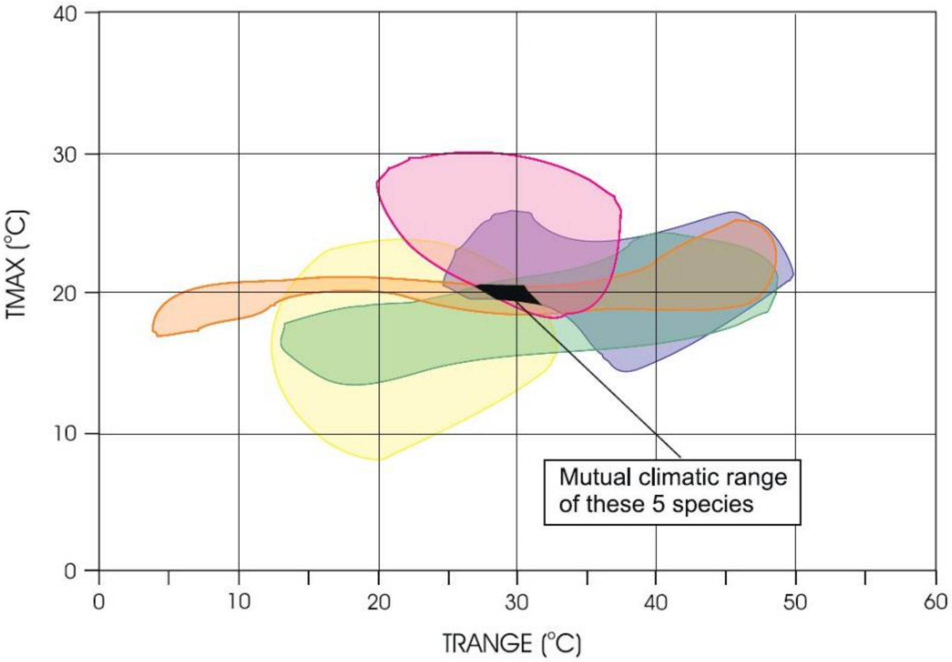


Figure 2. Hypothetical example of the overlap of climate envelopes for five species. The black area is the MCR estimate. (Elias, 2013)

2.4.1.1 Limitations of the MCR method

(1) Lack of modern species distributional data

The basis of the MCR method is the development of good quality species climate envelopes. However, in many cases we do not have sufficient knowledge of the species' distribution. Even for some well-studied groups, such as the species in family Carabidae, high-resolution distribution data are only available for populated regions, such as mid- and low latitudes of North America and Western Europe. Other regions are not well studied, especially in some remote areas, which are virtually uninhabited and hard to access. All practitioners are aware of the inadequacy in the beetle distributional data, but we have to use the available data for the moment, and hope to refine species climate envelopes in future. Getting beetle distributional data from remote regions is time consuming work and it will take many years of research to develop more reliable data at the appropriate continental scale. For some poorly known species, the species climate envelopes may be able to be modified by someone else who has personal expertise, or access to museum specimens in Siberian collections, for instance, or knowledge of foreign literature (e.g., in Russian, Mongolian, or Kazakh) or in the future when new data become available.

(2) Inaccurate climate data

The modern climate data employed in the MCR method are provided by the local meteorological stations. As discussed above, some remote regions lack sufficient meteorological stations. Thus, when a researcher uses a climatic model to estimate the climate parameters of modern beetle collection sites in remote areas, the data are not based on locally measured meteorological variables, but are rather interpolated values based on the nearest available meteorological data. In other words, the accurate climate data cannot be accessed because of lack of meteorological stations, thus the SCRs (species climate range), and consequently the MCRs derived from them, are based on smoothed climatic gradients; the true regional variance is probably underrepresented in the climatic database (Bray *et al.*, 2006). The reasonable density of climate stations in Western Europe can provide reliable climate data, while it is much more problematic for Eastern Europe and for Asia, where there are neither enough meteorological stations nor beetle collection data.

It is also worth noting that in mountainous terrains, the relationship of a beetle's distribution to local climatic conditions is more complex (Ponel *et al.*, 1999). Altitude is an important factor that influences climate parameters. Thus, in mountainous regions, the climate changes dramatically even in a short distance because of the difference in altitude. Temperatures cool with increasing elevation. However, there are different lapse rates in different regions of the world. Even a beetle species occurs near a meteorological station, the overlook of the significant difference of altitude between the meteorological station and the beetle collection site will lead to misunderstanding of the beetle's real preference.

2.4.1.2 MCR Calibration

Comparisons between predicted and observed modern temperatures for ranges of sites in Eurasia (Atkinson et al., 1987) and North America (Elias et al., 1996b) have shown that the MCR method is capable of predicting TMAX with reasonable accuracy and precision. Atkinson et al. (1987) reconstructed predicted versus observed TMAX and TMIN values based on the beetle species from 15 modern localities in Europe, Iceland, and Siberia, comparing the results with the mean temperature records from nearby meteorological stations. Linear regression equations were developed to compensate for systematic over-prediction of very cold temperatures and under-prediction of very warm temperatures in both the TMAX and TMIN estimates of temperature based on modern faunal assemblages. The TMAX regression formula for European faunas has an r^2 value of 0.94 and a standard deviation of 0.83^0C (Atkinson et al., 1987). The TMIN regression formula for European faunas has an r^2 value of 0.94 and a standard deviation of 2.42℃ (Atkinson et al., 1987) (upper half of figure 3). The same test has been made by Elias (1996) to correct the systematic errors in North American MCR estimates, which based on 35 modern beetle assemblages (lower half of figure 3). The TMAX regression formula for North American faunas is very similar, with an r^2 value of 0.94 and the TMIN regression formula for North American faunas has an r^2 value of 0.82.

Ecologically, as discussed above, it makes sense that beetles, like all other cold-blooded animals, are not good predictors of winter temperatures. In cold regions, exposure to winter air temperatures can be lethal for cold-blooded organisms. Thus, TMIN estimates are only good for generalized trends in average winter temperatures.

Elias (1998) also tested the reliability of using the MCR method to reconstruct mean annul precipitation (MAP) from insect fossil assemblages sampled from North American desert regions. Surprisingly, the results shown that the MAP regression formula has an r^2 value of 0.806, while the TMAX regression formula has an r^2 value of only 0,608. This means the beetles predicted more accurate values in MAP reconstruction than in TMAX reconstruction, which suggests that in arid regions, the precipitation is mainly controlling the beetles' distribution rather than the summer temperature (Elias, 1998).

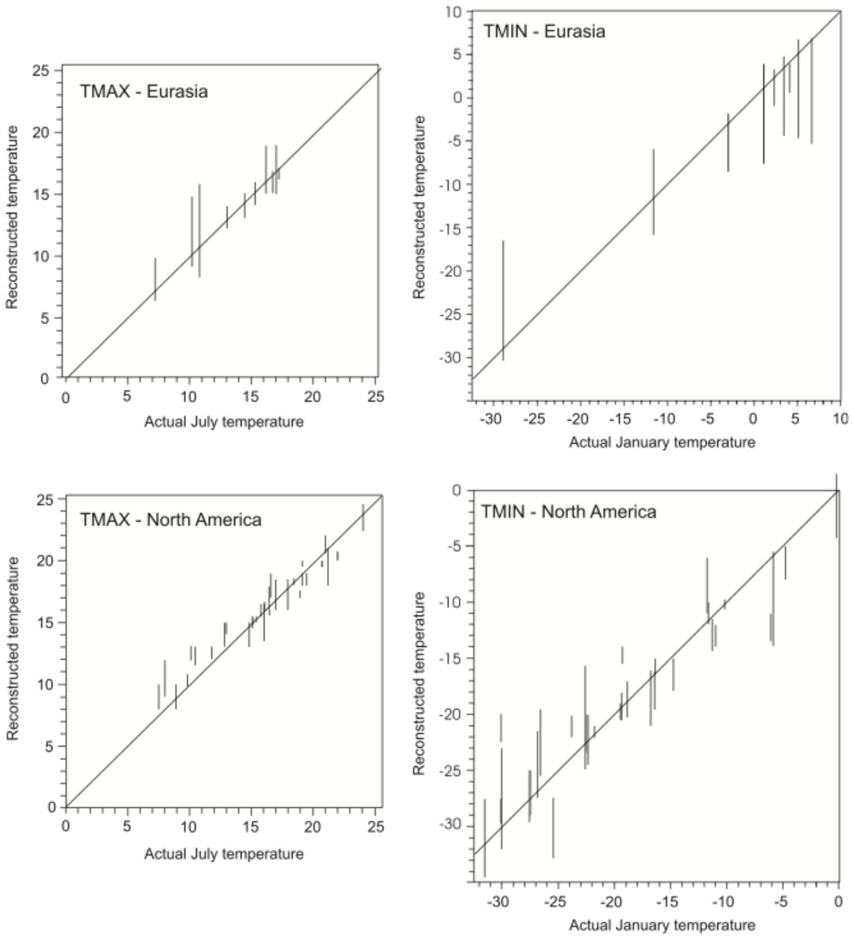


Figure 3. Graphs depicting the results of tests of predicted versus observed TMAX and TMIN for predatory and scavenging species of beetles living in Eurasia (upper two graphs) and in North America (lower two graphs). The vertical bars on each graph indicate the MCR estimate based on species found today at localities for which meteorological data are available. The diagonal lines show where the MCR estimates would fall if the predicted results matched the observed data. Note that for both Eurasian and North American data sets, there is a systematic underestimate in the coldest temperature ranges of both TMAX and TMIN, and a systematic overestimation of the warmest temperature ranges. Note also that TMAX estimates tend to be more tightly constrained than TMIN estimates, as discussed in the text. The upper two graphs are after Atkinson et al. (1987). The lower two graphs are after Elias et al. (1996b).

However, because there are no data available on frequency variations of beetle taxa throughout their distributional ranges, it is difficult to statistically determine the link between beetle distributions and climate data (Bray *et al.*, 2006). Statistical problems arise with the use of regression equations to correct systematic deviations in MCR estimates. The point estimates and ranges used in this approach have no defined probability. Atkinson *et al.* (1987) use the median value of each MCR as the point estimates plotted in the regressions, although the majority of the calculated MCR ranges plotted on the regression line. However, if the MCRs have any other distribution (log normal, multimodal for instance) then the median value of MCR cannot represent the estimate of the “true value”. Only the data that exhibit a normal (Gaussian) distribution in climate space can use the mean point estimate method (i.e., the linear regression method) (Bray et al., 2006). Sinka (1993) states that beetle distributions in climate space are probably normally distributed, and he suggested weighting against the extreme distributions (the margins of the SCRs) to generate normally distributed data to improve the precision of MCR method. However, the resulting MCRs were less in accord with the known climate of test sites, which strongly indicates that at least some beetles do not have Gaussian distributions within climate space, and that regression methods are therefore inappropriate for calibrating the bias.

2.4.1.3 Ubiquity Analysis

A lack of statistical control is a serious weakness with the MCR approach at present. Huppert and Solow (2004) argued that the link between beetle distributions and modern climatic parameters cannot be tested robustly using conventional statistical methods, because of the uncertainties in MCR reconstructions, even those based on relatively abundant modern distribution data for European or North American beetles. In order to test how the uncertainties in MCR estimates might be better constrained, Bray *et al.* (2006) used a technique known as Ubiquity Analysis, and produced Ubiquity SCRs for beetle taxa. The ubiquity of a beetle species’ distribution in climate space is defined by how much of a particular sector of climate space (a particular combination of TMAX and TRANGE, for example) a species actually occupies. In other words, it shows frequency of occurrence of each species in the various cells of TMAX vs TMIN in a climate space graph. For example, as figure 4 shows, the higher value of ubiquity represents higher frequency of beetle species occurring in this piece of climate space.

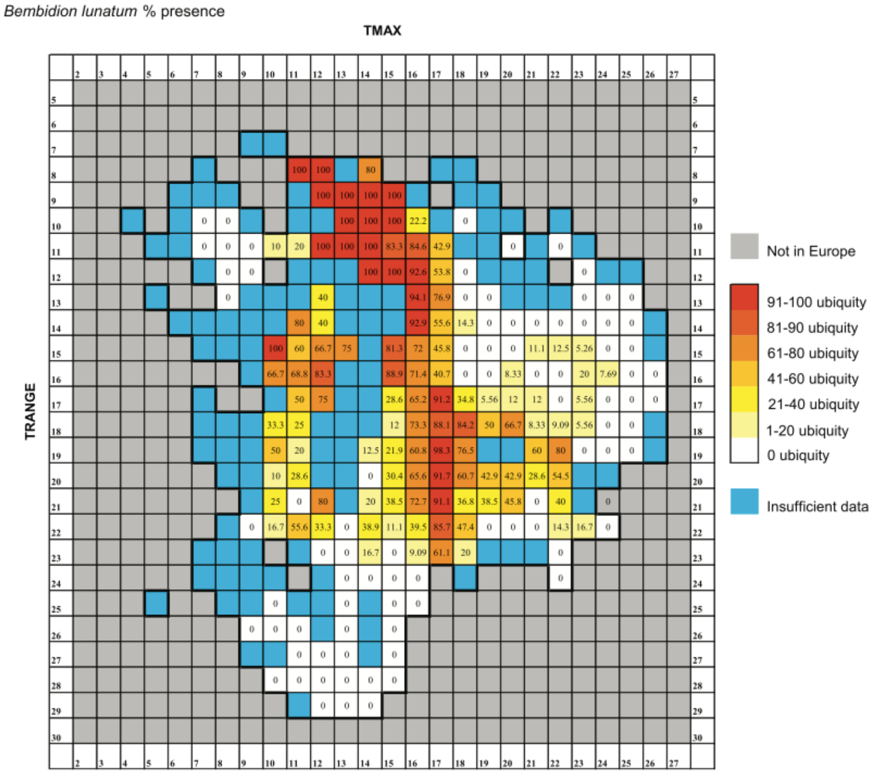


Figure 4. Ubiquity species climate envelopes for *Bembidion lunatum* (European occurrences only) with multiple centers of ubiquity (yellow and red grid cells). From Bray et al., 2006

Bray et al. studied 44 species, while the results show only six of these species have SCRs that are normally distributed in climate space. The remainder have bimodel, tri-model, or other modes of distribution (Figure 4). This study suggests that the linear regression models cannot be widely used. However, the ubiquity SCRs should be developed for more beetle species and more regions, to better understand three- dimensional ubiquity SCR plots as probability surfaces that can be combined to form ubiquity MCRs. This is a huge amount of work, but we have the hope that these will generate MCR estimates with improved precision and better constrained errors compared with those currently in use.

At this moment, the indicator species could be very useful in some cases to help us get more accurate data in the species climate envelopes, as they have restricted climatic tolerances. For example, the beetle species *Amara alpina* can only survives in Arctic regions, where the mean July temperature is below 10 degrees centigrade. Thus, if the species *Amara alpina* appears in a beetle assemblage, that means the average summer temperature in this region at that time was no more than 10 degrees centigrade (figure 5)

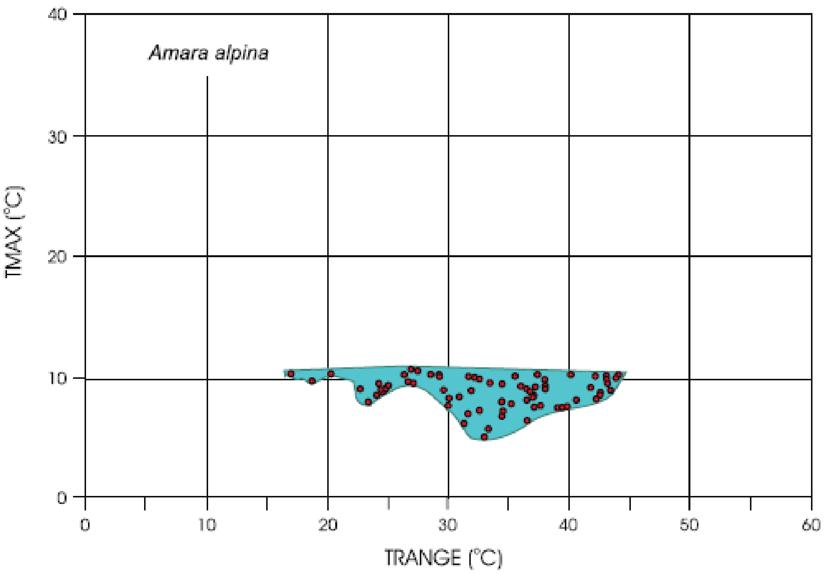


Figure 5. Species climate range of *Amara alpina*. From Elias, 2013.

There are, however, a number of problems that still need to be addressed for the future development of the MCR technique. Since the improved climate data will reduce some of the uncertainty in MCR estimates, highly resolved climate data are necessary. It is important to increase available beetle distributional data in new regions, especially for Asia. Numbers of important fossil species have modern ranges that are exclusively Asiatic; fossil specimens of these species, such as *Tachinus jacuticus* and *Aphodius holdereri* have been found Pleistocene assemblages from Western Europe. This is a long-range objective, and this research project will be a first step for this kind of research in China. Russian palaeoentomologist Svetlana Kuzmina worked with the late Andrei Sher to develop the QINSIB database (Quaternary Insects of Siberia) that contains modern distribution maps for beetle species found in Siberian Pleistocene fossil assemblages. These distribution data are now available on the web (Kuzmina, 2014).

2.4.2 The application of MCR in Late Pleistocene and early Holocene palaeoclimatic reconstructions

Coope summarized the Late glacial record from data assembled over more than 20 years, showing the climatic variation during the Late glacial in Britain. As shown in figure 5, temperatures rose extremely rapidly at about 13,000 cal. yr BP, and again at 10,000 cal. yr BP in the early Holocene. These rapid, large scale changes are not shown in pollen diagrams until centuries or millennia after the insect responses, because the vegetation response to the environmental change has often lagged behind the response of insects. Atkinson et al. (1987) calibrated these data with the linear regression model (figure 6): the heavy dark line represents the calibrated estimate values. However, as discussed above, the linear regression model should not be used in this case; the real results are between the thin black lines. In spite of this problem, it cannot be denied that fossil beetle proxy data provide valuable palaeotemperature data, because beetles are sensitive, reliable indicators of thermal regime. Also, MCR analyses provide what appear to be reliable values of the temperature range during the Late glacial, although they fail to provide a single point estimate of the temperature.

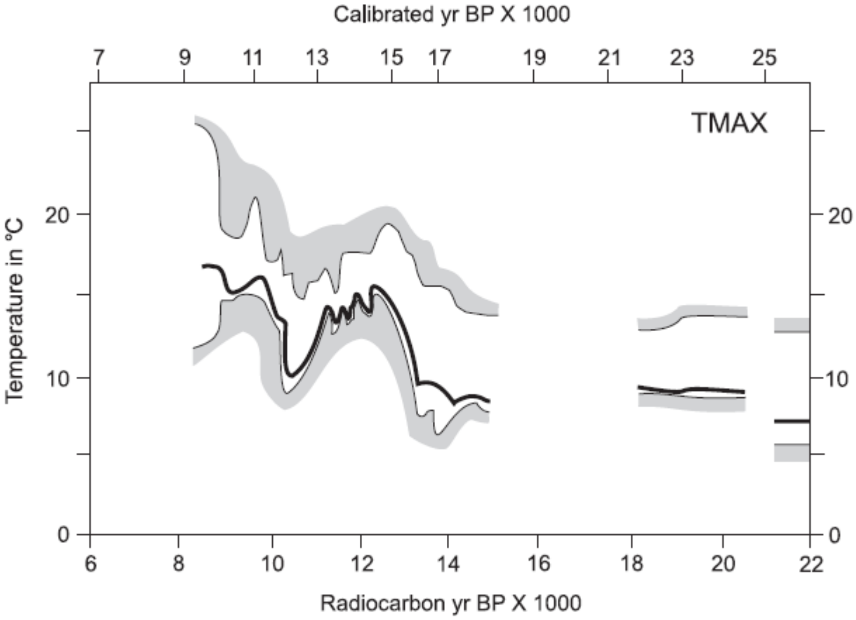


Figure 6. MCR TMAX estimates for the British Late glacial. From Atkinson et al., 1987.

Elias (2000) made MCR reconstructions from the Lateglacial beetle assemblages in arctic Alaska. As figure 7 shows, a dramatic increase of temperature occurred between 13,500 cal. yr BP and 12,900 cal. yr BP, and followed by an abrupt cooling until around 11,500 cal. yr BP. After that, the temperatures rose again and recovered to warmer than modern temperature between 10,500 and 10,000 cal. yr BP. Postglacial warming apparently was amplified in the Arctic, as it is today in global warming (Miller et al., 2010). Note that Elias (2000) did not attempt to calibrate the MCR results or to draw lines between data points. Rather, he showed the original MCR estimates for each fauna. Also note that the TMAX values shown in the

Alaskan reconstruction are departures from modern TMAX values at each study site. This is because Alaska is a huge region, and modern TMAX values vary greatly across the region. Atkinson et al.'s (1987) TMAX reconstruction is shown as reconstructed TMAX without any standardization. This is because modern TMAX values vary only little across Britain.

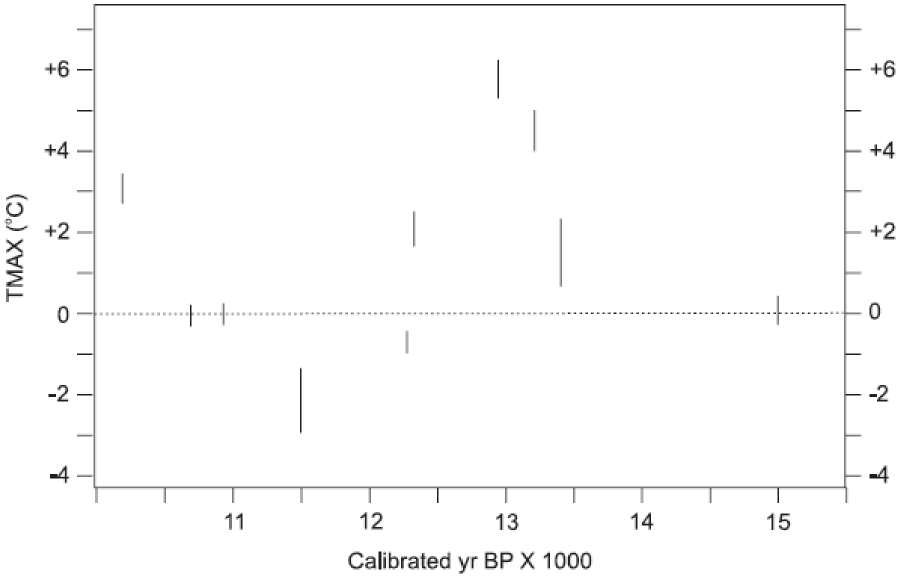
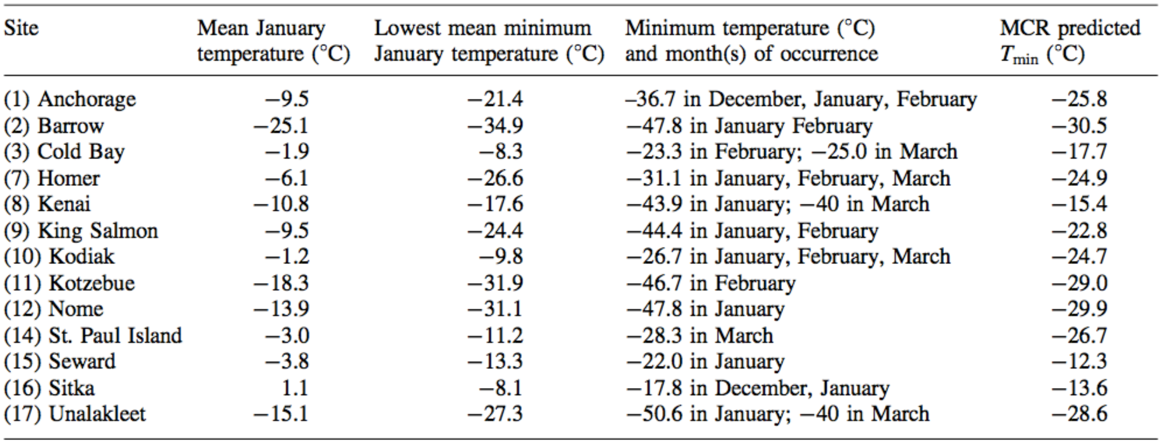


Figure 7 . Departures from modern mean July temperatures for sites in arctic Alaska. From Elias, 2000.

When Elias et al. (1999) were developing climate envelopes from fossil assemblages in Eastern Beringia, they found that the MCR predictions fit the observed TMAX reasonably well, but the predictions for the TMIN for coastal sites were consistently below the observed values. By careful analysis of the daily winter temperature records for coastal towns in Alaska, Elias et al. (1999) found that the average January temperature (TMIN) does not represent the actual climatic variability of these localities, because some days in these coastal areas are extremely cold. Although these extremely cold days may last only a few days in January, they greatly affect the coastal beetle fauna. Only the species that can tolerate extreme low temperatures can survive in these localities. Thus, these cold-resistant species would predict lower temperatures than the TMIN. Table 1 shows that the MCR predicted TMIN well estimated the lowest mean minimum January temperature, instead of the general TMIN. Thus, it can be seen that the beetles are easily affected by the environment, so it is very important to consider the special conditions in different cases.



Site	Mean January temperature (°C)	Lowest mean minimum January temperature (°C)	Minimum temperature (°C) and month(s) of occurrence	MCR predicted $T_{\min}$ (°C)
(1) Anchorage	−9.5	−21.4	–36.7 in December, January, February	−25.8
(2) Barrow	−25.1	−34.9	−47.8 in January February	−30.5
(3) Cold Bay	−1.9	−8.3	−23.3 in February; −25.0 in March	−17.7
(7) Homer	−6.1	−26.6	−31.1 in January, February, March	−24.9
(8) Kenai	−10.8	−17.6	−43.9 in January; −40 in March	−15.4
(9) King Salmon	−9.5	−24.4	−44.4 in January, February	−22.8
(10) Kodiak	−1.2	−9.8	−26.7 in January, February, March	−24.7
(11) Kotzebue	−18.3	−31.9	−46.7 in February	−29.0
(12) Nome	−13.9	−31.1	−47.8 in January	−29.9
(14) St. Paul Island	−3.0	−11.2	−28.3 in March	−26.7
(15) Seward	−3.8	−13.3	−22.0 in January	−12.3
(16) Sitka	1.1	−8.1	−17.8 in December, January	−13.6
(17) Unalakleet	−15.1	−27.3	−50.6 in January; −40 in March	−28.6

Table 1. Modern mean January, mean January minimum, and absolute minimum winter temperatures as coastal Alaskan sites, compared with MCR predicted TMIN. From Elias et al. (1999).

2.5 Fossil beetles in archaeological research

The insect remains from some archaeological sites can be used for recognizing past environmental conditions and human activities, especially human living conditions and activities (Kenward, 1978). As in all palaeoenvironmental studies using insect fossils, in an environmental archaeological context, the researcher compiles information for the habitats associated with all the identified species in an assemblage, then uses this information to form an outline of the environmental conditions and the human activities associated with the insect fauna, which is the "mosaic" approach proposed by Osborne (1969), thouth this approach had been criticied (Kenward, 1978). One difference between purely palaeontological and archaeological work is that those working on archaeological sites must consider the extent to which human activities might affect beetle species composition and abundance. For example, if the appearance of a species or group of species in an assemblage is believed "inappropriate" then these species will be assumed to be imported by human beings, such as the appearance of Mediterranean food pests in Icelandic fossil assemblages (Kenward, 1978). Another difference about archaeological research is the consideration of the abundance of the species, and some statistical methods will be applied to acquire more details. For instance, Robinson (1983) was trying to establish past arable/pastoral ratios by using fossil beetle assemblages. Smith et al. (2014) attempted to use the abundance and diversity of dung beetles in fossil assemblages to indicate the cattle herd concentration.

Kenward (1978, p.5) suggested that the "application of a community approach, in which ecologically related groups of species are used to determine the past existence of their habitats, is a promising method". Each ecological group includes a range of species that together are associated with a particular ecological condition or human activity in the past. For example, Robinson (1981) applied ecological groups of beetles in the interpretation of insect assemblages from sites in Oxfordshire. In this research, fossil beetles were divided into ten groups: aquatic, pasture/dung, meadowland; wood and trees, marsh/aquatic plants, bare ground/arable, dung/foul organic material, Lathridiidae, synanthropic, and structural timbers. Each group provided specific information on elucidating the surrounding landscapes or human activities. For instance, pasture/dung beetles (*Geotrupes spp.*, *Colobopterus spp.*, *Aphodius spp.*, *and Onthophagus spp.*) provided evidence for the importance of pasture; synanthropic species (*Mycetophagus quadriguttatus, Tenebrio molitor, Ptinus fur, Tipnus unicolor, Stegobium paniceum,* and *Typhaea stercorea*) are associated with human habitation, which are related to straw or hay waste and probably live in thatch; the woodworm beetle (Anobium punctatum) is related to structural timbers (Robinson, 1981). This method has been applied in further studies (Robinson, 1983; Kenward, 1995; Smith et al., 2010). Usually, the aquatic beetle species (those that spend their entire adult life in the water) are eliminated from consideration if the deposits accumulated under water, in order to avoid the ecological skewing caused by the deposit itself. The results of these studies seem to be validated by other lines of evidence when expressed as a percentage of the total number of terrestrial individuals from the samples (Kenward, 1978).

For the investigation of very large numbers of samples, multivariate statistics have been applied. For example, Carrott and Kenward (2001) use detrended canonical correspondence analysis (DCCA) to test the groups from archaeological insect (mainly Coleoptera) assemblages in York. They investigated associations between groups of species, and identified the significance of those associations as indicators of past human living conditions and activities. Smith (2013) used detrended correspondence analysis on 131 insect faunas from 49 cesspits from eleven archaeological sites in London. He combined this approach with the study of other environmental evidence such as plant macrofossils, a potential indicator package suggested by Kenward and Hall (1997). The combined fossil evidence provided a natural grouping of organisms, including a range of stenotopic species. When taken together, the fossil evidence provides a large range of environmental indicators that help elucidate both natural and human environments. Overall, fossil beetles have been widely applied in the archaeological research to reveal past environmental conditions and human activities at or near archaeological sites. Because of the involvement of human beings, the use of fossil beetles in archaeological research is a much finer and more complicated process than it is in palaeoenvironmental studies from natural settings. Most statistical methods used in archaeological research requires enormous samples, otherwise the results might be affected by many factors, such as sampling sites, the type of deposit, and the population densities of beetle species. On the other hand, fossil beetle assemblages used in the palaeoenvironmental reconstruction of natural localities often do not yield large numbers of specimens per sample, even though large numbers of species may be identified. For instance, Coope and Angus (1975) identified 270 species of beetles from an interstadial deposit at the Isleworth site, England, but most species were represented by less than ten individuals. However, the approach of ecological groupings of beetles is a useful way to quantitatively interpret archaeological insects, and could be extended to other type of research. This approach will be tested in this research, as discussed below in the discussion chapter.

Chapter 3. Study area and sampling site

3.1 Overview of the Study area – Chinese Altai region

The Altai Mountains are a northwest- southeast trending mountain range in central Asia (Figure 8). The range extents from the Rubtsovsk region of Russia in the northwest to the Bayan-Öndör region of Mongolia in the southeast. These mountains cross parts of Russia, Kazakhstan, China and Mongolia. The Altai Mountains in China form the southern slope of the middle part of the range. This region is approximately 500 km long, with the higher and wider terrain in the northwest and lower and narrower terrain in the southeast. In China, the peaks of the Altai range from 3000m to 1000m above sea level (Hu et al., 2009).

Figure 8. Location of Altai region (Halashazi Wetland is the sample site).

The Chinese Altai region is located in the northern-most part of Xinjiang Province in China (figure 8), from the south of Altai mountains to the north of Dzungarian Basin, approximately between 45°00’00” and 49°10’45” N, 85°41’73” and 91°01’15” E. It is contiguous with Mongolia in the northeast, Russia in the north, and Kazakhstan in the west. Its total area is about 171,000 km^2, with 32% of mountainous region, 22% of hills, river valleys and plains, and 46% of Gobi desert (Hu et al., 2009). The terrain of the Altai region declines step by step from the north to the south. The landforms between the Altai Mountains and the Dzungarian Basin are hills and plains, due to the alluviation of the Ertix and Ulungur Rivers. The southern part of the Altai region borders on the Gurbantünggüt Desert, a region of both stable and unstable sand dunes (Hu et al., 2009).

The Altai region is situated in the Central hinterland of Eurasia, where summers are short and winters are cold and long. This is typical of a temperate continental climate. Based on the temperature data from year 1971 to 2000, the mean January temperature is -15.5°C, and the mean July temperature is 21.8°C. The location of the meteorological station is 47.8° N, 88.1°E, and the altitude is 738 m (Weather China, 2001).

The precipitation regime of Altai region is mainly affected by the Westerlies from the Atlantic Ocean, and also by cold wet airflow from the Arctic Ocean. In general, the plains are drier than the mountainous region, and the eastern part is drier than the western part: the mean annual precipitation in mountainous region is about 400 to 600 mm, though some areas receive 1000 mm; the mean annual precipitation in hills, plains and the southeastern part is less than 200 mm; the southern part has the lowest annual precipitation, which is only 95 mm on average (Weather China, 2001).

The surface runoffs of Altai region feed the Ertix River system, Ulungur River system and the Jimunai River system, a total of 56 rivers, with the whole catchment area 95,700 km^2 (Nuerlan, 2001).

In the Altai region, the vegetation types change significantly, according to altitude. Landscapes above 2300 m are dominated by mountain meadows; mountain forests are found between 1100 m to 2300 m, including *Pinus sylvestris*, *Picea obovata*, *Abies sibirica* and other species. Elevations less than 1100 m are covered in steppe vegetation; in the arid southern part supports only drought tolerant forage and sacsaoul (*Haloxylon ammodendron*) (Zhang and Hai, 2002).

3.2 Previous Holocene Studies in Altai region

3.2.1 Holocene palaeoclimate reconstruction

The Altai region in China, located in the middle of arid central Asia, may have been the transitional area between the Asian Monsoon-dominated climates from the east and the Westerlies-dominated climates from the west during the Holocene (Blyakharchuk et al., 2004, 2007, 2008; Harrison et al., 1996; Rudaya et al., 2009; Tarasow et al., 2000). The history of Holocene climate change in this region is therefore both sensitive and complex.

Table 2 and figure 9 list thirteen Holocene study sites in the Chinese Altai region and the nearby areas. Table 2 also shows their main findings. Most studies agree that there was a dry interval at the beginning of Holocene. However, as summarized in Table 3, there is less general agreement about subsequent climatic changes in this region.

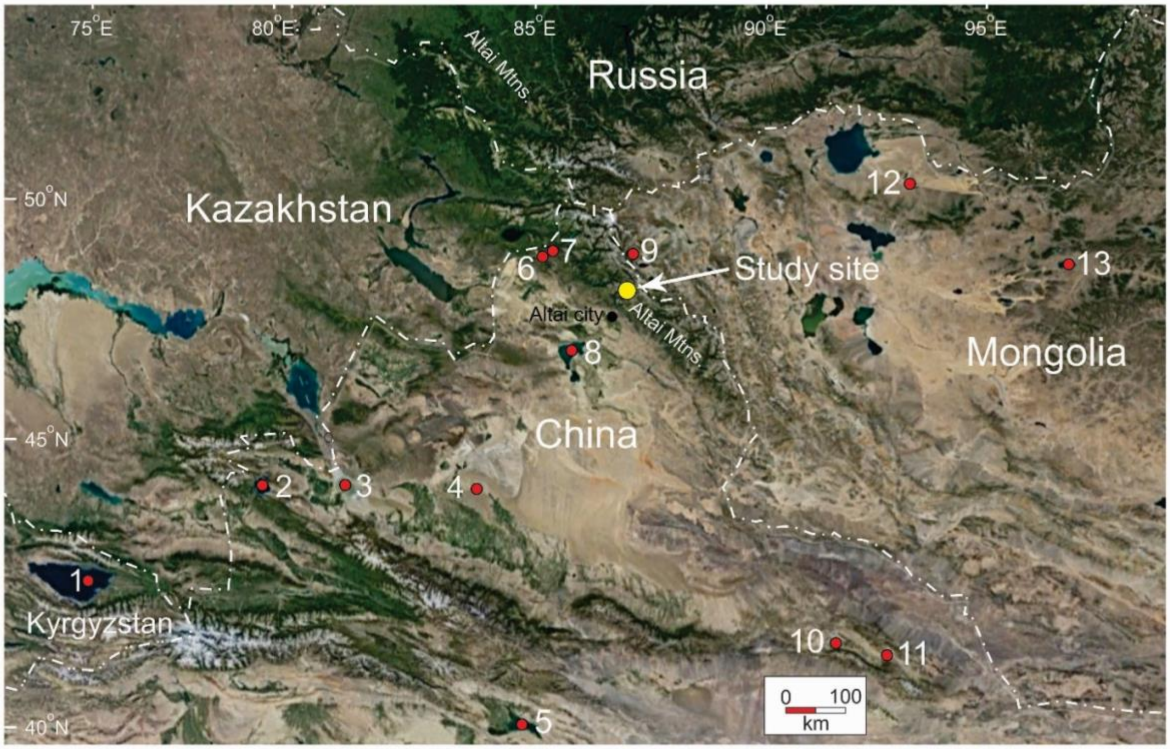


Figure 9. The Holocene study sites in the Chinese Altai region and the nearby areas. 1. Issyk-Kul Lake; 2. Sayram Lake; 3. Ebinur Lake; 4. Manas Lake; 5. Bosten Lake; 6. Tiershahan Wetland (Habahei Peat); 7. Narenxia Peat; 8. Ulungur Lake; 9. Hoton Nuur; 10. Barkol Lake; 11. Tuolekule Lake; 12. Bayan Nuur; 13. Telmen Lake.

Table 2. Holocene studies in the Chinese Altai region and nearby areas

NO.	Study Site	Location	Elevation (m.a.s.l)	Proxies used	Age (cal. yr BP)										Reference
					11k-10k	10k - 9k	9k-8k	8k-7k	7k-6k	6k-5k	5k-4k	4k-3k	3k-1k	After 1k	
1	Issyk-Kul Lake	42.50° N, 77.10°E	1606	Ostracod, stable isotope ($\delta^{18}O$, $\delta^{13}C$)	▨	▨	Wet	Wet	Dry	Dry	Dry	Dry	Dry	▨	Ricketts et al. (2001); Ferronskii et al. (2003)
2	Sayram Lake	44.60° N, 81.17°E	2072	Pollen	Warm and dry	Warm and moisture increased				Warm and dry	Cold and wet				Jiang et al., 2013
3	Ebinur Lake	44.32°N, 82.21°E	200	Pollen	Cold and dry (swamp or wetland)			Warm and wet (lake)						Dry	Song (2016); Wang et al. (2013)
4	Manas Lake	45.46° N, 85.55°E	251	$\delta^{18}O$, pollen		Warm and wet				Dry	Dry	Warm and wet	Dry	▨	Rhodes et al. (1996); Xu (2005)
				Pollen;	Cold and dry	Warm and wet						Dry	Dry	▨	Sun et al. 1994
5	Bosten Lake	42.00°N, 87.02°E	1047.5	Pollen, ostracod	Dry	Dry	Dry	Dry	Wet	Wet	Wet	Wet	Wet	▨	Huang (2006); Huang et al. (2009)
				Diatom	▨	▨	▨	Cold and wet	Warm and dry	Cold and wet	Dry	Dry	Cold and wet	▨	Yang (2008)
				Magnetic susceptibility, grain size	Dry	Dry	Dry	Dry	Wet	Wet	Less wet	Wet	Wet	▨	Zhang (2014)
6	Narenxia peat	48.48°N, 86.54°E	1760	Pollen	Warm and wet				Cold and dry			Warm and wet		Cold and dry	Feng et. al (2017)
7	Tiershahan Wetland (Habahe peat)	48.49°N, 86.57°E	1763	Pollen	▨	Dry	Dry	Wet	Wet	Wet	Warm and dry	Cold and wet		Warm and dry	Zhang (2016)
				Magnetic susceptibility	Cold (until 9.5k)		Warm	Warm	Warm	Warm	Warm	Cold	Cold	Cold	Zhang (2013)
				Plant macrofossil	Dry	Dry	Dry	Wet	Wet	Wet (until 4.6k)		Dry	Relatively wet		Sun (2012)
8	Ulungur Lake	47.20°N, 87.29°E	478.6	Ostracod, stable isotopes ($\delta^{18}O$, $\delta^{13}C$), pollen	Dry (low lake level)	Warm and dry		Cold and wet	Warm and wet (lake level rise)		Warm and dry (lake level decrease)		Warm and wet	▨	Jiang et al. (2008, 2007)
				Pollen		Warm and dry		Cold and dry	Wet	Wet	Wet	Wet	Wet	▨	Liu et al. (2008)

Table 2. (continued)

NO.	Study Site	Location	Elevation (m.a.s.l)	Proxies used	Age (cal. yr BP)										
					11k-10k	10k - 9k	9k-8k	8k-7k	7k-6k	6k-5k	5k-4k	4k-3k	3k-1k	After 1k	Reference
9	Hoton Nuur	48.37°N, 88.20°E	2083	Pollen, diatom	Dry and cold, steppe vegetation	Generally wetter and warmer than present					Cold and dry				Rudaya et al. (2009)
10	Barkol Lake	43.42°N, 92.54°E	1575	$\delta^{13}C$, grain size			Dry	Wet	Wet	Warm and wet		Cold	Dry		Lü (2011)
				Pollen; plant macrofossil; grain size	Dry	Dry	Dry	Warm and wet (4.2k-3.8k dry)				Drier than middle Holocene, wetter than early Holocene			Wang (2013); An et al. (2011); Tao et al. (2010); Tao (2011); Li (2009); Zheng (2010)
				Stable isotopes ($\delta^{18}O$, $\delta^{13}C$), grain size, carbonate contents		Dry and cold			Warm and wet		Warm and dry		Cold and wet	Cold and dry	Zhong et al. (2010)
11	Tuolekule Lake	43.30°N, 94.20°E	1890	Pollen	Dry	Dry	Dry	Warm and wet (4.5-3.8 dry)				Drier than the middle Holocene, wetter than the early Holocene			Tao (2011)
12	Bayan Nuur	50.00° N, 94.02°E	932	Diatom, pollen	Cold and wet (until 9.5k, lake depth 48m)		Dry (lake depth decreased to 4m)		Warm and wet (lake depth 4.4m)		Dry (lake depth 1m)	Cold and dry			Dorofeyuk and Tarasov (1998); Grunert et al. (2000)
13	Telmen Lake	48.83° N, 97.33°E	1789	Diatom, pollen				Dry	Dry	Dry	Wet	Wet	Wet		Peck et al. (2002); Fowell et al. (2003)

<table>
<tr><th>NO.</th><th>Study sites</th><th colspan="2">Early Holocene</th><th colspan="2">Middle Holocene</th><th colspan="2">Late Holocene</th></tr>
<tr><td>1</td><td>Issyk-Kul Lake</td><td colspan="3">Wet</td><td colspan="3">Dry</td></tr>
<tr><td>2</td><td>Sayram Lake</td><td colspan="3">Warm and dry</td><td colspan="3">Cold and wet</td></tr>
<tr><td>3</td><td>Ebinur Lake</td><td colspan="3">Cold and dry</td><td colspan="3">Warm and wet</td></tr>
<tr><td>4</td><td>Manas Lake</td><td colspan="3">Warm and wet</td><td colspan="3">Warm and dry</td></tr>
<tr><td>5</td><td>Bosten Lake</td><td colspan="3">Dry</td><td colspan="3">Wet</td></tr>
<tr><td>6</td><td>Narenxia Peat</td><td colspan="2">Warm and wet</td><td colspan="2">Cold and dry</td><td colspan="2">Warm and wet</td></tr>
<tr><td>7</td><td>Tiershahan Wetland</td><td colspan="3">Warm and dry</td><td colspan="3">Cold and wet</td></tr>
<tr><td>8</td><td>Ulungur Lake</td><td colspan="3">Warm and dry</td><td colspan="3">Warm and wet</td></tr>
<tr><td>9</td><td>Hoton Nuur</td><td colspan="3">Warm and wet</td><td colspan="3">Cold and dry</td></tr>
<tr><td>10</td><td>Barkol Lake</td><td colspan="2">Cold and dry</td><td colspan="2">Warm and wet</td><td colspan="2">Cold and dry</td></tr>
<tr><td>11</td><td>Tuolekule Lake</td><td colspan="2">Dry</td><td colspan="2">Warm and wet</td><td colspan="2">Dry</td></tr>
<tr><td>12</td><td>Bayan Nuur</td><td>Cold and wet</td><td colspan="2">Dry</td><td colspan="2">Warm and wet</td><td>Cold and dry</td></tr>
<tr><td>13</td><td>Telmen Lake</td><td colspan="2"></td><td colspan="2">Dry</td><td colspan="2">Wet</td></tr>
</table>

Table 3. A summarize of the Holocene climatic patterns from different study sites.

3.2.2 Dominant atmospheric circulation

Another research topic is the dominant atmospheric circulation control for central Asia climatic changes during the Holocene, and several hypotheses have been put forward:

(1) Westerlies domination

Since the meteorological records show that the modern precipitation in central Asia is controlled by the Westerlies, and monsoon rainfall does not extend as far inland as the study region (Li, 1991). Some researchers hold the view that the moisture availability in Xinjiang Province during the Holocene was also mainly affected by Westerlies rather than the Asian monsoon (Liu et al., 2008; Chen et al., 2008; Ran and Feng, 2013; Wang and Feng, 2013; Jiang, 2013).

Chen et al. (2008) synthesized palaeoclimate records from eleven lakes of the mid-latitude arid Asian region to evaluate spatial and temporal patterns of moisture changes during the Holocene (Figure 10). The results show that Arid Central Asia (ACA) as a whole experienced synchronous and coherent moisture changes during the Holocene, namely a dry early Holocene, a wetter early to mid-Holocene, and a moderately wet late Holocene, which is out-of-phase with the pattern of monsoonal Asia, as documented by numerous palaeoclimate records (Chen et al., 2008) (Figure 11). The Tibetan Plateau effectively blocks the Indian monsoon from reaching ACA (Figure 10)

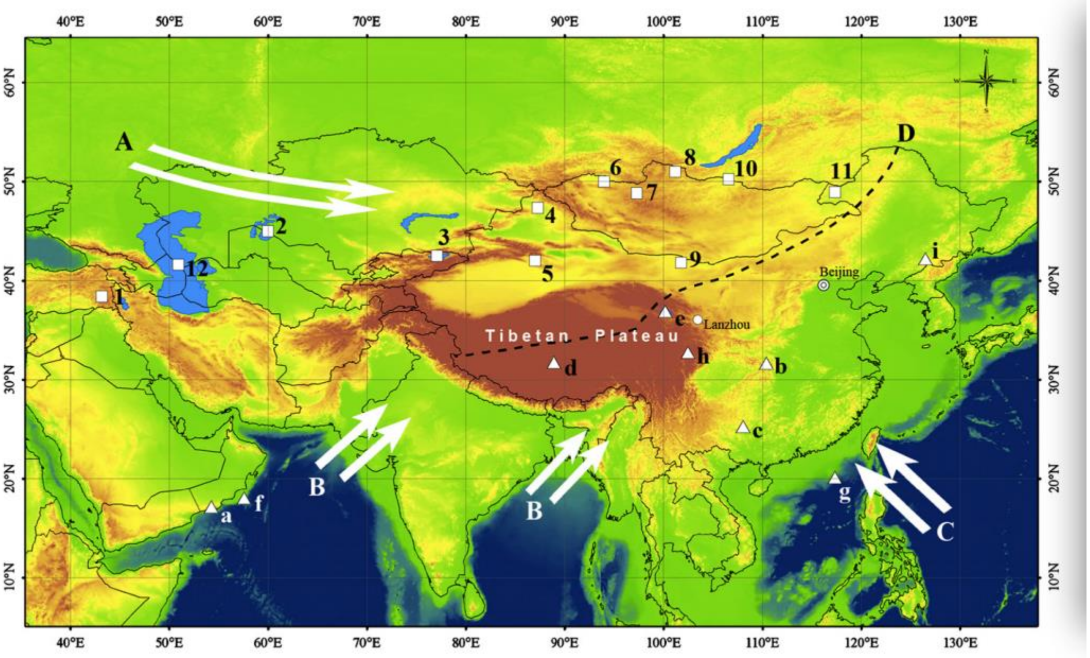


Figure 10. Overview map showing the palaeoclimatic study sites analyzed by Chen et al. (2008) in arid central Asia (numbers) and monsoonal Asia (lower case letters), and the dominant circulation systems (arrows with upper case letters) of the Westerlies (A), Indian monsoon (B), and East Asian monsoon (C). The modern Asian summer monsoon limit is shown by a dark dashed line. The sites in arid central Asia are:1. Lake Van; 2. Aral Sea; 3, Issyk-Kul Lake; 4, Wulungu Lake; 5, Bosten Lake; 6, Bayan Nuur;7, Telmen Lake; 8, Hovsgol Nuur; 9, Juyan Lake; 10, Gun Nuur; 11, Hulun Nuur; 12, Caspian Sea. The sites in monsoonal Asia (triangles) include speleothem records ((a) Qunf Cave, Southern Oman; (b) Shanbao Cave, central China; and (c) Dongge Cave, SW China), lake records ((d) Siling Lake and (e) Qinghai Lake), marine records ((f) Arabian Sea and (g) South China Sea), and peat records ((h) Hongyuan peat bog and (i) Hani peat bog). (Chen et al. 2008, p. 353)

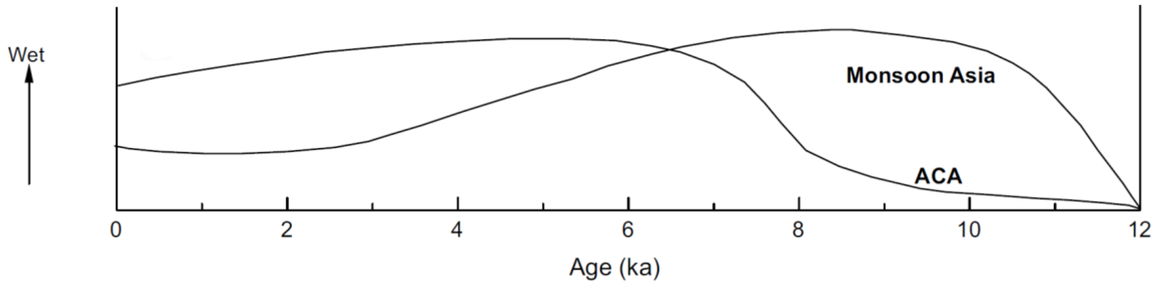


Figure 11. The out-of-phase relationship of Holocene moisture evolution between monsoon Asia and ACA. (Chen et al. 2008, p. 358)

Chen et al. (2008) suggest that summer insolation of the Northern Hemisphere played a key role in ACA moisture changes, but only after the ice sheets had disappeared. During the last deglaciation and early Holocene, the ice-sheets at high latitudes were still large compared with those of the mid- and late Holocene, modulating and reducing air temperature and the ocean surface temperature, even though summer insolation was higher (Koc et al., 1993; Kaplan and Wolfe, 2006). However, during the early Holocene, the maximum summer insolation enhanced the Asian summer monsoon (Staubwasser et al., 2002; Wang et al., 2005) and enhanced the temperature in low latitudes. As a result, this large meridional temperature gradient between high and low latitudes would have enhanced the mid-latitude Westerlies air-stream and also would have shifted the Westerlies jet stream southward, causing strong winds in the Arid Central Asian region. Also, the cold ocean surface would have reduced water evaporation from the North Atlantic Ocean. All of these would result in less precipitation and a dry climate in Arid Central Asia during the early Holocene.

Jiang (2013) proposed another hypothesis to explain the dry early Holocene. He considered that the influence of ice-sheet melting in high latitudes was not sufficient to affect the moisture decrease, but that the strengthened solar radiation decreased the temperature gradient between high and low latitudes, leading to weaker Westerlies in the mid-latitudes and less evaporation in western, upwind regions (Mediterranean, Black Sea, or Caspian Sea), thus resulting in a dry climate in Arid Central Asian during the early Holocene.

Wang et al. (2013) reconstructed a regional averaged moisture index (RA-moisture index) for the Holocene in the Xinjiang Area, based on their research at Ebinur Lake and moisture level reconstructions from other study sites in Xinjiang province, including Sayram Lake (Jiang et al., 2013), Ulungur Lake (Liu et al., 2008), Bosten Lake (Huang, 2006, 2009) and Barkol Lake (Tao et al., 2010) (figure 12c). As figure 12a shows, this RA-moisture index is different from the East Asian monsoon strength index (Dongge Cave data, Dykoski et al., 2005). Unexpectedly, the Holocene RA-moisture index in the Xinjiang region is also different from reconstructions of the mean effective moisture pattern in Arid Central Asia, as described by Chen et al. (2008), and likewise it is different from the moisture index of Central Asia reconstructed by Herzschuh (2006), in which the dominant forcing factors were regional uplift and descent of air masses, centered around the Tibetan Plateau (figure 12b). As discussed above, Chen et al. (2008) suggested a gradually decreased moisture in Arid Central Asian from ~8000 cal. yr BP, while the RA-moisture index shows the moisture increased from ~8000 cal. yr BP.

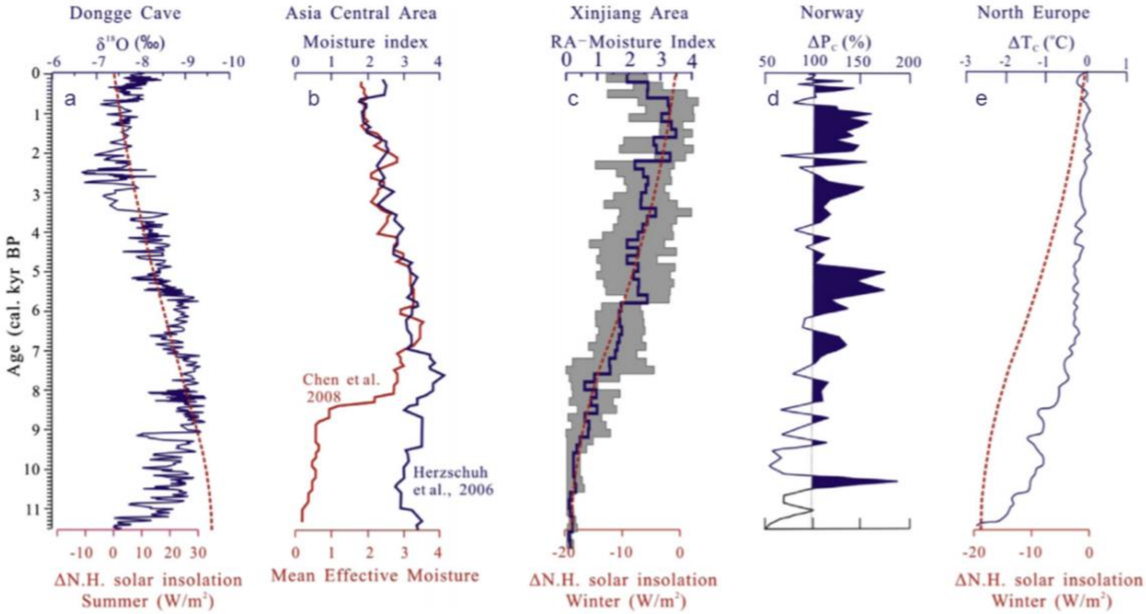


Figure 12. (a) the Holocene moisture evolution of Dongge Cave in Asian Monsoon area (blue line); Holocene summer solar insolation (red dashed line). (**b)** the Holocene moisture evolution in Central Asia area. **(c)** Holocene regional averaged moisture index in Xinjiang area (blue line); Holocene winter solar insolation (red dashed line). **(d)** Holocene winter precipitation variation in Norway. **(e)** Holocene mean winter temperature of northern Europe (blue line); Holocene winter solar insolation (red dashed line) (Wang et al. 2013).

However, as figure 12d and figure 12e show, the Holocene regional averaged moisture index in Xinjiang province is aligned with the positive cold-season precipitation variation, based on the Falgefonna record of Norway (Bakke et al., 2008), and it was aligned with the positive winter temperature deviation of northern Europe reconstructed from pollen data (Davis et al., 2003). Thus, Wang et al. (2005) hypothesized the Holocene precipitation in Xinjiang province may have been driven by winter precipitation and warming trends in northern Europe. In mid to late Holocene, the gradually increased winter insolation in northern Europe might have caused more evaporation in the North Atlantic Ocean, and therefore injected more moisture to the Westerlies system, thus bringing more precipitation to eastern, downwind regions, including Xinjiang province. However, this hypothesis needs more data support and different climatic influences should be factored in. Similarly, reduced summer solar insolation may also have caused less precipitation in Xinjiang province during summer, which would affect total moisture.

(2) Asian monsoon domination

Some other studies hold that the moisture brought by the Westerlies is not critical to environmental changes observed in central Asia, and the Asian monsoon made an important contribution to the humidity of the early-mid Holocene. Harrison et al. (1996) and Tarasov et al. (2000) speculated that the Asian monsoon extended to southern Siberia, including the entire Altai region. From 8000 yr BP to 6000 yr BP, lake data from Mongolia, western Siberia, and as far northwest as Yakutia register conditions wetter than present, which suggest that the expansion of the Asian monsoon was at a maximum in the mid-Holocene. However, this model lags behind the driving changes in insolation forcing by several thousand years (Harrison et al. 1996). This discrepancy remains to be explained.

Similarly, the studies from Wolungur Lake (Jiang et al., 2007, 2008), Manas Lake (Rhodes et al. ,1996; Xu, 2005), and Barkol Lake (Zhong et al. 2010) also suggested increased moisture during the early to middle Holocene, and these authors consider that this was caused by the strong influence of the South Asian monsoon. The Asian monsoon might have extended at least to northern Xinjiang Province, including the southern Altai region, during the Holocene warm intervals (Rhodes et al. ,1996), and the Westerlies once again dominated the northern Xinjiang region during late Holocene (Zhong et al. 2010).

(3) Different parts of Altai controlled by different climate systems

Rudaya et al. (2009) split the Altai region into three geographical regions: the eastern Altai within Mongolia, the western Altai within Kazakhstan, and the northern Altai within Russia. Based on their own research on Hoton Nuur, and other published data (Achit-Nur (Gunin et al., 1999), “kharkhiraa south side” (Schlütz, 2000) and Bayan Nuur ((Krengel, 2000; Grunert et al., 2000) in the eastern Altai; Ozerki Swamp and Karkaraly Mountains (Kremenetski et al., 1997; Tarasov et al., 1997) in the western Altai; and Ulagan Plateau (Blyakharchuk et al., 2004) in the northern Altai), Rudaya et al. (2009) suggested different climate systems controlled different regions during the different intervals. In the eastern Altai, it was warm and wet in the first half of Holocene (~11,000 to ~5000 cal. yr BP), and cold and dry in the second half of Holocene (~5000 cal. yr BP to present). The climate in this region aligned with Asian monsoon climate pattern. In the western Altai, it was warm and dry in the first half of the Holocene, and cold and wet in the second half of the Holocene. The climate in this region was aligned with the Westerly climate pattern. In the northern Altai, it was warm and wet in the first half of the Holocene, which may have been controlled by the Asian monsoon, and cold and wet in the second half of the Holocene, which may have been controlled by Westerlies.

(4) Influence from North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO)

Feng et al. (2017) compared their reconstruction of Holocene climate based on pollen from the Narenxia Peat site in the southern Altai Mountains to climatic forcings associated with the NAO and the ENSO, and concluded that a combination of NAO and ENSO forcings strongly affected climatic conditions in the southern Altai region. As figure 13 shows, the reconstructed NAO index variations (Trouet et al., 2009; Olsen, et al., 2012) are almost synchronous with reconstructed ENSO strength (Rein et al., 2005) in the past ~5200 years, and also are synchronized with the reconstructed precipitation and temperatures from Narenxia Peat. Feng et al. (2017) assumed that the approximate synchronieity between the NAO index and the ENSO strength also existed before 5200 cal. yr BP.

During the positive phase of the NAO, moisture from both the North Atlantic and the Mediterranean was carried east to the Central-Southwest Asia region (including northern Pakistan, southern Uzbekistan, Afghanistan, Tajikistan and southern Kazakhstan), transported by increased strength of Westerlies (Hurrell and Van Loon, 1997; Xu et al., 2016). On the other hand, the warm phase of ENSO in the western Pacific acted to weaken the Siberian High-Pressure system, allowing increased moisture to enter south-central Asia in the winter, spring and autumn (Syed et al., 2006, 2010). Thus, Feng et al. (2017) hypothesized that Holocene precipitation and temperatures in the Altai region, and throughout southern Siberia, may have been modulated by a combination of NAO and ENSO forcings.

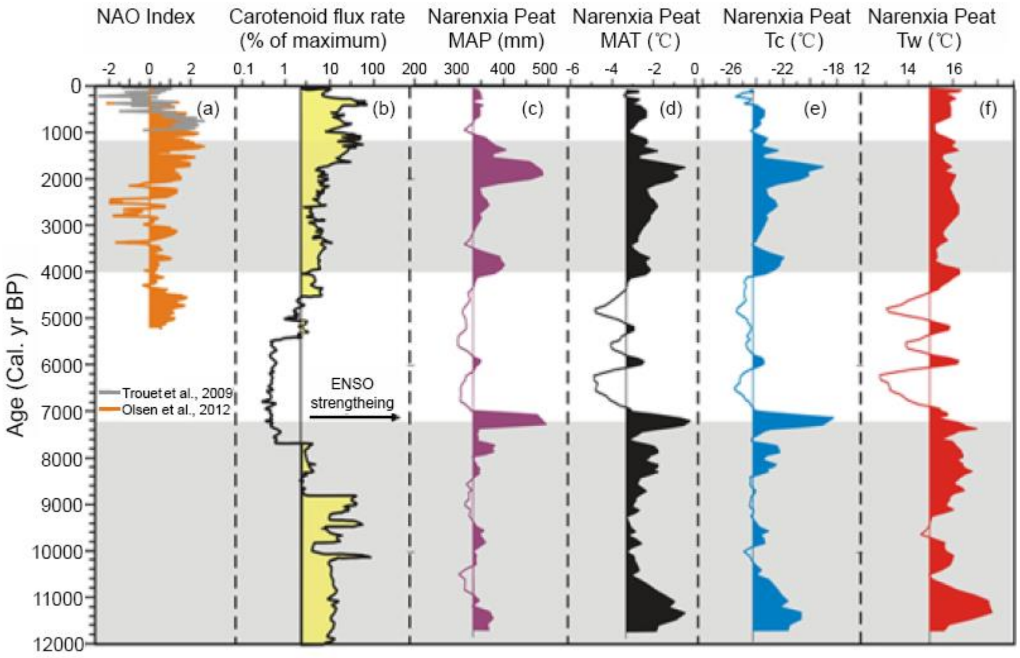


Figure 13. Comparison of the interpreted Holocene environmental change from Narenxia Peat with NAO index and Carotenoid flux rate. **(a)** the reconstructed NAO index variations from 5200 cal. yr BP. (**b)** the reconstructed ENSO strength from 12,000 cal. yr BP. **(c)** the reconstructed Holocene mean annual precipitation from Narenxia Peat. **(d)** the reconstructed Holocene mean annual temperature from Narenxia Peat. **(e)** the reconstructed Holocene cold-season temperature from Narenxia Peat. **(f)** the reconstructed Holocene warm-season temperature from Narenxia Peat.

In summary, the Holocene climate change in the Altai region or in Arid Central Asia was a complex process. Besides atmospheric circulation, the local topography (nearby rivers and mountains) of the study site also might have affected the results. The response time of the pollen signal to the climate change might also have caused the difference between reconstructions. For example, after the temperature increased and trees started to grow, it may have taken a few centuries for conifer pollen to reach concentrations sufficient to show in the pollen records (Elias, 1985). Thus, more studies using multiple proxies should be carried out in this region, in order to acquire more abundant and more accurate data.

3.3 Sampling sites

The sample sites for this project are located in the Halashazi Wetland. The peat in Halashazi Wetland was discovered by Li (1981) on a previous prospecting trip in the Altai Mountain region of China. The wetland is located to the north of Altai City, at the southern slope of the Altai Mountains (48°07’ N, 88°21 E) (figure 9). The altitude is 2450 m above sea level. Since the nearest meteorological station is in Altai city, the modern average seasonal temperatures of Halashazi wetland have been estimated, taking into account the elevational difference between the meteorological station and the study site. Thus, the difference in temperatures were reckoned on the basis of an elevational lapse rate of 0.6 °C per 100 m (Meteoblu, 2017). Based on this formula, the mean July temperature of the sampling site is about 11.5°C, and the mean January temperature is about -25.7 °C.

There are more than 50 peat hummocks in the Halashazi wetland with heights varying from 0.5 m to 5.0 m (figure 14). Oceanic moisture scarcely reaches this arid area, so the wetlands that developed here are extremely rare. While the Halashazi wetland contains a rich peat resource, the moisture that feeds the wetlands comes from streams flowing from the southern slopes of the Altai Mountains. Figure 15 shows the bedrock geology of the Chinese Altai Mountains (Yuan et al., 2006). The study site, Halashazi wetland is sitting on diorite and Cambrian Ordovician volcanic rocks.

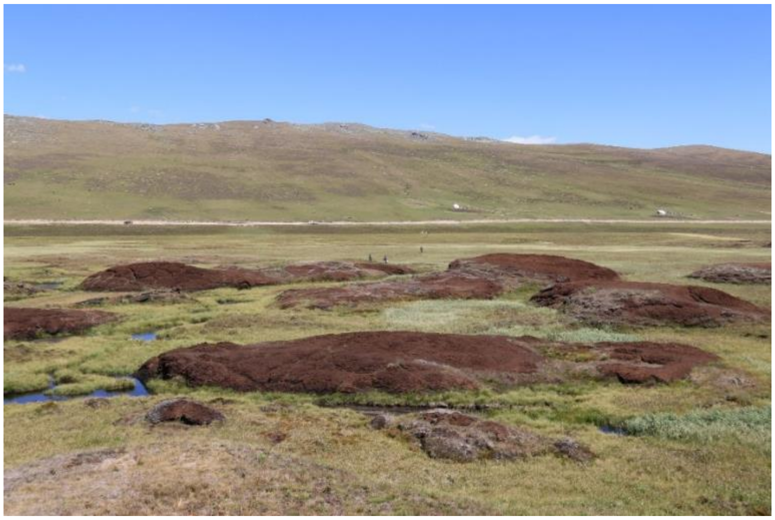


Figure 14. Peat hummocks in the Halashazi wetland. (Photo by the author)

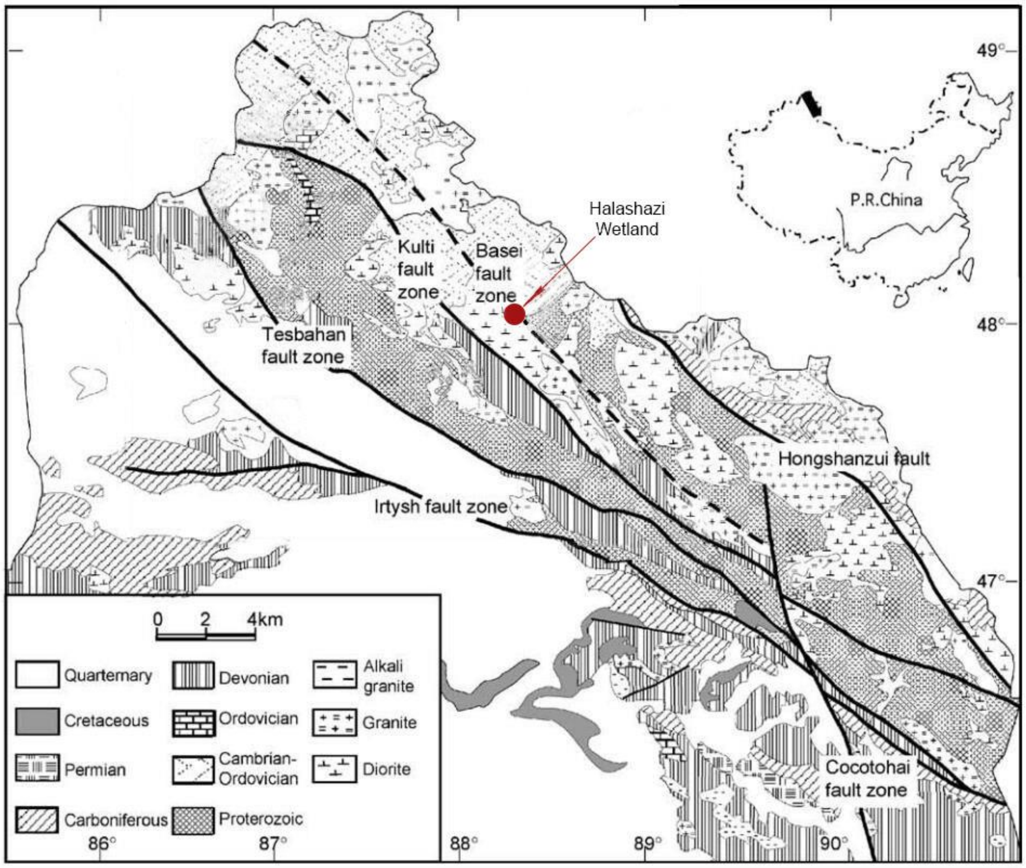


Figure 15. The bedrock geology of the Chinese Altai Mountains (Yuan et al., 2006).

The Halashazi wetland is located at the crossroad of the Altai Mountains and the Dzungarian Basin, where a boreal ecosystem meets an arid desert ecosystem (figure 16) (Ran et al. 2015). Since the site is located at an ecosystem boundary, the fossil beetle assemblages should show marked changes in response to changes of climate.

However, travel to the study region is highly restricted because of military sensitivity (proximity of Russian and Mongolia borders), and most indigenous peoples in this region are in the Kazakh ethnic group, Hui ethnic group, and Uygur ethnic group, who remain hostile (especially the Uygur ethnic group) to outsiders, so extensive field survey of potential sites in this region was not possible. Moreover, this site is extremely remote and difficult to reach, except by a four-wheel drive vehicle. But on the other hand, it is well away from human activity, so it has been left undisturbed. As such, it is a well-preserved and ideal site for palaeoclimate research.

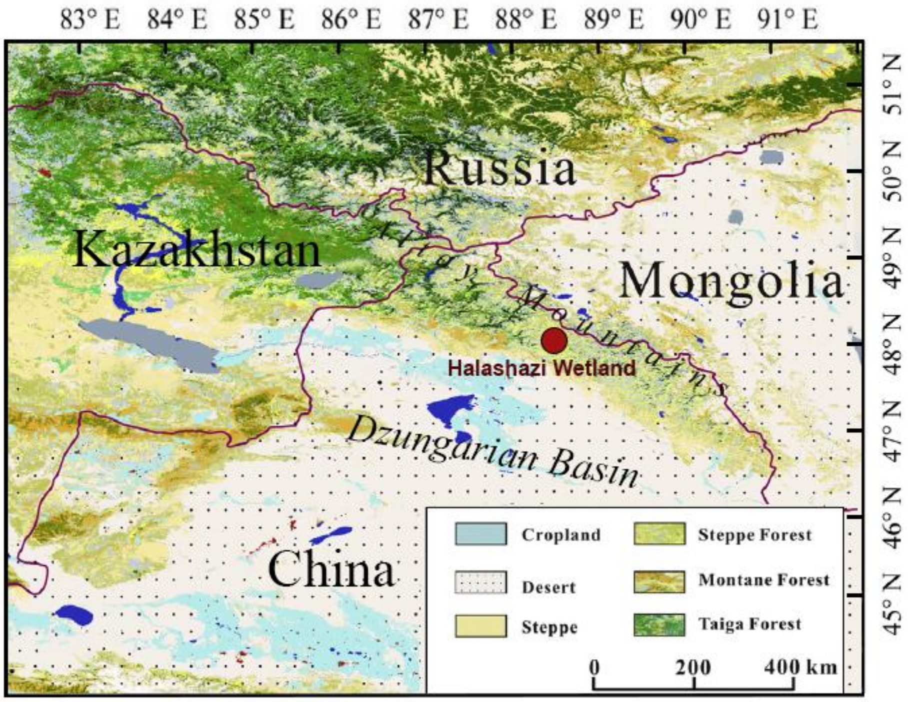


Figure 16. The distribution of vegetation from the Altai region (Ran et al. 2015).

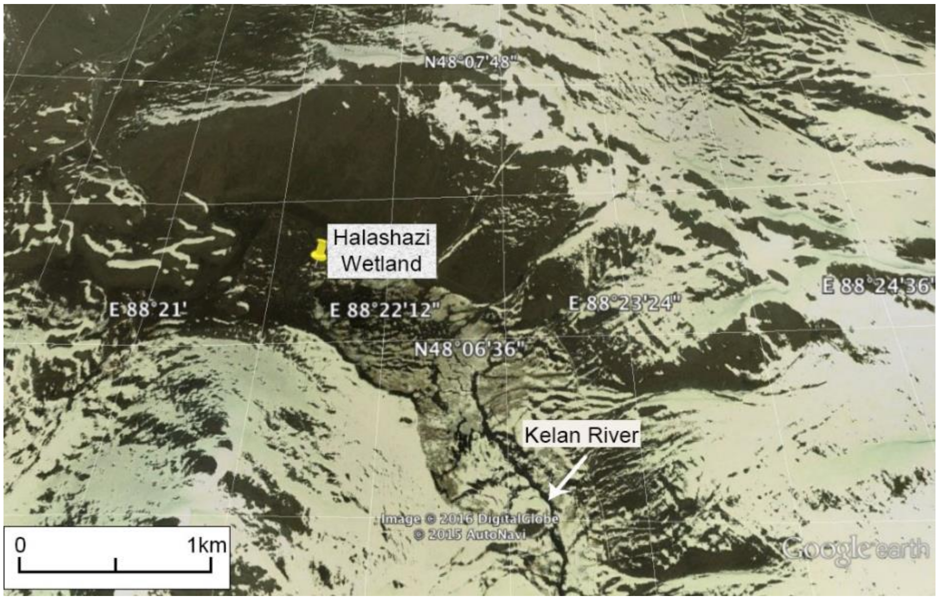


Figure 17. The topographic map of Halashazi wetland. (From Google Earth)

3.4 Peat accumulation at Halashazi

The map (figure 17) shows that the Halashazi wetland is located in a low-lying depression, surrounded by mountains on all sides. This led to the accumulation of water in the basin and the formation of wetland. The stream (headwaters of the Kelan River) shown in the south-central portion of the image likely fed the wetland throughout the time of peat formation. Peat preservation in the basin was enhanced by permafrost.

3.5 Sampling procedures

Two profiles have been taken in order to provide two sets of fossil assemblages for comparisons (figure 18, 19): profile 1, sampled on 26th July, 2014, is 1.5 m high, and 31 samples have been collected; profile 2 is about 200 m away from profile 1. It has been taken on 3rd August, 2015; the height is 2 m, and it yielded 40 samples.

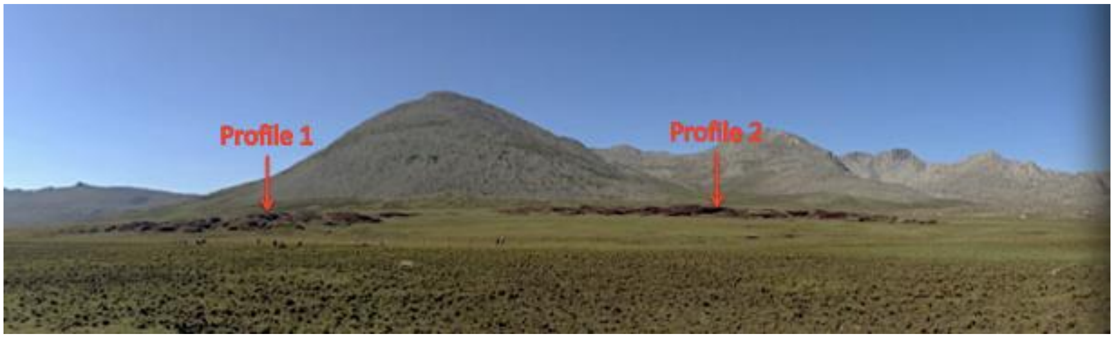


Figure 18. Halashazi wetland with approximate positions of the two profiles. (photo by the author)

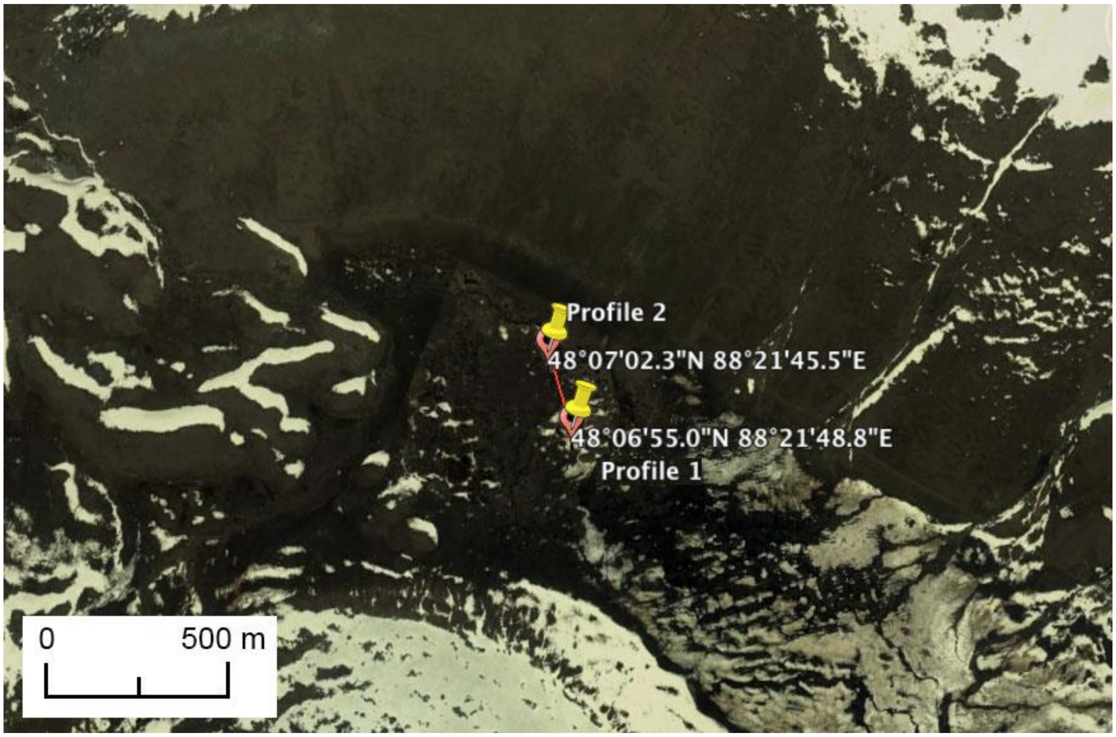


Figure 19. Positions of the sampled two profiles on topographic map. (From Google Earth)

It is very important to remove the weathered surface before sampling, to ensure the samples do not contain modern insects, as well as to ensure that modern carbon from recent organic material will not contaminate potential radiocarbon samples (Morgan, 1988). After cleaning the exposure, blocks of peat were cut with a knife, sealed in plastic samples bags, and labeled in stratigraphic sequence. In order to obtain enough beetle fossils, it is necessarily to collect large quantities of sediments. However, due to the high altitude of this site, it is hard to cut deep of the peat, because of the inside of the peat hummocks are frozen even in the summer. Thus, for profile 1, each block measuring approximately 30 cm wide by 15 cm deep (front to back) by 5 cm thick. Each sample was about 2 kilograms in weight. Samples were taken from the top of peat hummock downwards. Sampling below 70 cm at section 1 became too difficult because the peat frozen to solid below this depth. Therefor the lower part of the samples were taken from section 2 (figure 20).

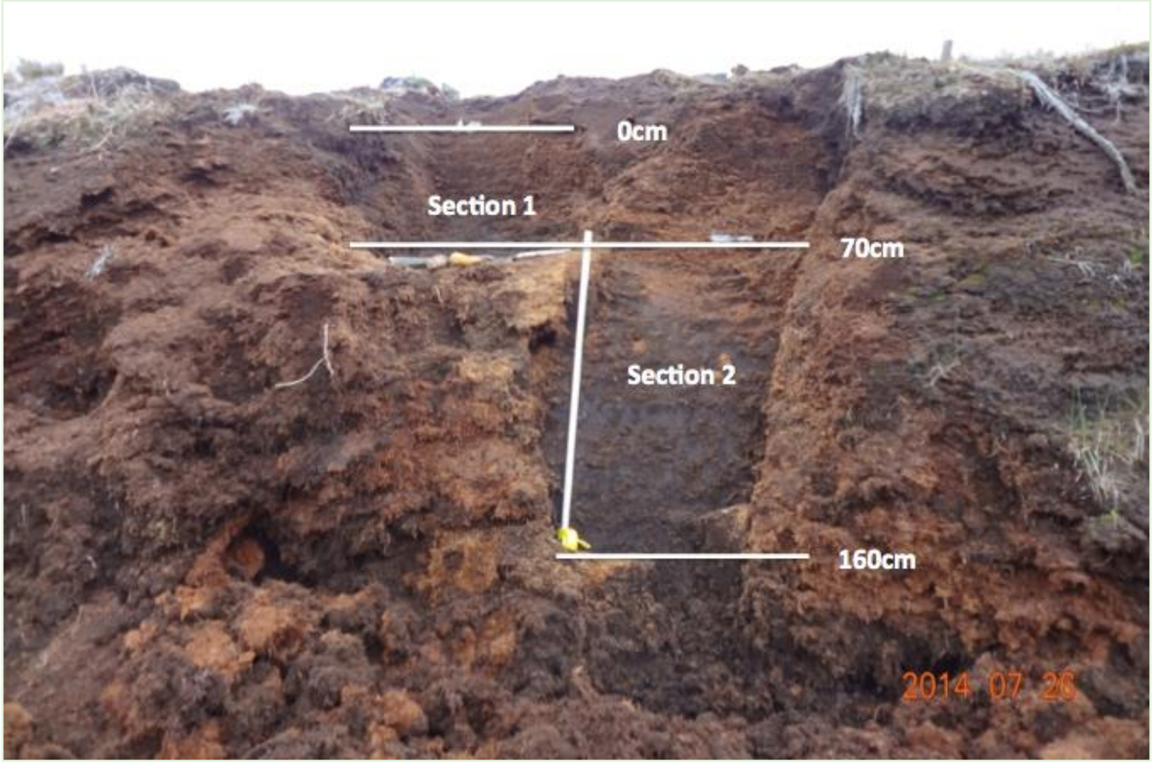


Figure 20. Peat profile 1 with the two sections. (Photo by the author)

In order to sample as deep as possible on the frozen peat hummock, to obtain older samples, profile 2 was sampled on a naturally collapsed peat hill. The inside of this peat hummock already was exposed at the bottom (figure 21). After cleaning the dried exposure, the peat blocks were cut every 5 cm from the top to the bottom. Since the peat could only be cut to a depth of 8 cm from front to back, the width of each block was widened to approximately 70 cm to ensure enough volume (two kilograms) of peat in each level.

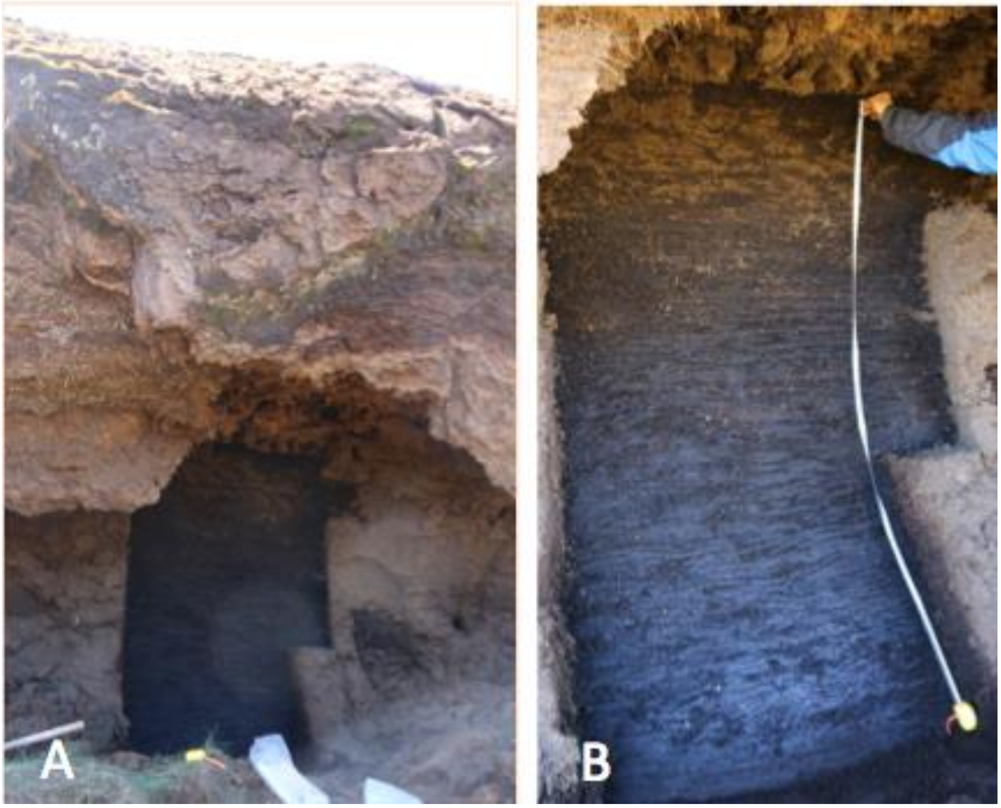


Figure 21. (A) Peat profile 2 on the naturally collapsed peat hummock. **(B)** Peat profile 2. (Photo by the author)

3.6 Peat description

Based on the Troels-Smith sediment description method (Troels-Smith, 1955), the details of the composition and level of humification of each sample have been listed in table 4. The plant remains in peat from both sampling sites are dominated by sedges (*Carex* spp.) and mosses (not *Sphagnum*). In Profile One, except layer 85-90 cm (mosses only), both sedges and mosses were found in every level of this profile. From 0 cm to 125 cm, the mosses are more abundant than sedges, while from 125 to 150, sedges are more abundant than mosses. In Profile Two, layer 0-5 cm contains only sedges. The rest of this profile (from 5 to 200 cm) is made up of moss peat. No woody plant remains were found, and no mineral layers were found. There is no evidence of reworking, just horizontally bedded layers of moderately humified peat. Based on visual observation, the sand and silt content of the samples was less than 5% in each sample.

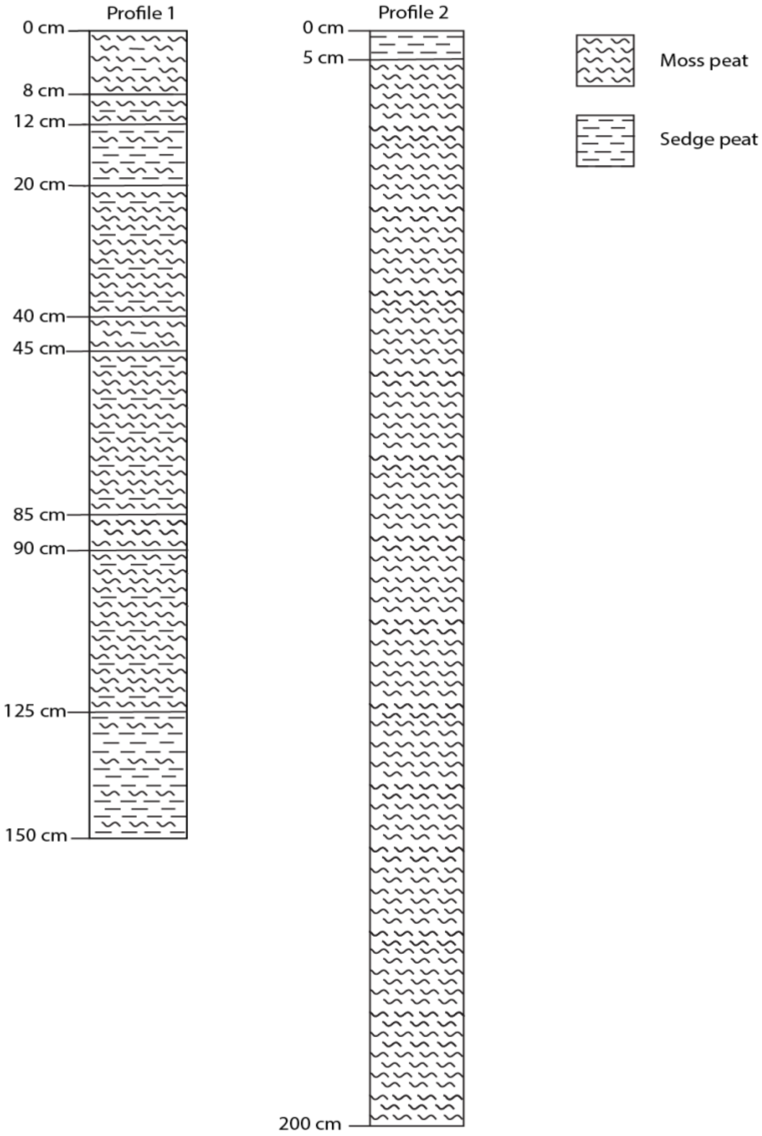


Figure 22. Peat stratigraphy from two sampled columns at study site.

Profile 1		Profile 2	
Depth (cm)	Description	Depth (cm)	Description
0-4	Th^{2} 3, Sh 1, Tb^{2+}	0-5	Tb^{1} 4
4-8	Th^{2} 3, Sh 1, Tb^{2+}	5-10	Th^{1} 3, Sh 1
8-12	Th^{2} 2, Tb^{2} 1, Sh 1	10-15	Th^{2} 3, Sh 1
12-16	Tb^{2} 2, Th^{2} 1, Sh 1	15-20	Th^{2} 3, Sh 1
16-20	Tb^{2} 2, Th^{2} 1, Sh 1	20-25	Th^{2} 3, Sh 1
20-25	Th^{2} 2, Tb^{2} 1, Sh 1	25-30	Th^{2} 3, Sh 1
25-30	Th^{2} 2, Tb^{2} 1, Sh 1	30-35	Th^{2} 3, Sh 1
30-35	Th^{2} 2, Tb^{2} 1, Sh 1	35-40	Th^{2} 3, Sh 1
35-40	Th^{2} 2, Tb^{2} 1, Sh 1	40-45	Th^{2} 3, Sh 1
40-45	Th^{2} 3, Sh 1, Tb^{2+}	45-50	Th^{2} 3, Sh 1
45-50	Th^{2} 2, Tb^{2} 1, Sh 1	50-55	Th^{2} 3, Sh 1
50-55	Th^{2} 2, Tb^{2} 1, Sh 1	55-60	Th^{2} 3, Sh 1
55-60	Th^{2} 2, Tb^{2} 1, Sh 1	60-65	Th^{2} 3, Sh 1
60-65	Th^{2} 2, Tb^{2} 1, Sh 1	65-70	Th^{2} 3, Sh 1
65-70	Th^{2} 2, Tb^{2} 1, Sh 1	70-75	Th^{2} 3, Sh 1
70-75	Th^{2} 3, Tb^{2} 1, Sh 1	75-80	Th^{2} 3, Sh 1
75-80	Th^{2} 2, Tb^{2} 1, Sh 1	80-85	Th^{2} 3, Sh 1
80-85	Th^{2} 2, Tb^{2} 1, Sh 1	85-90	Th^{2} 3, Sh 1
85-90	Th^{2} 3, Sh 1	90-95	Th^{2} 3, Sh 1
90-95	Th^{3} 2, Tb^{3} 1, Sh 1	95-100	Th^{2} 3, Sh 1
95-100	Th^{3} 2, Tb^{3} 1, Sh 1	100-105	Th^{2} 3, Sh 1
100-105	Th^{3} 2, Tb^{3} 1, Sh 1	105-110	Th^{2} 3, Sh 1
105-110	Th^{3} 2, Tb^{3} 1, Sh 1	110-115	Th^{2} 3, Sh 1
110-115	Th^{3} 2, Tb^{3} 1, Sh 1	115-120	Th^{2} 3, Sh 1
115-120	Th^{3} 2, Tb^{3} 1, Sh 1	120-125	Th^{2} 3, Sh 1
120-125	Th^{3} 2, Tb^{3} 1, Sh 1	125-130	Th^{2} 3, Sh 1
125-130	Tb^{2} 2, Th^{2} 1, Sh 1	130-135	Th^{2} 3, Sh 1
130-135	Tb^{2} 2, Th^{2} 1, Sh 1	135-140	Th^{2} 3, Sh 1
135-140	Tb^{2} 2, Th^{2} 1, Sh 1	140-145	Th^{2} 3, Sh 1
140-145	Tb^{2} 2, Th^{2} 1, Sh 1	145-150	Th^{2} 3, Sh 1
145-150	Tb^{2} 2, Th^{2} 1, Sh 1	150-155	Th^{2} 3, Sh 1
		155-160	Th^{2} 3, Sh 1
		160-165	Th^{2} 3, Sh 1
		165-170	Th^{2} 3, Sh 1
		170-175	Th^{3} 3, Sh 1
		175-180	Th^{3} 3, Sh 1
		180-185	Th^{3} 3, Sh 1
		185-190	Th^{3} 3, Sh 1
		190-195	Th^{3} 3, Sh 1
		195-200	Th^{3} 3, Sh 1

Table 4. Troels-Smith sediment description for two profiles. Components: Th = sedges, Tb = mosses, Sh = unidentifiable. The abundance of each component:0 = absent, 1 = up to ¼, 2 = ¼ to ½, 3 = ½ to ¾, 4 = whole, + = trace, less than ⅛. Humification is shown by superscript: 0 = no humification, 1 = slightly humification, 2 = half humification, 3 = very humification, 4 = completely humification (Troels-Smith, 1955).

3.7 Radiocarbon dating

AMS radiocarbon dating has been processed in the summer of 2016 in Lanzhou University, China. The plant remains form five samples have been selected from each profile for radiocarbon dating (table 5).

	Laboratory number	AMS ^{14}C date (uncal. yr BP)	Depth (cm)
Profile 1	LZU16206	3915 ± 25	4-8
	LZU 16207	4520 ± 25	30-35
	LZU 16208	4715 ± 25	65-70
	LZU 16209	4925 ± 25	95-100
	LZU 16210	5605 ± 25	145-150
Profile 2	LZU 16211	8500 ± 30	0-5
	LZU 16212	8525 ± 40	50-55
	LZU 16213	8940 ± 60	100-105
	LZU 16214	9150 ± 30	145-150
	LZU 16215	9255 ± 30	195-200

Table 5. The radiocarbon dates from Halashazi peat profiles. (AMS: accelerator mass spectrometry).

In order to acquire a reliable chronology, a formal Bayesian age model has been constructed for the radiocarbon ages in each profile (figure 23 and 24).

The AMS ^{14}C dates for the Halashazi peat profiles, along with the depth information, have been used in the Bayesian P_Sequence model. These data have been modeled to calculate the highest likelihood age ranges for every 5cm interval (Table 6 and 7), incorporating formal outlier detection (Bronk Ramsey, 2009a, b; 2013), and applying the IntCal13 calibration curve (Reimer et al., 2013).

The P_Sequence depositional model has been applied in Oxcal (Ramsey, 2013), with a variable K factor and automatic outlier detection, following Ramsey (2009a, b) with boundaries at the top and bottom. The outlier model selection used the general outlier model and outlier probabilities were set to 0.05%. The results of the modelling exercise are reported as 95%

confidence intervals, showing the highest probability density function and depositional model plots.

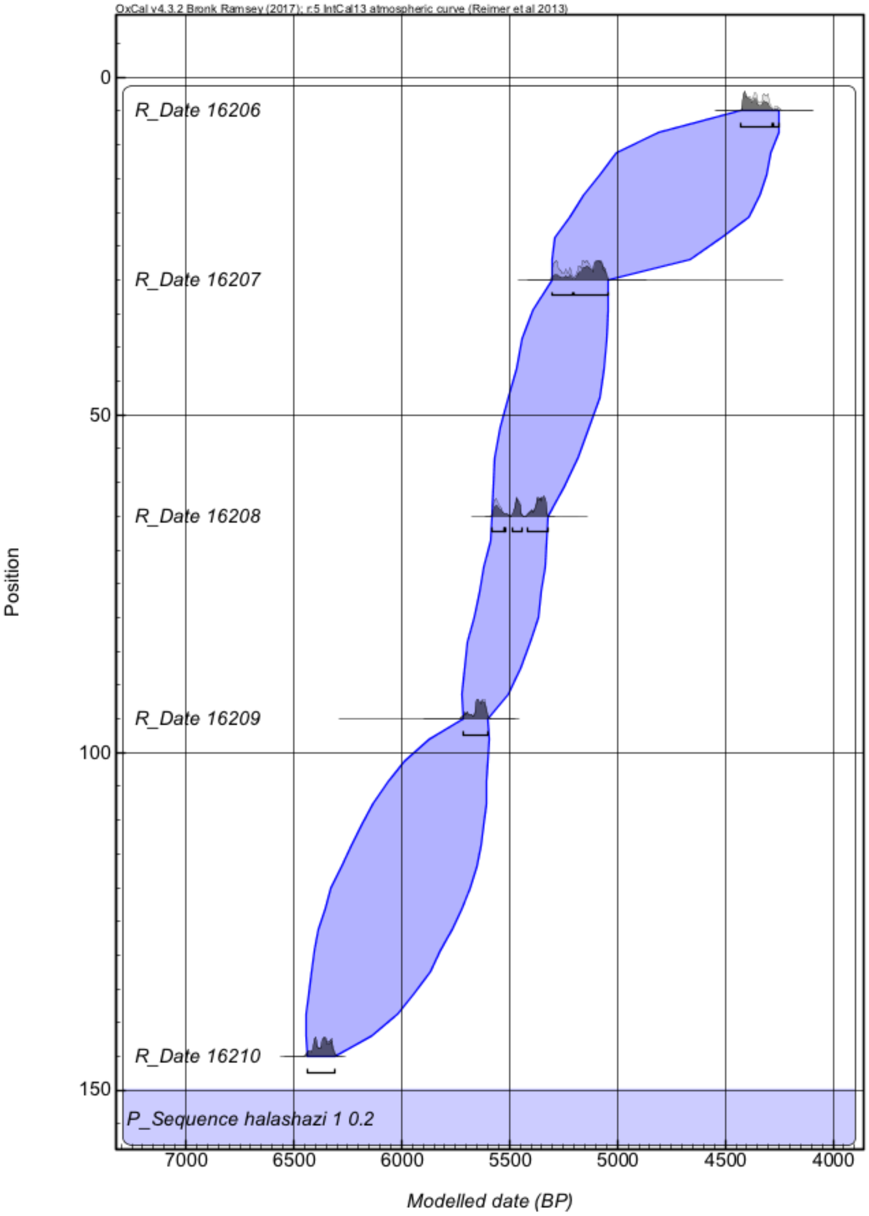


Figure 23. 95% confidence interval Highest Probability Density output for radiocarbon-based Bayesian age-depth model for Profile One (run using a Poisson process model). The model was constructed purely using AMS ^{14}C dates, for providing an independent age constraint.

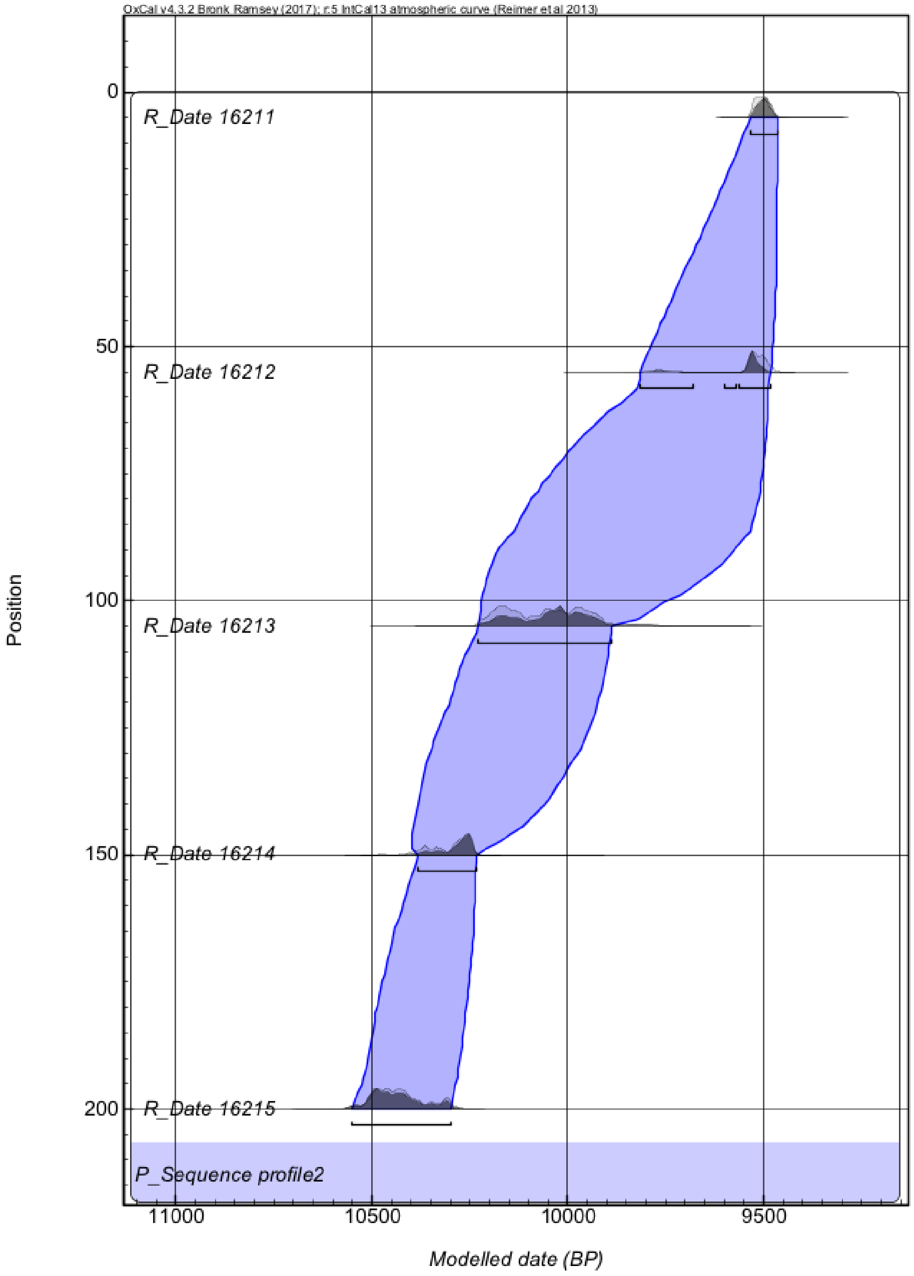


Figure 24. 95% confidence interval Highest Probability Density output for a radiocarbon-based Bayesian age-depth model for Profile Two (run using a Poisson process model). The model was constructed purely using AMS^{14}C dates, for providing independent age constraint.

Table 6. Calibrated age ranges of each sample in Profile One (calculated by the Bayesian P_Sequence model).

Name	Depth (cm)	Age (cal. yr BP)	Median
LZU16210	145-150	6309 – 6439	6374
Depth Model	140-145	6309 – 6444	6258
Depth Model	135-140	6072 – 6431	6179
Depth Model	130-135	5927 – 6406	6119
Depth Model	125-130	5832 – 6371	6058
Depth Model	120-125	5745 – 6331	6003
Depth Model	115-120	5675 – 6261	5951
Depth Model	110-115	5641 – 6171	5893
Depth Model	105-110	5615 – 6088	5847
Depth Model	100-105	5606 – 5938	5768
LZU16209	95-100	5598 – 5717	5658
Depth Model	90-95	5599 – 5720	5606
Depth Model	85-90	5492 – 5700	5557
Depth Model	80-85	5414 – 5666	5517
Depth Model	75-80	5368 – 5636	5493
Depth Model	70-75	5350 – 5596	5464
LZU16208	65-70	5332 – 5579	5451
Depth Model	60-65	5323 – 5573	5402
Depth Model	55-60	5231 – 5561	5370
Depth Model	50-55	5179 – 5523	5315
Depth Model	45-50	5107 – 5468	5272
Depth Model	40-45	5076 – 5424	5240
Depth Model	35-40	5056 – 5380	5213
LZU16207	30-35	5046 – 5305	5173
Depth Model	25-30	5041 – 5298	4949
Depth Model	20-25	4600 – 5219	4805
Depth Model	16-20	4391 – 5136	4731
Depth Model	12-16	4326 – 5042	4670
Depth Model	8-12	4298 – 4866	4561
LZU16206	4-8	4256 – 4509	4378

Table 7. Calibrated age ranges of each sample in Profile Two (calculated by the Bayesian P_Sequence model).

Name	Depth (cm)	Age (cal. yr BP)	Median
LZU16215	195-200	10298 – 10550	10424
Depth Model	190-195	10287 – 10527	10407
Depth Model	185-190	10279 – 10511	10395
Depth Model	180-185	10266 – 10498	10382
Depth Model	175-180	10260 – 10486	10373
Depth Model	170-175	10251 – 10475	10363
Depth Model	165-170	10247 – 10461	10354
Depth Model	160-165	10242 – 10444	10343
Depth Model	155-160	10237 – 10419	10328
Depth Model	150-155	10235 – 10401	10318
LZU16214	145-150	10232 – 10382	10307
Depth Model	140-145	10117 – 10395	10256
Depth Model	135-140	10061 – 10383	10222
Depth Model	130-135	10011 – 10369	10190
Depth Model	125-130	9978 – 10354	10166
Depth Model	120-125	9945 – 10327	10136
Depth Model	115-120	9924 – 10304	10114
Depth Model	110-115	9908 – 10280	10094
Depth Model	105-110	9899 – 10261	10080
LZU16213	100-105	9889 – 10229	10059
Depth Model	95-100	9753 – 10221	9987
Depth Model	90-95	9653 – 10205	9929
Depth Model	85-90	9569 – 10173	9871
Depth Model	80-85	9528 – 10126	9827
Depth Model	75-80	9513 – 10095	9804
Depth Model	70-75	9505 – 10045	9775
Depth Model	65-70	9499 – 9997	9748
Depth Model	60-65	9492 – 9918	9705
Depth Model	55-60	9490 – 9840	9665
LZU16212	50-55	9481 – 9815	9648
Depth Model	45-50	9477 – 9789	9633
Depth Model	40-45	9475 – 9763	9619
Depth Model	35-40	9471 – 9727	9599
Depth Model	30-35	9468 – 9700	9584
Depth Model	25-30	9468 – 9672	9570
Depth Model	20-25	9468 – 9644	9556
Depth Model	15-20	9468 – 9616	9542
Depth Model	10-15	9466 – 9584	9525
Depth Model	5-10	9463 – 9559	9511
LZU16211	0-5	9465 – 9535	9500

Note: For the sake of simplicity and clarity, the age data used in the dissertation is the median value, but the actual age range can be found in Table 6 and Table 7.

Chapter 4. Methodology

4.1 Extraction of beetle fossils

The extraction of beetle fossils is safe, cheap, easy and timesaving. The only chemicals involved in the process are kerosene (paraffin), ethanol, and detergent. There are five steps to extract insect fossils from sediments (Coope, 1969): 1. The peat block is soaked in water for 1 or 2 days to make the organic detritus soft and dispersed. 2. The organic fraction is sieved in a 0.3mm mesh by sluicing with water to remove silt, fine sand, and clay particles. 3. Paraffin floatation is used to concentrate insect fossils. The organic fraction is gently mixed with paraffin, and then cold water is added. The insects float on surface film because of the lipophilicity of chitin, while most plant macrofossils sink. 4. The oily fraction is decanted onto a 0.3mm screen, washed gently with detergent to remove oil, and then stored in 90% ethanol solution. 5. The residue is placed in a petri dish with ethanol, and a low power binocular microscope is used to sort specimens. The specimens are finally stored in 95% ethanol for identification.

4.2 Identification

4.2.1 Useful beetle exoskeleton parts for identification

The identification of beetles mostly relies on their exoskeletal characters. The fossils are rarely preserved intact. The main exoskeletal parts of beetles that are useful for identification are the head capsule, the pronotum (thoracic shield), and the elytra (wing covers). These sclerites have a variety of features, such as striae, carinae, grooves, tubercles, punctures, setae, and scales (figure 25). For example, punctures range from broad to narrow and deep to shallow; they may occur in patches, in dense small groups, in rows, or they may be widely dispersed; they may originally have contained a seta, or they may be only shallow, surface features. Generally, the exoskeletal parts of different species have different sizes, shapes, patterns or colors.

Microsculpture, some of which is visible only at high magnification (150-200X), is very useful in identifying fossil beetles (Lindroth, 1948), as the microlines are extraordinary constant within species, and do not degrade or alter with time. With the exception of a few beetles that are devoid of microsculpture, or only have patches of microsculpture at the margins of the pronotum and apex of the elytra, most species are completely covered with dense patterns of reticulate lines. In different species, the patterns range from isodiametric meshes to longitudinally or transversely elongated meshes, or they be broken into transverse rows of very fine lines, causing iridescence. Thus, identification can be made through the comparison of these characters of fossil beetles with modern, identified specimens.

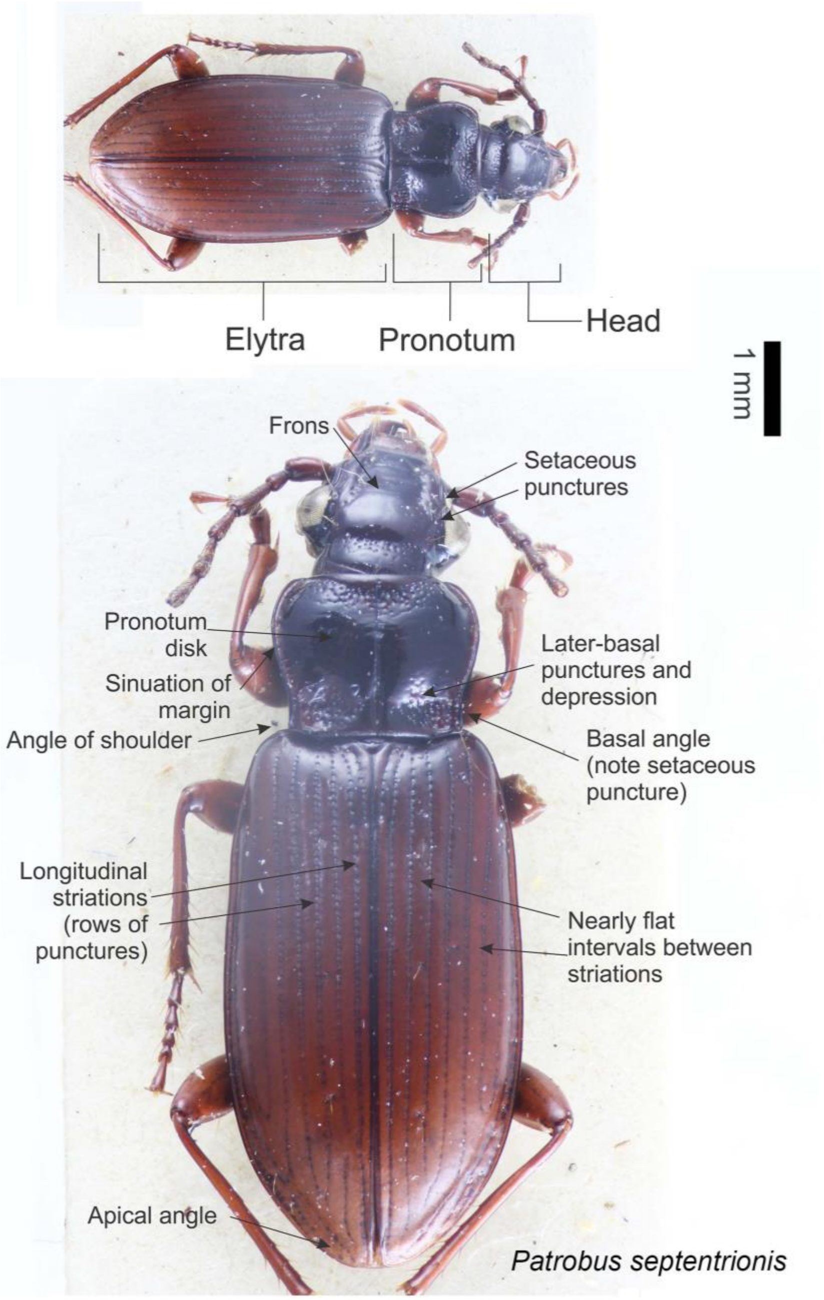


Figure 25. Useful characters for beetle identification.

The head capsule of many beetles is useful for their identification. Important features include the shape and position of the eyes, presence and kind of microsculpture, the position of certain setae (hairs) – often only represented by puncture marks on fossil specimens, and the shape of the head (rounded, flat, squared or elongated).

The pronotum (thoracic shield) has many useful diagnostic features that include shape, size, depth of impressions and punctures, placement of setigerous punctures, angles at apex and base, and microsculpture. Pronotum shape varies from flat to very convex, depending on taxonomic group. Some rove beetles, weevils, and bark beetles have highly convex pronota. Others (most ground beetles, some rove beetles, most water beetles, most dung beetles) have relatively flat pronota.

The elytron (wing cover) has diagnostic features that include size, shape, depth and nature of striations and punctures, placement of setigerous punctures, angles at shoulder and apex, and microsculpture. Pigmented color patterns are diagnostic for some species of Coccinellidae, Chrysomelidae, some Dytiscidae and Carabidae. Metallic coloration occurs in some Carabidae, Buprestidae, and others. This coloration is based on the refraction of light from the surface of the exoskeleton. Elytron shape varies from flat to very convex, but most are slightly arched, to cover the abdomen. The elytra of some families, notably Staphylinidae, are truncate.

When present, the male genitalia (aedeagus) as well as the terminal abdominal segments of some Staphylinidae are very diagnostic features. These features include shape, size, and configuration of lateral lobes of these sclerites.

4.2.2 Taxonomic literature

The identification of fossil beetle sclerites is a time-consuming process, since most dichotomous keys are for modern beetle identification that require entire specimens. But fortunately, numerous useful photographs and sketches can be found in some monographs of beetle families and genera, either of entire specimens or of important sclerites. For example, the series of studies on the ground beetles of Canada and Alaska written by Carl Lindroth (1961, 1963, 1966, 1968, 1969) and his revision of the Fennoscandian ground beetles (Lindroth, 1985, 1986) are useful resources for fossil ground beetle identification.

4.2.3 Images from websites

Many entomological web sites have been created that have excellent photos and taxonomic descriptions. For instance, the BioImages Website (http://www.bioimages.org.uk /html/Insecta. htm) offers more than 2,400 photos of European beetles. The website (http://www. koleopterologie.de/gallery/index.html), which was developed by a research group working on Rheinland Coleoptera, published multiple photos for over 800 beetle species. The website published by the Museum of Comparative Zoology at Harvard University also contains one of the most extensive type collections for North American beetles, with photographs of more than 13,000 species of beetles.

4.2.4 Museum Specimens

Although the photographs or sketches can help narrow the field, direct comparison of fossil beetle sclerites with identified modern species is the most important, final step of identification work to certain the species of fossil beetles. Only by doing so, it is possible to match the various characters of each species in a given group, from the body size to the surface microsculpture, with the fossil specimens.

The most identification work of this research was finished in the London Natural History Museum (NHM) with the help of Dr. Robert Angus. Based on the useful beetle exoskeletal parts mentioned above, a preliminary determination of the family and genus of the fossils was made. Many beetle species have very unique characteristics. They can be very confidently identified to genus level, and even to species. For example, the water scavenger beetle *Helophorus sibiricus*, has been identified by Robert Angus, a *Heloporus* specialist from the NHM, directly to the species level, based on the fossil size, the shape of the pronotum, and the striations and the pattern on the elytron.

Most beetle fossils in this research were easily identified to genus level. After the generic determination, I searched through photographic images and modern, identified material to select candidate species. Finally, modern specimens in the Natural History Museum were used to compare with the fossils species. In this step, it is necessary to check different individuals for one species, because for some species, the size or pattern may change between different individuals. It is important to select "reliable" characteristics to make the identification. Beside searching the images on websites and in the literature, we also checked all the species in the NHM modern collections, to maximize our success in finding candidate species.

The modern distribution of a species also plays an important role in narrowing down candidates for selection. In this research I found that nearly all the identified species have modern distributions in the northern and/or mountainous regions of Europe, Siberia, and Asia.

After comparisons, if the fossil beetle is an exact match for only one modern species, this essentially confirms that it is this species. It is then necessary to check the descriptions and distributions of this species in the literature to make further confirmation. However, some species cannot be distinguished on the basis of taxonomic features presented on their head, pronotum or elytron. The diagnostic characters may occur only on their genitalia, for instance, which are rarely preserved in association with the rest of the exoskeleton. In other instances, a species can be identified only by its pronotum, but the fossil remains are only elytra. So, some fossil specimens equally match multiple modern species.

In the case of fossils that are hard to identify to the genus level, or fossils which do not match any modern specimens in the museum, or for some fossil specimens whose identity cannot be confirmed, it is necessary to send photographs or the specimens themselves to taxonomic specialists, to ask for help. This was the case for several of the specimens in this study. Vladimír Navrátil identified fossil specimens of the ladybird *Ceratomegilla rickmersi*; Dr. Milos Knizek identified the bark beetle *Phloeotribus spinulosus*; Andreas Pütz identified the pill beetle *Cytilus sericeus*. A fossil specimen of the ground beetle Agonum was sent to Dr. Joachim Schmidt at the University Rostock, as the photograph did not show enough details for identification. Dr. Schmidt identified it as *A.quinquepunctatum*.

The beetle fossil assembles likely contain species new to science, as the study area is lacking in entomological study, and few modern collections have been made there. A new species – *Helophorus sinoglacialis* – has been found in this research. Dr. Robert Angus helped in the identification of *Helophorus*, and discovered a *Helophorus* fossil that did not match any known modern species. Fortunately, during this PhD project, Dr. Angus got an email from an entomologist, S. Ryndevich, concerning a strange modern *Helophorus* from the Chinese Altai. Angus described the modern *Helophorus* as a new species, and he realized the *Helophorus* fossil matches the modern new species (Angus et al., 2017).

4.3 Ecological statistics method

Each beetle species found in the fossil assemblages has been assigned to one ecological group. The details are shown in Table 9, Chapter 6. In each sample, the number of individuals of each species, the number of individuals in each group, and the total number of individuals have been recorded. Then the proportion of each ecological group has been calculated for each sample. The formula is as follow:

Proportion of each group = number of individuals in one ecological group divided by the total number of individuals.

Bar charts have been created for each sampling interval of the two profiles, showing the variations of individual numbers, both in total and in each ecological group, and variations of the proportion of each ecological group.

4.4 Bugs Coleopteran Ecology Package (BugsCEP)

In this project, the Mutual Climatic Range (MCR) programme in the Bugs Coleopteran Ecology Package (BugsCEP) was used. This is a program for Palaeoclimatological research, which aids in the reconstruction of climate from fossil beetle assemblages (Buckland, 2007). The species names and the depth of each sample are input into the program, and then the BugsCEP creates an MCR climate estimate (TMAX and TRANGE) for each sample. The output of the results are presented in both tabular and graph forms.

Chapter 5. Results

5.1 Identified fossil beetles

In total, 55 Coleoptera taxa representing 44 genera and 14 families have been found, and 37 species have been identified, including a new species *Helophorus sinoglacialis*. The fossil beetle fauna of the two profiles, and the minimum number of individuals of per sample have been listed in appendix one and two.

Since this is a new region for the study of fossil beetles, we lack detail knowledge of the modern local fauna. Some of the species found in this assemblage are even new to this region. So, it is necessary to explain the diagnostic features used in species identifications. The presentation of these taxonomic features makes the identifications more reliable and also provide a basis for further beetle studies. This section clearly explains how the beetle fossil sclerites found their "best match" species.

5.1.1 Species have been identified and their ecology and modern distribution

Carabidae

1) *Nebria nivalis* Paykull, 1798

The pronotum of *Nebria nivalis* is widest before the middle, and has a broadly sinuate side with a narrow posterior; its front angles project forward, and the hind angles are sharp at the tip; the basal margin is sinuate at the sides; both the front and base have deep depressions and punctures; the lateral seta are fixed outside a small longitudinal ridge, and this is the only *Nebria* species with anterior lateral setigerous punctures (figure 26 red arrows) (Lindorth, 1961). Based on these characters, the fossil pronotum matches *Nebria nivalis.*

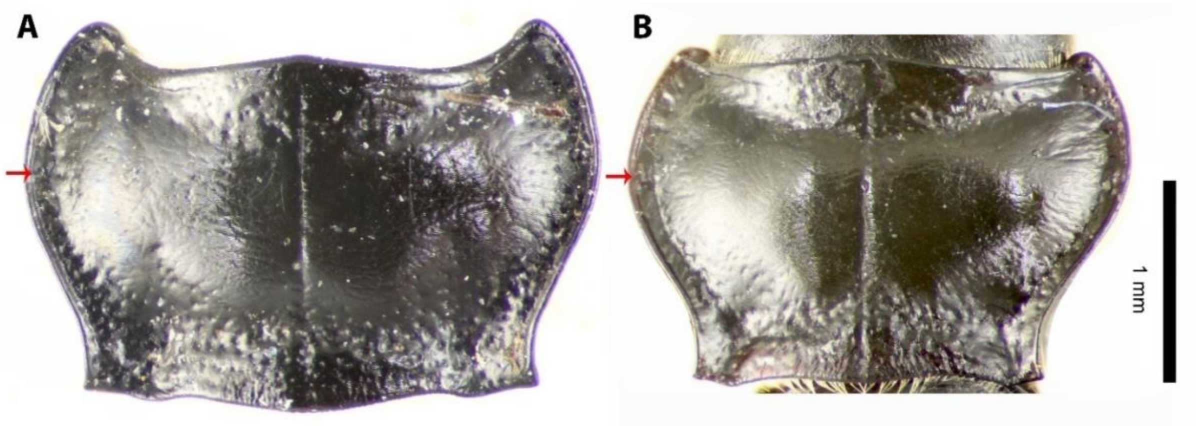


Figure 26. Pronotum of *Nebria nivalis.* **A** fossil specimen; **B** modern specimen (note: the modern specimen is smaller than the fossil).

Ecology

N. nivalis is the only *Nebria* of the northern tundra. The typical habitat of this species seems to be the northern margins of snowfields and above tree line, but it follows glacier outflows deep down into the forest region. It lives close to the water's edge, usually on barren banks (Lindroth, 1961).

Distribution

It is found from northern Europe to the Bering Sea coast in East Siberia (Farkač and Janata 2003: 88), and from the arctic plains in Alaska to Baffin Island and the western edge of Ungava Bay in northeasten Canada (Kavanaugh, 1978), and Greenland (Lindroth, 1961).

2) *Blethisa catenaria* Brown, 1944

Based on the size, the grooves on the head, and the shape of pronotum, the fossil looks similar to *Blethisa catenaria* and *Blethisa multipunctata*. But as figure 27 shows, *B. multipunctata* has a pair of strongly marked carinae and straight sides on the base of its pronotum, while *B. catenaria* does not (Lindroth, 1961). On this basis, the fossil has been identified as *Blethisa catenaria.*

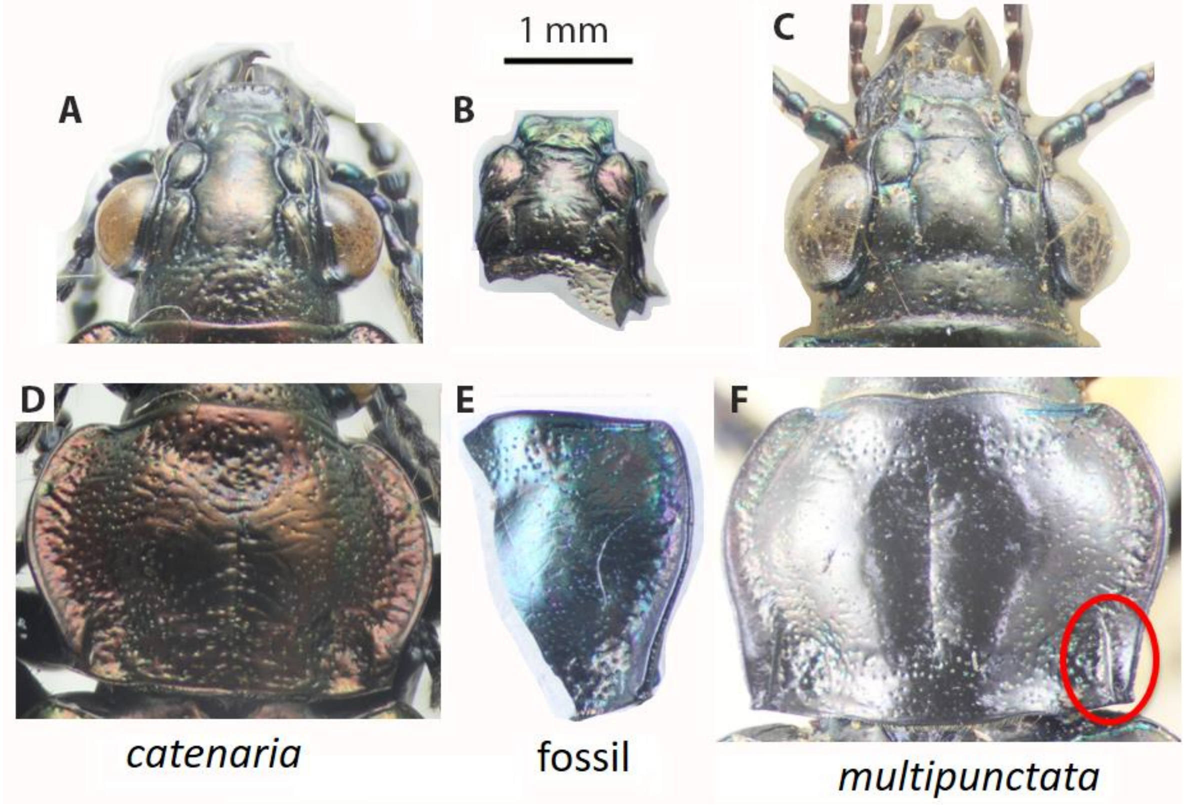


Figure 27. *Blethisa spp*. **A** modern *B. catenaria* head; **B** fossil *Blethisa* head; **C** modern *B. multipunctata* head; **D** modern *B. catenaria* pronotum; **E** fossil *Blethisa* pronotum; **F** modern *B. multipunctata* pronotum.

Ecology

B. catenaria is a ground-dwelling species, it lives on the tundra, and is always found on soft mud (mainly decaying mosses) at the margin of small pools. (Lindroth, 1961)

Distribution

B. catenaria is found in Northern European Russia, eastern Siberia (Goulet, 2003), and from western Alaska to the western shore of the Hudson Bay in northern Manitoba of Canada (Morgan et al. 2986; Nielsen et al. 1987).

Fossil remains from the Pliocene or early Pleistocene have been found in Meighen Island and Ellesmere Island of northern Canada, northwestern Greenland, and eastern Siberia (Böcher, 1995)

3) ***Elaphrus sibiricus*** **Motschulsky, 1844**

For *Elaphrus*, the tubercles on the elytra are an important feature for identification. By comparing the fossil with modern specimens, two candidates: *E. cupreus* and *E. sibiricus,* were selected. These two species are very closely related. As figure 28 shows, under high magnification, the tubercles on *E. sibiricus* elytra have punctures on their outer rings, while the outer rings of *E. sibiricus* tubercles are smoother. On this basis, the fossil was identified as *E. sibiricus.*

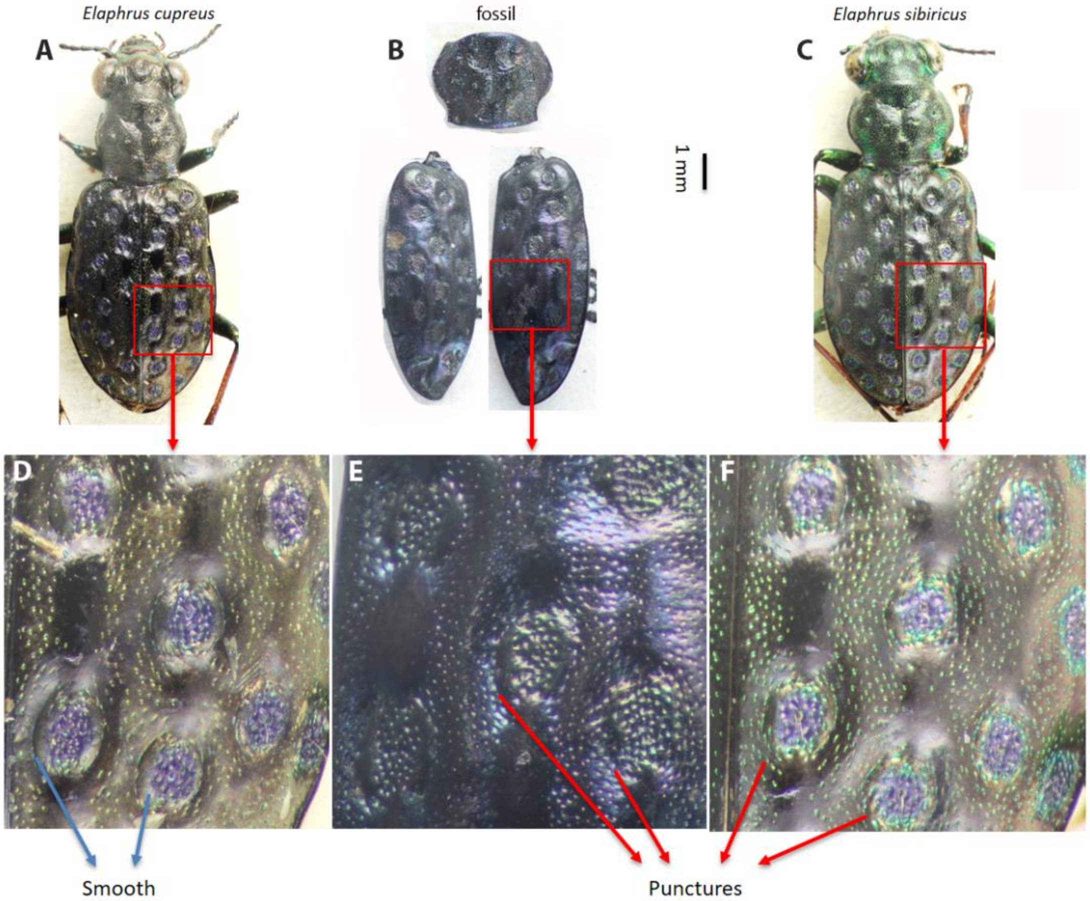


Figure 28. *Elaphrus* spp. and their elytral details. **A** modern *E. cupreus*; **B** pronotum and elytra of fossil *Elaphrus*; **C** modern *E. sibiricus*; **D** elytral details of modern *E. cupreus* **E** elytral details of fossil *Elaphrus*; **F** elytral details of modern *E. sibiricus.*

Ecology

E. sibiricus inhabits the banks of rivers and lakes. Its ecological requirements are similar to *Elaphrus cupreus* (Zinovyev, written communication, 2017), which is found on shaded, wet organic mud near small rivers, lakes, pools, and in marshy areas of forests. Adults occur on mosses, but rarely on Sphagum moss (Lindroth, 1945).

Distribution

This is an East-Palearctic species, extending from East Siberia (south-west Altai) to the Russian Far East (Zinovyev, written communication, 2017), northern Japan, Mongolia, and Inner Mongolia (Hailar) in China (Goulet, 2003).

4) *Bembidion lampros* Herbst, 1784

The supraorbital punctures (figure 29. red arrows) on the head are a typical character of *Bembidion*, and the defined sulcus along the inside of each eye is important for identifying some species of *Bembidion*. As figure 29 shows, the slightly arcuate furrows (red dashed lines) between the eyes of the fossil head match those of *Bembidion lampros* (Lindroth, 1963).

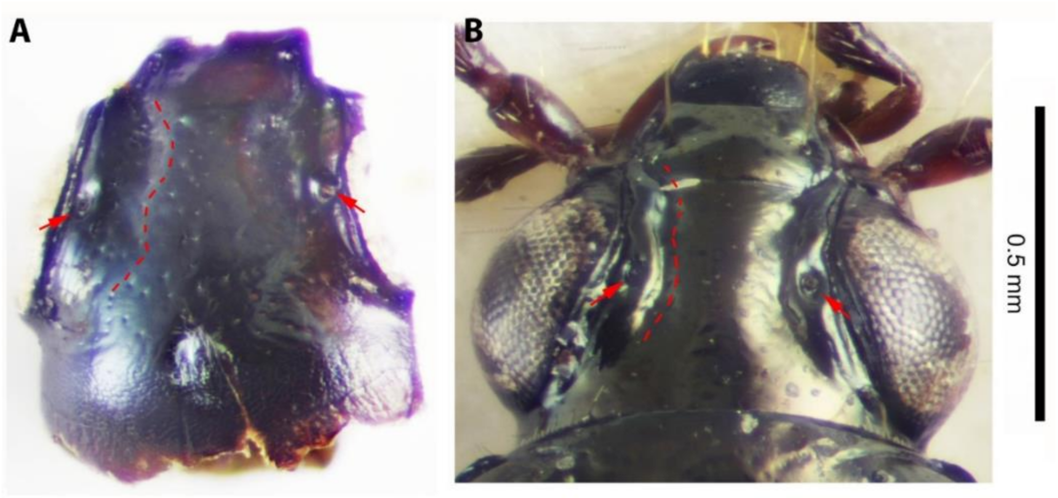


Figure 29. A fossil *Bembidion* head **B** modern *Bembidion lampros* head.

Ecology

In Europe, *B. lampros* lives on all kinds of open, sun-exposed ground (Lindroth, 1963)

Distribution

This Palaearctic species is found throughout Eurasia (Lindroth, 1963). And it was accidentally introduced into North America around the 1940s (Lindroth, 1955; Hatch 1949).

The fossil remains of this species from a Plio-Pleistocene sequence have been found in the northwestern Greenland (Böcher, 1995).

5) *Patrobus septentrionis* Dejean, 1828

The size, pronotum shape, pronotal punctures and depressions, and the straie of the elytra are important for the identification of *Patrobus*. This species often has deep frontal foveae on the head. For the pronotum, there is a complete anterior transverse impression, and the front margin is elevated at the middle before the impression (Lindorth, 1961); on the midline, it has a medially-deepened depression with a double row of punctures; the basal foveae are deep, and the basal punctures are quite variable. The elytra are flat and long, with sides diverging in the apical quarter; the straie continue almost to the apex (Luff and Turner, 2007). On this basis, the fossil was identified as *P. septentrionis* (figure 30).

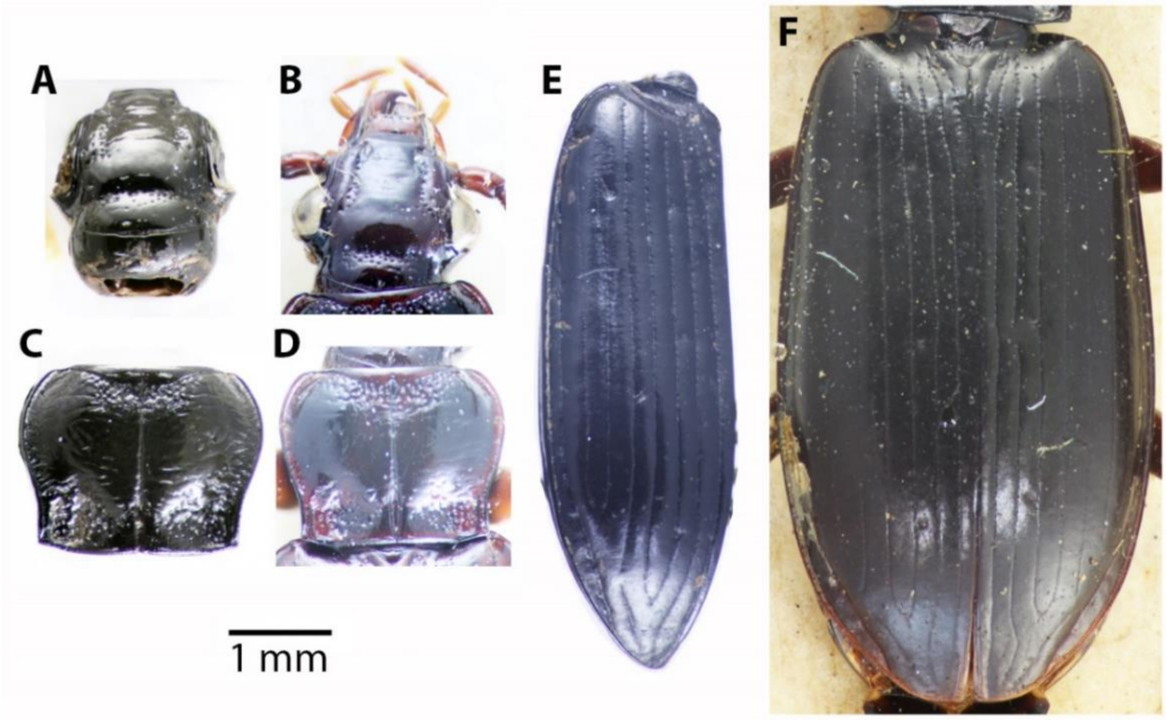


Figure 30. *Patrobus septentrionis*. **A** fossil head; **B** modern head; **C** fossil pronotum; **D** modern pronotum; **E** fossil elytron; **F** modern elytra.

Ecology

P. septentrionis is a cold-adapted species that lives in upland habitats (Luff and Turner, 2007), at the edge of ponds, lakes and slow streams. It is remarkable that some North American *P. septentrionis* (south Labrador, Aleutian and Pribilofs Islands) occur only on coastal tundra. However, in Eurasia, it usually lives on mountain tops and on the northern tundra (Lindroth, 1945)

Distribution

This is a circumpolar arctic-montane species. It is distributed from Scandinavia to North America, Greenland, Iceland (Lindroth, 1961) and North-West Siberia (Zamotajlov, 2003).

6) *Pterostichus agonus* Horn, 1880

Although this fossil fragment consists of only two small elytral pieces, their wavy and discontinuous striae and the interrupted intervals (by irregular depression) are very specific features, and these match *Pterostichus agonus* (figure 31).

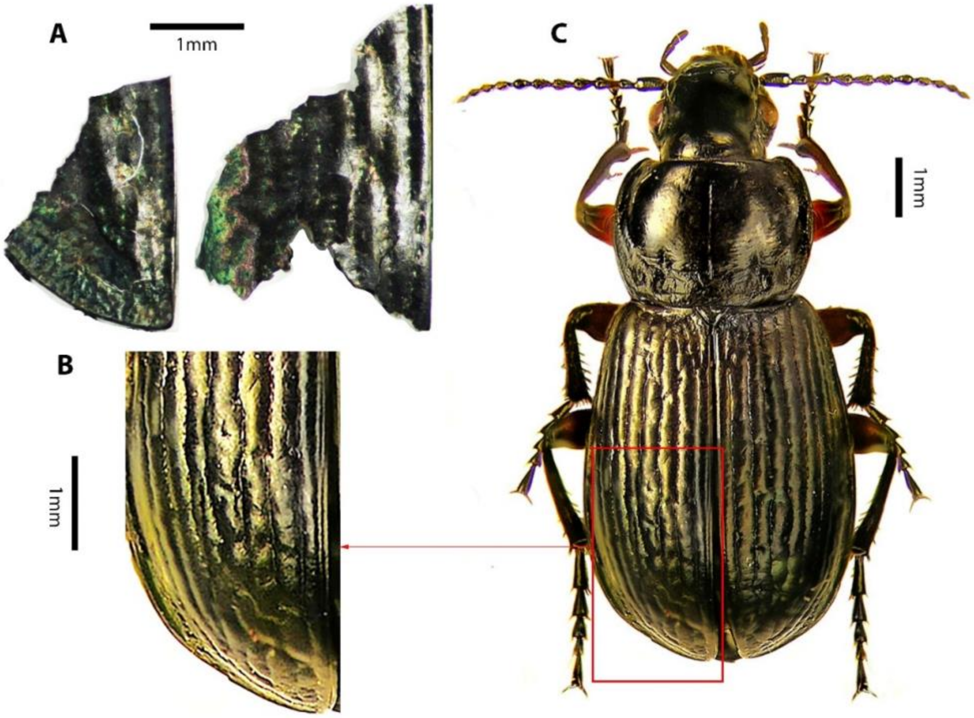


Figure 31. A fossil fragments of elytron; **B** modern *Pterostichus agonus* elytral apex; **C** modern *Pterostichus agonus* (image source: http://carabidae.org/gallery?taxon=9314).

Ecology

P. agonus has been found on moist tundra with sedge (*Eriophorum scheuchzeri* or *Carex aquatilis*), and *Saussurea alpina* (Lindorth, 1966).

Distribution

This is an Holarctic species, and has been found in northern Canada, Alaska, East Siberia and northeastern China (Lindorth, 1966; Bousquet 2003a).

7) *Pterostichus* (*Cryobius*) *brevicornis* Kirby, 1837

This fossil specimen has a pronotum with sinuate sides and denticulate hind angles, and each side has a deep latero-basal linear impression with punctures, which match *P. brevicornis* (Lindroth, 1966) (figure 32).

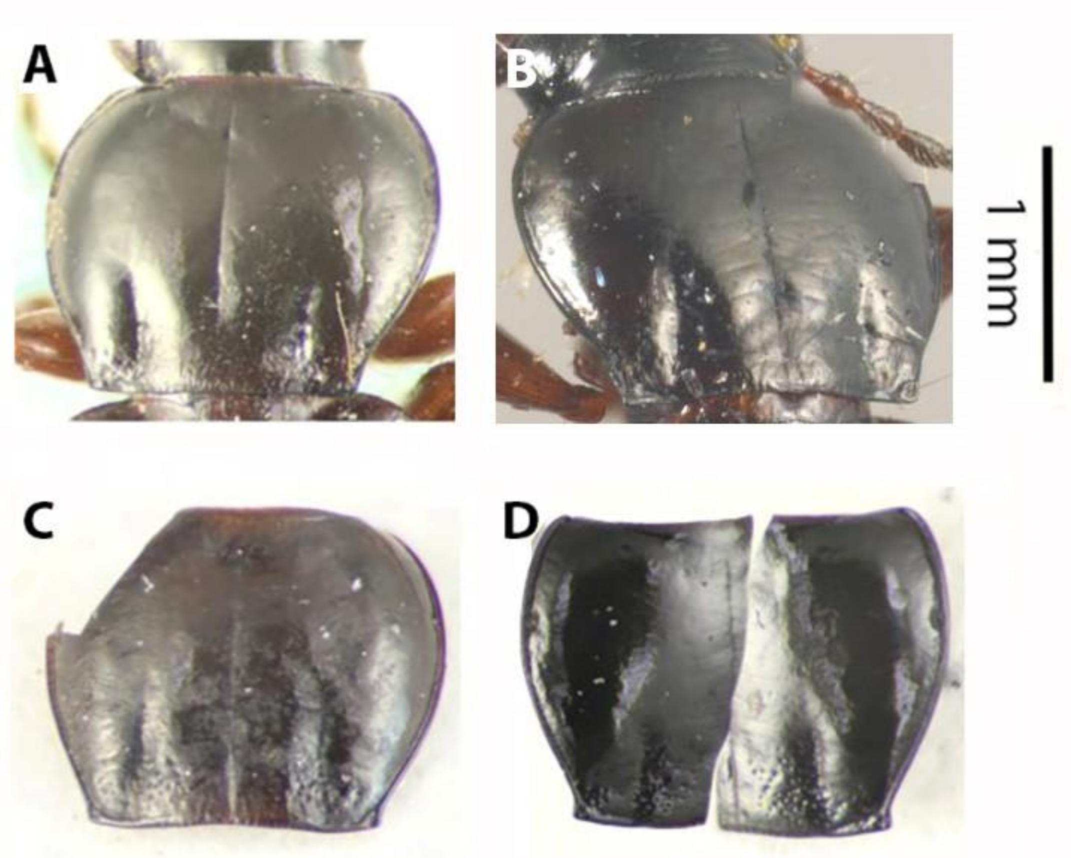


Figure 32. A modern *P. brevicornis* pronotum, specimen from Yukon, Canada; **B** modern *P. brevicornis* pronotum (image source: Spencer Entomological Collection) **C** and **D** fossil *P. brevicornis* pronota.

Ecology

P. brevicornis usually lives in either arctic or alpine tundra, or dry meadows, often among grass and leaves (Lindroth, 1966). It is abundant in riparian forests of the north part of West Siberia. It has also been found in coniferous forest near Ekaterinburg (Carabidae of the World, http://carabidae.org/gallery?taxon=9314, accessed in March 2017). It is mostly near tree line (Lindroth, 1966).

Distribution

It is found in northern Canada and Alaska (Lindroth, 1966). In Russia, it is found in several regions, including the Buryat Republic, the Chita region, East Sayan, the Irkutsk region, Khamar-Daban, Magadan, and in Yakutiya (Carabidae of the World, http://carabidae.org/gallery?taxon=9314, accessed in March 2017).

Fossil remains, which are older than 33,000 years B.P., have been found in southwestern Ontario (Warner et al., 1988), and in a Plio-Pleistocene sequence in northwestern Greenland (Böcher, 1995).

8) *Agonum consimile,* Gyllenhal, 1810

This fossil pronotum has rounded sides, slightly depressed in the front; the middle line does not extend to the base. The pronotum has depressions on the base; basal angles are obsolete but not disappeared, and contain one deep puncture. These features match *Agonum consimile* perfectly. The elytral striae of *A. consimile* are fine and impunctate; the dorsal punctures are small and often irregularly placed (Lindorth, 1966). As figure 33 shows, some of the dorsal punctures and the setae on the elytral apex of fossil match *A. consimile* (red arrows). But these elytral characters may be present on other *Agonum* species, so the identification of *A. consimile* in this research is based solely on the pronotum. The elytra could not be confidently identified to the species level.

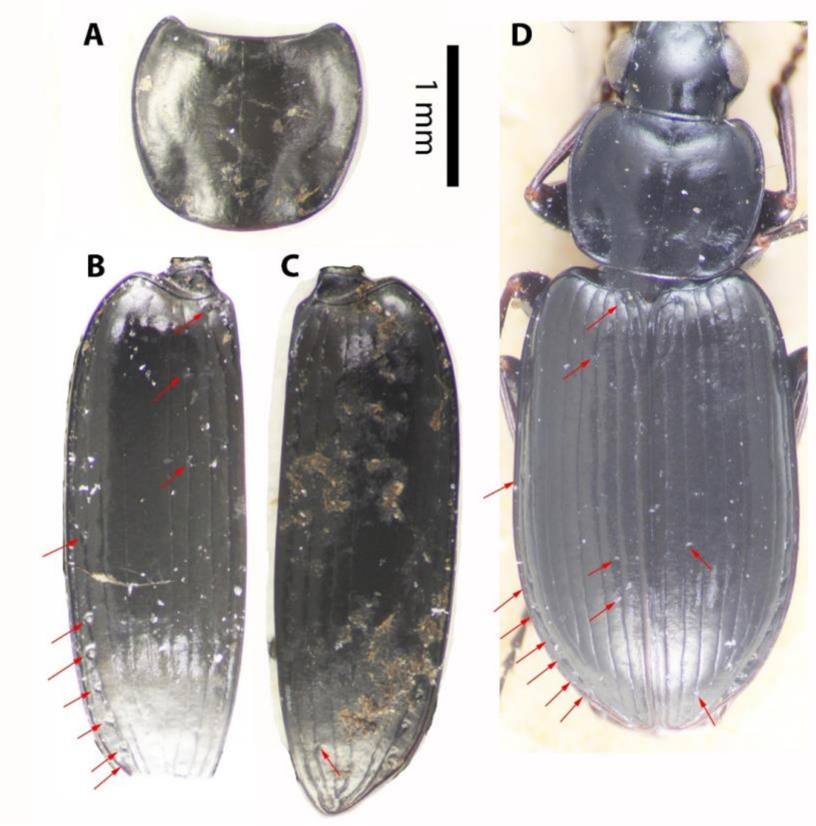


Figure 33. *Agonum consimile*. **A** fossil *A. consimile* pronotum; **B** fossil *A.* cf. *consimile* left elytron; **C** fossil *A.* cf. *consimile* right elytron; **D** modern *A. consimile*.

Ecology

A. consimile is a hygrophilous species; it lives at the edges of standing water (lakes, pools), always with soft soil and rich vegetation (sedges and a carpet of mosses, but rarely Sphagnum). The water in these lakes and pools is often pronouncedly warm (Lindorth, 1966).

Distribution

This is a Holarctic species, and has been found in the Palaearctic region, from Norway to the Russian Far East (Bousquet, 2003b). It is also known from Alaska to Vancouver Island (Lindroth, 1966), Cape Breton Island (Lindroth, 1954) and Newfoundland (Lindroth, 1955) in Canada, and the state of Washington in the United States (Glesne et al., 2000).

Fossil remains from and 15,400 B.P. to 14,000 B.P. have been found in central Iowa in the United States (Schwert 1992).

9) *Agonum quinquepunctatum* Motschulsky, 1844

This species has been identified by Dr. Joachim Schmidt from the University of Rostock, who is an expert on ground beetles. The specimens were posted to him and he confirmed their identity as *Agonum quinquepunctatum*, without any doubt. “It is one of the 10% of specimens which have the area around the elytral discal setae not markedly impressed” (Schmidt writing communication, 2017). Also, according to Lindroth (1966), the pronotum of *A. quinquepunctatum* has broad depressions instead of a linear impression, and it has punctures along the side as well as in basal foveae; the hind-angles are barely suggested. The elytra have rounded sides, and always have four to six dorsal punctures on the third interval. The fossil specimens match these features (figure 34). Unfortunately, the NHM does not have any modern specimens of this species in their collection.

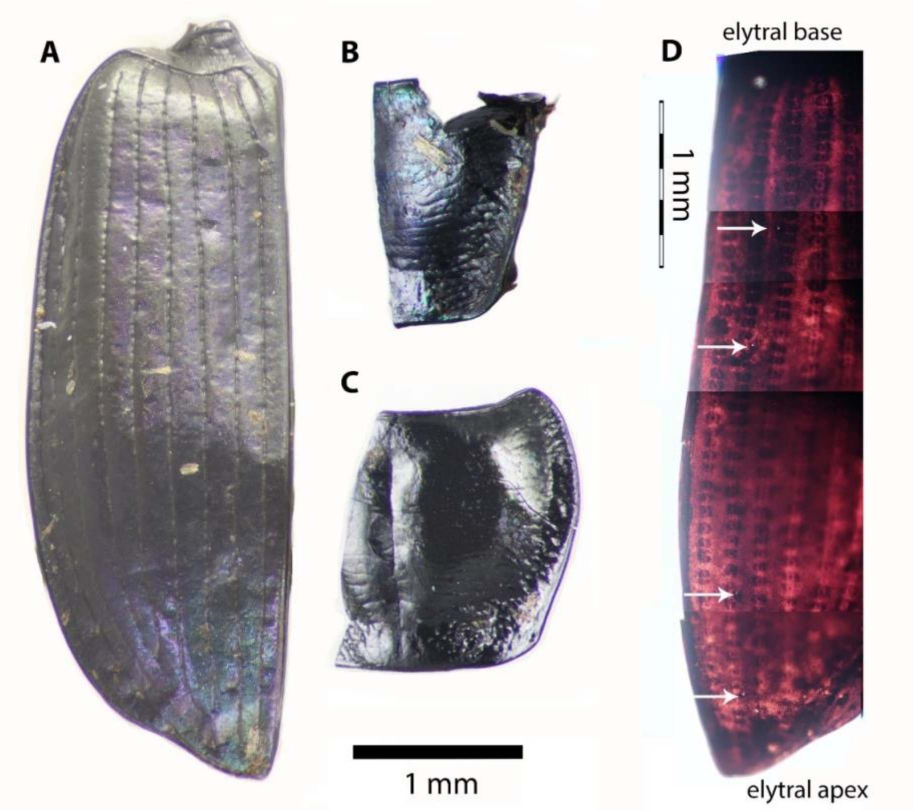


Figure 34. *Agonum quinquepunctatum.* **A** fossil *A. quinquepunctatum* elytron; **B** and **C** fossil fregments of *A. quinquepunctatum* pronotum; **D** ventral view of fossil *A. quinquepunctatum* elytron with lighting from below, which shows the dorsal punctures on third intervals (white arrows).

Ecology

A. quinquepunctatum have been found in peat bogs with *Sphagnum capillaceum* (Lindroth, 1966).

Distribution

This is a Holarctic species, and has been found in eastern and western Siberia, and from Alaska to Labrador in eastern Canada (Lindorth, 1966; Bousquet 2003b)

Fossil remains from 18,100 B.P. to 14,000 B.P. have been found in the central and southeastern Iowa (Baker et al. 1986; Schwert 1992).

Haliplidae

10) *Haliplus chinensis*

As figure 35 shows, the species *H. chinensis* appears to match the fossil specimen well. Both fossil and *H. chinensis* have smaller elytral serial punctures than *H. diruntus* and *H. variegatus*. Although the elytra of modern *H. chinensis* is slightly bigger than the fossil, it might be due to individual differences. And according to Vondel (1995), Xinjiang province is one of the localities for *H. chinensis*. The photograph of the *Haliplus* fossil has been send to Bernhard as well, and he agreed that the *H. chinensis* is the best match. Bernhard also suggested *H. diruptus* is a very variable species and could be a second candidate, but this species is so far only known from the eastern and southern China. Thus, this fossil *Haliplus* has been identified as *H. chinensis*.

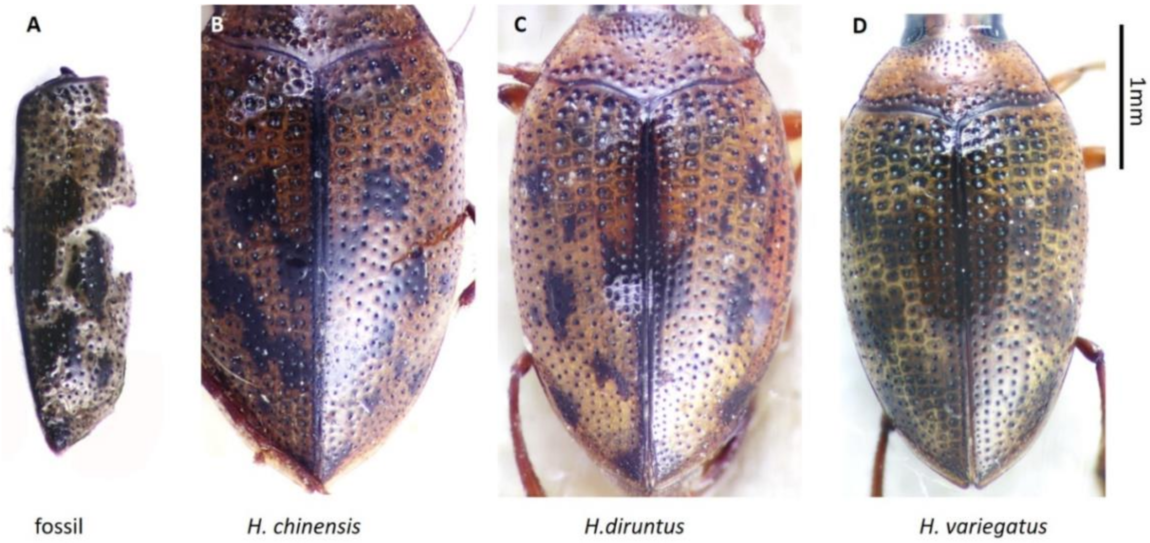


Figure 35. A fossil *Haliplus* elytron **B** modern *H. chinensis* **C** modern *H. diruntus* **D** modern *H. variegatus*.

Ecology

H. chinensis has been found at altitudes greater than 1800m (Vondel, 1995). And it is usually lives in vegetated pools with open water (Angus, written communication, 2017).

Distribution

This species is only known from China. It is widely distributed in China, which is found from Xinjiang, Inner Mongolia, Shanxi, Beijing and Qingdao in northern China, and Fujian, Jiangsu, Sichuan, Shanghai and Nanjing in northern China.

Dytiscidae

11) *Hydroporus notabilis* LeConte, 1850

Based on the size, the pale stripe on the lateral margins of the elytra, and the fine punctures of the elytra, the fossil matches *Hydroporus notabilis* (figure 36).

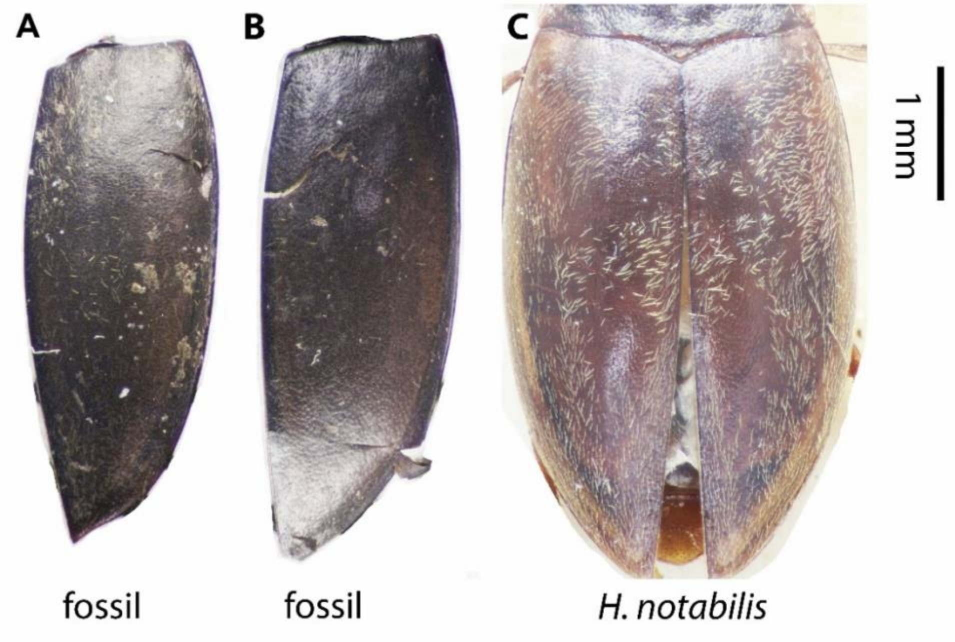


Figure 36. The elytra of fossil **(A and B)** and modern **(C)** *Hydroporus notabilis*

Ecology

H. notabilis usually lives in peaty pools with rich vegetation (Angus, written communication, 2017)

Distribution:

It is found from northern Europe to Siberia and the Far East of Russia, Mongolia, and the Nearctic Region (Nilsson and Hájek, 2015)**.**

12) *Hydroporus striola* (Gyllenhal, 1826)

According to the elytral size, the fossil potentially matches several *Hydroporus* species. Fortunately, the ventral side of the fossil pronotum was preserved. By comparing the prosternum with *H. striola, H. palustris* and *H. incognitus*, the shape and grooves of the fossil specimen match *H. striola* (figure 38). *H. striola* elytral markings are variable; typically, there is a faint pale stripe running from the shoulder to the tip of the elytron (Angus writing communication, 2016), which also shows on most of the fossil elytra (figure 37).

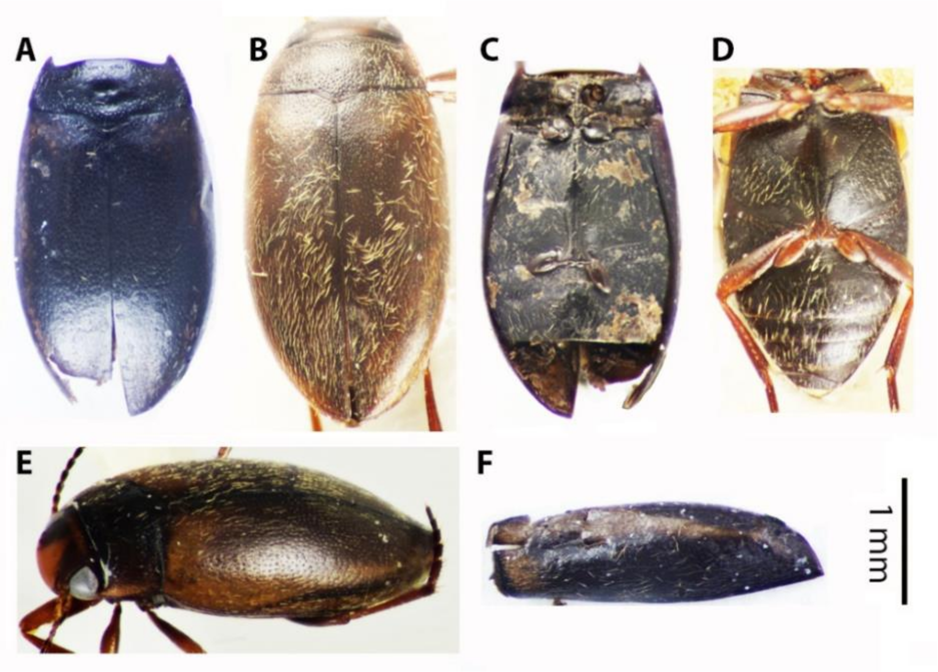


Figure 37. Fossil and modern *Hydroporus striola*. **A** pronotum and elytra of fossil *Hydroporus striola.* **B** pronotum and elytra of modern *Hydroporus striola.* **C** ventral side of fossil *Hydroporus striola.* **D** ventral side of modern *Hydroporus striola.* **E** elytron of modern *Hydroporus striola* with faint pale stripe. **F** elytron of fossil *Hydroporus striola*, which shows the faint pale stripe.

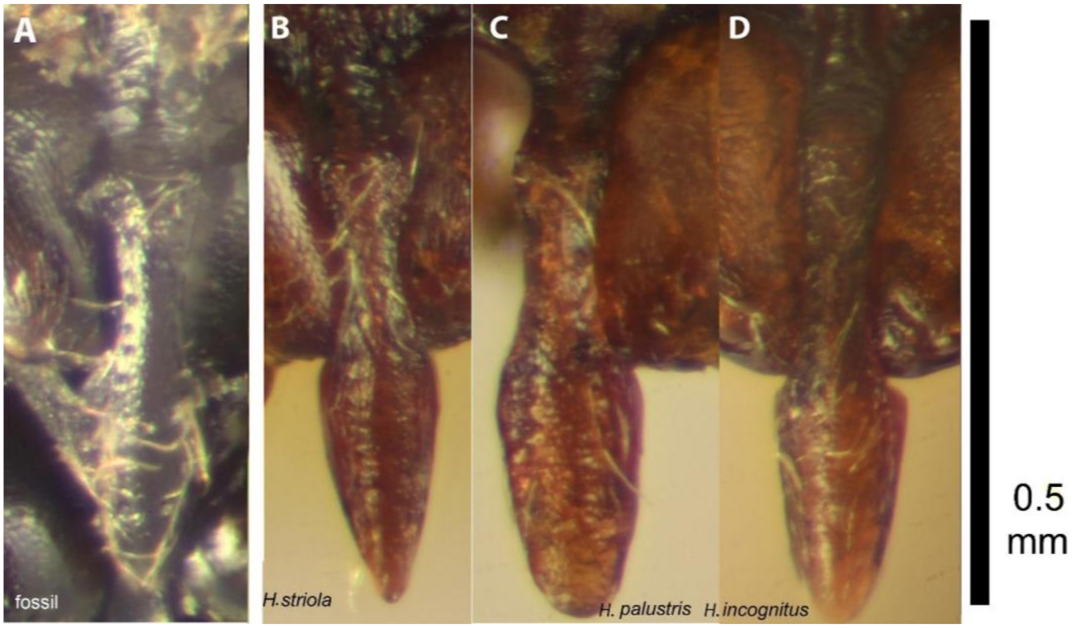


Figure 38. The prosternum of fossil *H. striola* **(A),** and modern prosterna of *H. striola* **(B),** *H. palustris* **(C)** and *H. incognitus* **(D).**

Ecology

H. striola inhabits small vegetated pools in marshland (Angus, written communication, 2017).

Distribution:

It is found from Europe to Kazakhstan and Siberia in Asia, and the Nearctic Region (Nilsson and Hájek, 2015).

13) ***Hydroporus umbrosus*** **(Gyllenhal, 1808)**

Hydroporus umbrosus and *Hydroporus angusi* are very similar to the fossil (figure 39), but high magnification photos of selected areas of the elytra show that the fossil belongs to *H. umbrosus* (figure 40).

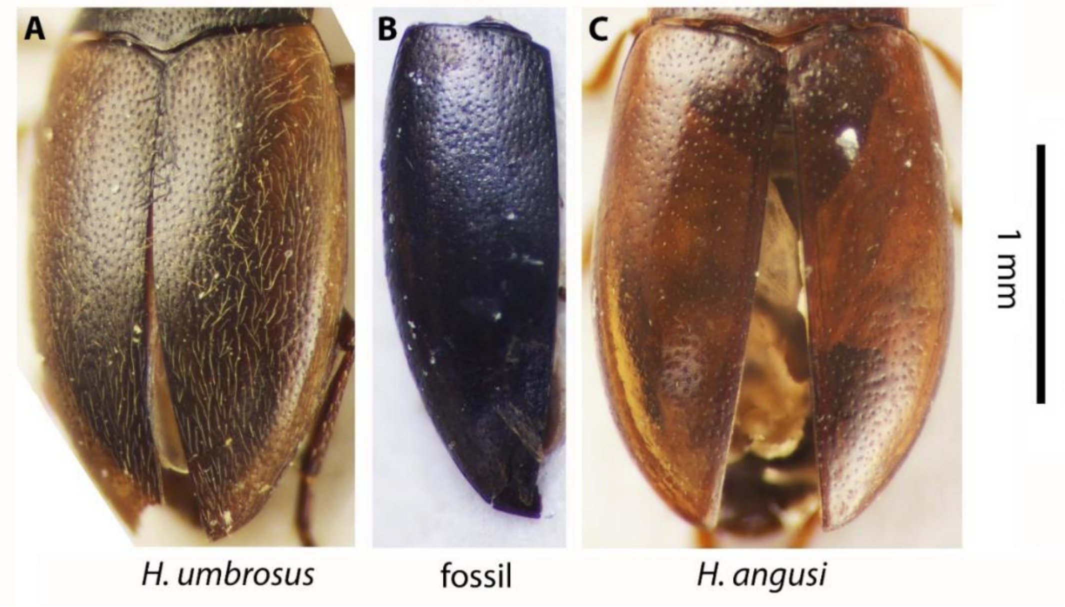


Figure 39. Modern *H. umbrosus* **(A),** fossil *H. umbrosus* **(B)** and modern *H. angusi* **(C).**

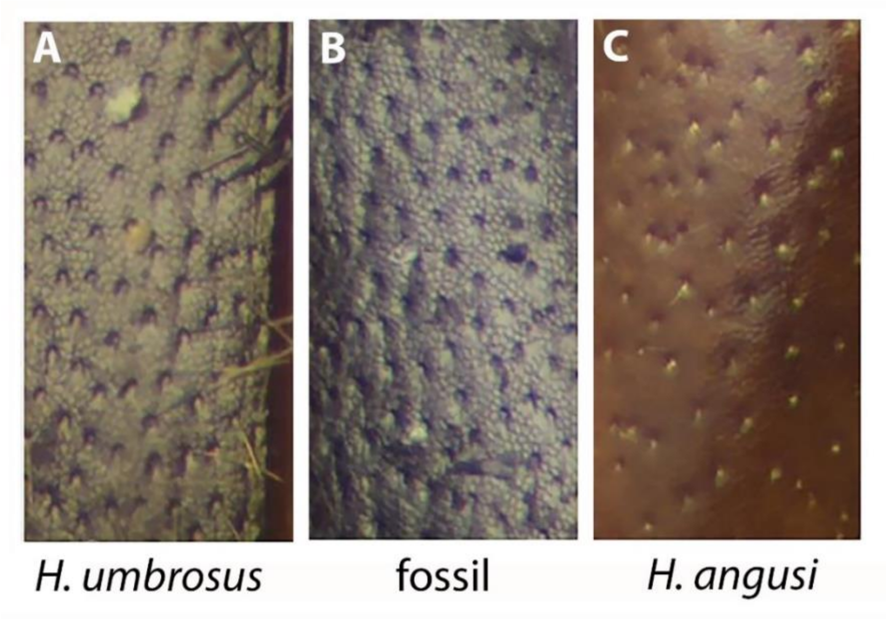


Figure 40. Details of elytral microsculpture and punctuation of fossil *H. umbrosus* **(B),** and modern specimens of *H. umbrosus* **(A)** and *H. angusi* **(C).**

Ecology

The habitat of *H. umbrosus* is in standing water, usually in marshes, ponds and ditches over peat (Garth and Friday, 2011).

Distribution

This species is distributed widely in Europe, and has also been found in Kazakhstan, Siberia and the Far East of Russia (Nilsson and Hájek, 2015).

14) *Hygrotus (Coelambus) impressopunctatus* (Schaller, 1783)

The size, the pattern and the punctures of the elytra are useful features for this identification. *Hygrotus impressopunctatus* has strongly punctured striae on the elytra, and the dorsal surface is covered with large coarse punctures, interspersed with small punctures (Foster and Friday, 2011) (figure 41).

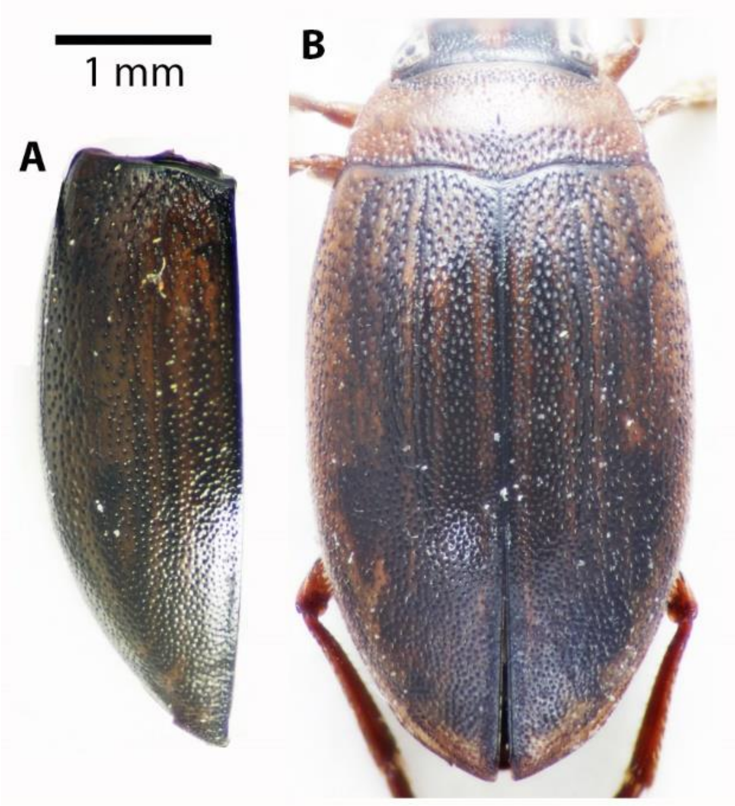


Figure 41. **A** The elytron of fossil *Hygrotus impressopunctatus*. **B** modern *Hygrotus impressopunctatus*.

Ecology

H. impressopunctatus typically lives in rich fens in lowland lakes, ponds and ditches, and is also found amongst Sphagnum in mesotrophic fens (Garth and Friday, 2011).

Distribution

This species has a Holarctic distribution. It is widely distributed in Europe, the Middle East, Siberia, Mongolia, northern China, Japan and the Nearctic region. (Nilsson and Hájek, 2015).

Helophoridae

15) *Helophorus pallidus* Gebler, 1830

Based on the shape, size, granulation, the pattern of the grooves, in addition to the rounded side of pronotum, the fossil has been identified as *Helophorus pallidus*. *H. pallidus* elytra have no scutellary stria, and a thick ridge runs along the elytral apex, just as in the fossil (figure 42).

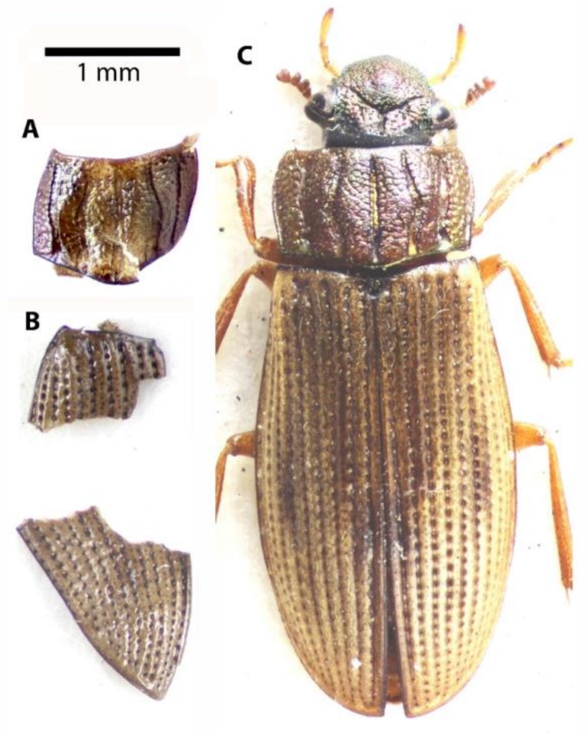


Figure 42. A pronotum of fossil *H. pallidus*. **B** Elytral fragments of fossil *H. pallidus*. **C** Modern *H. pallidus*

Ecology

Adult specimens *H. pallidus* usually can be found in the second half of the summer, and its normal habitat is grassy pools (Angus, 1992).

Distribution

In Europe, this species has been found in Estonia, Finland, Norway and Slovakia; in Asia, it is found from Siberia and the Far East of Russia (Löbl, I. and Löbl, D., 2015).

16) ***Helophorus sibiricus*** **(Motschulsky, 1860)**

With *Helophorus sibiricus*, both the size and shape of the pronotum and elytra are important. The fossil matches *H.* sibiricus, based on the pronotal granules and bristles, the layout of the grooves, the anterior angles; for the elytra, the identification is based on the nature of the striae and the ridged interstrial intervals (figure 43); on the head capsule, the overall shape, the basal narrow stem, and the size and strength of the granules match modern *Helophorus sibiricus* exactly (figure 44).

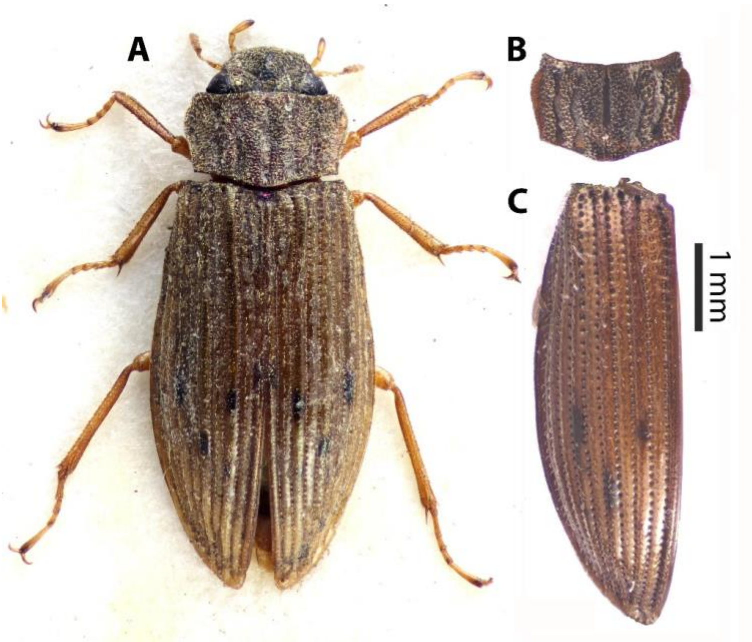


Figure 43. **A** modern *Helophorus sibiricus* specimens. **B** the pronotum of fossil *Helophorus sibiricus*. **C** the elytron of fossil *Helophorus sibiricus*.

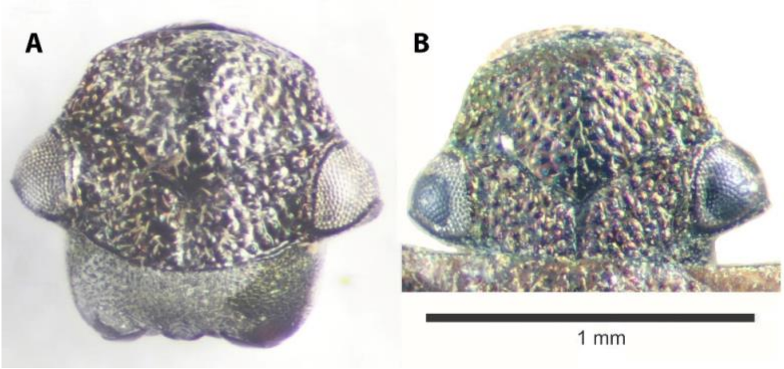


Figure 44. Head capsule of fossil *Helophorus sibiricus* **(A)** and modern *Helophorus sibiricus* **(B).**

Ecology

H. sibiricus is an aquatic species, found either by the edges of large rivers, in small streams, or in grassy pools (Angus, 1992).

Distribution

This is a northern species, found in northern Fennoscandia, and on high ground further south in Scandinavia. In Russia it is found in the far north (Polar Urals etc.), and extending eastwards across Siberia to Alaska and northern Canada (Angus, 1992). In Asia, it is found in northeast China (Heilongjiang), Japan and Mongolia (Löbl, I. and Löbl, D., 2015).

17) *Helophorus sinoglacialis* Angus, Ryndevich & Zhang, 2017

This is the new *Helophorus* species. At first the fossil was identified *as H. altaicus*. However, on the base of the elytra, *H. altaicus* has 5 rows of punctures, while both the modern *H. sinoglacialis* and the fossil have 6 rows of punctures (figure 45).

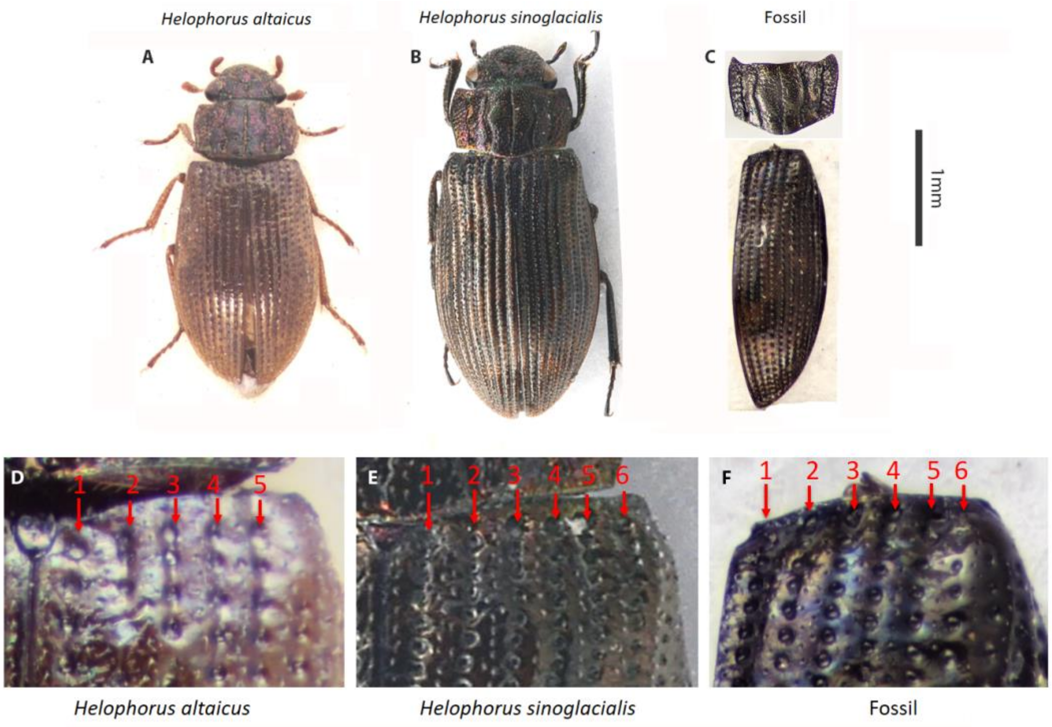


Figure 45. Modern *H. altaicus* **(A)**, modern *H. sinoglacialis* **(B)** and the pronotum and elytron of fossil *H. sinoglacialis* **(C)**; elytral details of modern *H. altaicus* **(D)**, modern *H. sinoglacialis* **(E)** and fossil *H. sinoglacialis* **(F)**.

Ecology

The *H. sinoglacialis* was collected in the gravel on the river bank. But according to the habitats of other *H. glacialis*-group species, the river at this site appears to be torrential and it seems unlikely to be the true habitat of the beetle. The fossil site hints at small pools being a more normal habitat (Angus et al. 2017).

Distribution

This species has only been found in the Altai region of China, and only one modern specimen has been collected.

Hydrophilidae

18) *Enochrus fuscipennis* (Thomson, 1884)

The identification of *Enochrus* is based on the pronotum, with a darker area in the middle, but this dark macula does not extend over the whole surface. The two species that fit this category are *E. quadripunctatus* and *E. fuscipennis*. The pronotum of *E. quadripunctatus* has a smaller central dark area, with four dark spots outside it (Figure 46 C). The fossil pronotum has a bigger central dark area, which is found in the pronotum of modern *E. fuscipennis* (Figure 46 D). Again, *E. fuscipennis* is typical of peaty places.

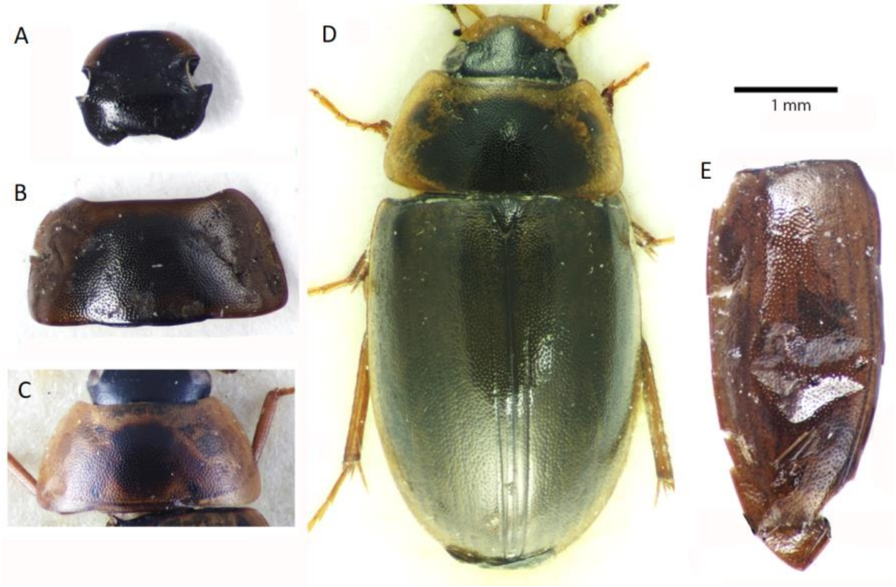


Figure 46. A fossil *Enochrus* head; **B** fossil *Enochrus* pronotum; **C** modern *E. quadripunctatus* pronotum; **D** modern *E. fuscipennis;* **E** fossil *Enochrus* elytron.

Ecology

E. fucipennis often lives in peaty vegetated pools (Angus, written communication, 2017).

Distribution

It is a widely distributed species from Europe to Iran, Kyrgyzstan, Turkey, Siberia and northern China (Löbl, I. and Löbl, D., 2015).

19) *Hydrobius subrotundus* (Stephens, 1829)

The position of elongate setae, called trichobothria, are important in the identification of *Hydrobius* (Fossen, 2016). The fossil's trichobothria are positioned in the intervals between the 2nd and 3rd row, and 4th and 5th row of serial punctures. This is the typical trichobothria positioning found in *H. fusipes* and *H. subrotumdus* (Figure 47). According to Fossen (2016), *H. subrotundus* generally have a more convex body than *H. fuscipes*, and the elytra of *H. subrotundus* is relatively wider than that of *H. fuscipes*. Figure 47 shows that the elytra of *H. subrotundus* is slightly wider than *H. fuscipes*, and the fossil has the widest elytron. Although the photographic angle may affect the appearance of the elytral width, the fossil elytron is much wider than *H. fuscipes*, therefore it is more like that of the *H. subrotundus*.

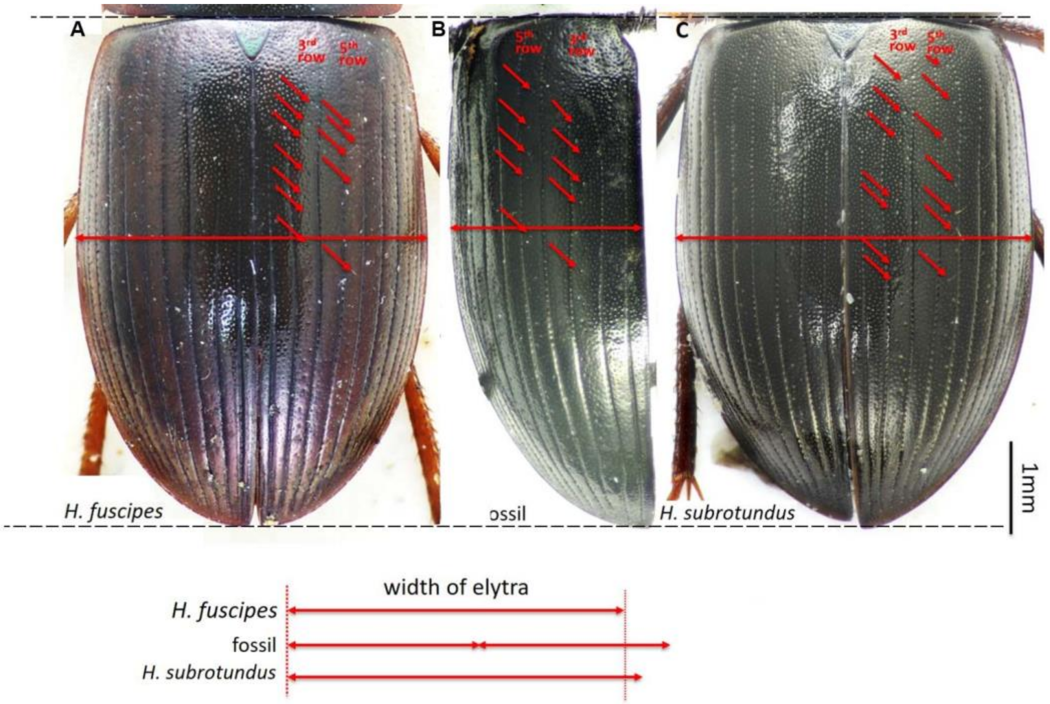


Figure 47. Comparison of the elytral width of *Hydrobius* and the relative position of trichobothria (red arrows) on the elytra of *Hydrobius*. **A** Modern *Hydrobius fuscipes* elytra; **B** Fossil *Hydrobius* eltron; **C** Modern *Hydrobius subrotundus* elytra.

Ecology

H. subrotundus usually likes shaded or colder waters. It is often found in more acidic waters and at the edges of slow flowing water with rich vegetation (Fossen et al., 2016).

Distribution

This species is known from Fennoscandia and Central Europe (Fossen et al., 2016).

Hydraenidae

20) *Ochthebius hungaricus* (Endrödy-Younga, 1968)

The fossil *Ochthebius* specimens have small random lines around the serial punctures on the elytra. Based on this and the size of elytra, *O. hungaricus, O. lurugosus* and *O.* minimus have been selected as candidates. As figure 48 shows, the best match for the fossil was *O. hungaricus*. In particular, both fossil and *O. hungaricus* elytra have wrinkles at the base.

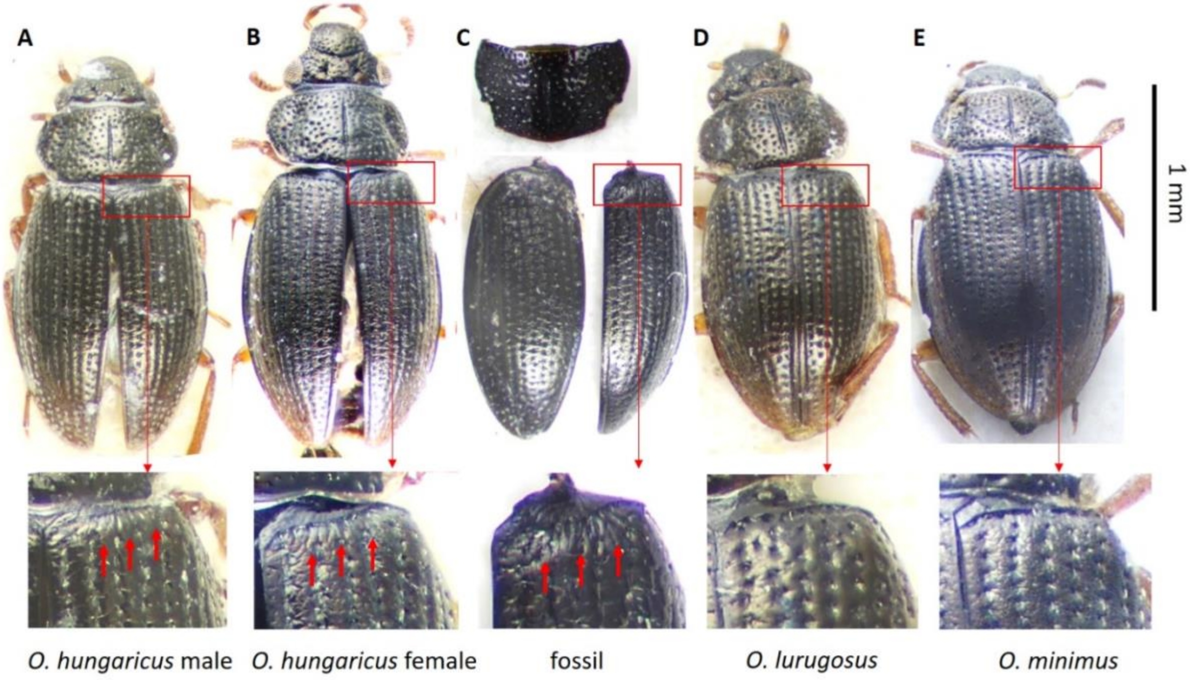


Figure 48. Comparison of the *Ochthebius* and its elytral base. *O. hungaricus* and the fossils have wrinkles at the elytral base (red arrows). **A** modern male of *O. hungaricus*; **B** modern female of *O. hungaricus*; **C** fossil *Ochthebius*; **D** modern *O. lurugosus*; **E** modern *O. minimus*.

Ecology

O. hungaricus lives in small vegetated pools, often with grassy edges (Angus, written communication, 2017).

Distribution

This species is distributed from Europe eastwards to the Altai region in Russia (Angus, written communication, 2017).

Silphidae

21) *Thanatophilus dispar* (Motschulsky, 1860)

The fossil *Thanatophilus* is only a fragment of left elytron apex. Based on the size, shape and the lines on the apex, *T. dispar*, *T. latericarinatus*, *T. minutus* and a new species (undescribed) from the Chinese city Harbin have been selected. Examination of the punctures on the apex (figure 49) shows that the fossil best matches either *T. dispar* or the new species from Harbin. The punctures of *T. latericarinatus* are further apart and those of *T. minutus* are too small. According to a Silphidae specialist, Dr. Ronald Madge from London Natural History Museum, only *T. dispar* and the new species from Harbin have little teeth on their elytral apex. These teeth are also apparent on the fossil (figure 50). But the undescribed species has so far only been found in Harbin, while *T. dispar* is widely distributed in Europe, Siberia, Mongolia and Northern China. Thus, the fossil *Thanatophilus* is more likely to be *T. dispar*.

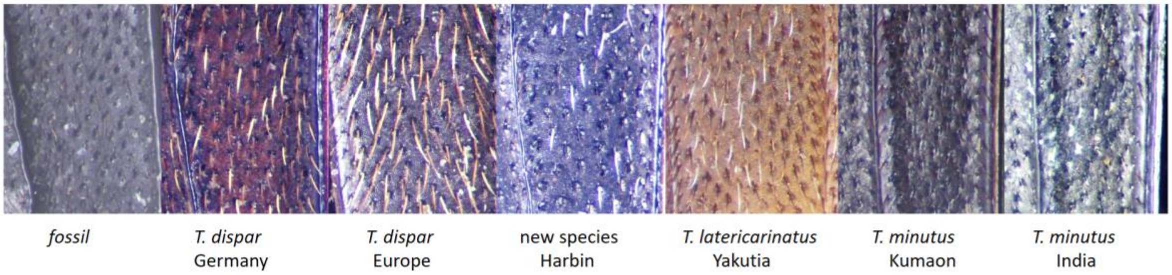


Figure 49. Comparison of the details of *Thanatophilus* elytral apex.

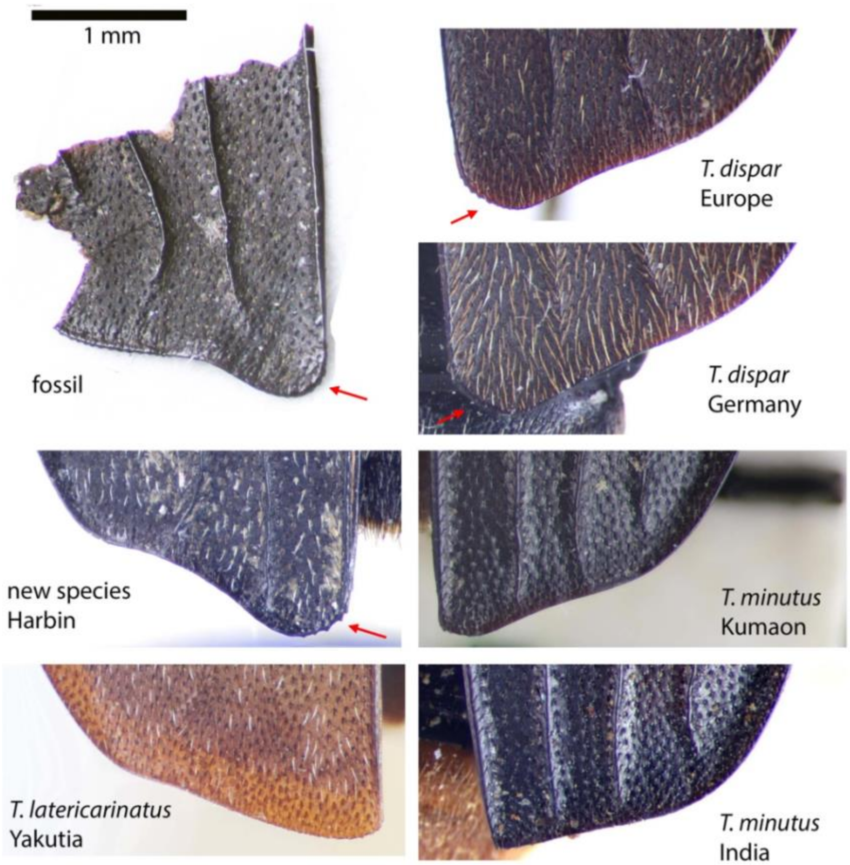


Figure 50. Comparison of the *Thanatophilus* elytral apex. Fossil, *T. dispar* and the undescribed species from Harbin, China have little teeth on their elytral apex (red arrows).

Ecology

T. dispar is a hygrophlilous species (Pearson, 1962b), that has been found from the carcasses of fish, birds and mammals. It has been found on littoral beaches, lake shores, in forests and woodland margins, and in grassland (Hyman, 1992; Nelson and Anderson, 1999; Koch, 1989; Sullivan, 1998).

Distribution

This species is distributed throughout Europe (Koch, 1989). It has also been found in central Siberia and Mongolia (http://www.discoverlife.org, accessed November 2017).

Staphylinidae

22) *Acidota crenata* (Fabricius, 1792)

Based on the size, shape, and the punctures of pronotum and elytra, and the small teeth on the elytral shoulder, this specimen matches *Acidota crenata* (figure 51).

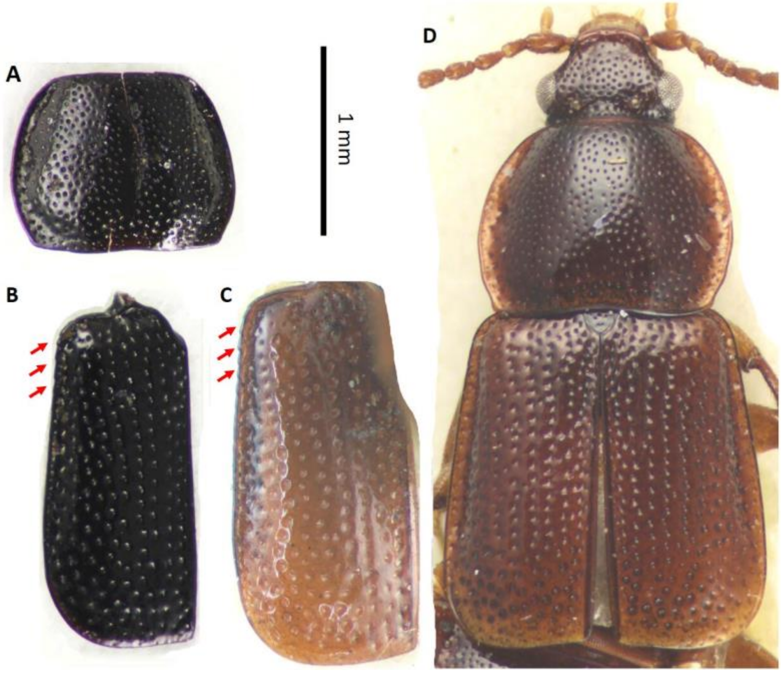


Figure 51. A fossil pronotum; **B** fossil elytron; **C** modern *Acidota crenata* elytron; **D** modern *Acidota crenata*. It is hard to see the small teeth on the elytral shoulder from the front of the specimens, but if the elytron is slightly tilted up, the teeth become obvious (red arrows).

Ecology

A. crenata lives in several different habitats. In forests, it inhabits moist areas under moss; in mountain areas, it is usually found under moist leaves and stones; in lower altitudes, it lives in *Sphagnum* and *Polytrichum* bogs; it also can be found in wet bog meadows (Horion, 1963).

Distribution

This species is widely distributed in the Holarctic. It is known from northern Europe, to the mountain areas of Central Europe, Siberia and Mongolia (Horion, 1963). In North America, it distributed from Alaska to Newfoundland and southern Quebec in eastern Canada, and south to the northeastern United States. And it also be found at high altitudes in Colorado and North Carolina of the United States (Campbell, 1983).

23) *Arpedium brachypterum* (Gravenhorst, 1802)

The head of the fossil *Arpedium* specimens have two little ocelli behind their large eyes (figure 52, red arrows). The pronotum has two large lateral punctures (figure 52, red circles). Considering the shape, size and the size of the punctures on pronotum, the fossil *Arpedium* best matches *Arpedium brachypterum.*

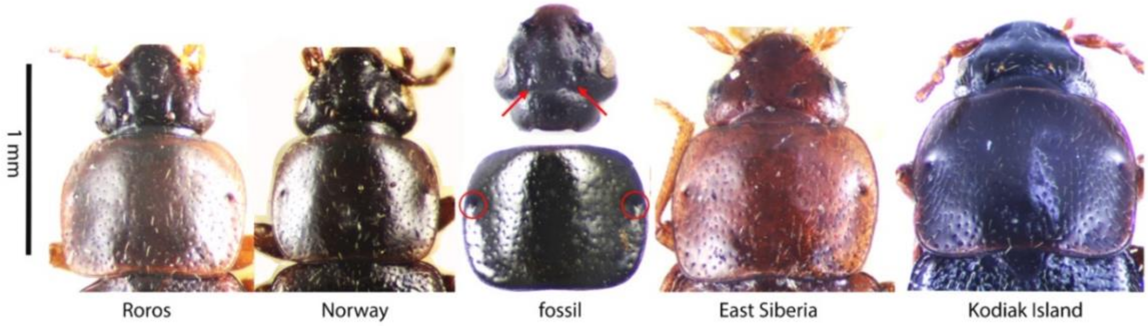


Figure 52. Comparison of modern Arpedium *brachypterum* from different collecting localities with the fossil *Arpedium brachypterum* (centre). The fossil *Arpedium brachypterum* specimen best matches the Norway specimen. Although the East Siberia and Kodiak Island specimens are larger than the fossil, the shape and other main characters are the same.

Ecology

In the Alps, *A. brachypterum* lives almost exclusively above tree line, especially in moist localities under stones, close to the edges of snowfields. In the northern regions of Europe, this species is usually found in the forest zone, but sometimes also occurs in the subalpine and alpine regions, to altitudes up to 1000 m, and has be found among moss in humid places in Sweden (Mani, 1968).

Distribution

This species is widely distributed in the northern Holarctic region. It is found from northern Europe, the mountains of central Europe, Siberia, Irkutsk (probably therefore in the Sayan and Altai mountains), and the Far East of Russia, Mongolia, and in the extreme northern parts of the continent (Munster, 1933). In North America, it is known from Alaska and northern Canada. And in the United States, there are disjunct alpine populations on the Mt. Washington in New Hampshire and the Mt. Katahdin in Maine (Campbell, 1984).

24) ***Olophrum. rotundicolle*** **(C. R. Sahlberg, 1817)**

Based on the size, shape and the punctures of the pronotum. This fossil pronotum matches *Olophrum rotundicolle* perfectly (figure 53).

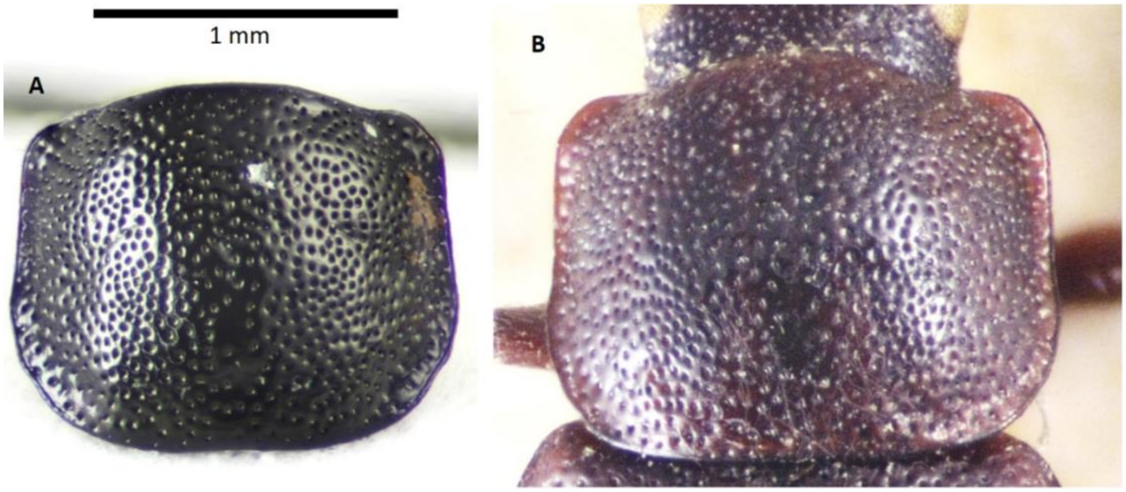


Figure 53. A fossil *Olophrum rotundicolle* pronotum; **B** modern *Olophrum rotundicolle* pronotum.

Ecology

O. rotundicolle is usually been found at the edge of streams, lakes, and bogs from moss or clumps of *Carex*. It is also found in moist *Salix* and *Alnus* spp. leaf litter, and floating debris instreams. In North America, this species occurs in arctic and alpine tundra (Campbell, 1983), where it has a very brief active season in summer (Elias, personal communication, 2017).

Distribution

This species is wildly distributed in the Holarctic. In the Palearctic region, it ranges from Scandinavia east to Siberia and the Far East of Russia (Löbl, I. and Löbl, D., 2015). In North America, this species ranges from Alaska to Newfoundland and southern Quebec in eastern Canada, and New York and Minnesota in the United States (Campbell, 1983). It is also found in isolated populations in the alpine zone of the Rocky Mountains.

25) *Olophrum boreale* (Paykul, 1792)

The pronotum of *Olophrum* is very important for identification. The fossil pronotum has two angles on the basal corners (figure 54, red arrows), which best match *Olophrum boreale.*

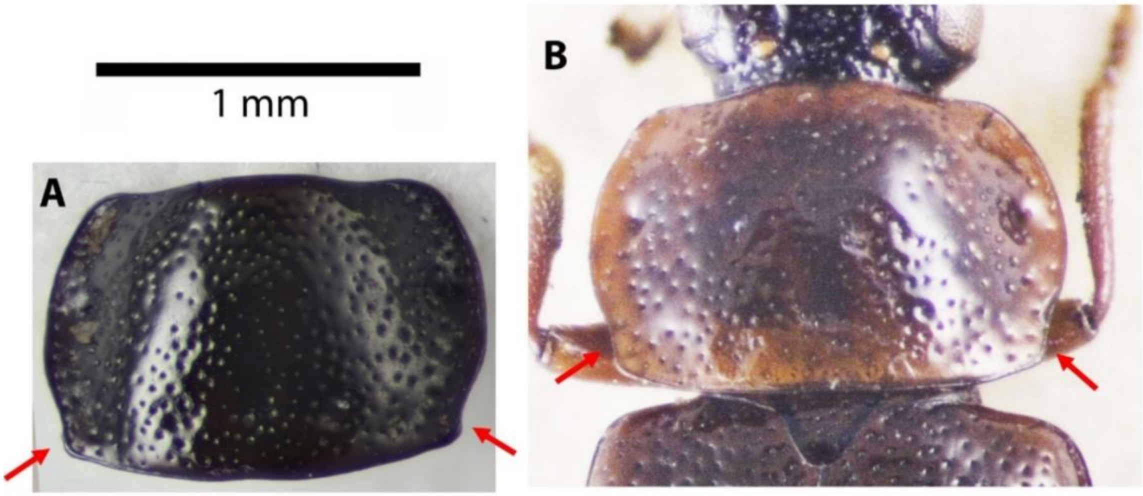


Figure 54. A fossil *Olophrum boreale* pronotum **B** modern *Olophrum boreale* pronotum

Ecology

O. boreale is frequently collected from alpine areas above tree line. It usually lives at the margin of bogs, lakes, springs, and streams with rich vegetation (sedges, *Equisetum*, *Typha*, moss, and various shrubs). It is also found among moist leaf litter, or under stones in moist areas (Campbell, 1983).

Distribution

This is a widely distributed Holarctic species. It is found from northern Fennoscandinavia through northern Russia to Novaya-Semlya and northern Siberia. In North America, it has been found from Alaska, eastwards cross the Yukon Territory and the Northwest Territories, to Quebec (Campbell, 1983).

26) *Bryophacis rufus* (Erichson, 1839)

The shape of the elytra and the relative position of trichobothria on the elytra are important for the identification of the genus *Bryophacis*. The species *Bryophacis rufus* has two rows of trichobothria on its elytra (Figure 55. red arrows). Some of the trichbothria punctures are obscured on the fossil specimen, but overall it matches *Bryophacis rufus* best.

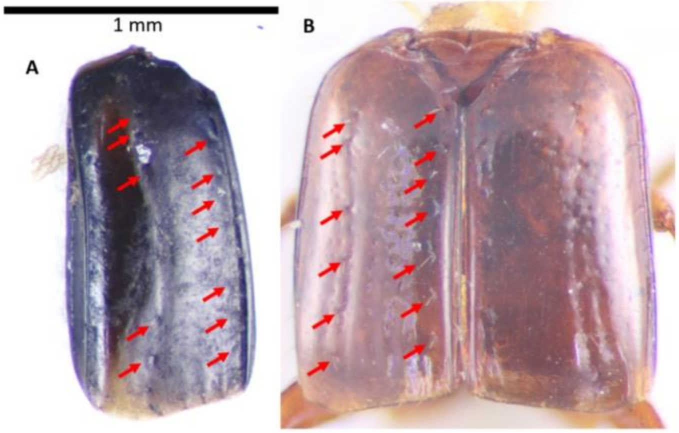


Figure 55. Fossil *Bryophacis rufus* elytron (**A**), modern *Bryophacis rufus* elytron; (**B**) the relative position of trichobothria (red arrows) on the elytra of *Bryophacis rufus*.

Ecology

B. rufus inhabits mountain forest, usually in the alpine zone. It has been found under moss or fallen leaves (Horion, 1967)

Distribution

This species is found across Europe as far north as Finland and east to Russia (Löbl, I. and Löbl, D., 2015).

27) *Gymnusa variegata* (Kiesenwetter, 1845)

Based on the shape and size of the fossil head and pronotum, *Gymnusa brevicollis, G. atra and G. variegata* are the possible candidates. As figure 56 shows, the size of the head of *G. atra* is almost as same as the fossil, while the eyes of *G. atra* are larger than the fossil. Also, the head of the fossil and the Polish specimen of *G. brevicollis* (figure 56 B) are similar in size, but the fossil pronotum is smaller than the Polish specimen (figure 57 B). Both the fossil head and the pronotum match *G. variegata*.

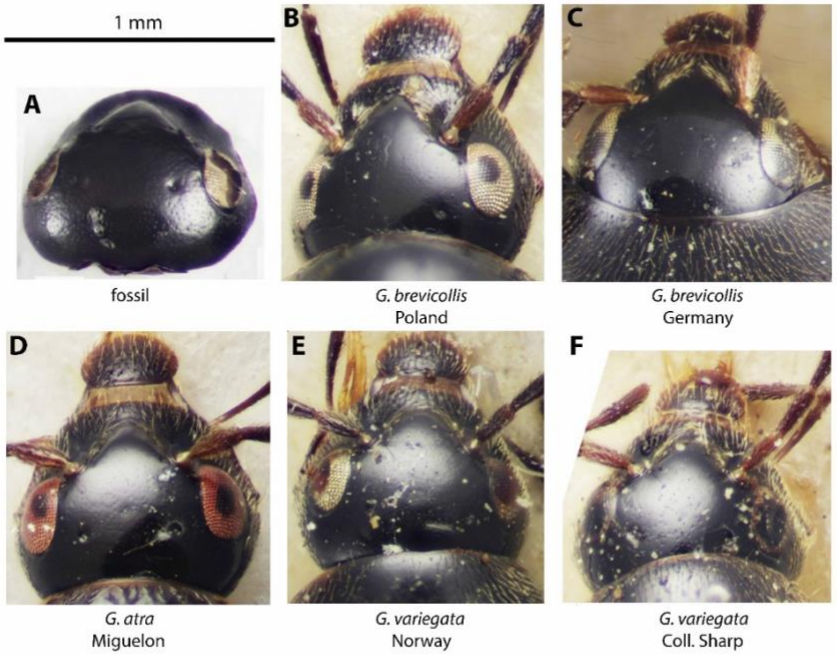


Figure 56. Comparison of the *Gymnusa* heads. **A** fossil *Gymnusa* head; **B** modern *G. brevicollis* head, specimen from Poland; **C** modern *G. brevicollis* head, specimen from Germany; **D** modern *G. atra* head, specimen from Miguelon, Spain; **E** modern *G. variegata* head, specimen from Norway; **F** modern *G. variegata* head, specimen collected by Sharp.

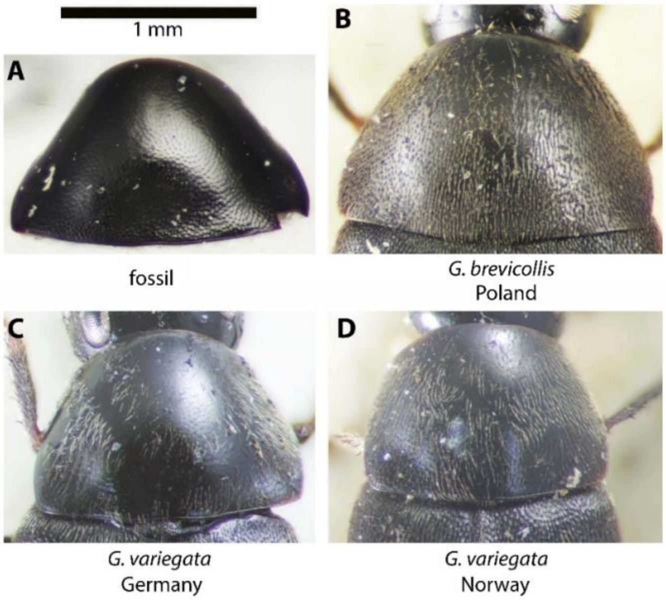


Figure 57. Comparison of *Gymnusa* pronota. **A** fossil *Gymnusa* pronotum; **B** modern *G. brevicollis* pronotum, specimen from Poland; **C** modern *G. variegata* pronotum, specimen from Germany; **D** modern *G. variegata* pronotum, specimen from Norway.

Ecology

The habitats of *G. variegata* is similar to *G. brevicollis*, which lives in swamps, sphagnum bogs, and marshy margins of lakes and slow flowing rivers (Klimaszewski, 1979). Specimens of *G. variegata* can also be found on mossy rocks in the middle of a stream (Smetana, 1960). Lohse (1974) regards it as mainly as a montane species.

Distribution

This species is distributed from Finland and western Russia to Central Europe, and eastward to the Ukraine. It is also found from Irkutsk in south central Russia (Klimaszewski, 1979).

Byrrhidae

28) *Cytilus sericeus* (Forster, 1771)

This identification has been confirmed by Andreas Pütz, a German Byrrhidae specialist. He is certain that the fossil *Cytilus* specimens belong to *Cytilus sericeus*, because the intermediate spaces between the striae are slightly vaulted and not coarsely wrinkled (figure 58).

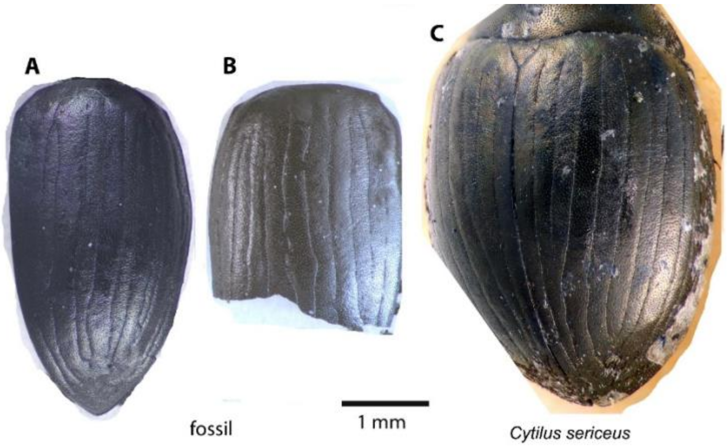


Figure 58. A fossil *C. sericeus* right elytron; **B** half fossil *C. sericeus* left elytron; **C** modern *C. sericeus.*

Ecology

C. sericeus feeds on mosses and lives among grasses and mosses (Pütz, 2007), in moist meadows and on patches of mosses in open ground (Lindroth, 1973).

Distribution

This is a very widely distributed Holarctic species. In China, it has been found from Gansu, Heilongjiang, Qinghai, Sichuan, and the Tian Shan Mountains of Xinjiang (Pütz, 2007).

Coccinellidae

29) *Hippodamia tredecimpunctata* (Linnaeus, 1758)

This is an easy identified species. Based on the elytral size, shape, color, and the number and position of the spots, the fossil *Hippodamia* elytra matches *Hippodamia tredecimpunctata* (figure 59).

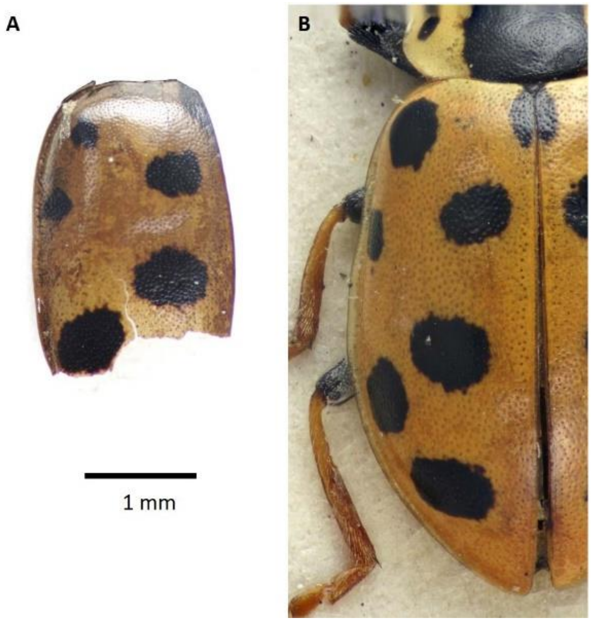


Figure 59. A fossil *H. tredecimpunctata* elytron fragment; **B** modern *H. tredecimpunctata* elytron.

Ecology

The habitats of this species include bogs, agricultural areas, parklands and grasslands (Belicek 1976, Kuznetsov, 1997), usually with vegetation of *Carex*, *Sparganium*, *Phragmites* and willows (Koch, 1989). It feeds on aphids and Erisyphaceae, and was also found from detritus, rotten hay, and under peeled bark (Nikitsky and Ukrainsky, 2016).

Distribution

This species is widely distributed in the Holarctic. It is known from Europe to the Middle East, Siberia, the Far East of Russia, Mongolia, China, Japan and South Korea. It is also widely distributed in North America (Nikitsky and Ukrainsky, 2016).

30) *Ceratomegilla rickmersi* (J. Weise, 1901)

At first *Hippodamia arctica* was considered as a possible candidate. However, Dr. Boris Korotyaev, a Coccinellidae expert from Russia, says there is no *H. arctica* elytra as dark as these fossil, and he thinks the pale side margins are wider than in *H. arctica*. He suggested three Asiatic species as candidates, but stated, "Yet I have found this broad margination of the elytra in the Asian *Ceratomegilla rickmersi*, *Hippodamia heydeni* and *Hippodamia andrewsi*, but all are never so dark" (Korotyaev, written communication, 2017). Another taxonomic expert in this group, Dr. Vladimír Navrátil from Czech University of Agriculture, was convinced that the fossils represent *Ceratomegilla rickmersi* (Navrátil, written communication, 2017) (figure 60). *C. rickmersi* does have dark specimens, and usually they have two bright spots and a pale margin on the elytra. Both *Hippodamia heydeni* and *Hippodamia andrewsi* do not have such dark specimens. Unfortunately, London Natural History Museum does not have any specimens of *C. rickmersi* for comparison.

Figure 60. fossil fragments of *C. rickmersi.* **A** larger left elytron specimen with several yellow spots; **B** and **C** smaller left elytra with two yellow spots; **D** smaller right elytron with one yellow spots; **E** and **F,** head capsules; **G** and **H** pronota.

Unfortunately, Dr. Vladimír Navrátil who identified this species has passed away, and there is no published information about this species.

Chrysomelidae

31) *Plagiodera versicolora* (Laicharting, 1781)

This identification been made by Dr. Michael Geiser, a Chrysomelidae expert from the London Natural History Museum. *Plagiodera versicolora* is the only *Plagiodera* species in the Palearctic, and it is very common in West Siberia. As figure 61 shows, the fossil matches the modern *Plagiodera versicolora.*

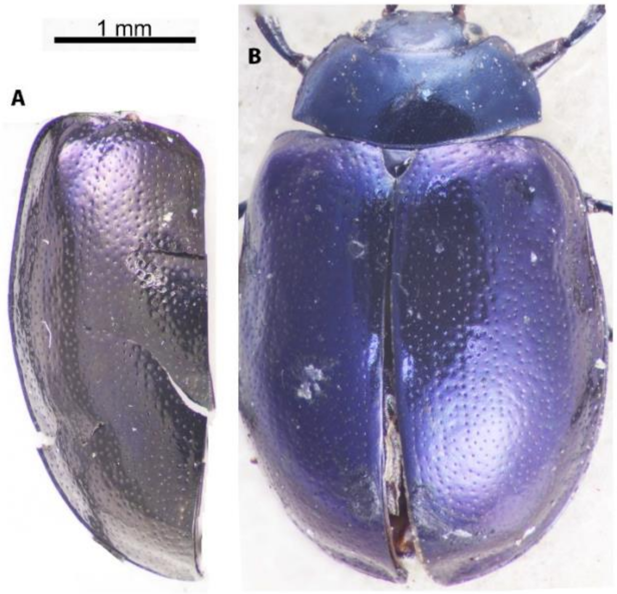


Figure 61. A fossil elytron of *Plagiodera versicolora*; **B** modern *Plagiodera versicolora*.

Ecology

P. versicolora lives on several species of *Salix* and *Populus* (Mohr, 1966; Franz, 1974; Koch, 1992).

Distribution

This species is widely distributed in the Palearctic and Oriental biogeographic provinces (Kippenberg, 2010).

32) *Phaedon armoraciae* (Linnaeus, 1758)

The fossil elytra have nine punctate longitudinal striae on the disc, a finely raised border, and fine and random punctures between striae. These featuresperfectly match those of *Phaedon armoraciae* (Watford Coleoptera Group,2017a) (figure 62).

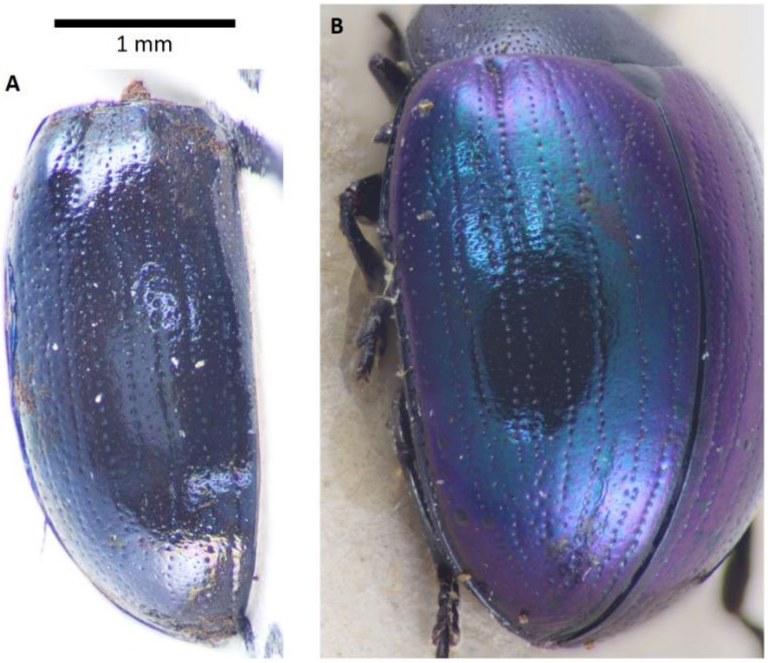


Figure 62. A fossil elytron of *Phaedon armoraciae*; **B** modern elytron of *Phaedon armoraciae*.

Ecology

P. armoraciae inhabits wetland. Adults are usually found from waterside vegetation (Watford Coleoptera Group, 2017a). Its host plants include *Veronica beccabunga*, *Veronica scutellata*, *Armoracia rusticana* (Steinhausen, 1994), *Nasturtium officinale, Nasturtium*, *Cochlearia pyrenaica* (Franz, 1974), and *Hippuris vulgaris* (Fuss et al., 2005).

Distribution

This species is widely distributed in the Palearctic, from Europe to Russia, Kazakhstan, Turkey, northern China (Hebei), and Mongolia (Kippenberg, 2010).

33) ***Galeruca tanaceti* (Linnaeus, 1758)**

The elytra of *Galeruca tanaceti* have a coarsely and densely punctured surface. The size and density of these punctures, and the explanate elytral side margin, are useful features for identification (Watford Coleoptera Group, 2017b). The fossil elytra match the modern *Galeruca tanaceti* (figure 63).

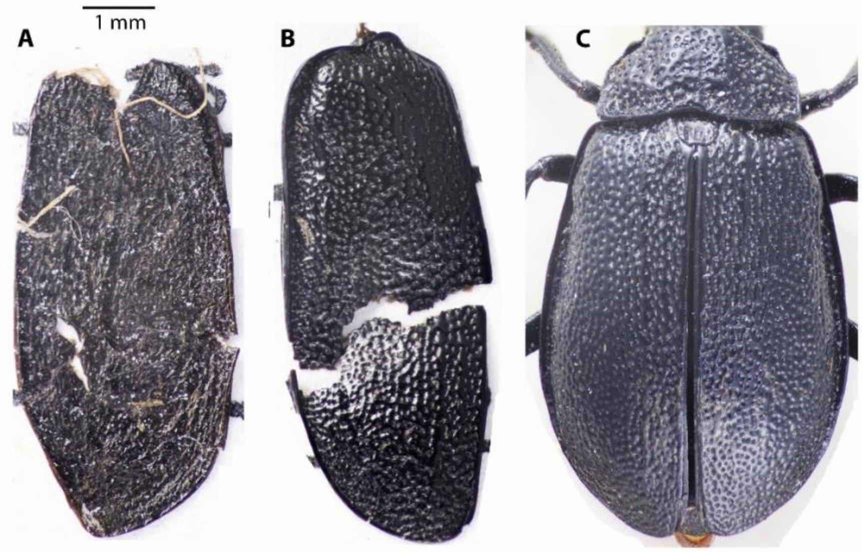


Figure 63. A and **B** fossil *Galeruca tanaceti* elytra. **C** modern *Galeruca tanaceti*.

Ecology

G. tanaceti is a polyphagous plant-feeding species. It inhabits grassy areas, usually in very dry environments (Natural Spot, no date). The host plants include *Centaurea nigra*, *Tanacetum vulgare*, *Achillea millefolium*, *Tussilago*, *Potentilla auserina*, *Cardamine pratensis*, *Sinapis arvensis*, *Succisa pratensis*, *Cirsium arvensis*, *Scabiosa columbaria*, and various *Veronica* species (Watford Coleoptera Group, 2017b).

Distribution

This Palearctic species is found from Europe, Central Asia, West Siberia, the Russia Altai Region, Japan, and North Africa (Morocco, Algeria and Tunisia) (Beenen, 2010).

34) ***Phyllotreta cruciferae*** **(Goeze, 1777)**

Based on the size and shape of the fossil elytron, *Phyllotreta cruciferae, P. nigripe and P. procera* are the possible candidates. In comparing these species, the elytral punctures of *Phyllotreta nigripe* are smaller, and the elytral surface of *Phyllotreta procera* is heavily reticulate between the punctures. Therefore, the fossil best matches *P. cruciferae* (figure 64).

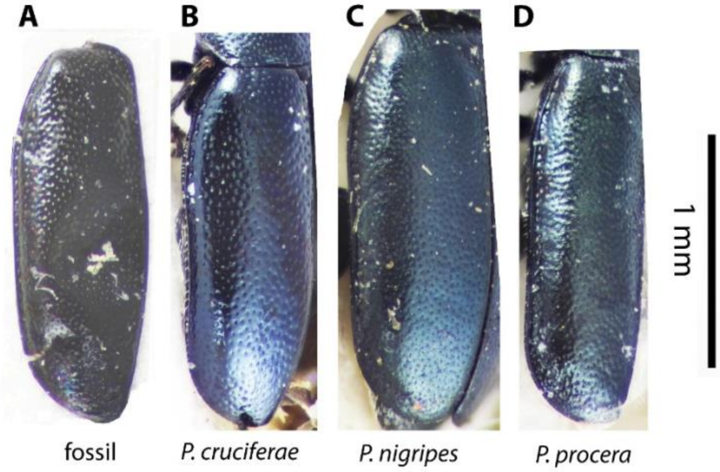


Figure 64. Comparison of the fossil *Phyllotreta* elytron with modern *Phyllotreta* species. **A** fossil elytron; **B** modern *P. cruciferae* elytron; **C** modern *P. nigripe* elytron; **D** modern *P. procera* elytron.

Ecology

The host plants for *P. cruciferae* mainly are mustard and *Cruciferae*, especially *Brassica* species (BugGuide, no date).

Distribution

This species is widely distributed in the Palearctic, except China, and is also found in the Nearctic (Döberl, 2010).

35) ***Chaetocnema obesa*** **(Boieldieu,1859)**

Based on the shape of elytra, the basal irregular punctures, and density of the punctures, this fossil matches *Chaetocnema obesa* (figure 65).

Figure 65. A fossil *Chaetocnema obesa* elytron; **B** modern *Chaetocnema obesa* elytron.

Ecology

C. obesa lives in swampy meadows, swamps, and the edges of rivers and lakes. It only feeds on a few plant taxa, including *Carex distans*, *Eleocharis palustris* and *Juncus spp.* (Koch, 1992; Mohr, 1966).

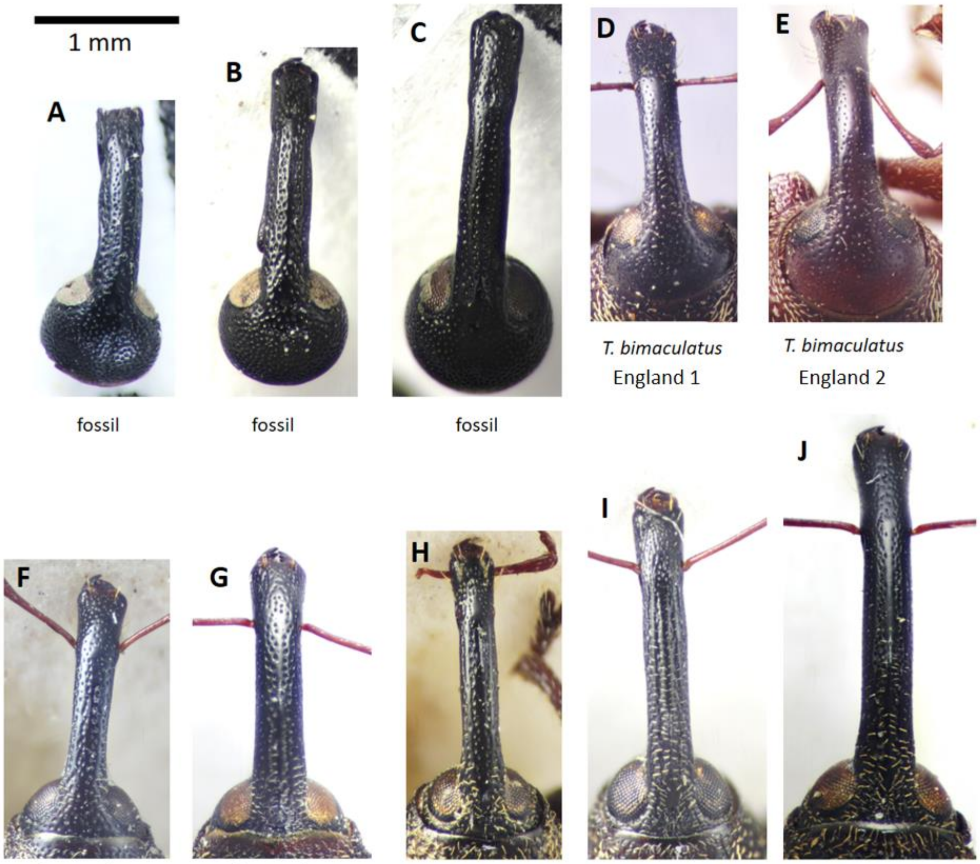
Distribution

This species is widely distributed in Central and Southern Europe, the Caucasus, Iraq, South Siberia, Kazakhastan, Mongolia and Tibet (Gruev, 1998). It is also known from Morocco, Algeria and Tunisia in North Africa (Döberl, 2010).

Erirhinidae

36) *Tournotaris bimaculatus* (Fabricius, 1787)

In size, shape, eye color, and the punctures on the head, pronotum and elytra, the fossil is most similar to *Tournotaris bimaculatus* and *Notaris scirpi*. Since the variations exist in different individuals from same species, several different specimens have been selected for each species, to ensure the identification based on reliable features. Over all, as figure 66 shows, even the heads of both species vary in the strength of the punctures, but it seems that *N. scirpi* has an elevated smooth region running along the middle of the rostrum, with a sort of depression running along each side. This is not so in *T. bimaculatus,* or the fossils. And also, *N. scirpi* has a longer and thinner rostrum. On the pronotum, the punctures of *N. scirpi* are generally coarser and closer together (figure 67).



fossil fossil fossil *T. bimaculatus* England 1 *T. bimaculatus* England 2

T. bimaculatus Coll. Sharp *T. bimaculatus* Yakutia *N. scirpi* Waterford *N. scirpi* Kent *N. scirpi* Slovakia

Figure 66. Comparation of fossil heads, modern *T. bimaculaus* heads and modern *N. scirpi* heads. **A – C** fossil heads; **D – G** heads of various modern *T. bimaculaus* specimens (**D** collected from England; **E** another specimen collected from Anglia; **F** collected by Sharp; **G** collected from Yakutia); **H – J** heads of different modern *N. scirpi* specimens (**H** collected from Waterford; **I** collected from Kent; **J** collected from Slovakia).

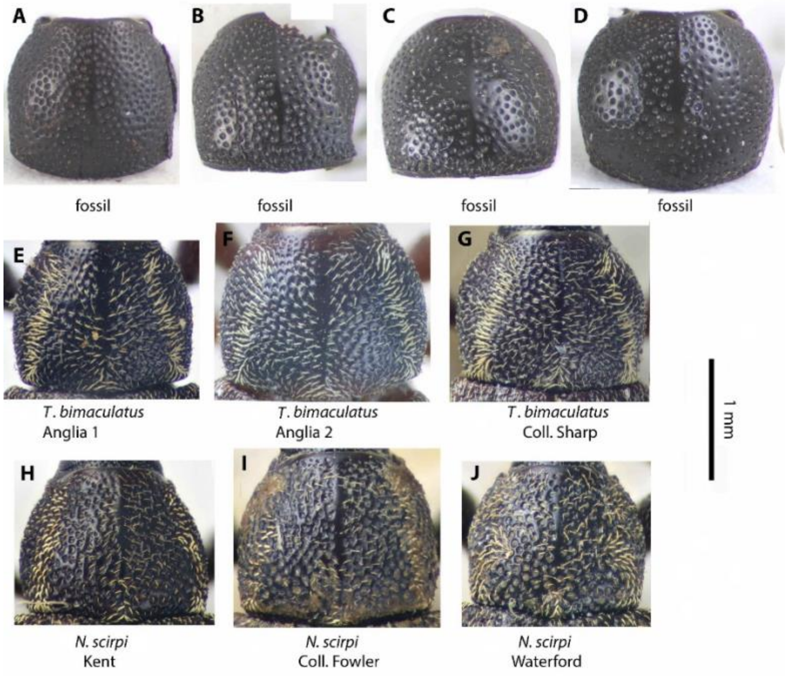


Figure 67. Comparation of fossil pronota, modern *T. bimaculaus* pronota and modern *N. scirpi* pronota. **A – D** fossil heads; **D – G** pronota of different modern *T. bimaculaus* specimens (**D** collected from Anglia; **E** another specimen collected from Anglia; **F** collected by Sharp); **H – J** pronota of different modern *N. scirpi* specimens (**H** collected from Kent, England; **I** collected by Fowler; **J** collected from Waterford, Ireland).

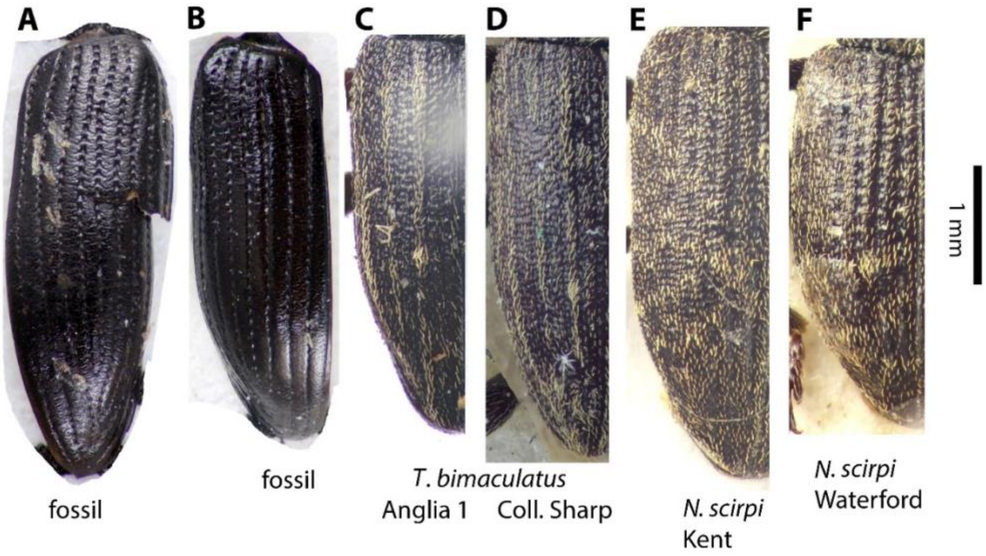


Figure 68. Comparation of fossil elytra, modern *T. bimaculaus* elytra and modern *N. scirpi* elytra. **A and B** fossil elytra; **C** elytron of modern *T. bimaculaus* collected from Anglia; **D** elytron of modern *T. bimaculaus* collected by Sharp; **E** elytron of modern *N. scirpi* collected from Kent; **F** elytron of modern *N. scirpi* collected from Waterford.

Ecology

This species lives on the banks of pools and marshes and in moist places. Host plants are *Typha latifolia L.* and *Phalaris arundinacea L.* (Caldara and O'Brien, 1995)

Distribution

This is a Holarctic species which ranges from Europe, Central Asia, Mongolia, Siberia, Japan, and North America (Caldara and O'Brien, 1995).

Scolytidae

37) *Phloeotribus spinulosus (Rey, 1883)*

This species was identified by Dr. Milos Knizek, a Czech Curculionidae specialist. He stated that all the visible morphological characters of this fossil fit *Phloeotribus spinulosus*, with its well developed, sharp spines (Knizek, written communication, 2017) (figure 69). It is a pholeophagous species that develops in spruce, usually on the lower branches of standing green trees, and is widely distributed in Palaearctic region.

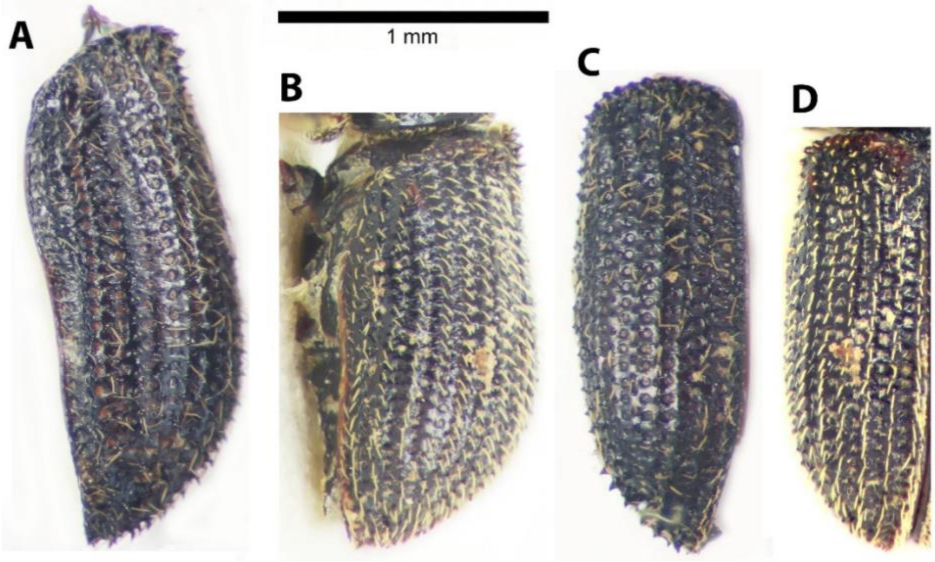


Figure 69. **A** lateral view of *P. spinulosus* fossil elytron; **B** lateral view of *P. spinulosus* modern elytron; **C** front view of *P. spinulosus* fossil elytron; **D** front view of *P. spinulosus* modern elytron.

Ecology

P. spinulosus is a phoelophagous species that develops in spruce, usually on the lower branches of standing green trees (Knizek, written communication, 2017).

Distribution

This species is widely distributed in Palaearctic region, known from Europe, Kazakhstan, Siberia, the Far East region of Russia, Mongolia and Japan (Knizek, 2011).

5.1.2 Taxa can only be identified to the genus or family level

1) *Trechus* (Carabidae)

The first striae on the elytral apex curves backwards at the apex (Lindroth, 1963) (figure 70. red arrows). This is a unique feature of *Trechus*. However, this fossil elytron does not match any modern *Trechus* specimens in the London Natural History Museum.

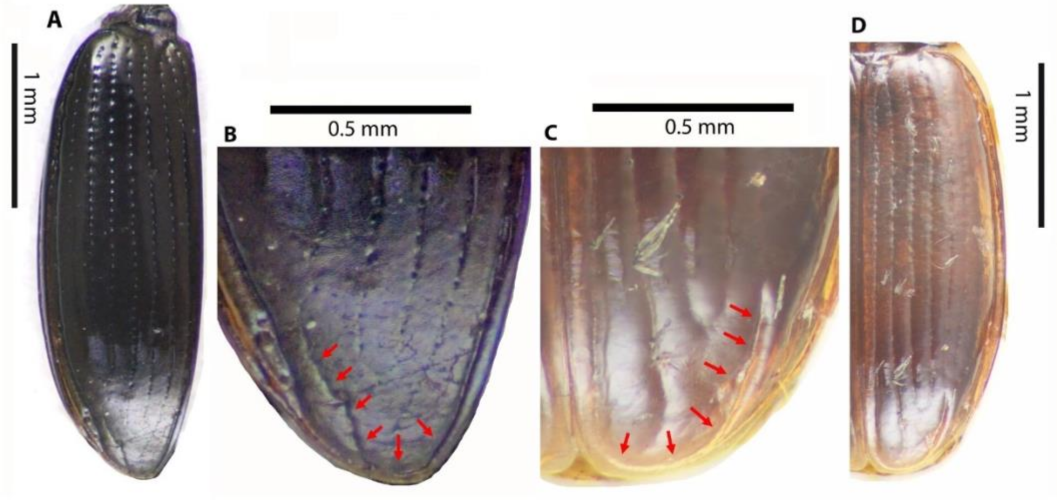


Figure 70. A fossil *Trechus* left elytron**; B** fossil *Trechus* elytral apex; **C** modern *Trechus apicalis* elytral apex; D modern *Trechus apicalis* right elytron.

2) *Chlaenius* (Carabidae)

By checking the modern collection of *Chlaenius* in the London Natural History Museum, the closest match is *Chlaenius stschukini*. However, the enlarged elytral detail shows that the fossil is different from *Chlaenius stschukini* (figure 71). The fossil specimen also been referred to a *Chlaenius* specialist, Dr. Alexandr Anischenko, but he also could not identify it.

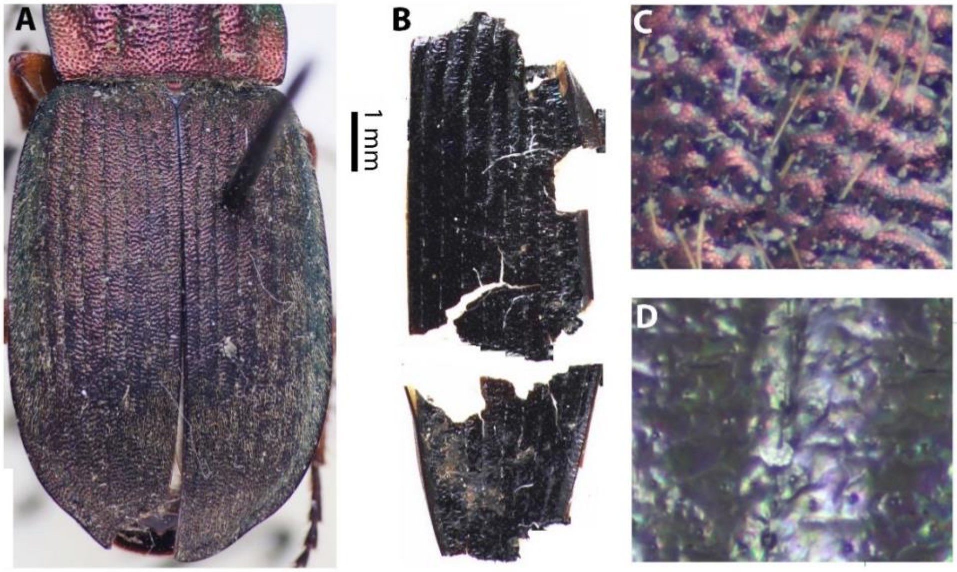


Figure 71. A modern *Chlaenius stschukini* elytra; **B** fossil fragments of elytron; **C** enlarged elytral detail of modern *Chlaenius stschukini* **D** enlarged elytral detail of fossil.

3) *Ilybius* (Dytiscidae)

Based on the size and shape of the fossil pronotum, I. aenescens, I. angustior, I guttiger and I. lenensis are the closest matches to the fossil. The I. angustior specimen is the only one dark enough to match the fossil, but the identification still cannot be confirmed (figure 72).

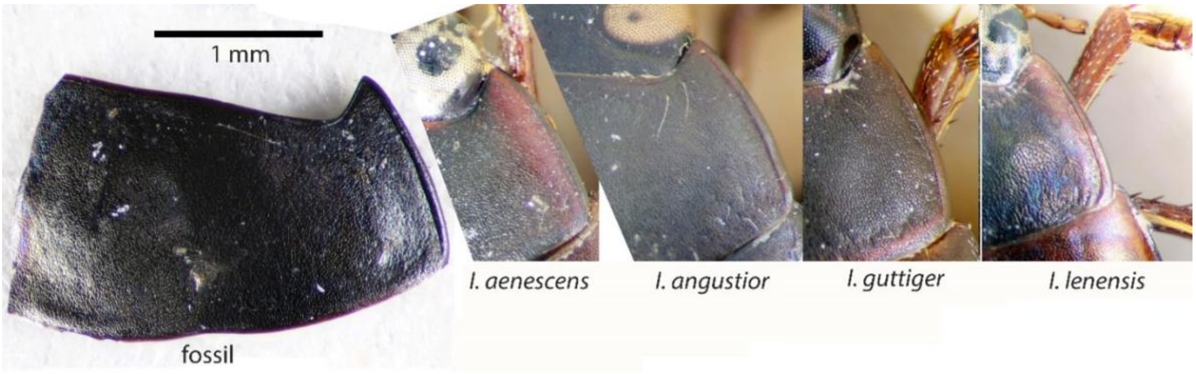


Figure 72. Comparison of fossil and modern *Ilybius* pronota.

4) *Colymbetes* (Dytiscidae)

The “finger print” pattern on the elytra is a specific feature of *Colymbetes*. But the fossil fragments are not large enough to identify the species (figure 73).

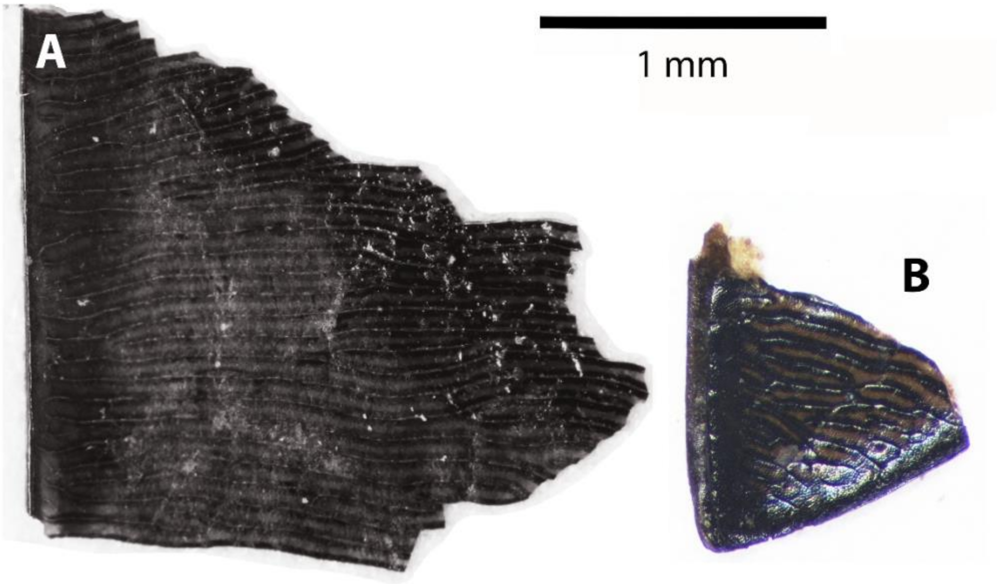


Figure 73. A fossil *Colymbetes* elytral fragment; **B** fossil *Colymbetes* elytral apex.

5) *Limnebius* (Hydrophilidae)

As figure 74 shows, the fossil elytron matches the female *L. parvulus* and *L. glabriventris*. However, according to Jäch (1993), the elytra of female *L. parvulus, L. glabriventris* and *L. shatrovskyi* cannot be confidently separated. So, the identification has to be to these three species.

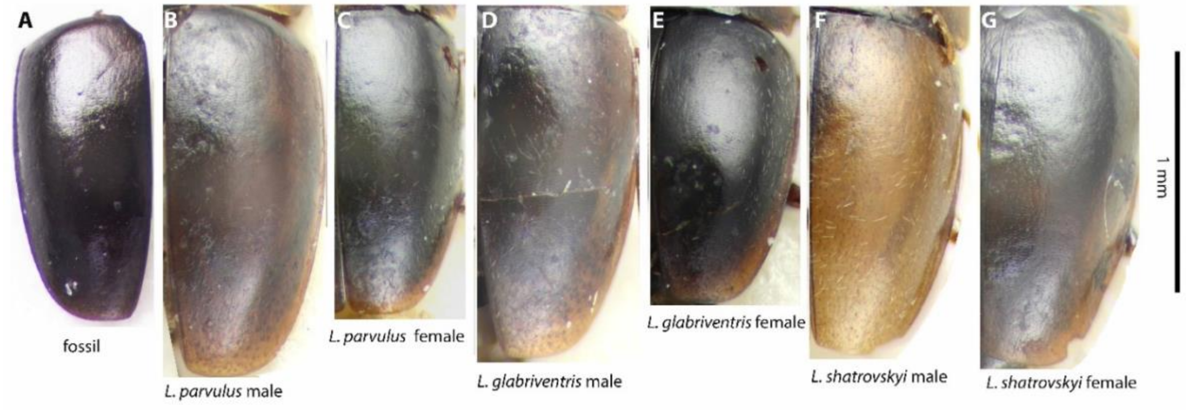


Figure 74. A fossil *Limnebius* elytron; **B** modern male *L. parvulus* elytron; **C** modern female *L. parvulus* elytron; **D** modern male *L. glabriventris* elytron; **E** modern female *L. glabriventris* elytron; **F** modern male *L. shatrovskyi* elytron; **G** modern female *L. shatrovskyi* elytron.

6) *Nargus* cf. *wilkini* (Leiodidae)

There is no modern specimen in the London Natural History Museum that matches this fossil elytron. The elytral shape and punctures of *Nargus wilkini* are similar to the fossil, but the modern specimens are larger than the fossil (figure 75).

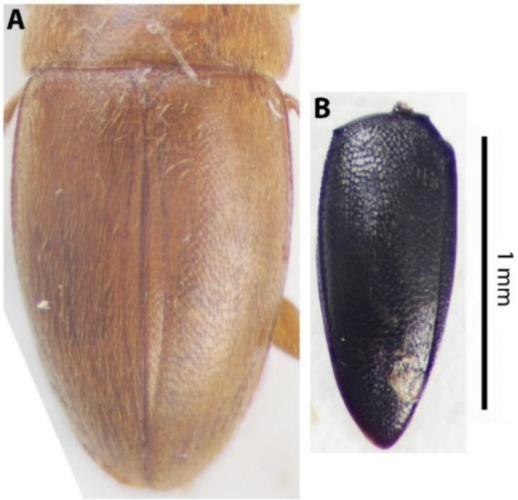


Figure 75. A modern *Nargus wilkini* elytra; **B** fossil *Nargus* elytron.

7) *cf. Eusphalerum* (Staphylinidae)

Based on the fossil pronotum and elytron, it is a Staphylinidae species (figure 76). But the genus cannot be confirmed. *Eusphalerum* is a possibility.

Figure 76. Fossil pronotum and elytron of cf. *Eusphalerum*.

8) *Stenus* (Staphylinidae)

Stenus species cannot be reliably identified only on the basis of the head, pronotum and elytron.

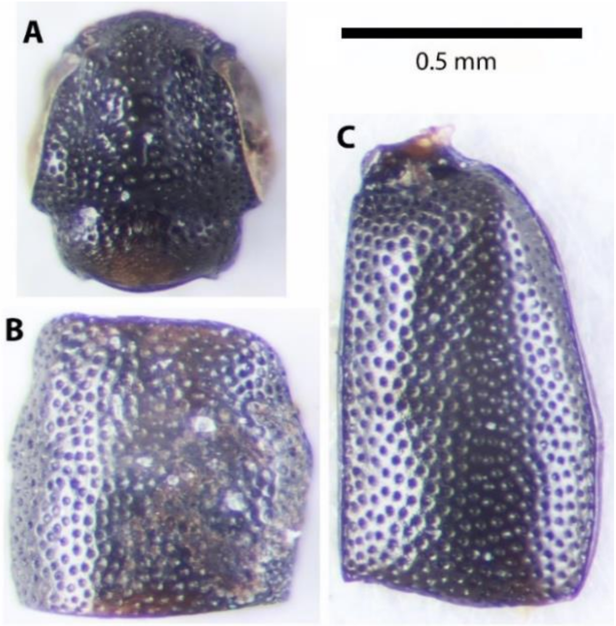


Figure 77. A fossil *Stenus* head; **B** fossil *Stenus* pronotum; **C** fossil *Stenus* right elytron.

9) ***Tetartopeus*** **(Staphylinidae)**

As figure 78 shows, the fossil pronotum matches *Tetartopeus kamschaticus* both in size and shape. To confirm the identification, a photograph of the fossil specimen was sent to Dr. Volker Assing, a specialist on this group. However, he suggests that without examination of the aedeagus, most *Tetartopeus* species are difficult to identify, even when whole specimens are available. Identification based exclusively on a pronotum is 'always close to wildly guessing' (Assing, written communication, 2017). Thus, *Tetartopeus kamschaticus* is the only likely match for this fossil specimen, but this is impossible to confirm.

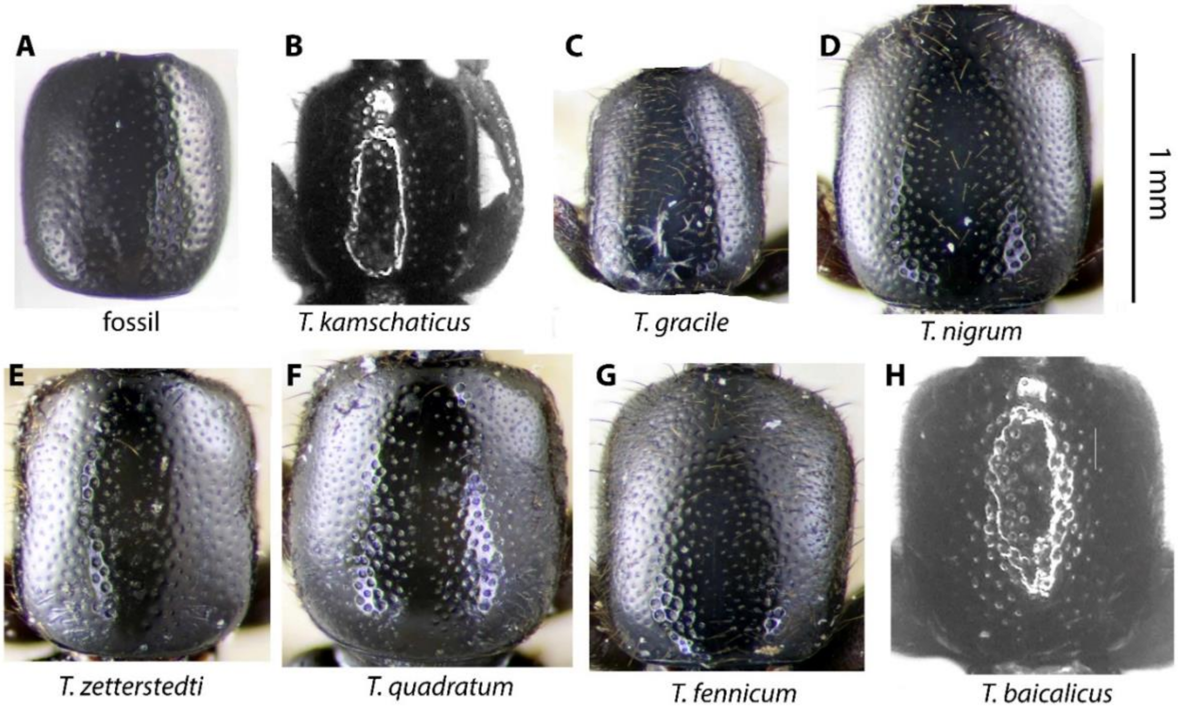


Figure 78. Comparison of *Tetartopeus* pronota. **A** fossil *Tetartopeus* pronotum; **B** modern *T. kamschativus* pronotum (image source: Assing, 2011); **C** modern *T. gracile* pronotum; **D** modern *T. nigrum* pronotum; **E** *T. zetterstedti* pronotum; **F** modern *T. quadratum* pronotum; **G** modern *T.fennicum* pronotum; **H** modern *T. baiccalicus* pronotum (image source: Assing, 2011)

10) *Quedius* (Staphylinidae)

Quedius is a large genus with hundreds of species, the identification on this genus requires a great deal of effort. In this fossil assemblage, two apparently different species of *Quedius* heads have been found, but both of them are difficult to identify to species. We did not find any modern specimens that match the small fossil head (figure 79. A – C). Based on the shape and size of the large fossil head, *Q. simplicifrons*, *Q. meridiocarpathicus,* and *Q. mulleri* have been selected. But the size of their eyes do not match the fossil.

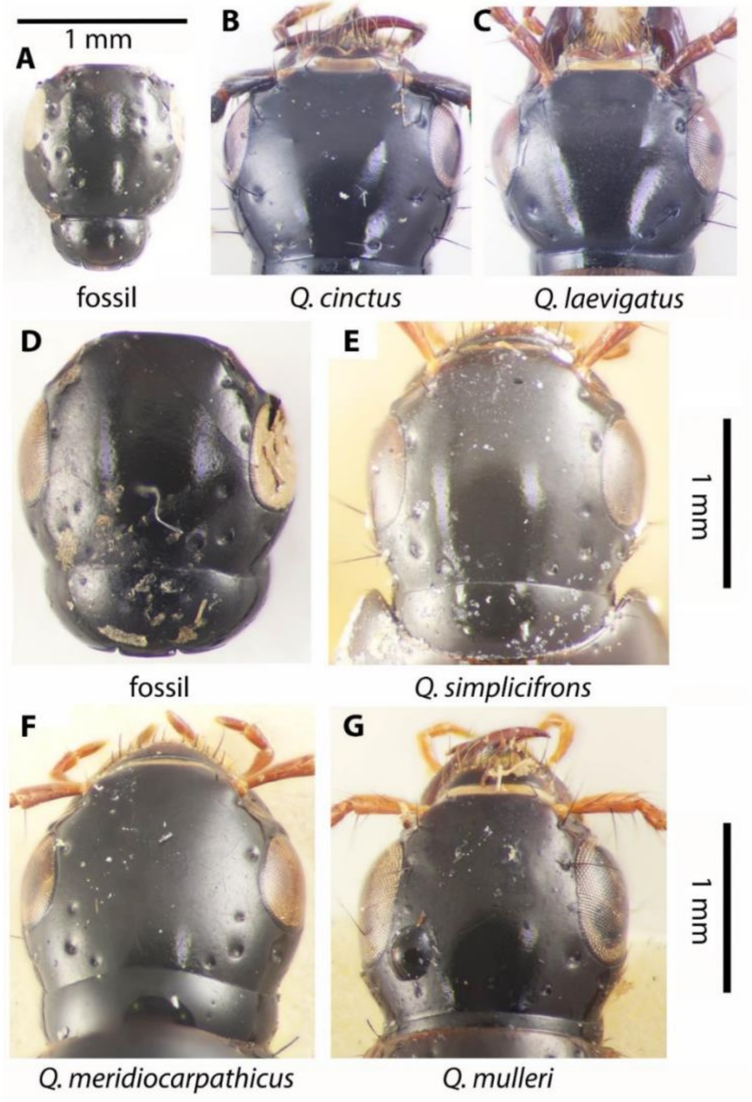


Figure 79. A small fossil *Quedius* head; **B** modern *Q. cinctus* head; **C** modern *Q. laevigatus* head; **D** larger fossil *Quedius* head; **E** modern *Q. simplicifrons* head; **F** modern *Q. meridiocarpathicus* head; **G** modern *Q. mulleri* head.

11) Pselaphidae

Dr. Ziwei Yin, a Chinese Pselaphidae specialist, suggested that this fossil elytra belongs to the tribe Pselaphini (figure 80), but according to him, it is impossible to identify the genus (Yin, written communication, 2017).

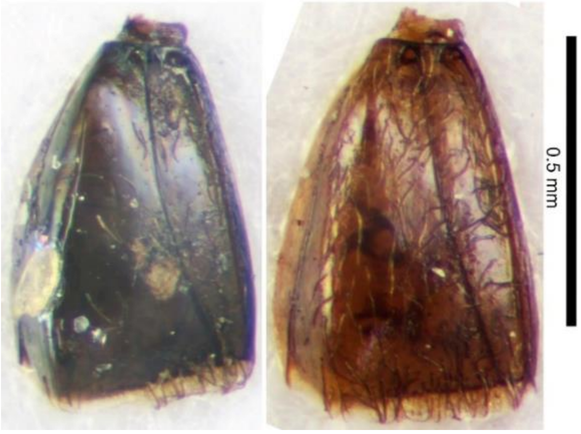


Figure 80. Fossil Pselaphini elytra.

12) *Nephus* (Coccinellidae)

By checking the modern specimens of *Nephus*, the best match for the fossil is *Nephus rubromaculatus*. But the pale spots on the elytron and the elytral size are different, and the photographs sent to a specialist did not elicit a response (figure 81). So, this species identification has not been confirmed.

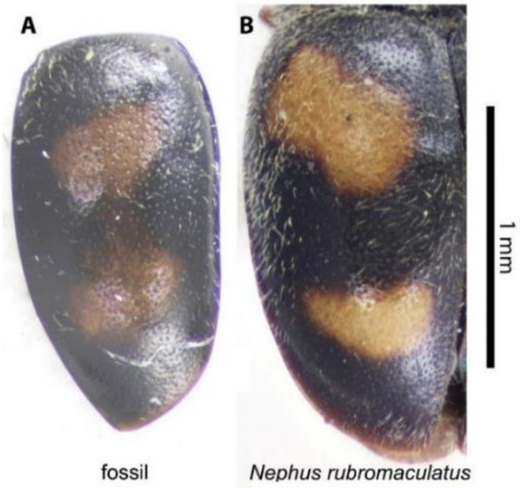


Figure 81. A fossil elytron; **B** modern *N. rubromaculatus* elytron.

13) *Corticaria* (Lathridiidae)

As figure 82 shows, the pronotum of *Corticaria baicalica* is too small, and *Corticaria geisha*, although the size matches the fossil, the color is too pale. Also, this species is only found in south China and Japan.

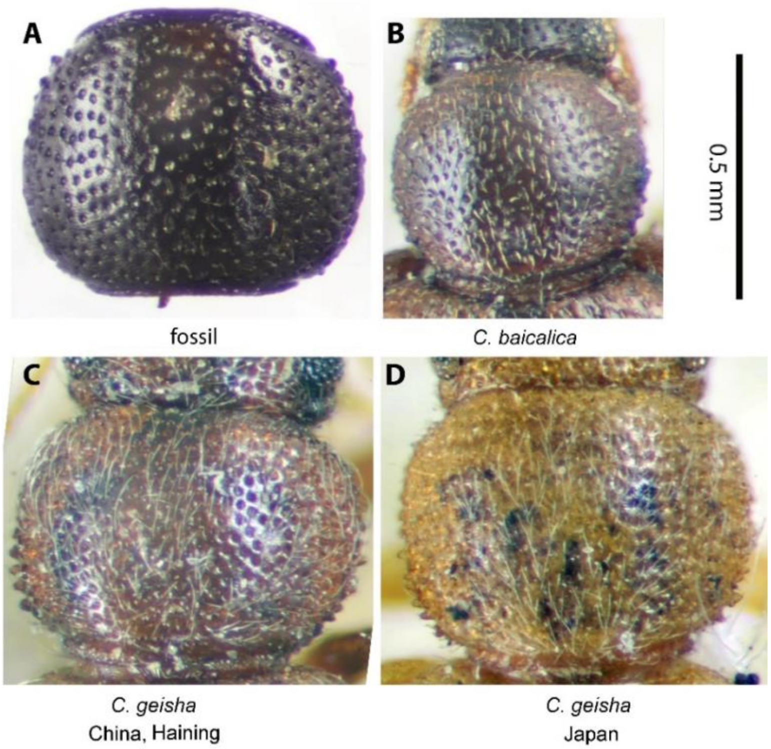


Figure 82. A fossil *Corticaria* pronotum; **B** modern *C. baicalica* pronotum; **C** modern *C. geisha* pronotum, Chinese specimen; **D** modern *C. geisha* pronotum, Japanese specimen.

14) *Smaragdina* (Chrysomelidae)

The only species found in the London Natural History Museum collection that has a blue pronotum and is similar to the size of fossil elytron is *Smaragdina obscuripes*. However, the shape of the pronotum does not match the fossil (figure 83).

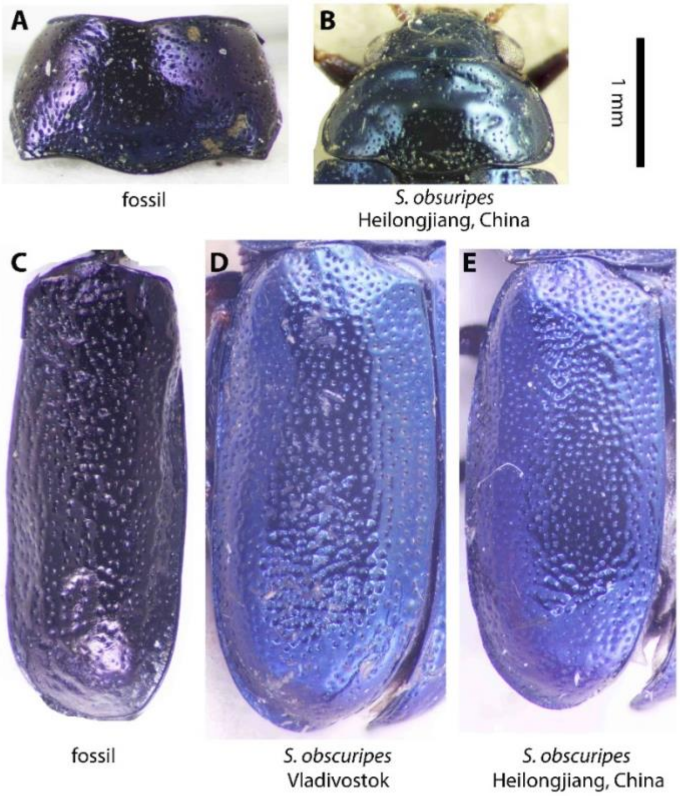


Figure 83. **A** fossil *Smaragdina* pronotum; **B** modern *S. obscuripes* pronotum, specimen from Heilongjiang, China; **C** fossil *Smaragdina* elytron; **D** modern *S. obscuripes* elytron, specimen from Vladivostok; **E** modern *S. obscuripes* elytron, specimen from Heilongjiang, China

15) *Altica* (Chrysomelidae)

Based only on the fossil head, pronotum and elytra, it is difficult to identify *Altica* to species (figure 84). *Altica* species are externally similar to each other, and they are often identifiable only by the aedeagus.

Figure 84. **A** fossil *Altica* head; **B** fossil *Altica* pronotum; **C – F** fossil *Altica* elytra.

16) *Cassida* (Chrysomelidae)

Based only on the fossil pronotum and elytra, *Cassida prasina* is a possible match for the fossil, but *C. prasina* does not match the dark pattern on the pronotum and elytron of the fossil (figure 85).

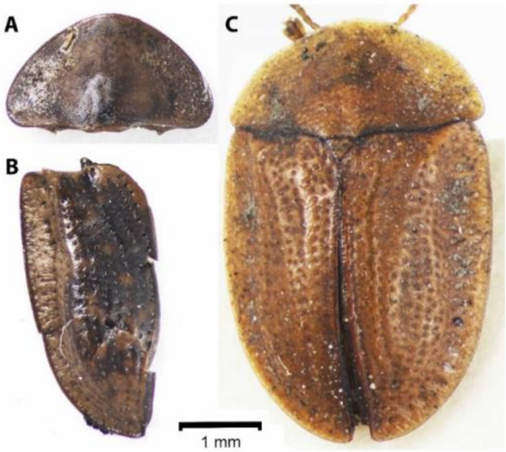


Figure 85. A fossil *Cassida* pronotum; **B** fossil *Cassida* elytron; **C** modern *Cassida prasina*.

17) *Trypodendron* (Scolytidae)

The species of *Trypodendron* vary a great deal in size and markings. As figure 86 shows, the specimen of *T. lineatum* matches the color pattern of the fossil, but it is larger. There are about five or six Palaearctic species, but the NHM does not have modern collections of them.

Figure 86. A fossil *Trypodendron* elytral fragment; **B** modern *T. lineatum* elytron.

Although specimens could only be identified to the genus, its occurrence can indicate the presence of trees.

5.2 Peat accumulation rates

Figure 87 and 88 show the variation of peat accumulation rates from the two profiles. For Profile One (from 6374 to 4378 cal. yr BP), peat accumulated faster from layer 75-80 cm to layer 35-40 cm (5493 to 5420 cal. yr BP), and slower in the other layers (almost less than 0.1 cm/year). For Profile Two (from 9500 to 10,424 cal. yr BP), the peat accumulated faster at the bottom (10424 to 10,318 cal. yr BP), and accumulated generally slower from layer 145-150 cm to layer 60-65 cm (10,307 to 9705 cal. yr BP), and faster again from layer 55-60 cm upwards (9665 to 9500 cal. yr BP). The average peat accumulation rate of Profile One is 0.073 cm/year, and the average peat accumulation rate of Profile Two is 0.21 cm/year, which is about three times faster than Profile One.

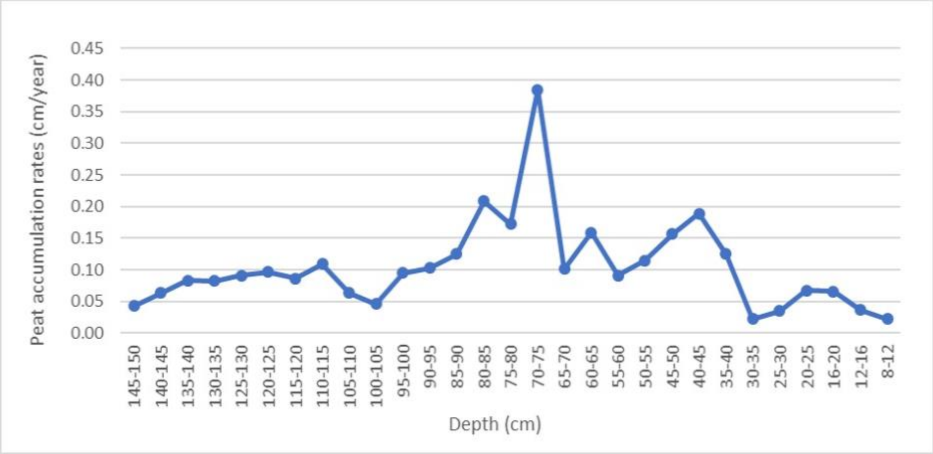


Figure 87. the variation of peat accumulation rates from Profile One.

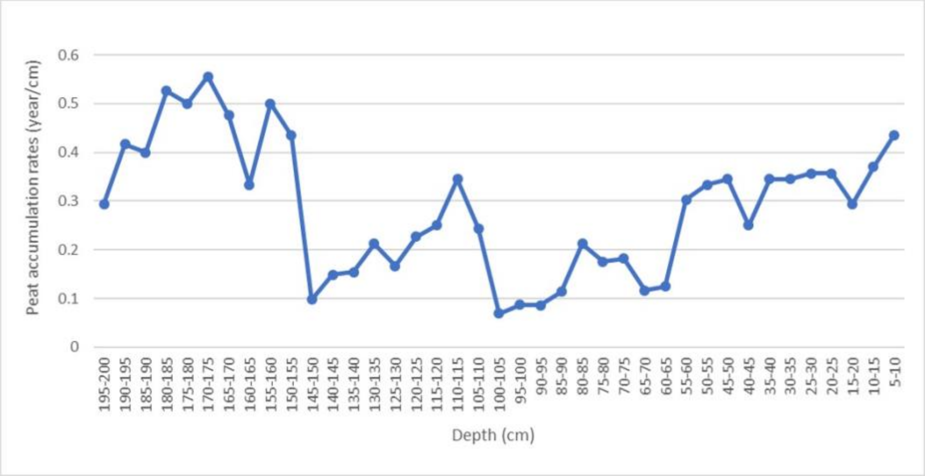


Figure 88. the variation of peat accumulation rates from Profile Two.

5.3 The Mutual Climatic Range result

The majority species in the BugsCEP are European fauna. Some Chinese species such as *Haliplus chinensis* or *Ceratomegilla rickmersi* are not included in this database. Fortunately, most of the beetle species identified from the Halashazi profiles are also found in Europe, thus the BugsCEP has the climate envelopes for them. Based on these species, the MCR estimates of palaeotemperature have been created. Unfortunately, a number of species in the fossil assemblages have wide temperature ranges (eurythermic). However, the MCR analyses still provided some useful information on palaeotempertures. Table 8 shows the species have been used in BugsCEP to create the MCR.

Number	Profile one	Profile two
1	*Nebria nivalis* (Payk.)	*Patrobus septentrionis* Dej.
2	*Bembidion lampros* (Hbst.)	*Pterostichus brevicornis* (Kirby)
3	*Agonum consimile* (Gyll.)	*Agonum consimile* (Gyll.)
4	*Hydroporus umbrosus* (Gyll.)	*Hydroporus notabilis* (LeC.)
5	*Hydroporus striola* (Gyll.)	*Hydroporus umbrosus* (Gyll.)
6	*Ochthebius hungaricus* (Endr. Y)	*Hydroporus striola* (Gyll.)
7	*Enochrus fuscipennis* (Thoms.)	*Ochthebius hungaricus* (Endr. Y)
8	*Thanatophilus dispar* (Hbst.)	*Helophorus sibiricus* (Mots.)
9	*Olophrum boreale* (Payk.)	*Helophorus pallidus* (Gebl.)
10	*Olophrum rotundicolle* (Sahl.)	*Enochrus fuscipennis* (Thoms.)
11	*Acidota crenata* (F.)	*Olophrum boreale* (Payk.)
12	*Gymnusa variegata* (Kies.)	*Olophrum rotundicolle* (Sahl.)
13	*Hippodamia tredecimpunctata* (L.)	*Acidota crenata* (F.)
14	*Galeruca tanaceti* (L.)	*Gymnusa variegata* Kies.
15	*Phyllotreta cruciferae* (Goeze)	*Cytilus sericeus* (Forst.)
16	*Chaetocnema obesa* (Boield.)	*Hippodamia tredecimpunctata* (L.)
17		*Phaedon armoraciae* (L.)
18		*Plagiodera versicolora* (Laich.)
19		*Galeruca tanaceti* (L.)
20		*Chaetocnema obesa* (Boield.)

Table 8. List of the species have been used to create MCR in the BugsCEP program.

5.3.1 MCR estimates for Profile one

16 species have been used in this profile to create the MCR estimates. In figure 89, the black bars represent the range of TMax and TMin during much of the middle Holocene (from 6374 to 4378 cal. yr BP), TMax and TMin values do not change significantly. The highest July temperature is around 15 °C, and the lowest July temperature is around 9 °C; the highest January temperature is around 0 °C, and the lowest January temperature is about -20 °C.

In layer 8-12 cm, the minimum TMax value was 13 °C. A comparison of the species in this sample with other samples shows that the presence of the ground beetle *Bembidion lampros* in this sample narrowed the range of TMax and indicated a warmer interval around 4561 cal. yr BP. And in the layer 20-25 cm, which is about 4805 cal. yr BP, the appearance of the ground beetle *Nebria nivalis* indicates a colder interval, with July temperatures between 9°C and 11 °C. Unfortunately, the assemblage from 75-80 cm contained only beetle species for which climatic data are unavailable, so I could not reconstruct the temperature for this period. Also, the assemblages from 120-130 cm and 135-145 cm, contained only eyrthermic species that have very wide temperature ranges. Thus, the MCR results from these layers are not useful.

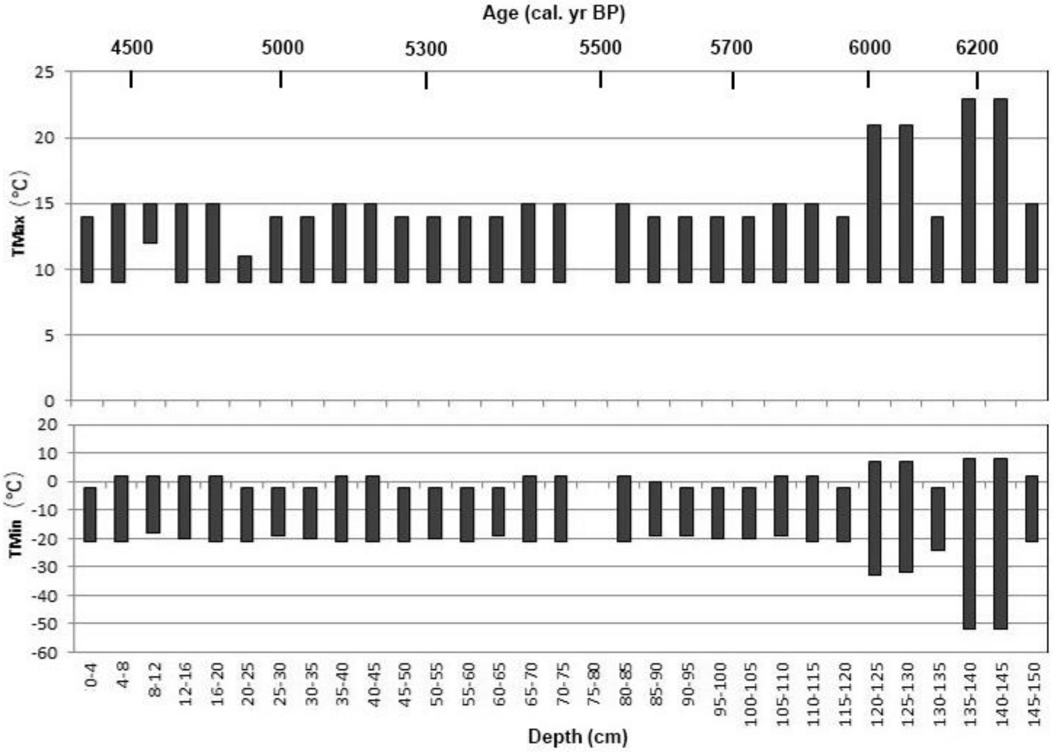


Figure 89. MCR estimates of TMax and TMin for Profile One (middle Holocene).

5.3.2 MCR estimates for Profile two

In Profile two, 20 species have been used in the MCR analysis. This profile represents the early Holocene, and dates from 10,424 cal. yr BP to 9500 cal. yr BP. As the MCR results show (figure 90), the temperature does change significantly during this interval. Most TMax values range between about 9 °C and 14 °C, and the TMin values range between about -19 °C and -3°C. Compared with Profile one, the range of temperatures in this profile are slightly narrower, but the temperature estimates from the early Holocene and the late Holocene assemblages do not show large differences. In Profile two, the assemblages from samples 45-50 cm, 120-125 cm, 145-150 cm, 175-180 cm and 190-195 cm show a slightly narrower range of both TMax and TMin. These estimates have the highest minimum mean July temperatures and the lowest maximum mean January temperatures (Figure 90). This is due to the presence of *Pterostichus brevicornis* in these samples. Again, the range of temperatures from the sample 0-5 cm is virtually useless, because this assemblage only contains eurythermic species

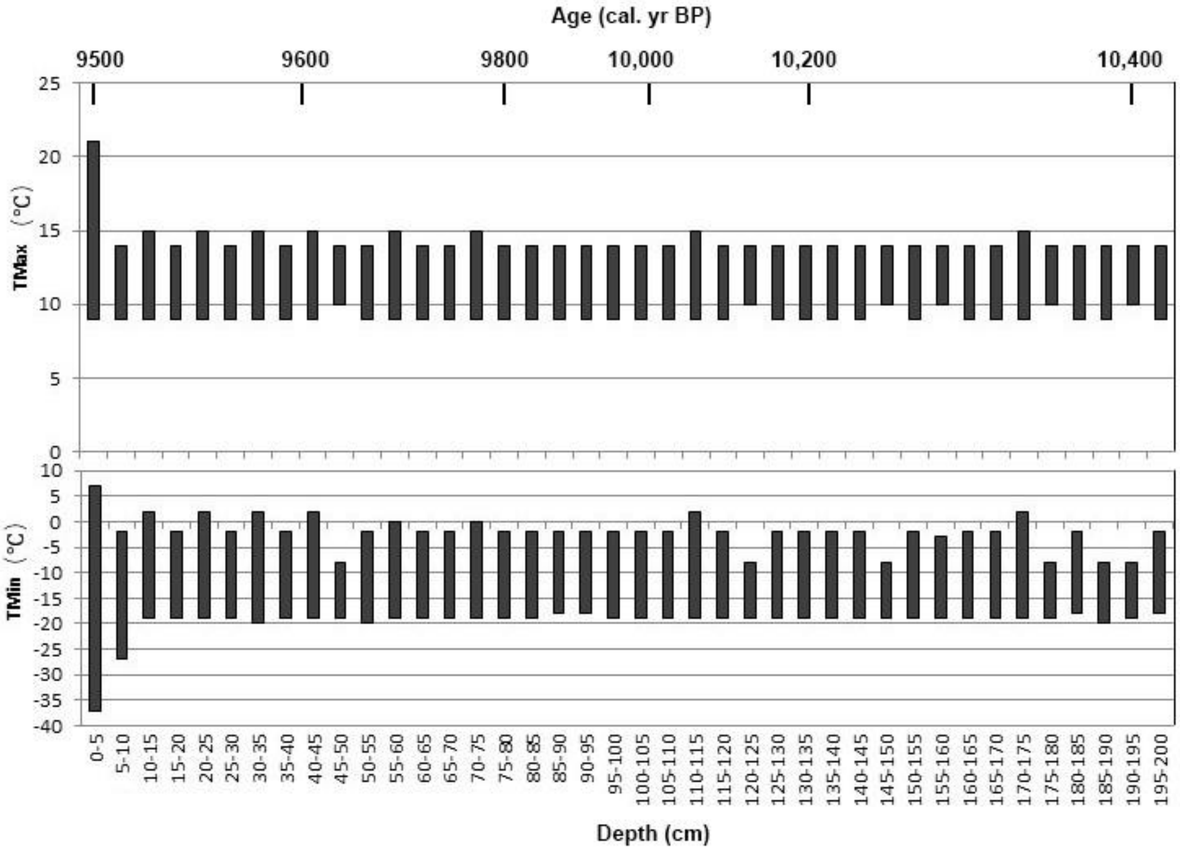


Figure 90. MCR estimates of TMax and TMin for Profile Two (early Holocene).

5.3.3 Reasons for poorly constrained MCR estimates

Unfortunately, most of the MCR estimates did not provide well-constrained reconstructions of palaeotemperature in this project. The TMAX and TMIN temperatures do not vary substantially through time, and the ranges of estimated temperatures are quite broad. One reason for the poorly constrained MCR estimates is the lack of stenothermic species in the fossil assemblages. In most intervals, all of the species used in the MCR estimates have a wide range of temperature tolerances, leading to wide ranges of temperature overlaps of the climate envelopes of these species.

Another reason for the poorly constrained estimates is the small number of identified species in the faunal assemblages. Because the sampled peat was frozen, it was extremely difficult to cut the kind of continuous and deep (both from front to back and from top to bottom) profile that might have yielded larger fossil assemblages. Even though the largest possible sediment samples were taken, the number of fossil beetle specimens extracted from the samples were disappointingly small. On the other hand, the peat samples taken from permafrost were subject to less disturbance, and exhibited the excellent preservation seen in permanently frozen specimens (Elias, 2013). Future regional studies should employ a larger field team, using powered equipment (e.g., chainsaws) to obtain larger quantity samples that would likely yield more abundant, diverse faunal assemblages.

The third reason for the lack of well-constrained MCR estimates is that the faunal assemblages contained some Chinese taxa for which species climate envelopes have not yet been developed. Since this is the first fossil beetle study in this area and in China, about one-third of taxa were not identified to the species level. As discussed above, 28 species were identified from Profile One, and 16 of these species have been used in the MCR analysis; 49 species were identified from Profile Two, and only 20 of these species have had species climate envelopes developed, allowing their use in MCR analysis. Therefore, this is one of the main causes of poorly-constrained MCR estimates in this project. At present, most of the Chinese species do not have sufficient collection locality records to allow the preparation of species climate envelopes. The process is also hindered by the lack of meteorological data associated with their collecting localities. In order to solve this problem, it will be necessary to carry out extensive further studies of the distribution and ecology of the modern beetle fauna of the study area, and then construct climate envelopes for these species. This process will take at least one to two years of additional research to complete.

Chapter 6. Discussion

6.1 Ecological groups of beetles

As discussed above, the ecological groups of beetles have often been used to reconstruct past environments as part of archaeological research. Of course, many insect fossil studies have been purely palaeontological in nature – not associated with human habitations. The best of such studies have dealt with large, diverse faunal assemblages. However, the present study has neither large numbers of samples or large faunal diversity, nor have the assemblages been disturbed by human beings. However, the analysis of "ecological groups" still provides some information on the palaeoecology of the study site. Under natural conditions (without human interference), changes in the composition of species in fossil assemblages is usually driven by environmental drivers, such as changes in temperature and moisture. Because many beetle species have relatively narrow thermal tolerances, their presence in an assemblage give a clear indication of a specific temperature range. Thus, the appearance of high- temperature- tolerant species indicates a warm environment. Conversely, the presence of cold adapted species indicates lower temperature conditions, regardless of their relative proportion in the assemblage (as long as the other species in the assemblage are adapted to a wide range of temperatures, including the lower temperatures indicated by the cold-adapted species). However, soil moisture might also affect the composition of beetle assemblages, especially in arid regions.

The following section uses statistical analysis of the various ecological groups found in the fossil assemblages as an independent means of palaeoenvironmental study. The analysis focuses on past moisture conditions. It does not provide a specific value, such as the past mean annual precipitation, but it might show the variation of beetle species in relation to changes in past moisture conditions. Based on their moisture requirements, each species found in the fossil assemblages has been assigned to one ecological group. These ecological groups include water- associated species, open landscape species, and woodland associated species (Table 9). Because of the small number of samples, the aquatic species were not excluded from the analysis, and have been assigned as water associated species.

Table 9. Ecological groups (based on the moisture requirements of beetles)

	Ecological Groups	**Definition**	**Species**
Water associated	Aquatic	Aquatic species which spend the majority of their adult life in water.	*Helophorus sibiricus; Helophorus pallidus; Hydrobius subrotundus; Haliplus chinensis; Ochthebius hungaricus; Ilybius spp.; Colymbetes spp.*
	Water side	Species usually living at the edge of ponds, lakes or slow streams.	*Blethisa catenaria; Elaphrus sibiricus; Nebria nivalis; Patrobus septentrionis; Pterostichus agonus; Agonum consimile; Olophrum boreale; Olophrum rotundicolle; Thanatophilus dispar; Hydrobius subrotundus*
	Peat bogs, fens and marshland	Hygrophilous species, found across a variety of semi-aquatic environments, such as peat bogs, marsh, swamp, and fens.	*Agonum quinquepunctatum; Hygrotus impressopunctatus; Hydroporus notabilis; Hydroporus striola; Hydroporus umbrosus; Helophorus sinoglacialis; Enochrus fuscipennis; Acidota crenata; Gymnusa variegata*
	Aquatic Plants	Chrysomelidae and Curculionidae species which feed exclusively on aquatic or waterside plants.	*Phaedon armoraciae; Plagiodera versicolora; Chaetocnema obesa; Tournotaris bimaculatus*
	Moist localities	Species that live in moist localities (but not strictly 'wetlands') among moss or under stones.	*Arpedium brachypterum*
Open landscape	Grassland	Species found on grassland and meadows.	*Pterostichus brevicornis; Hippodamia tredecimpunctata; Cytilus sericeus: Phyllotreta cruciferae;*
	Leaves	Species found under moss or fallen leaves	*Bryophacis rufus;*
	Dry areas	Species that live in grassy areas with dry environments or sun-exposed ground	*Bembidion lampros; Galeruca tanaceti;*
Woodland associate	Trees	Species that live in woodland and develop in trees.	*Phloeotribus spinulosus; Trypodendron spp.*

6.1.1 Analysis of the ecological groups for Profile One

In total, 28 species and 492 individuals have been found in this profile. The number of individuals in each sample has been listed in table 10. As figure 91 shows, the number of individuals in profile one changed dramatically through time, as did the variation of the proportion of water- associated species. The proportion of open landscape species and woodland associated species were too small to be considered. The number of individuals in the samples from this profile are very small; some layers only have six or seven individuals, and the largest sample has only 28 individuals. Another problem is that most of the unidentified species are rove beetle (Staphylinidae), which generally occur at very high population densities (Kenward, 1978:3). Because the modern rove beetle fauna of the study region is poorly known, more than half of the samples have over 50 percent unidentified specimens of Staphylinidae (figure 92). Unfortunately, because of these problems, the past moisture conditions cannot be determined simply based on the proportion of water-associated species.

6.1.2 Analysis of the ecological groups for Profile Two

This profile contained a total of 49 species and 1,751 individuals. The number of individuals in each sample in Profile Two have been listed in table 11. Compared with those from Profile One, this profile has more individuals per sample (Figure 93). Especially from 75 cm to 200 cm, most samples have more than 40 individuals, and the 80-85 cm layer has 79 individuals. The proportion of water- associated species obviously increase from layer 60-65 cm downwards, and remain at more than 50 percent (Figure 94). The total number of individuals, the individuals of water- associated species, and the proportion of water associated species increased from layer 75-80 cm downwards. This change may have come about for many reasons, such changes in population densities, changes in the local water table causing changes of the formation of the deposit and changes in the richness of aquatic vegetation. However, within this constrained profile, the number of individuals and the proportion of water-associated species in the samples from 75 cm to 200 cm was about two- thirds larger than that proportion in samples from 0 cm to 75 cm. Based on this large difference, changes in local moisture conditions could be considered a main impact factor. Therefore, the samples from 75 to 200 cm, probably represent at least local wetter conditions.

Table 10. The number of indivaduls of each ecological group and the proportions of Profile One

Depth (cm)	Water associated							Open landscape					Woodland		Unidentified species		Total number of specimen
	Aquatic	Water side	Peat bogs, fens and marshland	Aquatic Plants	Moist localities	Total	Proportions (%)	Grassland	Leaves	Dry area	Total	Proportions (%)	Trees	Proportions (%)	Total	Proportions (%)	
0-4	0	3	2	0	0	5	38.46	0	0	0	0	0	0	0	8	61.54	13
4-8	0	1	2	0	0	3	50.00	0	0	0	0	0	0	0	3	50.00	6
8-12	0	3	1	0	0	4	22.22	0	0	1	1	5.56	0	0	13	72.22	18
12-16	0	6	4	0	0	10	43.48	0	0	0	0	0	0	0	13	56.52	23
16-20	0	6	3	0	0	9	64.29	0	0	0	0	0	0	0	5	35.71	14
20-25	0	8	4	0	0	12	54.55	1	0	0	1	4.55	0	0	9	40.91	22
25-30	0	7	8	0	0	15	60.00	0	0	0	0	0	0	0	10	40.00	25
30-35	0	14	8	0	0	22	78.57	0	0	0	0	0	0	0	6	21.43	28
35-40	0	8	7	0	0	15	62.50	0	0	0	0	0	0	0	9	37.50	24
40-45	0	2	4	1	0	7	58.33	0	0	0	0	0	0	0	5	41.67	12
45-50	0	10	9	0	1	20	76.92	0	0	0	0	0	0	0	6	23.08	26
50-55	1	9	6	0	0	16	66.67	0	0	0	0	0	0	0	8	33.33	24
55-60	0	6	7	0	0	13	86.67	0	0	0	0	0	0	0	2	13.33	15
60-65	1	5	9	0	1	16	64.00	0	0	1	1	4.00	0	0	8	32.00	25
65-70	0	1	5	0	0	6	50.00	0	0	0	0	0	1	8.33	5	41.67	12

Table 10. (continued)

Depth (cm)	Water associated							Open landscape					Woodland		Unidentified species		Total number of specimen
	Aquatic	Water side	Peat bogs, fens and marshland	Aquatic Plants	Moist localities	Total	Proportion (%)	Grassland	Leaves	Dry area	Total	Proportion (%)	Trees	Proportion (%)	Total	Proportion (%)	
70-75	0	1	4	0	0	5	45.45	0	1	0	1	9.10	0	0	5	45.45	11
75-80	0	0	2	0	0	2	25.00	0	0	0	0	0	0	0	6	75.00	8
80-85	0	1	6	1	0	8	47.06	0	0	0	0	0	0	0	9	52.94	17
85-90	0	2	3	0	1	6	37.50	0	0	0	0	0	0	0	10	62.50	16
90-95	0	5	5	0	0	10	50.00	0	0	0	0	0	0	0	10	50.00	20
95-100	0	5	3	0	0	8	40.00	0	0	0	0	0	0	0	12	60.00	20
100-105	0	6	6	0	1	13	72.22	0	0	0	0	0	0	0	5	27.78	18
105-110	0	1	8	0	0	9	60.00	0	0	0	0	0	0	0	6	40.00	15
110-115	0	1	4	0	0	5	50.00	0	0	0	0	0	0	0	5	50.00	10
115-120	0	3	5	1	2	11	68.75	0	0	0	0	0	0	0	5	31.25	16
120-125	0	0	4	0	0	4	50.00	0	0	0	0	0	0	0	4	50.00	8
125-130	0	0	5	0	0	5	41.67	0	0	0	0	0	0	0	7	58.33	12
130-135	0	1	3	0	0	4	57.14	0	0	0	0	0	0	0	3	42.68	7
135-140	0	0	2	0	0	2	28.57	0	0	0	0	0	0	0	5	71.43	7
140-145	0	0	2	0	0	2	33.33	0	0	0	0	0	0	0	4	66.67	6

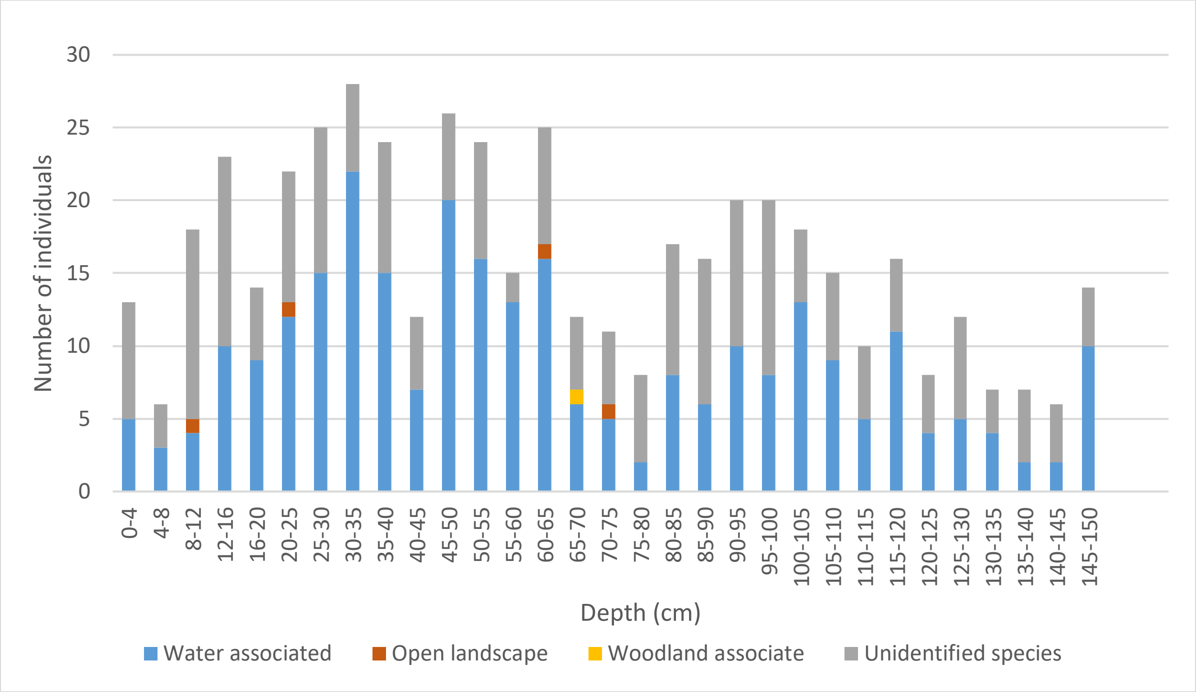


Figure 91. The number of individuals of water associated species, open landscape species, woodland associated species and unidentified species of Profile One.

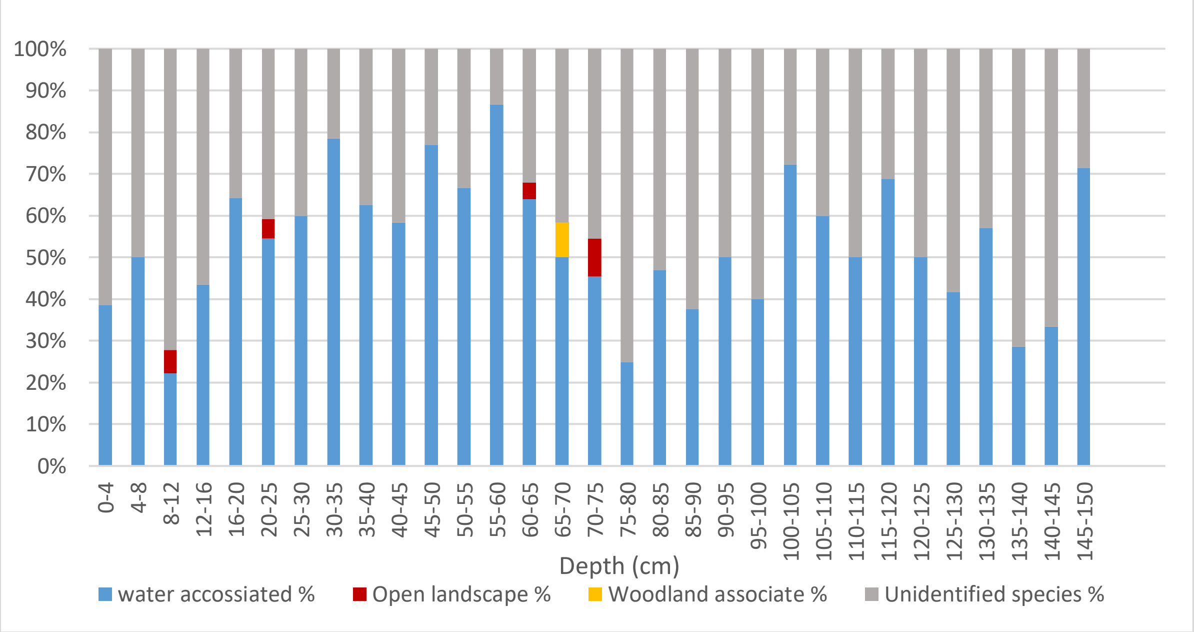


Figure 92. The variation trend of the proportion of water associated species of Profile One

Table 11. the number of individuals of each ecological group of Profile Two.

Depth (cm)	Water associated							Open landscape					Woodland		Unidentified species		Total number of specimen
	Aquatic	Water side	Peat bogs, fens and marshland	Aquatic Plants	Moist localities	Total	Proportion (%)	Grassland	Leaves	Dry area	Total	Proportion (%)	Trees	Proportion (%)	Total	Proportion (%)	
0-5	0	0	2	0	0	2	15.38	0	0	0	0	0	0	0	11	84.62	13
5-10	0	1	1	0	0	2	11.11	0	0	1	1	5.56	0	0	15	83.33	18
10-15	4	1	7	0	0	12	38.71	0	0	0	0	0	0	0	19	61.29	31
15-20	2	3	3	0	0	8	23.53	0	0	0	0	0	0	0	26	76.47	34
20-25	1	1	5	0	0	7	28.00	0	0	0	0	0	0	0	18	72.00	25
25-30	5	2	6	0	0	13	34.21	0	0	0	0	0	1	2.63	24	63.16	38
30-35	0	2	5	0	0	7	35.00	0	0	0	0	0	0	0	13	65.00	20
35-40	3	2	4	2	0	11	40.74	0	0	0	0	0	0	0	16	59.26	27
40-45	1	1	5	0	0	7	26.92	1	0	0	1	3.85	0	0	18	69.23	26
45-50	1	2	10	0	0	13	43.33	1	0	0	1	3.33	0	0	16	53.33	30
50-55	2	5	6	0	0	13	39.39	0	0	0	0	0	0	0	20	60.61	33
55-60	0	2	4	2	0	8	27.59	0	0	0	0	0	2	6.90	19	65.52	29
60-65	2	5	5	2	1	15	51.72	0	0	0	0	0	0	0	14	48.28	29
65-70	1	5	7	6	4	23	65.71	0	0	0	0	0	0	0	12	34.29	35
70-75	4	3	9	7	4	27	71.05	0	0	0	0	0	0	0	11	28.95	38
75-80	6	11	14	7	3	41	67.21	0	0	0	0	0	0	0	20	32.79	61
80-85	4	11	14	3	11	43	54.43	0	0	0	0	0	0	0	36	45.57	79
85-90	2	7	7	2	12	30	56.60	0	0	0	0	0	0	0	23	43.40	53
90-95	2	14	12	1	5	34	59.65	0	0	0	0	0	0	0	23	40.35	57
95-100	2	9	17	2	7	37	64.91	0	0	0	0	0	0	0	20	35.09	57

Table 11. (continued)

Depth (cm)	Water associated							Open landscape					Woodland		Unidentified species		Total number of specimen
	Aquatic	Water side	Peat bogs, fens and marshland	Aquatic Plants	Moist localities	Total	Proportion (%)	Grassland	Leaves	Dry area	Total	Proportion (%)	Trees	Proportion (%)	Total	Proportion (%)	
100-105	2	10	18	1	1	32	72.73	0	0	0	0	0	0	0	12	27.27	44
105-110	1	7	14	2	0	24	61.54	0	0	0	0	0	0	0	15	38.46	39
110-115	1	4	19	1	1	26	60.47	0	0	0	0	0	0	0	17	39.53	43
115-120	1	5	12	3	3	24	57.14	0	0	0	0	0	0	0	18	42.86	42
120-125	1	11	15	5	2	34	70.83	1	0	0	1	2.08	0	0	13	27.08	48
125-130	2	7	10	4	1	24	57.14	0	0	0	0	0	0	0	18	42.86	42
130-135	3	15	9	2	3	32	71.11	0	0	0	0	0	0	0	13	28.89	45
135-140	1	10	7	2	3	23	52.27	0	0	0	0	0	0	0	21	47.73	44
140-145	0	8	7	3	2	20	55.56	0	0	0	0	0	0	0	16	44.44	36
145-150	3	4	13	3	3	26	61.90	1	1	0	2	4.76	0	0	14	33.33	42
150-155	1	12	16	3	13	45	61.64	0	0	0	0	0	0	0	28	38.36	73
155-160	2	11	21	3	2	39	72.22	0	0	0	0	0	0	0	15	27.78	54
160-165	2	9	18	6	4	39	70.91	0	0	0	0	0	0	0	16	29.09	55
165-170	2	8	16	4	3	33	64.71	0	0	0	0	0	0	0	18	35.29	51
170-175	3	8	14	3	9	37	74.00	0	0	0	0	0	0	0	13	26.00	50
175-180	1	13	10	2	7	33	63.46	1	0	0	1	1.92	0	0	18	34.62	52
180-185	6	11	12	4	13	46	62.16	0	0	0	0	0	0	0	28	37.84	74
185-190	3	8	6	3	7	27	54.00	1	0	0	1	2.00	0	0	22	44.00	50
190-195	1	4	8	7	14	34	54.84	1	0	0	1	1.61	0	0	27	43.55	62
195-200	0	11	13	4	18	46	64.79	2	1	0	3	4.23	0	0	22	30.99	71

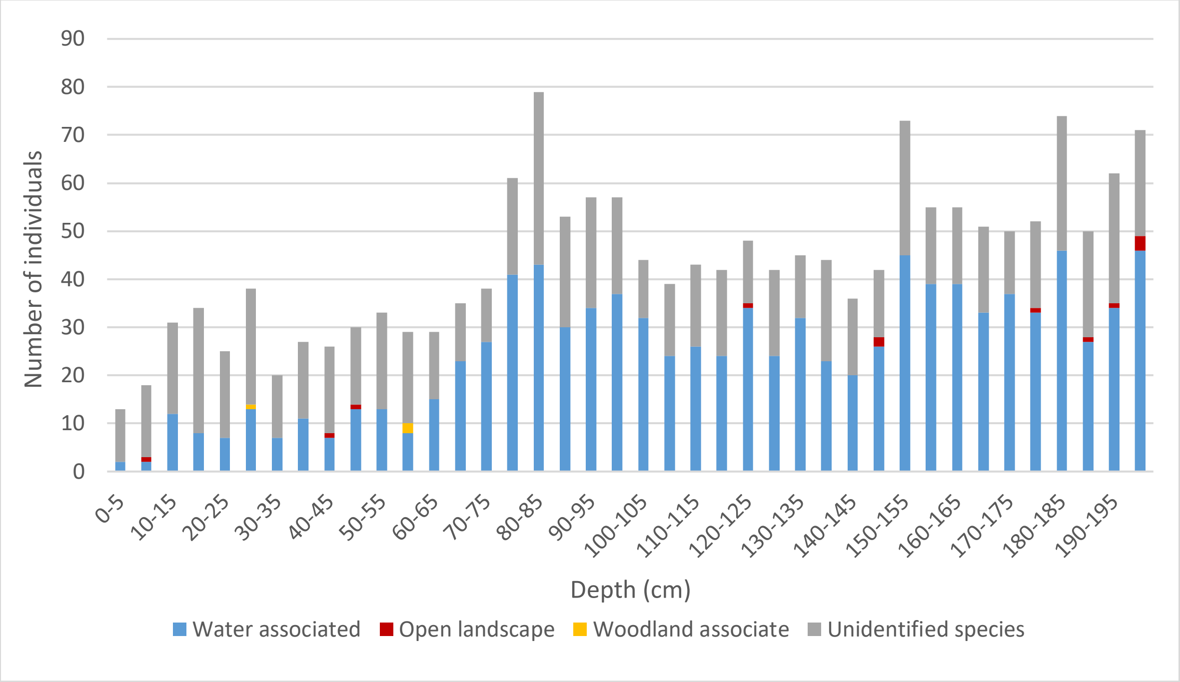


Figure 93. the number of individuals of water associated species, open landscape species, woodland associated species and unidentified species of Profile Two.

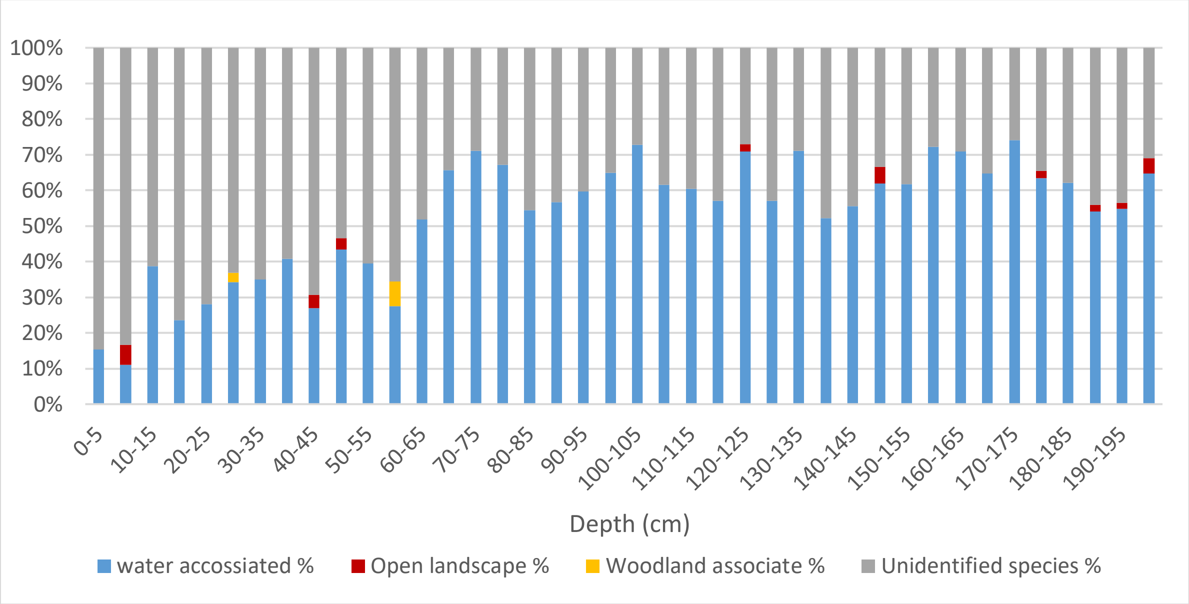


Figure 94. The variation trend of the proportion of water associated species of Profile Two.

Overall, statistical analysis of ecological groups requires large numbers of identified species in the samples. Unfortunately, this research yielded only small faunal assemblages, and many assemblages contain unidentified species. Another limiting factor in the project was that peat accumulates mainly in water, so fossil peats usually are dominated by water- associated species. However, the assemblage data do provide some information about past climates, albeit limited. The woodland associated species are very few, but they are relative to the local presence of trees.

6.2 Insect taphonomy in peat deposits

A comparison of the two profiles shows that Profile Two has far greater species diversity, and also has many more individuals, both in total and within each sample. Even though the samples from both profiles contained the same volume of sediment (about two kilograms per sample), there is a substantial difference in diversity and abundance of fossils. These differences may have been caused by several factors. The two profiles were collected from two different localities, about 200 meters apart. There were very likely differences in the palaeoenvironmental settings of the two sampling sites, such as differences in local hydrology and aquatic vegetation cover. The edges of lake shores or wetland margins that remain wet during the growing season usually have more abundant aquatic plant cover. This, in turn, may have helped in the accumulation and preservation of peat deposits. Local hydrological conditions may be affected by many factors. For example, the distance of the sample localities to nearby ponds, and the proximity to streams or springs. Low-lying lands usually collect more water.

As stated above in the literature review, anoxic environment could help the preservation of fossil insect, rapid peat accumulation rates aid in the rapid burial of insect remains in lacustrine environments, placing them in anoxic sediments, thus retarding decomposition. Therefore, the different peat accumulation rates in this study are an important preservational factor, which influences the abundance and diversity of insect remains from these two profiles.

The differences in local environmental conditions are evidenced by the differences noted in the peat accumulation rates for the two profiles. As discussed above, the average peat accumulation rate of Profile One is 0.073 cm/year, and the average peat accumulation rate of Profile Two is 0.21 cm/year, which is about three times greater than in Profile One. The higher accumulation rates are usually associated with wetter conditions and richer plant cover. Rapid peat accumulation also reduces the exposure time of insect remains to atmospheric oxygen.

Exposure on the surface leads to rapid decomposition of dead insects. However, insect carcasses rapidly buried in aquatic peat soon enter an anoxic environment in which decomposition is greatly retarded. Peat accumulation rates may only have been driven by local moisture conditions. So, given local variability in these conditions, it cannot be simply concluded that more fossil remains from one profile indicate wetter climate than at the other profile. The peat deposits only reflect local moisture conditions. In order to reconstruct a regional history of precipitation levels, it would be necessary to collect more samples from additional regional study sites, in order to obtain a regional reconstruction.

6.3 Palaeoenvironmental reconstruction

6.3.1 Early Holocene interpretation (Profile two: ~10,424 to ~9500 cal. yr BP)

Most species in these fossil assemblages inhabit moist environments, and live along the edge of water, such as peaty pools, bogs or ponds with rich vegetation. Thus, the early Holocene probably was a wet interval. The dominant vegetation was moss. The estimated mean July temperatures ranged from 9 ℃ to 15 ℃. This range of temperatures is close to the modern temperature (11.6 ℃). The estimated mean January temperature, which ranges from - 20 ℃ and 0 ℃ is warmer than the modern mean January temperature (-25.7 ℃). But as stated above in the literature review, beetles are active mainly in the summer, then they shelter in protected environments (such as mud, beneath snow, in piles of leaves) during winter. Thus, fossil beetles provide more reliable indications of summer temperature, and less accurate estimates of winter temperature. Although the estimated temperature range is wide and does not show significant variation, the appearance of three cold adapted species (the ground beetle *Patrobus septentrionis*, and the rove beetles *Arpedium brachypterum* and *Olophrum boreale*) and two bark beetle species *Phloeotribus spinulosus* and *Trypodendron sp*.) in this fossil assemblage help define the temperature changes during the early Holocene more clearly. Instead of providing a specific temperature estimate, the indicator species usually provide information on environments, such as vegetation cover or altitude of tree line, therefor inferring climatic conditions.

200-60 cm (from 10,424 to 9705 cal. yr BP)

In this interval, the specimens of *Patrobus septentrionis*, *Arpedium brachypterum* and *Olophrum boreale* were found in almost all of the layers. *P. septentrionis* usually lives on mountain tops and on the northern tundra; *A. brachypterum* lives almost exclusively above tree line, close to the edges of snowfields; *O. boreale* usually lives in alpine areas above tree line. These three species are semi-montane species that can only survive in cold environments and live above tree line. Variations of tree line reflect temperature changes. The modern tree line in the study region is about 2300 m above the sea level (Zhang and Hai, 2002), while the altitude of the study site is 2450 m, and today there are no trees near the sample site. These semi-montane, cold-adapted species could indicate a relatively cold climate, at least as cold as today, or even colder. Thus, from 10,424 to 9705 cal. yr BP, the appearance of cold-adapted species in all of the layers indicate a relatively cold interval.

60-20 cm (from 9665 to 9556 cal. yr BP)

The cold adapted species were not found in any of these samples, while two bark beetle taxa (*Phloeotribus spinulosus* and *Trypodendron sp.*) were found in layer 60-55 cm (9665 cal. yr BP). Also, a *Phloeotribus spinulosus* specimen was found in layer 30-25 cm (9570 cal. yr BP). These species live on spruce, usually on the lower branches of standing green trees (Knizek, written communication, 2017). Bark beetles spend nearly all of their lives in and around their host trees, emerging only once to find a mate (Elias, personal communication, 2017). Thus, it is likely that these specimens represent beetles that actually lived at or very close to the study site. The appearance of bark beetles in the fossil assemblages indicates the possibility of the presence of trees near the site. However, there were only three specimens found in this profile (two specimens in layer 60-55 cm and one specimen layer 30-25 cm). As emphasised by Ponel et al. (1995) and Ponel and Richoux (1997), air-transport of insects is quite common in mountains and strong ascending currents could cause long distance transport from lower elevatrions. Smith et al. (2000) have found that pine bark beetles can fly some distance and end up in deposits they do not represent. Thus, we cannot rule out the possibility that these bark beetle fossils might have been transported by winds from lower altitude areas or that they flew from somewhere else to the Halashazi Wetland. Kenward (2006) analysed the spatial relationships between insect remains and woodland and trees from a range of modern deposits. He discovered that there was a general trend for the proportions of tree-associated insects from higher values in woodland and near to isolated trees, to low or zero values where there were no trees. However, the proportions of tree-associated insects varied greatly. Sometimes low values occurred in woods or near trees (Kenward, 2006). Thus, based solely on the presence three bark beetle fossils, it is hard to determine if tree line was at or above the study site during this interval. But the complete disappearance of the cold adapted species in layer 200 – 60 cm may indicate a warmer interval.

Another obvious variation in the sequence is the disappearance of the weevil *Tournotaris bimaculatus* from layer 60-55 cm, onwards. Otherwise, this species was found in every layer from 200-60 cm. This species lives on the banks of pools and marshes and in moist places. Its host plants are *Typha latifolia L.* and *Phalaris arundinacea L.* (Caldara and Brien, 1995). The larvae of this beetle inhabit the stems of these aquatic plants, so they require the presence of standing water (Hoffman, 1958). This indicates the possibility of climatic amelioration around 9665 cal. yr BP (60-55 cm), and this climate change may have affected the local hydrology, causing the nearby lake or wetland margins to recede. In addition to this, as discussed above in the ecological groups section, both total number of individuals and the proportion of water-associated species decrease markedly from this layer upwards (9665 cal. yr BP), which may also indicate the reduction of local moisture.

20-0 cm (9542 to 9500 cal. yr BP)

In layer 20-15 cm (9542 cal. yr BP), the presence of the cold adapted beetle *Patrobus septentrionis* indicates the temperature probably decreased from 9542 cal. yr BP and the study area might have become cold again. However, again, there is only one single individual which may have been blown to the site by winds.

In summary, the interval from 10,424 to 9705 cal. yr BP (200-60 cm), was probably a cold and wet period, and the study site was above tree line. From 9665 to 9500 cal. yr BP (60-0 cm), it was probably warmer and drier.

6.3.2 Middle Holocene interpretation (Profile one: 6374 to 4378 cal. yr BP)

Most fossil beetles found in this profile live in moist environments and marshy areas, and are found in or at the edge of small pools, bogs or slow flowing streams with rich vegetation. Some species, such as the rove beetle *Olophrum boreale* and *Arpedium brachypterum*, which usually live above tree line frequently occur in the following assemblages: 150-145 cm (6374 cal. yr BP), 120-115 cm (5951 cal. yr BP), 105-100 cm (5768 cal. yr BP), 90-85 cm (5557 cal. yr BP), 65-60 cm (5402 cal. yr BP), 50-45 cm (5272 cal. yr BP), 16-12 cm (4670 cal. yr BP). Thus, during most of the Middle Holocene, the study site was probably a wetland above tree line with small pools, bogs or streams. The vegetation is dominated by either moss or sedge, or both. The estimated mean July temperatures were from 9 ℃ to 14 ℃, and the estimated mean January temperatures were from -21 ℃ to 0 ℃. These ranges of temperatures are similar to those from the MCR results of the early Holocene. The TMAX values were close to the modern temperature at the site (11.6 ℃), and the TMIN values were warmer than the modern mean January temperature (-25.7 ℃). As in the early Holocene record, the middle Holocene MCR results do not provide many details on the variation of temperature. However, there are some intervals that have some special indicator species and these provide more specific information as discussed below.

70-65 cm (~5451 cal. yr BP)

In this interval, a specimen of the bark beetle *Phloeotribus spinulosus* has been found. The appearance of bark beetles indicates the possibility of the presence of trees near the study site. However, as stated above, this single specimen might have been carried by winds from lower altitude areas. So, around 5500 cal. yr BP, tree line might have moved towards higher elevations, which was likely caused by the onset of conditions warmer than present. However, but the bark beetle single specimen provides only flimsy evidence for this conclusion.

65-60 cm (~5402 cal. yr BP)

Just after the last interval during which bark beetles appeared, a specimen of the leaf beetle *Galeruca tanaceti* was found in this fossil assemblage. This species usually lives in very dry environments. Also, the fossil specimen of the rove beetle *Arpedium brachypterum* occurs in this layer. This species lives almost exclusively above tree line. Based on these taxa, this interval probably reflects a drier and colder climate.

25-20 cm (~4805 cal. yr BP)

The MCR results show that this is a colder interval with the estimated TMax between 9 ℃ and 11 ℃, which is slightly lower than the modern mean July temperature. But the fossil beetle assemblages contain species that live in pools and or around margins of water. A leaf beetle *Phyllotreta cruciferae* found in this assemblage also indicates the presence of *Cruciferae* species. So, the climate at this stage was probably relatively cold and wet.

20-16 cm (~4731 cal. yr BP)

This assemblage contained the carrion beetle *Thanatophilus dispar*. This is evidence that there were birds or mammals living in the study area.

12-8 cm (~4561 cal. yr BP)

The ground beetle *Bembidion lampros* occurred in this fossil assemblage. This beetle species inhabits sun-exposed ground. But there were also other species present that live around small pools and bogs. This might reflect a relatively drier stage, but apparently the ground did not dry out. Also, in this interval, the estimated mean July temperature is higher than the modern value. Compared with layer 20-25m (4805 cal. yr BP), the temperature raised significantly. Thus, the interval around 4561 cal. yr BP was probably warmer and drier.

In summary, during most of the interval from 6374 to 5464 cal. yr BP (150 cm -70 cm), was probably a cold period, and the study site was above tree line. Around 5451 cal. yr BP (70-65 cm), it was probably warmer than present, and the tree line might moved to higher elevation; around 5402 cal. yr BP (65-60 cm), the site was probably colder, and tree line moved back to lower elevations; from 5370 to 4949 cal. yr BP (60-25 cm), local conditions were probably cold period again; around 4805 cal. yr BP (25-20 cm), the estimated mean July temperature was only 9 ℃ to 11 ℃, which represented a cold interval; around 4561 cal. yr BP (12-8 cm), the interval was probably warm and relatively dry. TMAX raised to 13 ℃ to 15℃, which is warmer than present. From 8-0 cm (4378 cal. yr BP), the return of cold-adapted beetles signals the return to cold conditions.

6.4 Comparison of the beetle record with other proxies

6.4.1 Studies from the Halashazi site

1) peat cellulose carbon isotope ($\delta^{13}C$)

Huang (2015) analyzed the carbon isotopic record from peat cellulose samples spanning the last 11,500 cal. yr BP, taken from a peat core (ATM10-C7) taken from the Halashazi wetland. Huang's preliminarily interpretation was that the $\delta^{13}C$ record of Altay peat cellulose is primarily a palaeotemperature indicator. Higher $\delta^{13}C$ indicates warmer climate, lower $\delta^{13}C$ indicates colder climate. Figure 95 shows the variation of the $\delta^{13}C$ from the peat core. There are four stages in the palaeotemperature evolution sequence: 11,400 to 9900 cal. yr BP is a low temperature stage; 9900 to 6200 cal. yr BP is a high temperature stage, but with some brief cold fluctuations; 6200 to 3900 ka BP is a relatively low temperature stage; 3900 cal. yr BP to present is a relatively high temperature stage.

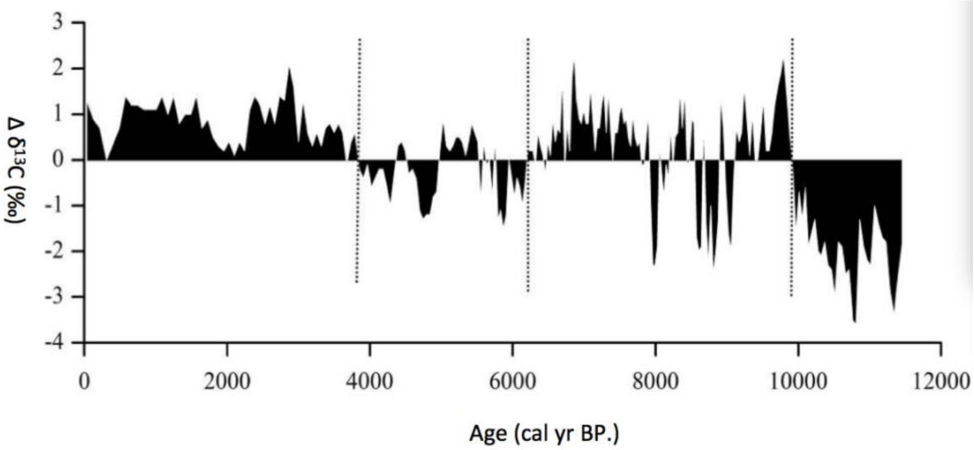


Figure 95. $\Delta\ \delta^{13}C$ (‰) of Halashazi peat cellulose. From Huang (unbublished Master desertation of Lanzhou University, 2015)

Compared with the fossil beetle record, both of the records show a colder early Holocene (figure 96). However, the fossil beetle records show this cold interval lasted until ~9700 yr BP, followed by a century of warmer temperatures, and then become cold again. On the other hand, the $\delta^{13}C$ record indicates an earlier and longer warm interval, which is from 9900 to 6200 cal. yr BP (figure 96).

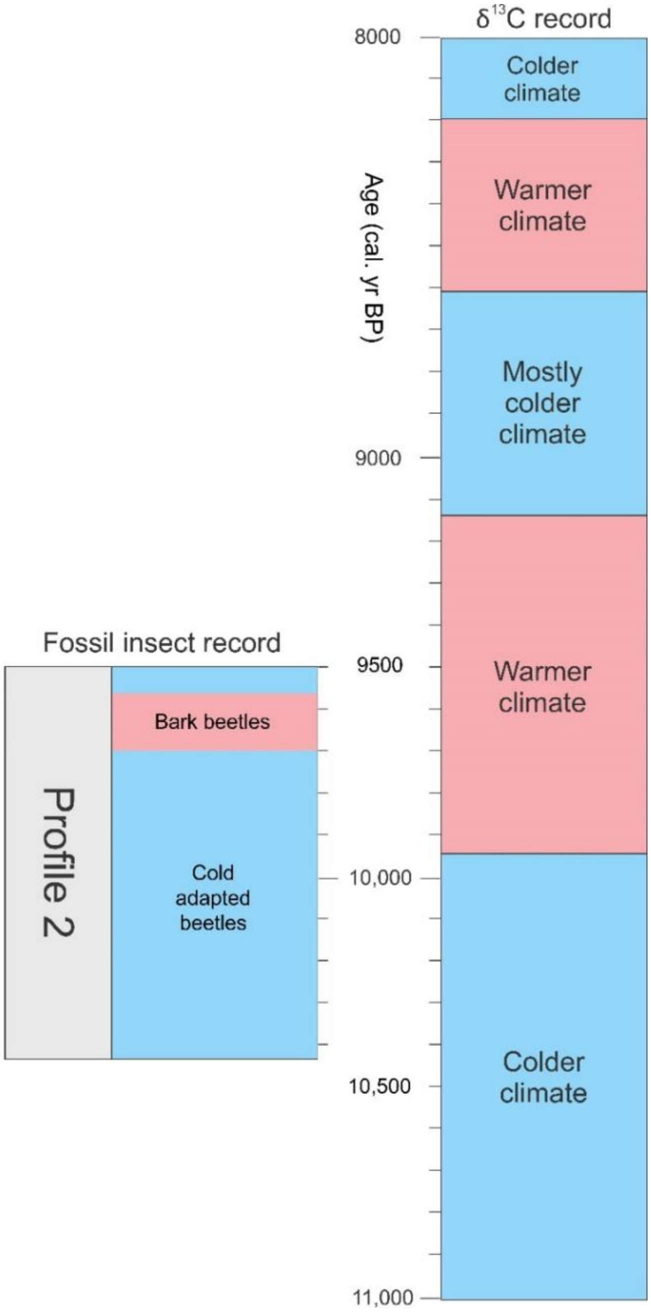


Figure 96. The comparsion of early Holocene interpretions from the Halashazi fossil beetle record and the δ^{13}C record.

For the middle Holocene, the beetle fossil record almost matches the δ^{13}C record, except for two colder intervals (around 6400 and 5300 cal. yr BP), which are only shown in fossil beetle record. Both of the fossil beetle record and δ^{13}C record agree that there was a transition from colder to warmer climate around 5500 and 4600 cal. yr BP (figure 97).

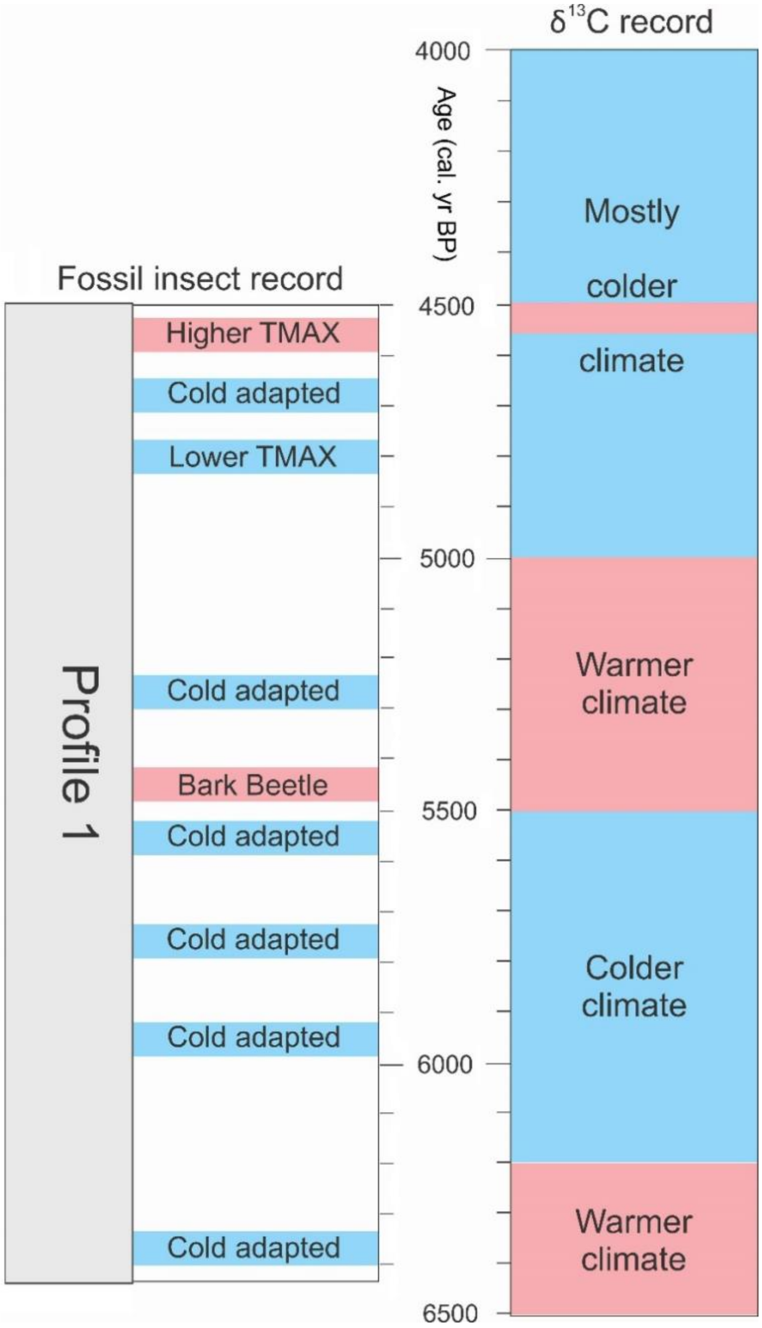


Figure 97. The comparsion of middle Holocene interpretations from the Halashazi fossil beetle record and the δ^{13}C record.

2) Pollen

The figure of plant remains (figure 98) and pollen record (figure 99) were provided by Yan Zhao from Lanzhou University. This is unpublished reseach from a peat core (ATM10-C6) in the Halashazi Wetland. The composition of plant remains shown in figure 98 are different from those in the insect study samples. As discussed above, the plant remains in Profile One (middle Holocene) from my study are similar with those in peat core ATM10-C6, which consists of sedges and mosses. The dominant plant remains in Profile Two (early Holocene) from my study are mosses rather than sedges. This difference of plant remains in the early Holocene is probably casued by the different sampled localities. But overall, the plant remains from Halashazi peat are mainly mosses and sedges, and no woody plant remains have been found in either study.

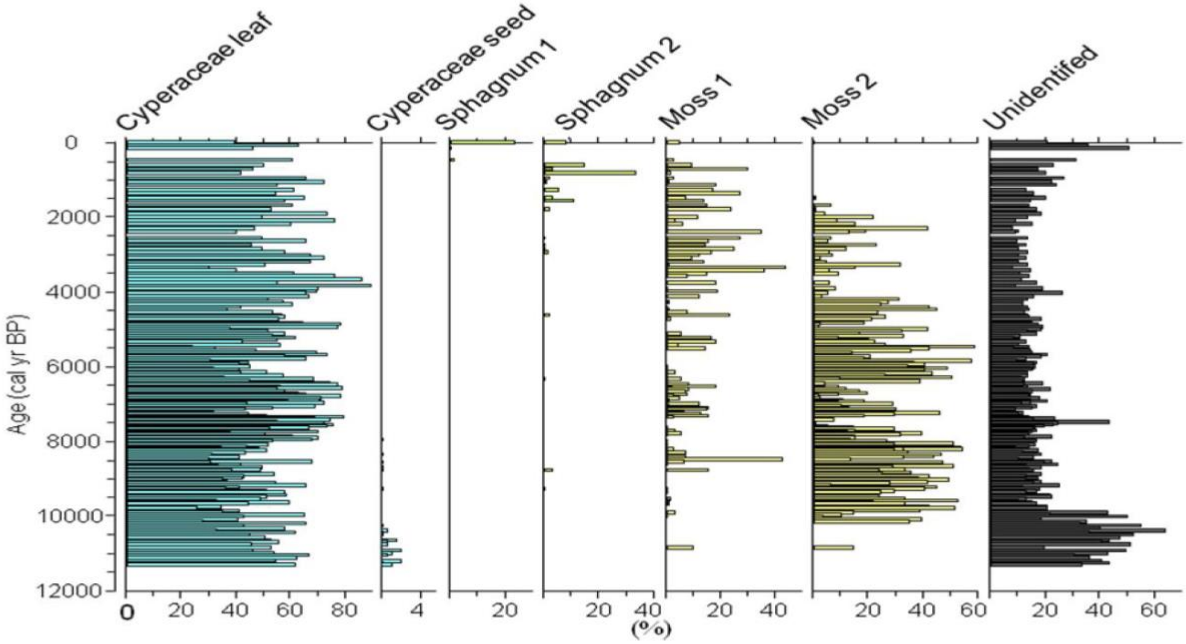


Figure 98. The plant remains from Halashazi Peat. From Yan Zhao, Lanzhou University (Unpublished).

Figure 99 shows the pollen records of Halashazi Wetland. *Artemisia* and Cyperaceae are the most abundant taxa in this reord. In a regional context, *Artemisia* is typically a desert-steppe genus that usually indicates dry climate. The family Cyperaceae includes mostly sedges, and in a regional context, sedges generally grow in wet habitats. However, the family Cyperaceae also includes the genus *Kobresia*, that grows on dry upland localities, especially at high elevations in Asia (Hultén, 1968). As Yurtsev (2001) noted, The dominant plants of cold-region steppes of Central Asia, including the Altai region, include *Festuca, Poa, Calamagrostis* (grasses), as well as *Kobresia*. Since the pollen of Cyperaceae cannot easily be identified to the generic level, it is impossible to determine whether the Cyperaceae signal from the Halashazi Peat pollen record represents the wet-adapted *Carex*, or the dry-adapted *Kobresia*. However, it would appear, based on the plant macrofossil remains, that most, if not all of the Cyperaceae pollen in the Halashazi record comes from sedges.

In addition, Chenopodiaceae also is a desert-steppe family. *Picea* and *Betula* pollen probably came from cool coniferous forest or cool mixed forest (Feng et al. 2017). So based on the pollen record in figure 99, the core can be roughly divided into four pollen zones. From 11,500 to 11,000 cal. yr BP, there is a spike in *Artemisia* percentages combined with a low level of Cyperaceae, which indicates a dry interval. From 11,000 to 9700 cal. yr BP, Cyperaceae levels are greater than 75 percent, while *Artemisia* is less than 15 percent, which indicates a wetter interval. From 9700 to 1500 cal. yr BP, the percentage of Cyperaceae declines from about 60 percent to 25 percent, while the percentage of *Artemisia* increasesfrom about 35 percent to 55 percecnt. This represent a gradual drying of the climate. The interval after 1500 cal. yr BP, it an arid interval with low Cyperaceae percentages (less than 20 percent) and high *Artemisia* percentages (more than 60 percent).

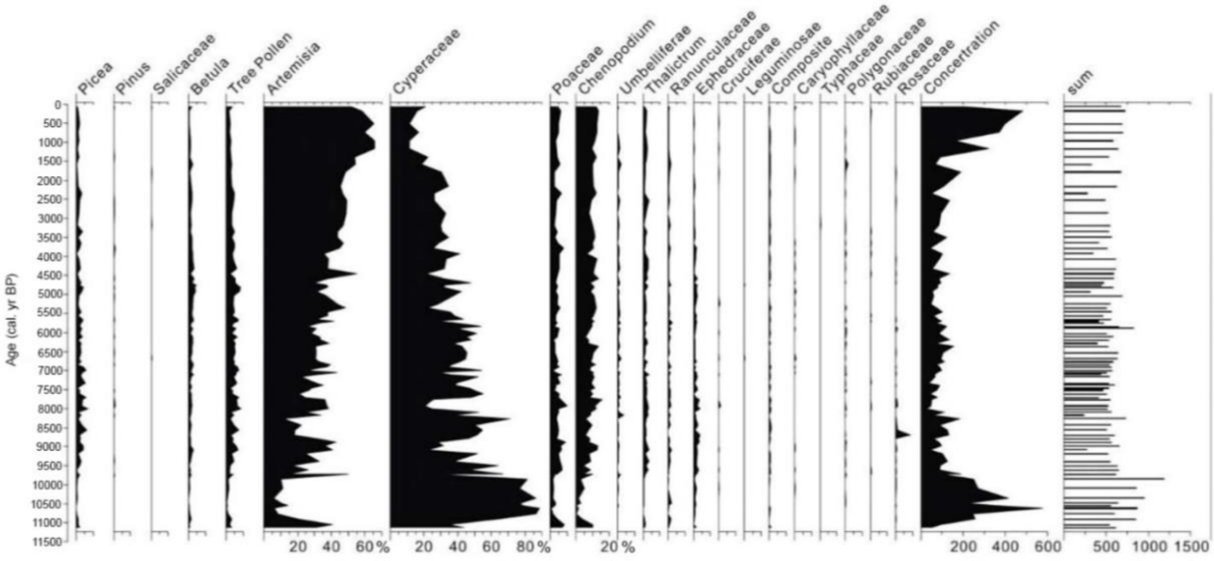


Figure 99. The pollen record from Halashazi wetland. From Yan Zhao, Lanzhou University (Unpublished).

As discussed above, fossil beetle record also showed a possible decrease of local moisture around 9700 cal. yr BP (based on a marked decline in both total number of individuals and the percentage of water-associated beetles, and the disappearance of the weevil *Tournotaris* *bimaculatus,* which feeds on aquatic plants). As noted above, this decline of moisture also showed in the pollen record, which indicates a probably dryer climate around 9700 cal. yr BP at least in Halashazi Wetland.

Another notable issue in the pollen record concerns spruce pollen. The percentage of *Picea* pollen in the Halashazi pollen study was never more than five percent throughout the Holocene. Due to the low percentage, it is hard to determine whether spruce actually lived in the study area, or whether the *Picea* pollen grains were transported by wind from somewhere else. As noted by Elias (2013), it can be extremely difficult to determine the threshold at which the number of spruce pollen grains should be considered to be of local origin. A few spruce pollen grains deposited in an early Holocene landscape may very well have arrived at a site from stands of trees growing many hundreds of kilometers away. Palynologists have adopted the conservative approach of taking the 10% spruce pollen threshold (i.e., the number of spruce pollen grains in a sample equals at least 10% of all grains counted) as indicative of the local presence of spruce for sites in Alaska and the Yukon (Ritchie, 1984). In the fossil beetle record, the specimens of bark beetles appeared around 9665, 9570 and 5451 cal. yr BP. Interestingly, at these times, *Picea* pollen percentages were less than two percent. Therefore, the appearance of the bark beetle fossils may have been due to transport by winds. Plant macrofossils may be taken as far stronger evidence of the presence of trees at a study site. Thus, Hu et al. (1995) found spruce needles in samples from a lake in southwestern Alaska that contained as low as 1% spruce pollen. They stated that the conventional criterion of 10% *Picea* pollen may be too conservative for judging the local presence of spruce trees, and that regional patterns of Holocene spread of spruce need to be re-examined, emphasizing the need for macrofossil studies. So, there is still the possibility that the presence of bark beetle fossils indicates the close proximity of spruce trees to the study site. One explanation for this is that the trees growing near Halashazi Wetland did not produce pollen, or only produced a little pollen at those times. Elias (1982a) discovered this situation in his study from Ennadai Lake in the Northwest Territories of Canada. During a climatic cooling in the Holocene, the spruces near Ennadai Lake apparently stopped producing pollen, or produced significantly less pollen than at other times. The decline of conifer pollen indicated either a retreat of northern tree line during a cold interval, or a cessation of spruce pollen production at the northern tree limit. However, the fossils of the carpenter ant and bark beetles reveal the continued presence of trees during this interval. Thus, the insect evidence shows that the trees remained, but stopped producing pollen. It has been shown that trees growing near northern tree line may stop producing pollen during cold intervals, in order to save metabolic energy, and that they recommence pollen production when the climate ameliorates (Elliott, 1979). Thus, during these intervals when bark beetle fossils have been found, there might indeed have been trees near Halashazi Wetland. However, the climate probably was not warm enough for the trees to produce abundant pollen. Since only a very few bark beetle fossils have been found, it is very difficult to confirm that whether these bark beetle fossils in the samples were carried by winds or whether the beetles lived there, indicating the presence of trees near the Halashazi Wetland. In order to solve this problem, it is necessary to have more studies in the Halashazi Wetland and nearby sites. If additional studies yield abundant bark beetle fossils, it is more likely that tree line moved uphill, and that it was at or above the study site. Otherwise, if further studies only yield a few bark beetle fossils, it is more likely they lived somewhere else and were wind-transported to the site(s).

In summary, the climate interpreted from the fossil beetle record generally matches the interpretation of cellulose carbon isotope record and the pollen record from Halashazi, with some notable exceptions.

Both the fossil beetle record and $\delta^{13}C$ record show a colder early Holocene, and two climatic transitions (from colder to warmer) around 5500 and 4600 cal. yr BP. However, there are also differences between the fossil beetle record and the $\delta^{13}C$ record. The fossil beetle record provides more details in terms of the local site, because the carbon in cellulose ultimately comes from atmospheric CO_2, thus the $\delta^{13}C$ record reflects more regional conditions. In addition, the $\delta^{13}C$ record provides only a qualitative analysis, which only shows general trends in Holocene temperatures. It does not provide specific temperature values, and also cannot compare with the modern temperatures. Thus, it is difficult to compare $\delta^{13}C$ reconstructions with other kinds of proxies, as the $\delta^{13}C$ record yields only general trends of warming and cooling. On the other hand, the fossil beetle record provides quantitative temperature reconstructions, which yield a specific range of palaeotemperature values by MCR method. Although in this project, it only yielded well-constrained values for two intervals. Even without the MCR results, the presence of cold-adapted beetle species provides more details on past climates. In this study, the appearance of the cold-adapted species may be taken as an indication of climatic conditions as least as cold as today, and possibly colder.

In comparing the insect and pollen records, it is apparent that both show a decrease of moisture around 9700 cal. yr BP, at least at the study site. The bark beetle fossils provide evidence of the possible presence of trees at or very near the site during three specific intervals, whereas the spruce pollen values at the site never exceeded five percent, and there were no spruce macrofossils found in the palaeobotanical study by Zhao (unpublished). However, these bark beetle fossils could also have been blown in from lower elevations, so this reconstruction needs further studies to be resolved.

6.4.2 Studies from the Chinese Altai region and nearby area

Based on the fossil beetle record from the Halashazi Wetland, the climate was generally wet and cold during the early Holocene from 10,500 to 9500 cal. yr BP, and relatively dry (based on the pollen record) and cold during the middle Holocene from 6300 to 4300 cal. yr BP. Compared with the other studies from the Chinese Altai region, listed in table 2, none of these studies fully agree with the interpretation based on the fossil beetle record from Halashazi Wetland. In terms of the early Holocene, most study sites recorded a dry interval until about 8000 cal. yr BP. One exception was the study from Bayan Nuur (Figure 9, number 12), which was interpreted as a cold and wet interval from about 11,000 to 9500 cal. yr BP. The study from Narenxia peat (Figure 9, number 6), agrees with the reconstruction of a cold and dry middle Holocene.

Since this project did not yield a continuous Holocene peat sequence, but rather produced fossil beetle records for two discrete Holocene intervals, it is hard to determine what climatic forcings affected the Holocene climate change in the Halashazi Wetland. One assumption is the wetter early Holocene might have been caused by melt water from the Altai Mountain glaciers of the Late Pleistocene. This would have been driven by high summer insolation levels in the early Holocene (figure 100).

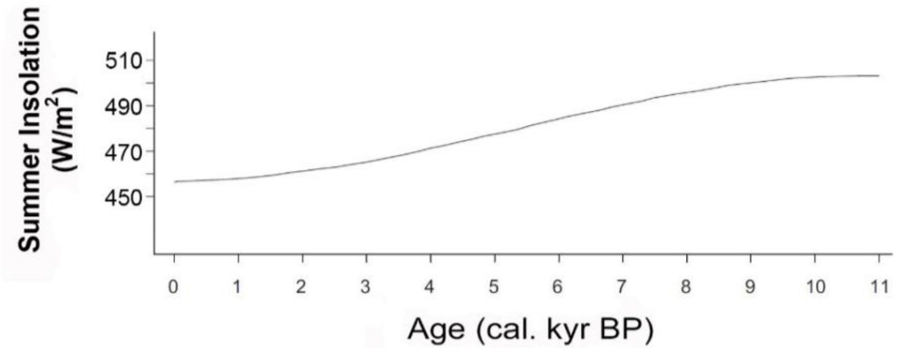


Figure 100. Northern Hemisphere 65°N summer insolation (Berger and Loutre, 1991).

As discussed above, the palaeoenvironmental studies in the Altai region have produced a variety of different interpretations of Holocene climate change. Some of these differences may be due to local topography. So, it is reasonable that reconstruction of Holocene climate change from the Halashazi Wetland does not agree with any of the other regional reconstructions based on other proxies. It is just shows a history of local environmental change for two discrete intervals of the Holocene. Some studies (e.g., Chen et al, 2008) have attempted to correlate their local studies with the macroclimate of the entire Arid Central Asian region. This is an enormous area, and as shown on the map (figure 9), only a few of palaeoenvironmental studies have thus far been done there. Much more work needs to be done before a comprehensive view of Holocene climate change in Arid Central Asia can be obtained.

6.5 Zoogeography

6.5.1 New distribution records

Of the 37 beetle species identified from the Early and Middle Holocene insect faunal assemblages of the Halashazi Wetland,12 species have modern records from China, and only five species have been recorded from the study region in Xinjiang province. While 24 species from the site are found today in Europe, and 34 species occur in Siberia. This research expanded the distribution records for those undetected beetle species in the study region.

6.5.2 Altai Mountain range as a dispersal corridor

As discussed above in the literature review, Elias (2014) studied the Late Pleistocene fossil beetle assemblages from Rocky Mountain region of North America. Twenty-three percent of the 200 identified beetle species are no longer resident in Rocky Mountains, and none of the 200 species is extinct. Interestingly, some beetle species that used to live in the southern Rocky Mountains during the Late Quaternary are now found only in the Pacific Northwest region. The beetle record clearly indicates that there was an insect migration corridor between the Rocky Mountains and the Pacific Northwest region that remained open for much of the Late Pleistocene, and persisted until the last millennium. According to the modern distribution of the identified beetle species in the Halashazi study, the beetle species found in the fossil assemblages are predominantly found today in northern Asia. Of the 37 identified beetle species, 34 species (92%) have modern records in Siberia. So, the Altai Mountains probably served as dispersal corridor for these beetle species. Beetles might move between the Halashazi Wetland and the Siberian regions along the Altai Mountains in response to large-scale fluctuations of climate. However, more studies of the fossil beetles from different sites (both in southern Altai and in northern Altai) and from different time periods (especially intervals of large-scale climate change), and the study of the modern beetles from the northern Altai region are required to test this theory.

Chapter 7. Conclusions

This project used Quaternary beetle assemblages to reconstruct early and middle Holocene environments in the southern Altai region of northwest China. This was a pilot study for Quaternary entomology in this region and has never before been done in China. It has successfully served as a proof of concept for fossil beetle research in temperate/boreal regions in China.

Two different peat profiles were sampled from Halashazi Wetland, with profile depths of 160 cm and 200 cm respectively. Based on AMS radiocarbon dating results, the peat in Profile One ranges in age from ca. 6374 to ca. 4378 cal. yr BP, and the peat in Profile Two ranges in age from ca.10424 to ca. 9500 cal. yr BP.

In total, 54 Coleoptera taxa representing 44 genera and 14 families have been found, and 37 species have been identified, including a new species *Helophorus sinoglacialis*. The majority of the fossil beetle species identified belong to the Holarctic boreo-arctic fauna, and indicate a cold steppe or tundra ecosystem. Of the 37 identified beetle species, 34 species (92%) are found today in the Siberian region.

Quantified temperature estimates have been made using the Mutual Climate Range (MCR) method. Indicator beetle species (cold adept species and bark beetles) have helped to identify both cold and warm intervals, and moisture conditions have been estimated on the basis of water associated species. Overall, the early Holocene (Profile Two) can be divided into two stages: a cold and wet interval from ~10,424 to ~ 9705 cal. yr BP, and a warmer and drier interval from ~ 9705 to ~ 9500 cal. yr BP. The reconstruction of climate change during the middle Holocene (Profile Two) is more complicated: first there was a cold and relatively dry interval from ~ 6374 to ~5451 cal. yr BP, followed by a temperature rise around 5451 cal. yr BP, then another cold and dry interval from ~ 5402 to ~ 4805 cal. yr BP. There was a warm interval around 4561 cal. yr BP, followed by another cold interval from ~ 4500 to ~ 4378 cal. yr BP. Generally, the fossil beetle record indicates a cold and wet early Holocene (from ~10424 to ~ 9500 cal. yr BP) and a relativly cold and dry middle Holocene (from ~6374 to ~ 4378 cal. yr BP) at the Halashazi Wetland.

Compared with the peat cellulose carbon isotope ($\delta^{13}C$) record and the pollen record from Halashazi Wetland, the palaeoenvironmental reconstructions based on the fossil beetle record generally match the interpretations of these other two proxies. However, the appearance of bark beetle fossils (*Phloeotribus spinulosus* and *Trypodendron sp*.) demonstrate the possibility of the presence of trees at or very near the site around 9665, 9570 and 5451 cal. yr BP, whereas the spruce pollen values at the site never exceeded five percent, and there were no spruce macrofossils found in the palaeobotanical study.

This project demonstrated the successful use of the MCR method in the study region, largely because species climate envelopes already exist for the Holarctic boreo-arctic species identified. However, the smallness of the identified fauna greatly limited the precision of the MCR estimates. Thus, more studies are needed in order to obtain more precise palaeotemperature estimates from MCR analysis, and also to acquire more precise details of the history of environmental changes in this study region.

The first priority for future studies is the collection of modern beetles from the study site. About one-third of the beetle taxa in the Halashazi fossil assemblages could not be identified. Since the identification of fossil beetles is based on comparison with modern specimens, inadequate knowledge of the modern beetle taxa in the study area is a great hindrance to the identification of fossil beetles. It seems likely that the modern beetle fauna of this region contains numerous beetle species that are currently unknown to science.

The second priority for future research is the development of species climate envelopes for Chinese beetle taxa. Although most identified beetle species in this project already have species climate envelopes, the modern ranges and ecological tolerances of some Chinese beetle taxa are poorly known. The collection of these data is a time-consuming process, beginning with the documentation of modern collecting localities of each species, followed by the determination of mean seasonal temperature data and mean annual precipitation data for the collection localities. The lack of meteorological stations in some remote regions of northern China and surrounding nations is a major problem that can only be overcome through the development of gridded climate An example of this method for estimating climate parameters for remote sites was described in Elias et al., (1996b), wherein a 25 km North American climate database was used to pair climate parameters with the modern beetle collection sites, using the geographically nearest grid location to each collecting site.

The third priority for future work is the collection of continuous peat sequences and larger samples. Due to limitations in funding and manpower, the samples obtained in this project were too small to yield abundant, diverse insect faunas. Thus, future regional studies should employ a larger field team, using powered equipment (e.g., chainsaws) to obtain larger quantity samples that would likely yield more abundant, diverse faunal assemblages.

Finally, it must be acknowledged that macrofossil studies such as this reveal only local conditions, so that this project reveals only a history of environmental change at the sample site. Thus, the fourth priority for future work would be to develop a regional climatic reconstruction based on the study of many additional sites in the region.

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Appendix 1. Fossil beetle fauna of Profile One, in minimum number of individuals per sample

Profile One	Depth (cm) and minimum number of individuals										
Taxon	0 | 4	4 | 8	8 | 12	12 | 16	16 | 20	20 | 25	25 | 30	30 | 35	35 | 40	40 | 45	45 | 50
Carabidae											
Nebria nivalis Paykull	-	-	-	-	-	1	-	-	-	-	-
Elaphrus sibiricus Motschulsky	-	-	-	-	-	1	-	-	-	-	-
Bembidion lampros Herbst	-	-	1	-	-	-	-	-	-	-	-
Agonum consimile Gyllenhal	1	-	-	-	-	-	3	2	-	-	4
Agonum spp.	-	-	2	4	-	-	2	1	3	2	-
Dytiscidae											
Ilybius spp.											
Hydroporus striola Gyllenhal	-	-	-	1	-	-	-	3	-	-	-
Hydroporus umbrosus Gyllenhal	-	-	-	-	-	-	1	-	-	-	-
Hydroporus spp.	-	-	-	-	-	1	1	-	-	1	1
Helophoridae											
Helophorus spp.	-	-	-	-	-	1	-	-	-	-	-
Helophorus sinoglacialis Angus, Rydevich and Zhang	1	-	-	-	-	-	-	-	-	-	-
Hydrophilidae											
Enochrus fuscipennis	-	1	1	3	2	2	4	1	1	1	4
Hydraenidae											
Ochthebius hungaricus Endrödy-Younga	-	-	-	-	-	-	-	-	-	-	-
Silphidae											
Thanatophilus dispar Motschulsky	-	-	-	-	1	-	-	-	-	-	-
Staphylinidae											
Acidota crenata Fabricius	-	-	-	-	-	-	-	-	-	-	-
Arpedium brachypterum Gravenhorst	-	-	-	-	-	-	-	-	-	-	1
Olophrum rotundicolle C.R.Sahlberg	2	1	3	5	5	6	4	12	8	2	6
Olophrum boreale Paykull	-	-	-	1	-	-	-	-	-	-	-
Bryophacis rufus Erichson	-	-	-	-	-	-	-	-	-	-	-
Gymnusa variegata Kiesenwetter	1	1	-	-	1	-	2	4	6	2	4
Stenus spp.	6	3	9	8	5	6	7	4	3	2	4
Tetartopeus spp.	-	-	-	-	-	-	-	-	1	-	-
Quedius spp.	1	-	2	1	-	3	1	1	2	1	1
Pselaphinae spp.	-	-	-	-	-	-	2	-	-	-	-
Coccinellidae											
Ceratomegilla rickmersi Weise	-	-	-	-	-	-	-	-	-	-	-
Chrysomelidae											
Galeruca tanaceti Linnaeus	-	-	-	-	-	-	-	-	-	-	-
Phyllotreta cruciferae Goeze	-	-	-	-	-	1	-	-	-	-	-
Chaetocnema obsea Boieldieu	-	-	-	-	-	-	-	-	-	1	-
Curculionidae											
Phloeotribus spinulosus Rey	-	-	-	-	-	-	-	-	-	-	-

Appendix 1. (continued)

Profile One	Depth (cm) and minimum number of individuals										
Taxon	50 | 55	55 | 60	60 | 65	65 | 70	70 | 75	75 | 80	80 | 85	85 | 90	90 | 95	95 | 100	100 | 105
Carabidae											
Nebria nivalis Paykull	-	-	-	-	-	-	-	-	-	-	-
Elaphrus sibiricus Motschulsky	-	-	-	-	-	-	-	-	-	-	-
Bembidion lampros Herbst	-	-	-	-	-	-	-	-	-	-	-
Agonum consimile Gyllenhal	3	4	2	-	-	-	-	-	1	1	2
Agonum spp.	-	-	2	1	-	1	2	1	-	1	-
Dytiscidae											
Ilybius spp.	-	-	1	-	-	-	-	-	-	-	-
Hydroporus striola Gyllenhal	1	-	-	-	-	-	-	1	1	1	2
Hydroporus umbrosus Gyllenhal	-	-	-	-	-	-	-	-	1	-	-
Hydroporus spp.	-	-	1	1	1	1	-	-	-	-	-
Helophoridae											
Helophorus spp.	-	-	1	-	-	-	-	-	-	1	-
Helophorus sinoglacialis Angus	-	-	-	-	-	-	-	-	-	-	-
Hydrophilidae											
Enochrus fuscipennis Thomson	3	5	5	2	3	1	4	1	2	1	3
Hydraenidae											
Ochthebius hungaricus Endrödy-Younga	1	-	-	-	-	-	-	-	-	-	-
Silphidae											
Thanatophilus dispar Motschulsky	-	-	-	-	-	-	-	-	-	-	-
Staphylinidae											
Acidota crenata Fabricius	-	-	-	-	-	-	-	-	-	-	-
Arpedium brachypterum Gravenhorst	-	-	1	-	-	-	-	1	-	-	1
Olophrum rotundicolle C.R.Sahlberg	6	2	3	1	1	-	1	1	4	4	4
Olophrum boreale Paykull	-	-	-	-	-	-	-	1	-	-	-
Bryophacis rufus Erichson	-	-	-	-	1	-	-	-	-	-	-
Gymnusa variegata Kiesenwetter	2	2	2	2	-	-	2	1	1	-	1
Stenus spp.	4	1	1	3	4	3	4	3	7	3	3
Tetartopeus spp.	-	-	-	-	-	1	-	-	1	1	1
Quedius spp.	3	1	3	-	1	1	3	5	1	6	1
Pselaphinae spp.	-	-	-	-	-	-	-	-	-	-	-
Coccinellidae											
Ceratomegilla rickmersi Weise	1	-	1	1	-	-	-	1	1	1	-
Chrysomelidae											
Galeruca tanaceti Linnaeus	-	-	1	-	-	-	-	-	-	-	-
Phyllotreta cruciferae Goeze	-	-	-	-	-	-	-	-	-	-	-
Chaetocnema obsea Boieldieu	-	-	-	-	-	-	1	-	-	-	-
Curculionidae											
Phloeotribus spinulosus Rey	-	-	-	1	-	-	-	-	-	-	-

Appendix 1. (continued)

Profile One	Depth (cm) and minimum number of individuals								
Taxon	105 | 110	110 | 115	115 | 120	120 | 125	125 | 130	130 | 135	135 | 140	140 | 145	145 | 150
Carabidae									
Nebria nivalis Paykull	-	-	-	-	-	-	-	-	-
Elaphrus sibiricus Motschulsky	-	-	-	-	-	-	-	-	-
Bembidion lampros Herbst	-	-	-	-	-	-	-	-	-
Agonum consimile Gyllenhal	-	-	2	-	-	1	-	-	-
Agonum spp.	-	-	-	1	1	-	-	-	-
Dytiscidae									
Ilybius spp.	-	-	-	-	-	-	-	-	-
Hydroporus striola Gyllenhal	1	-	-	-	1	-	-	-	-
Hydroporus umbrosus Gyllenhal	2	-	-	1	-	1	1	1	-
Hydroporus spp.	-	1	-	-	-	-	-	-	1
Helophoridae									
Helophorus spp.	-	-	-	-	-	-	-	-	-
Helophorus sinoglacialis Angus	-	-	-	-	-	-	-	-	1
Hydrophilidae									
Enochrus fuscipennis Thomson	3	3	4	1	2	2	1	1	2
Hydraenidae									
Ochthebius hungaricus Endrödy-Younga	-	-	-	-	-	-	-	-	1
Silphidae									
Thanatophilus dispar Motschulsky	-	-	-	-	-	-	-	-	-
Staphylinidae									
Acidota crenata Fabricius	-	-	-	-	-	-	-	-	1
Arpedium brachypterum Gravenhorst	-	-	2	-	-	-	-	-	1
Olophrum rotundicolle C.R.Sahlberg	1	1	1	-	-	-	-	-	2
Olophrum boreale Paykull	-	-	-	-	-	-	-	-	-
Bryophacis rufus Erichson	-	-	-	-	-	-	-	-	-
Gymnusa variegata Kiesenwetter	2	-	1	2	2	-	-	-	1
Stenus spp.	5	3	3	1	1	2	2	2	2
Tetartopeus spp.	-	1	-	-	2	-	-	-	-
Quedius spp.	1	1	1	2	3	1	2	2	2
Pselaphinae spp.	-	-	-	-	-	-	-	-	-
Coccinellidae									
Ceratomegilla rickmersi Weise	-	-	1	-	-	-	1	-	-
Chrysomelidae									
Galeruca tanaceti Linnaeus	-	-	-	-	-	-	-	-	-
Phyllotreta cruciferae Goeze	-	-	-	-	-	-	-	-	-
Chaetocnema obsea Boieldieu	-	-	1	-	-	-	-	-	-
Curculionidae									
Phloeotribus spinulosus Rey	-	-	-	-	-	-	-	-	-

2. Fossil beetle fauna of Profile Two, in minimum number of individuals per sample.

Profile Two	Depth (cm) and minimum number of individuals									
Taxon	0 | 5	5 | 10	10 | 15	15 | 20	20 | 25	25 | 30	30 | 35	35 | 40	40 | 45	45 | 50
Carabidae										
Trechus spp.	-	1	-	-	-	-	-	-	-	-
Blethisa catenaria Brown	-	-	-	-	-	-	-	-	-	-
Elaphrus sibiricus Motschulsky	-	-	-	-	-	-	-	-	-	-
Patrobus septentrionis Dejean	-	-	-	1	-	-	-	-	-	-
Pterostichus agonus Horn	-	-	-	-	-	-	-	-	-	-
Pterostichus brevicornis Kirby	-	-	-	-	-	-	-	-	-	1
Agonum consimile Gyllenhal,	-	1	-	1	-	-	-	1	-	1
Agonum quinquepunctatum Motschulsky	-	-	-	-	-	-	-	-	-	-
Agomum spp.	1	-	3	2	2	3	2	1	2	-
Haliplidae										
Haliplus chinensis Falkenstromöm	-	-	-	-	-	-	-	-	-	-
Dytiscidae										
Ilybius spp.	-	-	4	2	-	4	-	2	-	1
Colymbetes spp.	-	-	-	-	-	-	-	-	-	-
Hydroporus notabilis LeConte	-	-	-	-	-	-	-	-	-	-
Hydroporus striola Gyllenhal	-	-	1	-	3	4	3	-	3	3
Hydroporus umbrosus Gyllenhal	-	-	3	1	2	-	-	2	1	2
Hygrotus impressopunctatus Schaller	-	-	-	-	-	-	-	-	-	3
Helophoridae										
Helophorus pallidus Gebler	-	-	-	-	-	-	-	-	-	-
Helophorus sibiricus Motschulsky	-	-	-	-	-	1	-	-	-	-
Helophorus sinoglacialis Angus	-	1	2	1	-	-	1	1	1	1
Hydrophilidae										
Enochrus fuscipennis Thomson	1	-	-	1	-	-	-	-	-	-
Hydrobius subrotundus Stephens	-	-	-	-	-	-	-	-	-	-
Hydraenidae										
Limnebius spp.	-	-	-	-	-	-	-	-	-	-
Ochthebius hungaricus Endrödy-Younga	-	-	-	-	1	-	-	1	1	-
Leiodidae										
Nargus sp.	-	-	-	-	-	-	-	-	-	-

Appendix 2. (continued)

Profile Two	Depth (cm) and minimum number of individuals									
Taxon	0 | 5	5 | 10	10 | 15	15 | 20	20 | 25	25 | 30	30 | 35	35 | 40	40 | 45	45 | 50
Staphylinidae										
Acidota crenata Fabricius	-	-	-	-	-	-	-	-	-	-
Arpedium brachypterum Gravenhorst	-	-	-	-	-	-	-	-	-	-
Olophrum rotundicolle C.R.Sahlberg	-	-	1	1	1	2	2	1	1	1
Olophrum boreale Paykull	-	-	-	-	-	-	-	-	-	-
cf. Eusphalerum spp.	-	-	-	1	-	2	1	-	-	-
Bryophacis rufus Erichson	-	-	-	-	-	-	-	-	-	-
Gymnusa variegata Kiesenwetter	1	-	1	-	-	2	1	1	-	1
Stenus spp.	9	10	9	19	10	13	6	11	9	13
Tetartopaeus spp.	-	1	-	-	-	-	1	-	1	1
Quedius spp.	1	-	1	1	-	1	1	-	1	1
Byrrhidae										
Cytilus sericeus Forster	-	-	-	-	-	-	-	-	-	-
Coccinellidae										
Ceratomegilla rickmersi Weise	-	2	5	3	5	5	2	3	4	1
Nephus sp.	-	-	-	-	-	-	-	-	-	-
Hippodamia tredecimpunctata Linnaeus	-	-	-	-	-	-	-	-	1	-
Latridiidae										
Corticaria spp.	-	-	-	-	-	-	-	-	-	-
Chrysomelidae										
Plagiodera versicolora Laicharting	-	-	-	-	-	-	-	1	-	-
Smaragdina spp.	-	1	1	-	-	-	-	-	-	-
Phaedon armoraciae Linnaeus	-	-	-	-	-	-	-	1	-	-
Galeruca tanaceti Linnaeus	-	1	-	-	-	-	-	-	-	-
Altica spp.	-	-	-	-	1	-	-	1	1	-
Chaetocnema obesa Boieldieu	-	-	-	-	-	-	-	-	-	-
Cassida spp.	-	-	-	-	-	-	-	-	-	-
Erirhinidae										
Tournotaris bimaculatus Fabricius	-	-	-	-	-	-	-	-	-	-
Curculionidae										
Trypodendron sp.	-	-	-	-	-	-	-	-	-	-
Phloeotribus spinulosus Rey	-	-	-	-	-	1	-	-	-	-

Appendix 2. (continued)

Profile Two	Depth (cm) and minimum number of individuals									
Taxon	50 | 55	55 | 60	60 | 65	65 | 70	70 | 75	75 | 80	80 | 85	85 | 90	90 | 95	95 | 100
Carabidae										
Trechus spp.	-	-	-	-	-	-	-	-	-	-
Blethisa catenaria Brown	-	-	-	-	-	-	1	-	-	-
Elaphrus sibiricus Motschulsky	-	-	-	-	-	-	-	-	-	-
Patrobus septentrionis Dejean	-	-	-	1	-	1	1	-	-	-
Pterostichus agonus Horn	-	-	-	-	-	-	-	-	-	-
Pterostichus brevicornis Kirby	-	-	-	-	-	-	-	-	-	-
Agonum consimile Gyllenhal	3	-	3	1	-	2	1	2	4	2
Agonum quinquepunctatum Motschulsky	-	-	-	-	-	-	-	-	1	-
Agonum spp.	-	1	-	1	2	-	3	-	-	2
Haliplidae										
Haliplus chinensis Falkenstromöm	-	-	-	1	-	-	-	-	-	-
Dytiscidae										
Ilybius spp.	-	-	2	-	2	3	1	1	1	1
Colymbetes spp.	-	-	-	-	-	-	1	-	-	-
Hydroporus notabilis LeConte	1	2	-	-	2	1	1	-	2	-
Hydroporus striola Gyllenhal	3	1	1	3		2	1	1	2	6
Hydroporus umbrosus Gyllenhal	-	1	2	2	6	9	9	5	5	6
Hygrotus impressopunctatus Schaller	1	-	1	-	-	-	1	-	1	4
Helophoridae										
Helophorus pallidus Gebler	-	-	-	-	-	-	-	-	-	-
Helophorus sibiricus Motschulsky	-	-	-	-	-	-	-	-	-	-
Helophorus sinoglacialis Angus	-	-	1	1	-	-	-	1	1	1
Hydrophilidae										
Enochrus fuscipennis Thomson	-	-	-	-	-	1	1	-	-	-
Hydrobius subrotundus Stephens	-	1	1	1	-	-	1	-	-	-
Hydraenidae										
Limnebius spp.	-	-	-	-	-	3	2	-	1	1
Ochthebius hungaricus Endrödy-Younga	2	-	-	-	2	-	-	1	-	-
Leiodidae										
Nargus sp.	-	-	1	-	-	-	-	-	-	-

Appendix 2. (continued)

Profile Two	Depth (cm) and minimum number of individuals									
Taxon	50 | 55	55 | 60	60 | 65	65 | 70	70 | 75	75 | 80	80 | 85	85 | 90	90 | 95	95 | 100
Staphylinidae										
Acidota crenata Fabricius	-	-	-	-	-	--	-	-	-	-
Arpedium brachypterum Gravenhorst	-	-	1	4	4	3	11	12	5	7
Olophrum rotundicolle C.R.Sahlberg	2	1	1	2	3	8	7	4	7	7
Olophrum boreale Paykull	-	-	-	-	-	-	-	1	3	-
cf. Eusphalerum spp.	2	2	-	1	-	11	22	17	9	10
Bryophacis rufus Erichson,	-	-	-	-	-	-	-	-	-	-
Gymnusa variegata Kiesenwetter	1	-	-	1	1	1	1	-	-	-
Stenus spp.	16	13	10	6	8	4	7	2	5	5
Tetartopaeus spp.	1	-	-	-	-	1	1	-	-	-
Quedius spp.	-	1	2	1	-	-	1	-	1	-
Byrrhidae										
Cytilus sericeus Forster	-	-	-	-	-	-	-	-	-	-
Coccinellidae										
Ceratomegilla rickmersi Weise	1	2	1	3	-	2	2	4	7	3
Nephus sp.	-	-	-	-	-	-	-	-	-	-
Hippodamia tredecimpunctata Linnaeus	-	-	-	-	-	-	-	-	-	-
Latridiidae										
Corticaria spp.	-	-	-	-	-	-	-	-	1	-
Chrysomelidae										
Plagiodera versicolora Laicharting	-	-	-	-	-	-	-	-	-	-
Smaragdina spp.	-	-	-	-	-	-	-	-	-	-
Phaedon armoraciae Linnaeus	-	-	-	-	-	-	-	-	-	-
Galeruca tanaceti Linnaeus	-	-	-	-	-	-	-	-	-	-
Altica spp.	-	-	-	-	1	2	-	-	-	-
Chaetocnema obesa Boieldieu	-	-	-	-	-	-	-	-	-	-
Cassida spp.	-	-	-	-	-	-	-	-	-	-
Erirhinidae										
Tournotaris bimaculatus Fabricius	-	2	2	6	7	7	3	2	1	2
Curculionidae										
Trypodendron sp.	-	1	-	-	-	-	-	-	-	-
Phloeotribus spinulosus Rey	-	1	-	-	-	-	-	-	-	-

Appendix 2. (continued)

Profile Two	Depth (cm) and minimum number of individuals									
Taxon	100 | 105	105 | 110	110 | 115	115 | 120	120 | 125	125 | 130	130 | 135	135 | 140	140 | 145	145 | 150
Carabidae										
Trechus spp.	-	-	-	-	-	-	-	-	-	-
Blethisa catenaria Brown	-	-	-	-	-	-	-	-	1	-
Elaphrus sibiricus Motschulsky	-	-	-	-	-	-	-	-	1	-
Patrobus septentrionis Dejean	-	-	-	-	1	-	-	-	2	-
Pterostichus agonus Horn	-	-	1	-	-	-	-	-	-	-
Pterostichus brevicornis Kirby	-	-	-	-	1	-	-	-	-	1
Agonum consimile Gyllenhal	2	1	-	1	1	1	4	2	1	1
Agonum quinquepunctatum Motschulsky	-	-	-	1	1	-	-	-		
Agomum spp.	1	-	-	2	1	1	-	-	1	1
Haliplidae										
Haliplus chinensis Falkenstromöm	-	-	-	-	-	-	-	-	-	-
Dytiscidae										
Ilybius spp.	2	-	1	1	1	1	1	-	-	1
Colymbetes spp.	-	1	-	-	-	-	-	-	-	-
Hydroporus notabilis LeConte										
Hydroporus striola Gyllenhal	7	5	11	3	3	6	7	3	2	5
Hydroporus umbrosus Gyllenhal	6	5	3	4	7	4	1	2	4	4
Hygrotus impressopunctatus Schaller	3	3	3	1	1	-	-	-	1	1
Helophoridae										
Helophorus pallidus Gebler	-	-	-	-	-	-	-	-	-	-
Helophorus sibiricus Motschulsky	-	-	-	-	-	-	-	-	-	-
Helophorus sinoglacialis Angus	1	-	-	-	-	-	1	1	-	-
Hydrophilidae										
Enochrus fuscipennis Thomson	-	1	-	-	-	-	-	-	-	1
Hydrobius subrotundus Stephens	-	-	-	-	1	1	-	-	-	-
Hydraenidae										
Limnebius spp.	-	-	-	-	-	-	1	1	-	2
Ochthebius hungaricus Endrödy-Younga	-	-	-	-	-	1	1	-	-	-
Leiodidae										
Nargus sp.	-	-	-	-	-	-	-	-	-	-

Appendix 2. (continued)

Profile Two	Depth (cm) and minimum number of individuals									
Taxon	100 | 105	105 | 110	110 | 115	115 | 120	120 | 125	125 | 130	130 | 135	135 | 140	140 | 145	145 | 150
Staphylinidae										
Acidota crenata Fabricius	-	-	-	-	-	-	-	-	-	-
Arpedium brachypterum Gravenhorst	1	-	1	3	2	1	3	3	2	3
Olophrum rotundicolle C.R.Sahlberg	8	6	3	4	8	5	11	8	3	3
Olophrum boreale Paykull										
cf. Eusphalerum spp.	3	5	5	4	2	6	3	7	6	2
Bryophacis rufus Erichson										1
Gymnusa variegata Kiesenwetter	1	-	2	3	3	-	-	1	-	2
Stenus spp.	4	6	6	4	2	5	3	2	3	2
Tetartopaeus spp.					1	1		2		1
Quedius spp.	2	1	-	1	1	-	1	2	1	2
Byrrhidae										
Cytilus sericeus Forster	-	-	-	-	-	-	-	-	-	-
Coccinellidae										
Ceratomegilla rickmersi Weise	2	3	6	6	4	3	5	5	4	5
Nephus sp.	-	-	-	-	-	-	-	-	-	1
Hippodamia tredecimpunctata Linnaeus	-	-	-	-	-	-	-	-	-	-
Latridiidae										
Corticaria spp.	-	-	-	-	-	-	-	1	-	-
Chrysomelidae										
Plagiodera versicolora Laicharting	-	-	-	-	-	-	-	-	-	-
Smaragdina spp.	-	-	-	-	-	-	-	1	-	-
Phaedon armoraciae Linnaeus	-	-	-	-	-	-	-	-	-	-
Galeruca tanaceti Linnaeus	-	-	-	-	-	-	-	-	-	-
Altica spp.	-	-	-	-	1	1	1	1	1	-
Chaetocnema obesa Boieldieu	-	-	-	-	-	-	-	-	-	-
Cassida spp.	-	-	-	1	1	1	-	-	-	-
Erirhinidae										
Tournotaris bimaculatus Fabricius	1	2	1	3	5	4	2	2	3	3
Curculionidae										
Trypodendron sp.	-	-	-	-	-	-	-	-	-	-
Phloeotribus spinulosus Rey	-	-	-	-	-	-	-	-	-	-

Appendix 2. (continued)

Profile Two	Depth (cm) and minimum number of individuals									
Taxon	150 | 155	155 | 160	160 | 165	165 | 170	170 | 175	175 | 180	180 | 185	185 | 190	190 | 195	195 | 200
Carabidae										
Trechus spp.	-	-	-	-	-	-	-	-	-	-
Blethisa catenaria Brown	-	-	1	-	-	-	-	-	-	1
Elaphrus sibiricus Motschulsky	-	-	-	-	-	-	-	-	-	2
Patrobus septentrionis Dejean	-	3	-	-	-	-	-	-	1	-
Pterostichus agonus Horn	-	-	-	-	-	-	-	-	-	-
Pterostichus brevicornis Kirby	-	-	-	-	-	1	-	1	1	-
Agonum consimile Gyllenhal	3	1	1	2	0	2	1	1	-	1
Agonum quinquepunctatum Motschulsky	2	-	-	-	-	-	-	-	-	-
Agomum spp.	1	1	1	-	2	-	-	-	-	-
Haliplidae										
Haliplus chinensis Falkenstromöm,	-	-	-	-	-	-	-	-	-	-
Dytiscidae										
Ilybius spp.	-	-	1	1	-	-	1	1	-	-
Colymbetes spp.	-	-	-	-	-	-	1	-	-	-
Hydroporus notabilis LeConte	-	1	1	-	-	-	1	1	2	2
Hydroporus striola Gyllenhal	5	7	9	6	5	5	6	3	2	6
Hydroporus umbrosus Gyllenhal	6	11	8	9	9	4	4	-	3	3
Hygrotus impressopunctatus Schaller	-	1	-	-	-	-	-	-	1	1
Helophoridae										
Helophorus pallidus Gebler	-	-	-	-	-	-	1	-	1	-
Helophorus sibiricus Motschulsky	-	1	-	-	-	-	-	-	-	-
Helophorus sinoglacialis Angus	1	-	-	-	-	-	-	1	-	1
Hydrophilidae										
Enochrus fuscipennis Thomson	-	-	-	-	-	-	-	-	-	-
Hydrobius subrotundus Stephens	-	-	1	-	-	1	1	1	-	1
Hydraenidae										
Limnebius spp.	1	1	1	1	3	1	3	2	-	-
Ochthebius hungaricus Endrödy-Younga	-	-	-	-	-	-	-	-	-	-
Leiodidae										
Nargus sp.	-	-	-	-	-	-	-	-	-	-

Appendix 2. (continued)

Profile Two	Depth (cm) and minimum number of individuals									
Taxon	150 | 155	155 | 160	160 | 165	165 | 170	170 | 175	175 | 180	180 | 185	185 | 190	190 | 195	195 | 200
Staphylinidae										
Acidota crenata Fabricius	-	-	-	1	-	1	-	-	-	-
Arpedium brachypterum Gravenhorst	13	2	4	3	9	7	13	7	14	18
Olophrum rotundicolle C.R.Sahlberg	9	7	6	6	8	10	7	6	3	4
Olophrum boreale Paykull	-	-	-	-	-	-	2	-	-	2
cf. Eusphalerum spp.	15	6	5	5	3	5	18	13	18	16
Bryophacis rufus Erichson	-	-	-	-	-	-	-	-	-	1
Gymnusa variegata Kiesenwetter	2	1	-	-	-	-	1	1	-	-
Stenus spp.	3	1	1	2	2	4	2	2	2	3
Tetartopaeus spp.	2	1	2	1	-	2	-	-	1	-
Quedius spp.	4	1	4	5	2	2	3	2	2	2
Byrrhidae										
Cytilus sericeus Forster	-	-	-	-	-	-	-	-	-	2
Coccinellidae										
Ceratomegilla rickmersi Weise	2	3	2	3	3	1	3	3	2	1
Nephus sp.	-	-	-	-	-	-	-	-	-	-
Hippodamia tredecimpunctata Linnaeus	-	-	-	-	-	-	-	-	-	-
Latridiidae										
Corticaria spp.	-	-	-	1	-	-	-	-	-	-
Chrysomelidae										
Plagiodera versicolora Laicharting	-	-	-	-	-	-	-	-	1	-
Smaragdina spp.	-	-	-	-	-	-	1	-	-	-
Phaedon armoraciae Linnaeus	-	-	-	-	-	-	-	-	-	-
Galeruca tanaceti Linnaeus	-	-	-	-	-	-	-	-	-	-
Altica spp.	1	2	1	1	1	4	1	2	2	-
Chaetocnema obesa Boieldieu	-	-	-	-	-	-	-	-	2	-
Cassida spp.	-	-	-	-	-	-	-	-	-	-
Erirhinidae										
Tournotaris bimaculatus Fabricius	3	3	6	4	3	2	4	3	4	4
Curculionidae										
Trypodendron sp.	-	-	-	-	-	-	-	-	-	-
Phloeotribus spinulosus Rey	-	-	-	-	-	-	-	-	-	-