



**Insect evidence for environmental and climate changes
from Younger Dryas to Sub-Boreal in a river floodplain
at St-Momelin (St-Omer basin, northern France),
Coleoptera and Trichoptera.**

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Abstract

The St-Omer area is a rapidly subsiding basin in which long sequences of Weichselian and Holocene sediments are preserved. A core 21 m long, extracted from near St-Momelin about ten km north of St-Omer, has been analysed for insect fossils. Four Faunal Units (SMi-1 to SMi-4) are described based on changes in both coleopteran and trichopteran assemblages. The basal Faunal Unit (SMi-1) includes many cold-adapted species and is attributed to the Younger Dryas chronozone. The transition to Holocene sedimentation was abrupt. Faunal units SMi-2 to SMi-4 are attributable to the Holocene. They lack all the cold-adapted species found in the basal sediments and in their place are insect assemblages very similar to the present day fauna in this region. This sequence spans the period from the Pre-Boreal to the Sub-Boreal. Faunal Unit SMi-2 includes insects from the Pre-Boreal, the Boreal and most of the Atlantic periods. This fauna was fairly sparse and made up largely of species living in freshwater habitats. The Faunal Unit SMi-3 includes the insect assemblages from the Late-Atlantic to Sub-Boreal periods. This fauna was much more diverse and indicated a river meandering across its floodplain and bordered by a mature forest at a time when the climate was warmer than that of the present day. This chronostratigraphical sequence of events is supported by ^{14}C dates and by lithological data. Thermal climatic conditions have been quantified using the Mutual Climatic Range method. During the Younger Dryas period (SMi-1), T_{max} (the mean July temperature) was in the region of 10 °C and T_{min} (the mean temperature of January/February) was close to -11/-12 °C. After the sudden climatic amelioration at the start of the Holocene (SMi-2 to SMi-4) T_{max} probably fluctuated throughout the early Holocene between 16 °C to 19 °C and T_{min} between 0 °C to 5 °C; figures that are close to those of the present day. This climatic history is compared with others in northern Europe.

1. Introduction

Continuous sequences of insect assemblages spanning the Lateglacial-Holocene transition are extremely rare in continental Europe, especially at low altitude. Several insect faunas that span this transition are also known from lowland sites in Britain (Ashworth, 1972; Walker et al., 1993, 2003). Faunas of this age are known from high altitudes in southern France (Ponel and Coope, 1990; Ponel et al., 1992, 2001). The St-Omer basin is an area of continued subsidence which has acted as a sediment trap in which a thick organic sequence accumulated, ranging in age from Early Weichselian (Würmian) to Holocene (e.g., up to 20 m of Holocene sediments are present in places) (Mansy et al., 2003). It provides an opportunity to investigate the palaeoecological history reflected in the insect faunas from the Lateglacial/Holocene transition at a low altitude site in northern France. Furthermore, because of the proximity of the St-Omer basin to the coastline it also provides evidence of the relationship between the ecology development, sea level changes and the varying dynamics of the adjacent river system (Denys and Baeteman, 1995; Shennan and Horton, 2002; Waller and Long, 2003). It is in a geographically and temporally crucial situation in which the Holocene marine transgression started to invade the North Sea embayment (Gibbard, 1995).

Several earlier palaeoecological studies in the St-Omer basin, have shown an extended sequence of Early-

Weichselian and Holocene deposits at Watten and St-Momelin (Van der Woude and Roeleveld, 1985; Sommé et al., 1994; Emontspohl, 1995). Up to now these have been based principally on pollen analysis and little or no attention has been paid to other aspects of the palaeontological record.

In 2000 a large multidisciplinary programme was launched (Gandouin, 2003; Meurisse et al., 2005) in order to investigate the environmental changes in the St-Omer basin and along the French coast of the Strait of Dover. The aim of this programme is to reconstruct the dynamics of the postglacial sea level rise, environmental and climate changes, from the Younger Dryas to the Sub-Atlantic periods (NB, The chronostratigraphic units of Mangerud et al. (1974) are used throughout this paper) using a set of reliable ecological indicators i.e. stratigraphy, sedimentology, pollen, molluscs, and insect fossils. A secure geochronological framework also had to be established. This vast programme is at present at various stages of completion. The vegetation dynamics in the St-Omer region from Pre-Boreal to Sub-Atlantic have been analyzed by Gandouin (2003). Preliminary and methodological studies of chironomid fossil assemblages in river floodplains have been given by Gandouin et al. (2005, 2006).

Almost nothing is known from the French side of the Channel about the assemblages of other fossil insects that date from this critical period. In the Paris basin, sequences of insect faunas spanning the Bølling-Allerød interstadial

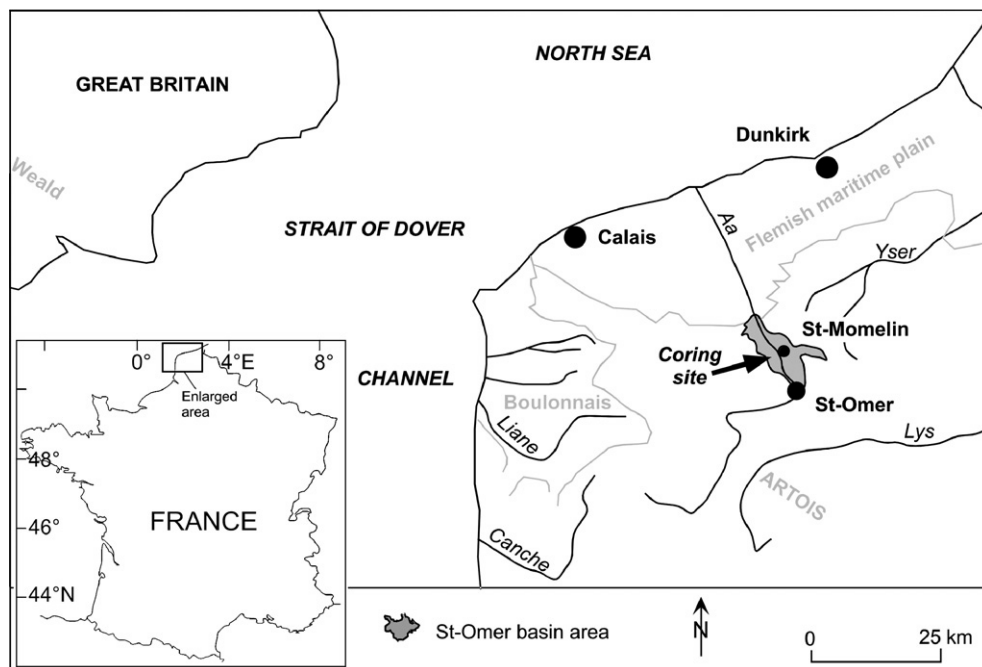


Fig. 1. Geographical location of the study site.

have been described from Conty and Houdancourt (Ponel et al., 2005) but the Younger Dryas sediments were not fossiliferous. The coleopteran record from the St-Omer basin is especially significant since it includes these Younger Dryas faunas and thus completes our knowledge of the transition into the Holocene in northern France. On the British side of the Channel an important coleopteran sequence spanning this critical period has been described from the excavations at Hollywell Coombe associated with the northern terminal of the Channel Tunnel near Folkestone (Coope, 1998). Further afield useful comparison can be made with a Younger Dryas coleopteran assemblage from Jersey in the west (Jones et al., 2004) or with the insect sequence spanning the Late glacial interstadial and the Younger Dryas from Notsel in the Mark valley in the Netherlands (Bohncke et al., 1987).

In this paper we present an almost continuous record of insect assemblage from the Younger Dryas to the Sub-Boreal periods. The present study is focused on insects (with the exception of the Chironomidae, which will be published elsewhere). By far the most abundant and diverse identifiable fossils are the Coleoptera (beetles) because they have such robust skeletons and survive well as fossils in anaerobic, waterlogged sediments. Furthermore, their morphological complexity often enables them to be identified to the species level. Previous studies have shown them to be sensitive indicators of Quaternary environments and climates (Coope, 1977; Ponel, 1995). Trichoptera are also abundant and well preserved in this sequence. Other orders of insect such as Hymenoptera, Hemiptera and Megaloptera also occur frequently in these deposits but have not been investigated in detail here.

The St-Momelin area is at present the subject of a series of works at various stages of completion. They are devoted to chironomids (Gandouin et al., in press), molluscs, pollen, and a concluding multiproxy synthetic analysis is also scheduled.

2. Study site

The site was described in detail by Gandouin et al. (2005) and only a brief summary will be given here. It is located in the "Pas-de-Calais" (Northern France) (Fig. 1), in the valley of the river Aa. The catchment of the river is 56,000 ha/560 km². The solid substrate is of mostly chalk, but downstream it extends onto Eocene clay. In its lower reaches it is located predominantly in an area of subsidence; the St-Omer basin stretching from Arques to Watten (Mansy et al., 2003). This basin (about 4000 ha/40 km²) is situated about 30 km inland from the North Sea coast. The connection between the basin and the maritime plain is a single narrow outlet near Watten, about 1 km wide. The river gradient within the basin is very low, amounting to only around 0.1‰. Thus the topography of the valley, the calcareous nature of the river coupled with the continuous subsidence of the area make it an excellent sedimentary trap likely to preserve long-term (i.e., high resolution) palaeoenvironmental records. Its low altitude means that from time to time incursions of the sea into the basin and subsequent regressions were readily recorded in the sedimentary sequence. Thus the basin served as an estuary during the Holocene Calais and Dunkirk transgressions, and was occupied by a fluvial and marshy ecosystem during marine regressions (Van der Woude and Roeleveld, 1985). Because insects have never managed to become adapted to fully marine environments, it is only during the terrestrial phases that the insect fauna provides detailed palaeoenvironmental and palaeoclimatic information.

Today the St-Omer region has a temperate oceanic climate; the mean temperatures of the warmest and the coldest month are about 18 °C and 3 °C respectively (Gandouin, 2003) and the mean annual temperature is close to 10.5 °C. It has an annual rainfall amounting to about 800 mm (Gehu, 1970). The modern landscape

Table 1

¹⁴C dates assigned to sediments from St-Momelin

Depth (cm)	Laboratory identification code	Material	¹³ C/ ¹² C ratio	Conventional ¹⁴ C Age (uncal. BP)	Cal. BP	Cal. BC
650	Hv — 24808	Peat	−28.9‰	4180 ± 45	4825–4575	2875–2625
700	Hv — 24807	Peat	−29.0‰	5040 ± 55	5890–5720	3940–3770
1000	Hv — 24806	Fine gyttja	−29.7‰	5810 ± 50	6710–6540	4760–4590
1600	Beta — 161065	Peat	−28.1‰	7740 ± 60	8620–8400	6670–6450
1625–1630	Beta — 161066	Peat	−28.2‰	8610 ± 70	9720–9500	7770–7550
1700	Beta — 161067	Peat	−29.1‰	9450 ± 70	11070–10940 / 10860–10520	9120–8990 / 8910–8570

The calibrated age ranges were based on the INTCAL98 calibration procedure, using the intercept method (Stuiver et al., 1998). All measurements were performed on bulk sediment with a conventional radiocarbon dating procedure.

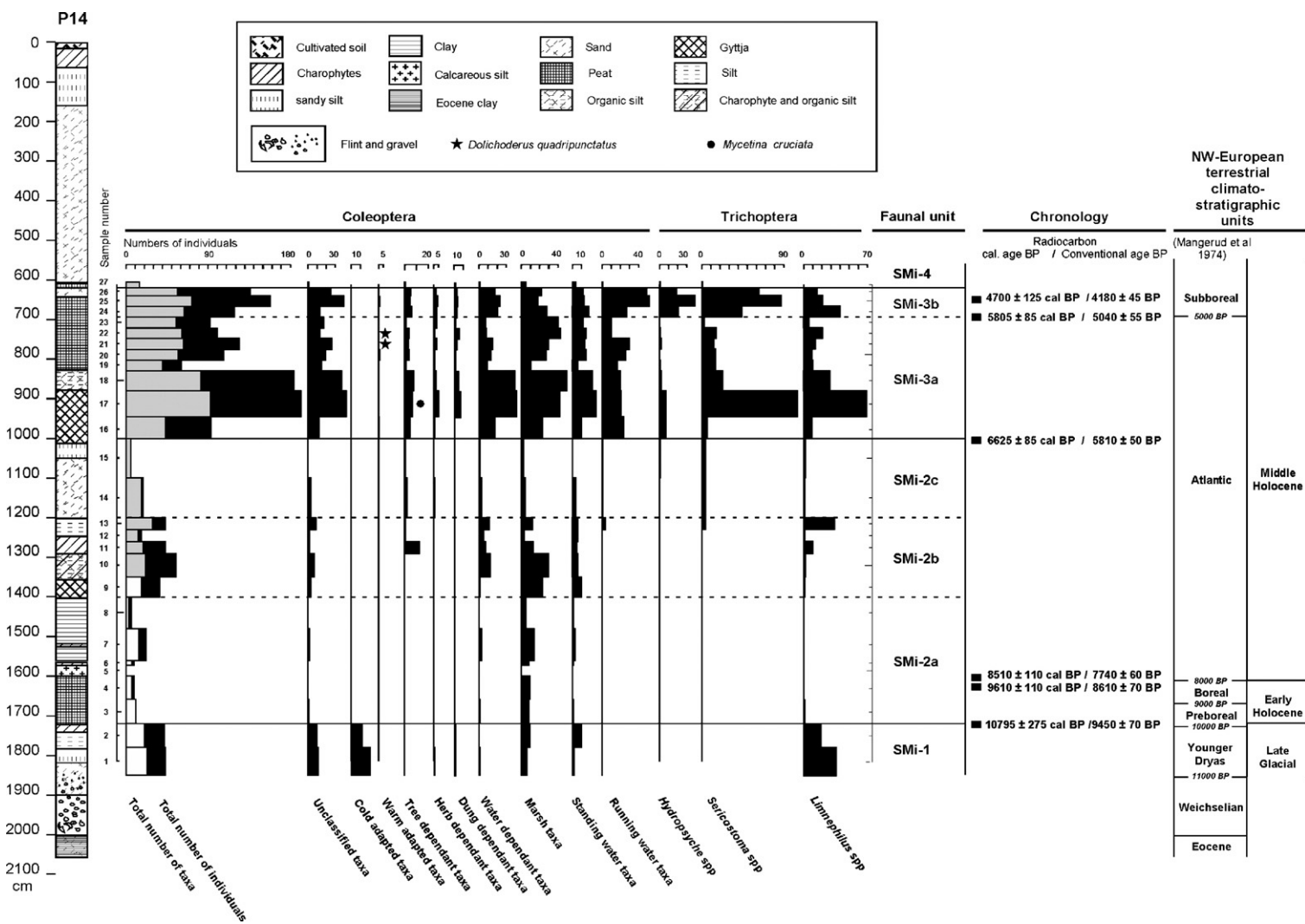


Fig. 2. Synthetic insect diagram from St-Momelin showing the lithological sequence; the fauna subdivided according to ecological groups; radiocarbon dates (2σ) and climatostratigraphical units.

corresponds today to a mosaic of cultivated and built up areas, with scattered remnants of seminatural vegetation of willow and alder woodlands, peat-bogs, and wet grasslands.

2.1. Field work

Sedimentary samples were obtained entirely by means of boreholes carried out on the cultivated St-Momelin marsh (N50°47'06", E2°14'42", alt. 2 m NGF). A screw-auger corer 10 cm wide was used. The sedimentary sequence consisted of alternating riverine and marine sands and silts. The freshwater organic deposits consisting of charophytic peaty sediments, true peat and gyttja. At this site the Quaternary sediments were almost 21 m thick and rested upon Eocene clays. The uppermost 1 m of sediment was not sampled because of the likelihood of contamination by modern agriculture. No samples were obtained from between levels 1 m and 6 m because the sandy sediment could not be retained by the corer. Below this level the samples were carefully extracted from the auger using the techniques already used successfully at Dingé (Andrieu et al., 1997) and at La Côte (Field et al., 2000).

2.2. Chronology and lithostratigraphy of the St-Momelin borehole

The radiocarbon ages obtained from bulk samples (Table 1) were calibrated with the INTCAL98 calibration curve, using the intercept method (Stuiver et al., 1998). All dates correspond to the Holocene period (Fig. 2). The older date (10795 ± 275 cal. BP) was taken from sediment overlying an undated minerogenic fossiliferous layer made of fluvial gravels and calcareous sandy-silty sediments (1850–1740 cm).

The lithology matches the general pattern observed in North Sea coastal plains (e.g., Baeteman and De Gans, 1993), in which Tertiary and Pleistocene basal sediments are overlain by Holocene sediments. A terrestrial and freshwater peat layer is characteristic of the infilling of the ancient Lateglacial river channel during early-Holocene times (Berendsen and Stouthamer, 2000). Holocene sea level rises lead to the formation of two main marine sedimentary layers (Calais and Dunkirk transgressions), intercalated within the late Atlantic/Sub-Boreal peat corresponding to a decrease in the rate of sea level rise or a possible minor marine regression (Gandouin, 2003). During this period, the St-Omer hydrographic system consisted of a river system meandering through a vast marshy region (Van der Woude and Roeleveld, 1985; Gandouin et al., 2005).

3. Insect analysis

Only the freshwater organic sediments were sampled for insect remains. The boundaries between samples were determined largely by sedimentary limits: thin sedimentary units were collected as single samples, whilst thicker ones were cut into several subequal pieces. The total weight of sediment for insect analysis was about 65 kg, and the average weight per sample about 2.4 kg. Insect fragments were extracted according to the standard paraffin flotation method described by Coope (1986). The fragments are preserved in tubes of 30% alcohol to prevent fungal attack. Identifications were made by comparison of these fragments with modern specimens. In Table 2 the nomenclature and taxonomic order of the Coleoptera and Trichoptera follow respectively that of Lucht (1987) and Moretti (1983), and the numbers opposite each name and in each sample column, indicate the minimum number of individuals of that taxon in each sample and is estimated by using the maximum number of any identifiable skeletal element. Biological and ecological symbols adjacent to each taxon are mainly drawn from Koch (1989–1992) for the Coleoptera, unless otherwise stated, and from Moretti (1983) and from Tachet (2000) for Trichoptera. Coleoptera dominate this assemblage with 265 taxa out of a total of 274. The rest include representatives of the Orders Trichoptera, Heteroptera, Hymenoptera (Formicidae) and Megaloptera. Almost 60% of beetle taxa were identified to the level of species or species-group.

The sequence of 27 insect assemblages (STO1 to STO27) was divided into 4 main Faunal Units (named SMi-1 to SMi-4) based on the variation of beetle ecological categories and number of individuals of Trichoptera genera (Fig. 2). These Faunal Units were drawn up independently of pollen or lithological considerations. SMi-2 was divided into three subunits a, b, and c, indicated by the marked increase in the total numbers of taxa and individuals in SMi-2b. SMi-3 was divided into two secondary subunits a and b, based on variations in the relative numbers of standing and running water insect species.

Below 18.50 m, the coarse sand and gravels did not yield any insect remains.

3.1. Faunal Unit SMi-1, samples 1–2 (18.5–17.2 m)

The beetle fauna from this unit is characterised by the presence of numerous cold-adapted species such as *Bembidion virens*, *Patrobis assimilis*, *Helophorus glacialis*, *Pycnoglypta lurida*, *Mannerheimia arctica*, *Eucnecosum brachypterum*, *Boreaphilus henningianus*

Table 2
Insects from St-Momelin

		SMi-1				SMi-2a				SMi-2b				SMi-2c				SMi-3a				SMi-3b				SMi-4			
		STO1	STO2	STO3	STO4	STO5	STO6	STO7	STO8	STO9	STO10	STO11	STO12	STO13	STO14	STO15	STO16	STO17	STO18	STO19	STO20	STO21	STO22	STO23	STO24	STO25	STO26	STO27	
COLEOPTERA																													
Carabidae																													
<i>Nebria brevicollis</i> (F.)	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	
<i>Elaphrus cupreus</i> Duft.	wet	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	
<i>Clivina</i> sp.	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	
<i>Dyschirius globosus</i> (Hbst.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	1	-	1	-	1	-	
<i>Bembidion lampros</i> (Hbst.)	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	
* <i>Bembidion virens</i> Gyll.	c	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Bembidion</i> cf. <i>tibiale</i> (Duft.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Bembidion</i> cf. <i>decorum</i> (Zenk.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	
<i>Bembidion assimile</i> Gyll.	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	-	-	1	-	2	-	-	-	-	-	
<i>Bembidion doris</i> (Panz.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
<i>Bembidion iricolor</i> Bedel	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	
<i>Bembidion</i> spp.	u	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	1	1	-	
* <i>Patrobus assimilis</i> Chaud.	c	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Pterostichus strenuus</i> (Panz.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	1	-	-	-	1	1	-	-	-	
<i>Pterostichus diligens</i> (Sturm)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	
<i>Pterostichus vernalis</i> (Panz.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
<i>Pterostichus nigrita</i> (Payk.)	wet	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	1	-	-	-	-	-	-	-	-	
<i>Pterostichus minor</i> (Gyll.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	2	-	2	2	-	-	
<i>Pterostichus</i> s.l. spp.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
<i>Agonum (Euophilus) micans</i> (Nicol.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	
<i>Agonum (Euophilus) scitulum</i> Dej.	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	
<i>Agonum (Euophilus) cf. piceum</i> (L.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Agonum (Euophilus) thoreyi</i> Dej.	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	
<i>Agonum (Euophilus) sp.</i>	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	1	
<i>Amara quenseli</i> (Schönh.)	c	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Oodes helopioides</i> (F.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	-	
<i>Badister sodalis</i> (Duft.)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	
<i>Badister (Baudia) sp.</i>	wet	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
<i>Odacantha melanura</i> (L.)	wet	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2	-	1	-	2	-	-	
<i>Dromius longiceps</i> Dej.	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	
Haliplidae																													
<i>Haliplus confinis</i> Steph. group	s	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Haliplus lineolatus</i> Mannh.	s	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Haliplus immaculatus</i> Gerh.	s	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
<i>Haliplus</i> sp.	s	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	
Dytiscidae																													
<i>Guignotus pusillus</i> (F.)	s	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
? <i>Coelambus</i> sp.	s	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Hygrotus inaequalis</i> (F.)	s	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	
<i>Hydroporus cf. palustris</i> (L.)	s	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	1	-	-	
<i>Hydroporus</i> s.l. sp.	s	-	-	-	-	-	1	-	-	-	-	-	-	-	-	2	1	-	1	-	1	-	1	-	1	-	-	-	
<i>Potamonectes depressus</i> (F.) <i>elegans</i> (Panz.)	s	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
<i>Noterus clavicornis</i> (Geer)	s	-	-	-	-	-	-	3	1	2	1	1	1	-	-	1	1	-	-	1	1	2	1	1	-	-	-	-	
<i>Agabus bipustulatus</i> (L.)	s	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
<i>Agabus</i> sp.	s	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-	-	
<i>Ilybius</i> sp.	s	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1	1	-	-	-	-	-	
<i>Nartus grapei</i> (Gyll.)	s	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	
<i>Colymbetes</i> sp.	s	1	1	-	-	-	-	-	-	-	-	1	-	-	-	1	1	1	1	1	1	1	1	1	1	1	-	-	

<i>Acilius</i> sp.	s	—	—	—	—	—	—	1	—	—	1	—	—	—	1	—	1	1	1	—	—	1	—	—	—	—	—
<i>Dytiscus</i> sp.	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—
Gyrinidae																											
<i>Gyrinus urinator</i> Ill.	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
<i>°Gyrinus suffriani</i> Scriba	s	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	3	4	—	—	—	—	—	—	—
<i>Gyrinus caspius</i> Ménétr.	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Gyrinus</i> sp.	s	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	1	1	2	—	—	—	2	2	1	1
<i>Orectochilus villosus</i> (Müll.)	r	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1	1	1	—	2	1	1
Hydraenidae																											
<i>Hydraena testacea</i> Curt.	s	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	1	—	—	—	—	1	—	—	—	—	—
<i>Hydraena</i> spp.	w	—	—	1	—	—	—	—	—	1	3	1	1	5	2	—	7	14	18	4	6	4	2	3	10	7	6
<i>Ochthebius bicolon</i> Germ./auriculatus Rey	w	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	3	—	—
<i>Ochthebius minimus</i> (F.)	w	—	—	—	—	—	—	—	—	—	7	—	—	—	—	—	7	11	—	—	—	5	3	—	1	3	5
<i>Ochthebius</i> gr. <i>marinus</i> (Payk.)	w	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ochthebius</i> spp.	w	—	—	—	—	—	—	1	—	—	—	6	3	5	—	1	—	—	13	1	3	—	—	2	2	6	—
<i>Limnebius</i> spp.	w	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	2	14	7	2	1	1	—	3	2	4	—
<i>Hydrochus</i> sp.	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—
<i>Helophorus glacialis</i> Villa	c	7	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helophorus brevipalpis</i> Bedel	s	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helophorus</i> spp.	s	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	1	1	—
Hydrophilidae																											
<i>Coelostoma orbiculare</i> (F.)	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	1	—	1	—	1	1
<i>Coelostoma hispanicum</i> (Küst.)	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
<i>Cercyon ustulatus</i> (Preyssl.)	d	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	1	—	—	—
<i>Cercyon tristis</i> (Ill.)	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3	1	—	2	2	—	—	2	—	2
<i>Cercyon sternalis</i> Sharp	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
<i>Cercyon</i> spp.	d	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	1	—	—	—	1
<i>Megasternum boletophagum</i> (Marsh.)	d	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	1	3	—	—	2	—	—
<i>Paracynus aeneus</i> (Germ.)	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
<i>Hydrobius fuscipes</i> (L.)	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—	—	1	—	1
<i>Limnoxenus niger</i> (Zschach)	s	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Anacaena</i> spp.	s	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	1	1	1	—	1	1	1	—
<i>Laccobius</i> spp.	s	—	—	—	—	—	—	1	—	4	1	—	1	1	—	—	1	1	1	—	1	1	1	—	1	1	—
<i>Enochrus</i> spp.	s	—	—	1	—	—	—	1	—	—	1	—	3	1	1	—	—	1	3	—	—	—	1	1	—	—	—
<i>Cymbiodyta marginella</i> (F.)	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
<i>Chaetarthria seminulum</i> (Hbst.)/ <i>similis</i> Woll.	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	1	1	—	1	2	1	2	1
<i>Hydrophilus caraboides</i> (L.)// <i>flavipes</i> (Stev.)	s	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hydrous</i> sp.	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Histeridae																											
<i>G.</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Silphidae																											
<i>Thanatophilus</i> sp.	u	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Silpha</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Phosphuga atrata</i> (L.)	u	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	1	1	—	—	1
Catopidae																											
<i>Nargus</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Choleva</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—
Scydmaenidae																											
<i>Neuraphes</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—

(continued on next page)

[illegible][illegible]

<i>Falagria sulcatula</i> (Grav.)	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Drusilla canaliculata</i> (F.)	u	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
<i>Aleocharinae</i> indet.	u	6	7	-	-	-	-	-	-	1	1	-	-	1	-	2	4	2	2	2	3	-	1	4	5	-	
<i>Staphylinidae</i> indet.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	1	-	4	-	-	
Pselaphidae																											
<i>Bryaxis</i> spp.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	2	4	3	1	5	2	-	2	1	1	1	-	
<i>Rybaxis laminata</i> (Motsch.)	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	
<i>Pselaphus heisei</i> Hbst.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
Cantharidae																											
<i>Cantharis</i> sp.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	
<i>Rhagonycha</i> sp.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	
Malachiidae																											
<i>Anthocomus coccineus</i> (Schall.)	wet	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	1	-	-	-	-	-	-	
<i>Malachiidae</i> indet.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
Melyridae																											
? <i>Dasytes</i> sp.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
Elateridae																											
<i>Adrastus</i> sp.	t	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-	-	-	
<i>Denticollis linearis</i> (L.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	
<i>Hypnoidus</i> cf. <i>rivularius</i> (Gyll.)	c	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Zoroehrus dermestoides</i> (Herbst)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	
<i>Elateridae</i> indet.	u	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	1	-	1	1	2	2	2	1	1	-	
Eucnemidae																											
<i>Dromaeolus barnabita</i> (Villa)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
<i>Dirhagus lepidus</i> (Rosh.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	
Throscidae																											
<i>Throscus</i> sp.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
Buprestidae																											
<i>Trachys minutus</i> (L.)	t	-	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Dascillidae																											
<i>Dascillus cervinus</i> (L.)	wet	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	
Helodidae																											
<i>Cyphon</i> spp.	wet	-	2	1	-	-	1	1	-	1	2	1	1	1	-	3	1	2	1	3	4	1	3	4	3	2	-
Dryopidae																											
<i>Dryops</i> sp.	w	-	-	-	-	-	1	-	-	2	-	1	1	-	-	1	2	1	1	3	5	2	2	3	2	2	-
<i>Elmis</i> cf. <i>aenea</i> (Müll.)	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	2	2	5	2	1	1	3	6	5	-
<i>Esolus parallelepipeds</i> (Müll.)	r	-	-	-	-	-	-	-	-	-	-	-	-	1	4	3	6	4	11	14	6	2	11	26	26	-	
<i>Oulimnius tuberculatus</i> (Müll.)/ * <i>trogloodytes</i> (Gyll.)	r	-	-	-	-	-	-	-	-	-	-	-	4	1	-	12	10	9	6	5	5	-	4	1	5	5	-
<i>Limnius volckmari</i> (Panz.)	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	1	3	2	1	1	7	5	5	-	
cf. <i>Normandia nitens</i> (Müll.)	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	3	-	3	1	6	1	2	3	9	7	-
Byrrhidae																											
<i>Simplocaria semistriata</i> (F.)	u	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

(continued on next page)

Table 2 (continued)

		SMi-1	SMi-2a		SMi-2b				SMi-2c				SMi-3a				SMi-3b				SMi-4							
		STO1	STO2	STO3	STO4	STO5	STO6	STO7	STO8	STO9	STO10	STO11	STO12	STO13	STO14	STO15	STO16	STO17	STO18	STO19	STO20	STO21	STO22	STO23	STO24	STO25	STO26	STO27
<i>Cytilus sericeus</i> (Forster)	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Byrrhus</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Nitidulidae																												
<i>Cateretes</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—
<i>Brachypterus urticae</i> (F.)	h	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
<i>Meligethes</i> sp.	h	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	—	—
<i>Epuraea</i> sp.	t	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Cucujidae																												
<i>Psammocerus bipunctatus</i> (F.)	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	—	1	—	—	—	—	—	—	—	—
<i>Laemophloeus</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Cryptophagidae																												
<i>Telmatophilus</i> sp.	h	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
<i>Cryptophagus</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Atomaria mesomelaena</i> (Hbst.)	wet	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—
<i>Atomaria</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—	—	1	—	—	—	1	—	—
Phalacridae																												
<i>Phalacrus caricis</i> Sturm	wet	—	—	—	—	—	1	—	—	2	—	—	—	1	—	—	1	2	—	—	—	—	—	1	1	—	—	—
<i>Phalacridae</i> indet.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—
Lathridiidae																												
<i>Lathridius</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Enicmus</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Corticariini</i> indet.	u	—	1	—	—	—	—	2	—	—	—	—	1	2	—	—	1	1	4	1	—	2	—	—	1	—	1	—
Colydiidae																												
<i>Cerylon</i> cf. <i>ferrugineum</i> Steph.	t	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Endomychidae																												
<i>Mycetina cruciata</i> (Schall.)	t	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Coccinellidae																												
<i>Anisosticta novemdecimpunctata</i> (L.)	wet	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Semiadalia notata</i> (Laich.)	u	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sphindidae																												
<i>Aspidiphorus orbiculatus</i> (Gyll.)	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—
Cisidae																												
<i>G.</i> sp.	u	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Anobiidae																												
<i>Ernobius</i> sp.	t	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	1	—	—
<i>Anobium</i> s.l. sp.	t	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	1	—
Anthicidae																												
<i>Anthicus gracilis</i> (Panz.)	wet	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Alleculidae																												
<i>Gonodera luperus</i> (Hbst.)	t	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—

Tenebrionidae																												
<i>Eledona agricola</i> (Hbst.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	
Scarabaeidae																												
<i>Onthophagus</i> gr. <i>ovatus</i> (L.)	d	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
<i>Onthophagus</i> sp.	d	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aegialia sabuleti</i> (Panz.)	wet	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxyomus sylvestris</i> (Scop.)	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Aphodius depressus</i> (Kug.)	d	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aphodius</i> spp.	d	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	1	1	-	1	1	1	1	1	-
<i>Cetonia aurata</i> (L.)	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Chrysomelidae																												
<i>Macrolea appendiculata</i> (Panz.)	wet	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Donacia clavipes</i> F.	wet	-	-	-	1	-	1	4	-	6	1	-	-	-	-	1	6	15	-	-	-	-	-	-	1	-	-	-
<i>Donacia dentata</i> Hoppe	wet	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Donacia versicolore</i> (Brahm)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	2	-	-	-	-
<i>Donacia aquatica</i> (L.)	wet	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Donacia</i> cf. <i>marginata</i> Hoppe	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	1	1	1	-	-	-	1
<i>Donacia thalassina</i> Germ.	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Donacia</i> cf. <i>vulgaris</i> Zschach	wet	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Donacia cinerea</i> Hbst.	wet	-	-	1	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Donacia</i> spp.	wet	-	-	1	-	-	-	-	-	-	1	1	1	-	-	-	1	3	1	3	1	4	-	-	1	-	-	-
<i>Plateumaris discolor</i> (Panz.)	wet	-	-	-	-	-	-	-	-	9	2	-	-	-	-	-	1	-	1	-	-	2	-	-	-	-	-	-
<i>Plateumaris sericea</i> (L.)	wet	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	-	-	-
<i>Plateumaris braccata</i> (Scop.)	wet	-	-	-	2	-	3	5	4	6	-	1	-	-	-	-	3	2	1	2	4	4	-	-	-	-	-	-
<i>Plateumaris</i> cf. <i>rustica</i> (Kunze)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	2	-	1	-	-	-
<i>Plateumaris consimilis</i> (Schränk)	wet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Plateumaris</i> spp.	wet	-	-	1	1	-	-	1	-	1	2	2	-	1	-	-	-	1	1	2	-	8	7	5	-	3	-	-
<i>Donacia</i> / <i>Plateumaris</i> sp.	wet	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-
<i>Prasocuris phellandrii</i> (L.)	wet	-	-	-	-	-	-	-	1	-	-	-	1	-	-	1	1	-	-	-	1	1	-	-	-	-	-	-
<i>Plagiodera versicolora</i> (Laich.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Melasoma aenea</i> (L.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
<i>Phyllodecta</i> sp.	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Agelastica alni</i> (L.)	t	-	-	-	-	-	-	-	-	-	-	-	1	2	1	3	1	1	1	1	1	-	1	1	2	1	-	-
<i>Phyllotreta</i> sp.	h	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-
<i>Halitica</i> sp.	h	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Epitrix pubescens</i> (Koch)	h	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Alticinae</i> indet.	u	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-
Bruchidae																												
<i>Bruchus</i> / <i>Bruchidius</i> spp.	h	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Scolytidae																												
<i>Scolytus</i> sp.	t	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hylesinus crenatus</i> (F.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
<i>Leperisinus varius</i> (F.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	1	-	-
<i>Ernopus fagi</i> (F.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Taphrorychus bicolor</i> (Hbst.)/ <i>villifrons</i> (Duf.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Xyleborus dispar</i> (F.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
<i>Xyleborus saxeseni</i> (Ratz.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	1	-
Curculionidae																												
<i>Pselaphorhynchites</i> sp.	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Apion</i> (<i>Melanapion</i>) <i>minimum</i> (Hbst.)	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
<i>Apion</i> spp.	h	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	1	-	1	-	-	-	-

(continued on next page)

Table 2 (continued)

		SMi-1	SMi-2a		SMi-2b							SMi-2c							SMi-3a							SMi-3b							SMi-4	
		STO1	STO2	STO3	STO4	STO5	STO6	STO7	STO8	STO9	STO10	STO11	STO12	STO13	STO14	STO15	STO16	STO17	STO18	STO19	STO20	STO21	STO22	STO23	STO24	STO25	STO26	STO27						
<i>Otiorhynchus</i> sp.	u	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–					
<i>Phyllobius/Polydrusus</i> spp.	u	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1	2	–	1	–	1	–	–	–	1	–					
<i>Sitona</i> sp.	h	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–					
<i>Rhyncolus chloropus</i> (L.)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–					
<i>Stereocorynes truncorum</i> (Germ.)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–					
<i>Rhyncolus</i> sl. sp.	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–					
<i>Bagous</i> spp.	s	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	1	3	2	–	–	–	1	–	–	1	–	–	1					
<i>Tanysphyrus</i> cf. <i>lemnae</i> (Payk.)	s	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	1	–	1	1	1	–	3	3	2	3	–						
<i>Notaris bimaculatus</i> (F.)	wet	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–					
<i>Notaris scirpi</i> (F.)	wet	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–					
<i>Notaris aethiops</i> (F.)	c	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–					
<i>Thryogenes</i> sp.	wet	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	1					
<i>Tychius picrostris</i> (F.)	h	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–					
<i>Anthonomus</i> cf. <i>pedicularius</i> (L.)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–					
<i>Curculio pyrrhoceras</i> (Marsh.)	t	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–					
<i>Curculio</i> sp. (≠ <i>nucum</i> L.)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1					
<i>Hylobius</i> cf. <i>transversovittatus</i> (Goeze)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–					
<i>Hypera</i> sp.	h	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–					
<i>Limnobaris</i> sp.	wet	–	–	1	1	–	–	–	–	1	–	–	–	–	–	–	2	–	–	–	–	–	1	1	–	1	–	–	–					
<i>Eubrychius velutus</i> (Beck.)	wet	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–					
<i>Drupenatus nasturtii</i> (Germ.)	wet	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	–					
<i>Ceutorhynchus</i> sl. spp.	h	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1	–	–	–	–	1	–	–	–					
<i>Gymnetron labile</i> (Hbst.)	h	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–					
<i>Gymnetron</i> cf. <i>pascuorum</i> (Gyll.)	h	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–					
<i>Gymnetron</i> sp.	h	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–					
<i>Rhynchaenus</i> cf. <i>pilosus</i> (F.)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–					
<i>Rhynchaenus stigma</i> (Germ.)/ <i>pseudostigma</i> (Temp.)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–					
<i>Rhynchaenus</i> cf. <i>angustifrons</i> (West)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–					
<i>Rhynchaenus</i> sp.	u	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–					
<i>Rhamphus pulicarius</i> (Hbst.)/ <i>oxyacanthae</i> (Marsh.)	t	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	1	–	–	–	1	–	–	–					
<i>Curculionidae</i> indet.	u	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–					
HYMENOPTERA Formicidae																																		
<i>Dolichoderus quadripunctatus</i> (L.)		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–	–					
HETEROPTERA																																		
<i>Saldidae</i> indet.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–	1	1	–	1	–	1	–	–	–					
<i>Gerris</i> sp.		–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–					
<i>Heteroptera</i> indet.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1					
TRICHOPTERA																																		
<i>Hydropsyche</i> sp.		–	–	–	–	–	–	–	–	–	–	–	–	–	1	7	7	2	1	–	2	1	–	–	21	39	19	1						
<i>Sericostoma</i> sp.		–	–	–	–	–	–	–	–	–	–	–	4	4	4	6	105	23	15	15	13	16	3	44	87	63	1	–						
cf. <i>Limnephilus</i> sp.		36	19	1	–	–	–	–	1	2	10	1	34	1	2	9	69	29	10	9	13	21	6	40	21	15	–	–						
<i>Trichoptera</i> indet.		–	–	–	–	–	–	–	–	–	–	1	2	–	–	1	7	4	1	–	–	4	1	6	8	9	–	–						
MEGALOPTERA																																		
<i>Sialis</i> sp.		–	–	–	–	–	–	–	1	–	–	–	10	–	–	2	5	6	1	1	3	7	3	11	4	5	–	–						

Figures show the minimum numbers of individuals per sample. The nomenclature and taxonomic order for the Coleoptera and the Trichoptera follow respectively that of Lucht (1987) and Moretti (1983). (°) indicates the taxa identified from the study of male genitalia; (*) indicates the taxa that do not belong to the modern French fauna. Wet, marsh taxa; s, standing water taxa; r, running water taxa; w, water dependent taxa; t, tree dependent taxa; h, herb dependent taxa; d, dung dependent taxa; c, cold adapted taxa; u, unclassified taxa.

and *Notaris aethiops*. None of the thermophilous species present in the Holocene sediments were present in these samples.

Although this is a small assemblage, the beetles provide an ecologically consistent picture of the local environment at this time. *Bembidion virens* lives near water “on sterile, gravelly or stony river banks and lake shores” (Lindroth, 1985-1986). *Patrobus assimilis* inhabits a wide range of environments such as open country, forests, heaths, swamp and lake shores. *Amara quenseli* is a species of dry unshaded habitats where the soil is usually sand and gravel and where the vegetation is sparse. *Helophorus glacialis* is abundant in this Faunal Unit. It lives in small shallow dark-bottomed pools at the edges of snow patches, where the water is always near to freezing-point (Hansen, 1987). *Pycnoglypta lurida*, *Olophrum fuscum*, *Arpedium quadrum*, *Eucnecus brachypterum*, and *Boreaphilus hennigianus* are predatory species found in damp places amongst moss and plant debris (Palm, 1948; Zanetti, 1987). *Gymnusa brevicollis* is also a wetland staphylinid associated with mosses and accumulations of decaying plant remains such as *Phragmites*, *Carex*, and *Juncus*. *Aegialia sabuleti* is today extremely rare in France but common in northern Europe where it is found in sandy places at the roots of plants. In south-west France (Dordogne) this species seems to be associated with layers of dead leaves and other plant detritus buried at some depth in sandy deposits along river valleys, and in abandoned stream channels (Delpy, 2000). *Simplocaria semistriata* feeds exclusively on mosses. Two other phytophagous Coleoptera are weevils: *Notaris bimaculatus* is oligophagous on *Phalaris arundinacea*, *Glyceria maxima*, *Spartina anglica* and *Typha latifolia*. *Notaris aethiops* is more polyphagous, it is reported on various Poaceae, *Sparganium ramosum*, *Iris pseudacorus* and *Carex gracilis*. The shallow pools of standing water are indicated by *Colymbetes* sp., *Ochthebius* cf. *marinus*, *Helophorus glacialis*, *Helophorus brevipalpis*, and *Helophorus* sp. There are no beetles in this assemblage that indicate the local presence of trees.

In summary, this is a fauna of open, sandy or gravelly habitats with sparse vegetation growing in the drier places and reedy plants and mosses where the soil was moist. Damp accumulations of vegetable debris were probably widespread. Snow patches probably existed into the summer months from which melt water fed shallow pools. The absence of any running water species suggests that, at this time, the site was probably located at some distance from the main channel of the river Aa.

3.2. Faunal Unit SMI-2, samples 3–15 (17.2–10 m)

The most characteristic feature of this Faunal Unit is the complete absence of the cold-adapted species and the presence of relatively thermophilous species whose ranges only just reach southern Fennoscandia. These species include *Odacantha melanura*, *Guignotus pusillus*, *Gyrinus suffriani*, *Hydraena testacea*, *Limnoxenus niger*, *Hydrophilus caraboides*, *Lesteva heeri*, *Anthonomus coccineus*, and *Esolus parallelepipedus*. In spite of the evidence for climatic warming at this time, insect fossils were remarkably scarce with an average of only 21 individuals per sample.

An environmentally significant species is the predator *Odacantha melanura* which has rather narrow habitat requirements. It is associated with clayey or muddy margins of eutrophic lakes and ponds where there is dense and tall growth of reedy plants such as *Phragmites*, and sometimes also *Typha* and *Glyceria* (Lindroth, 1985-1986). *Pterostichus nigrita* lives beside freshwater of all types often where there is tall vegetation. The “whirligig beetle” *Gyrinus suffriani* is also often found in fens choked by *Phragmites* where it hunts on the surface of the water for insects accidentally stranded there by the surface tension. *Noterus clavicornis* (relatively common from samples STO9 to STO13), is also a predator that lives in shallow standing water where there is abundant vegetation. It is often found in brackish water or in localities very near to the sea (Holmen, 1987). Species indicative of running-water such as *Oulimnius* and *Esolus* appear near to the top of this Faunal Unit. Both are detritus feeders.

Aquatic or semi-aquatic phytophagous species become more common in this Faunal Unit. They indicate both submerged and emergent pond-weeds and reedy vegetation. *Eubrychius velutus* is a fast swimming weevil that feeds principally on *Myriophyllum*. *Bagous* is also a sub-aquatic weevil that feeds on a variety of pond-weeds. *Tanysphyrus lemnae* feeds on the surface on the floating duckweed *Lemna*. *Donacia appendiculata* feeds on *Sparganium ramosum* and *Typha latifolia*. *Donacia clavipes* and *Plateumaris braccata* are largely restricted to *Phragmites communis*. *Donacia dentata* feeds on *Sagittaria sagittifolia* and also on *Alisma*. *Donacia cinerea* and other species of *Plateumaris* feed mostly on sedges. *Prasocuris phellandri* usually feeds on various aquatic Umbelliferae but occasionally on *Caltha palustris*.

Of particular importance here is the presence of tree-dependent beetles. *Trachys minutus* (locally abundant in sample STO11 only) is associated with many trees such as *Corylus*, *Salix* and *Populus*. *Agelastica alni*, regularly

present from sample STO13 upwards, feeds almost exclusively on *Alnus*. The larvae of *Curculio pyrrhoceras* develop in oakleaf galls produced by the attacks of the wasp *Cynips quercusfolii*.

In summary, the assemblages from faunal unit SMi-2 indicate standing, shallow water with much marshy vegetation in and about it. *Alnus* trees were common during the deposition of the upper part of this Faunal Unit and subsequently. The presence of oak trees suggests that better drained ground was not very far away. However, the rarity of ground-beetles suggests that much of the area may have been submerged in the immediated vicinity and that the margin of the marsh was probably located at some distance from the coring site.

3.3. Faunal Unit SMi-3, samples 16–26 (10–6.2 m)

This Faunal Unit includes most of the taxa that were present SMi-2 but also many more additional species indicating greatly increasing taxonomic diversity. It is likely that the terrestrial environments had become much more diversified either as a result of water regression or sedimentary infilling.

The local environment is now made up of a mosaic of varied micro-biotopes. Two subunits of SMi-3 can be established on the basis of variations in the proportions of running and standing water. The relative abundance of the riffle beetles *Elmis aenea*, *Esolus parallelipipedus*, *Oulimnius*, *Limnius volckmari* and *Normandia* indicate rapidly moving, well oxygenated water. They were much more abundant in the upper part of the zone (SMi-3b) compared with the lower part (SMi-3a), probably reflecting changes in the hydrological regime. The larval Trichoptera (caddisflies) provide additional information about the actual speed at which the water was flowing at this time. *Hydropsyche*, which becomes relatively abundant in SMi-3b, prefers mature rivers where the water has an average speed of 25–50 cm s⁻¹ whereas *Sericostoma* in SMi-3a prefers speeds below 25 cm s⁻¹ (Tachet, 2000). However many species of water beetles of the families Dytiscidae, Gyrinidae, Hydraenidae, and Hydrophilidae indicate the presence of standing or slowly moving water. These ecologically contrasting groups are not necessarily incompatible. The presence of both groups in this Faunal Unit suggests a river meandering across its floodplain between riffles to pools and that the sediment included members of both communities accidentally brought together for instance at time of flood.

Almost 30 taxa of predatory or scavenging ground beetles are all associated with marshy environments. These include *Dyschirius globosus*, *Bembidion* spp.,

Pterostichus spp., *Agonum* spp., *Oodes helopioides*, *Badister sodalis*, *Odacantha melanura* and *Dromius longiceps*. The silphid *Phosphuga atrata* is a specialist predator on snails.

Among the Staphylinidae, *Micropeplus porcatus*, *Olophrum fuscum* (already identified in faunal unit SMi-1), *Lesteva sicula heeri*, *Trogophloeus* sp., *Oxytelus rugosus* and *Stenus* spp. are well represented in almost every sample from SMi-3, all of these are associated with wet mud or decaying vegetal matter.

Several of the “semi-aquatic” phytophagous species occur for the first time in this Faunal Unit. *Donacia versicolore* is restricted to *Potamogeton natans*. *Donacia* cf. *marginata* is monophagous, feeding on *Sparganium ramosum*. *Donacia thalassina* is found on *Scirpus lacustris*. *Plateumaris consimilis* feeds on various species of *Carex*. *Drupenatus nasturtii* is monophagous on *Nasturtium officinale*. *Phalacrus caricis*, already identified in the previous faunal unit, lives on flowers of *Carex* that have been infected by smut fungus.

Tree dependent species occur throughout SMi-3, but at relatively low numbers. Many of them are characteristic of the riverine forest, such as *Plagiodera versicolora* (associated with *Salix* and *Populus*); *Melasma aenea* (associated with *Alnus*), *Phyllodecta* sp. (genus containing half a dozen species in Europe, all of them living mainly on *Salix*, sometimes also on *Populus*). *Agelastica alni* is present throughout SMi-3 suggesting that alder was very abundant nearby. *Apion minimum* is a weevil associated with several species of *Salix*. Its larvae develop in galls produced by the sawfly *Pontania* on willow leaves. Several bark-beetles (e.g., Scolytidae) have larvae that feed on the cambium layer. *Scolytus* itself attacks many deciduous trees. *Hylesinus crenatus* is usually found under the bark of *Fraxinus*. *Ernoporus fagi* is restricted to *Fagus silvatica*. *Leperisinus varius* and *Taphrorychus bicolor/villifrons* all attack a variety of deciduous trees. *Xyleborus dispar* and *Xyleborus saxeseni* make their tunnels under the bark of a variety of trees including conifers.

Of particular interest is the range of saproxylophagous beetles at this level, indicating the abundant presence of old, dead trees and decaying wood nearby. The click-beetle *Denticollis linearis* is a common insect always found in forests where the adult beetle can be found on flowers and foliage, but whose larvae live in rotten wood. The weevils *Rhyncolus chloropus* and *Stereocorynes truncorum* can be found inside rotten trunks of many tree species. Species of *Cerylon* are abundant under dead bark of deciduous or coniferous trees where they prey upon other insects, especially on bark-beetles. *Ernobius* and *Anobium* (the familiar

woodworm beetle) are associated with dry dead wood preferably that has first been attacked by fungus (Hickin, 1963). *Eledona agricola* is a fungus feeder, dependent on *Laetiporus sulphureus*.

Several important species in this Faunal Unit are typical of pristine, undisturbed primeval forests for example *Mycetina cruciata*, *Dromaeolus barnabita* and *Dirrhagus lepidus*. The most significant of these species is *Mycetina cruciata*, which occurs in sample STO16. This species is associated with old forests not affected by human action ("urwald" forests), where it is found in wet rotten wood attacked by fungus. Today, *M. cruciata* seems to have a predominantly mountainous distribution in France although it has been found recently at low altitude in the Paris basin (Nérat, 2005); it is likely that this modern distribution pattern results from the eradication of most of the original lowland forests during the historic period. Today this species is extinct in Britain (Buckland and Dinnin, 1993). The last fossil British record is dated to 2980 ± 110 BP at Thorne Moors (Buckland, 1979), which is probably the most recent site (Late Bronze Age) to yield "urwald" assemblages in Britain. *Dromaeolus barnabita* (in STO18) and *Dirrhagus lepidus* (in STO24) are also species associated with ancient forests where dead timber is abundantly available. Both species are good indicators of pristine forests. *Dromaeolus barnabita* is found in isolated localities in most of continental Europe. According to Muona (1993) and Dinnin (1997) it lives in old forest where it excavates holes beneath bark on branches and trunks of various deciduous trees infected by white rot, pupating in hard wood close to the surface. Most larvae develop on the warmer, southern side of the tree. The same authors indicate that the modern distribution of this declining insect is discontinuous, with scattered localities in southern and central Europe. It is apparently a thermophilous species. It is now extinct in Britain, but there are neolithic fossil records from Runnymede (Robinson, 1991) and at Bole Ings (Dinnin, 1997). *Dirrhagus lepidus* is today very rare everywhere, it is known from Caucasus, Central Europe, northern Italy, and France where it is found in Pyrénées, Vosges, and in Departments Doubs and Savoie. It is apparently associated with various deciduous trees.

In addition to records of "urwald" Coleoptera, SMi-3 is also marked by large numbers of running water beetles, especially in SMi-3b. This conjunction of apparently unrelated events is interesting, since it is now believed that forest clearance during the Neolithic period had a severe impact on the fluvial benthic insect faunas (Smith, 2000), especially on the riffle beetles which are adapted to highly oxygenated rivers and live

exclusively at the bottom of streams, among gravels and shingles. It is likely that a secondary impact of the removal of the forest cover was an increase of soil erosion leading to a rise of alluviation processes in lowland areas, making the biotope unsuitable for Elmidae. Combined evidence from independent data, such as saproxylophagous and water beetles, suggests that forest cover in the St-Omer basin remained undisturbed during SMi-3, and that large scale forest clearance did not start in the region before 4700 cal. BP, the last date available at the end of SMi-3b. This is in agreement with the general scheme established in this part of Europe (Bell and Walker, 1992).

Of particular importance in this assemblage is the presence of two strongly halophilous species in SMi-3b. The ground beetle *Bembidion iricolor* is confined to the sea shore or upper estuaries (Lindroth, 1974) where it lives under plant litter and sea weed (Luff, 1998). The water beetle *Paracymus aeneus* lives at the edges of shallow, well vegetated and often temporary pools above the high tide mark (Hansen, 1987).

In summary the coleopteran assemblage from this Faunal Unit indicates a mature river meandering across a floodplain with alternating shallow riffles and pools of more slowly flowing water. It is likely that high tide was not far away though in the immediate vicinity aquatic habitats were dominated by fresh water. Nearby there was much marshy ground with abundant alder and willow trees in the wetter places and, on the drier ground, oaks and other deciduous trees growing. The forest was mature with much dead timber; standing dead trunks as well as prostrate logs lying in the marsh itself.

3.4. Faunal Unit SMi-4, sample 27 (6.06–6.2 m)

The uppermost Faunal Unit includes the insects from a single sample. It is marked by a very low number of taxa and of individuals, and by the disappearance of almost all the ecological categories mentioned above, with the exception of standing water and wetland species. However, there is no evidence to suggest that this impoverishment is due to any climatic deterioration. It is possible, since it is the uppermost sample, that some of the original fossil content has been lost by decomposition, perhaps due to groundwater percolation.

4. Climatic interpretation of the coleopteran assemblages

The interpretation of the climatic significance of coleopteran assemblages is based on the assumption that individual species have critical temperature preferences

which, to a large extent, are reflected by their geographical ranges. In this account the climatic significance of the assemblage from each Faunal Unit will be considered separately. Climatically critical species will be discussed first and then, for each Faunal Unit, a quantified estimate will be made of the palaeotemperature using the Mutual Climatic Range (MCR) method (Atkinson et al., 1987) and the Climatic Reconstruction Software package (Buckland, 2003). In these reconstructions only predatory or general scavenging beetle species have been used in order to avoid using phytophagous beetle species whose geographical ranges are *directly* dependent on those of their preferred host plant. These MCR estimates are thus independent of those derived from the palaeobotanical data. In the MCR estimates given below, T_{max} indicates the mean air temperature of the warmest month (July) and T_{min} indicates the mean air temperature of the coldest months (January and February).

4.1. Faunal Unit SMi-1

The predominance of cold-adapted species of beetle in this assemblage that do not occur today in northern France indicates that the climate at the time was much colder than that of the present day. Such species include *Bembidion virens*, *Patrobus assimilis*, *Amara quenseli*, *Helophorus glacialis*, *Pycnoglypta lurida*, *Olophrum fuscum*, *Mannerheimia arctica*, *Eucnecusum brachypterum* and *Boreaphilus henningianus* all of which have today boreo-montane distributions in Europe. *Aegialia sabuleti* is extremely rare in France but common in Fennoscandia as far north as Lappland and the Kola Peninsula. *Notaris aethiops* is a northern species found in isolated localities at high altitudes in Central Europe, in France it is restricted to a few lakes and peat bogs in the Massif Central.

Quantitative MCR estimates of the thermal climate at this time gave the following figures based on predatory and scavenging beetle species from this Faunal Unit:

T_{max} lay between 10 °C and 13 °C.
T_{min} lay between – 18 °C and – 2 °C.

It is likely that the actual figures lay towards the colder end of these estimates (Coope et al., 1998).

4.2. Faunal Unit SMi-2

The suite of relatively thermophilous beetle species in this Faunal Unit whose geographical ranges barely reach as far north as southern Scandinavia indicates that there had been a marked amelioration in the temperature by this time. Climatic conditions at this time were about as

warm as they are at the present day in northern France. This interpretation is supported by the complete disappearance of all the cold-adapted species so characteristic of the previous Faunal Unit.

Because of the small number of stenothermic species present in this Faunal Unit it has been necessary to utilise in this MCR estimation all the species from samples STO3 to STO15 that are also included in the MCR database. The temperature estimates for this Faunal Unit thus represent a mean value for a period that lasted for about 4000 years. The MCR estimates based on the predatory and scavenging beetle species from this Faunal Unit were as follows:

T_{max} lay between 16 °C and 21 °C.
T_{min} lay between – 3 °C and 3 °C.

It is likely that the actual figure for T_{max} lay towards the mid point of this range and that the actual figure for T_{min} lay near the upper limit of the range (Coope et al., 1998).

4.3. Faunal Unit SMi-3

Faunal unit SMi-3 clearly indicates a temperate climate, that may have been even warmer than it is today. Of special interest is the presence in two adjacent samples (STO21 and STO22) of the ant *Dolichoderus quadripunctatus*. This species is today common in southern France but is extremely rare further north (Seifert, 1996) and has not been recorded from Britain or Scandinavia (Collingwood, 1979). In northern France it is found only in isolated outposts, probably when favourable local conditions allow a warm microclimate to become established. It lives in colonies inside hollow twigs and branches of small deciduous trees and bushes, but never on coniferous trees. It is interesting to note that it is often found on *Ulmus*, *Populus*, and *Salix* alongside rivers (Bernard, 1968). This ant may safely be considered to be a thermophilous species.

Amongst the beetles, the presence of several southern taxa such as *Anthicus gracilis* in sample STO16 suggest that the climate was probably warmer than today. *Paracymus aeneus* in sample STO25 provides further evidence for warm conditions at this time since this rare water beetle is typically a Mediterranean-Atlantic species. There are however isolated records as far north as the extreme south of Scandinavia (Hansen, 1987). The species is usually considered to be relatively thermophilous (Hebauer and Klausnitzer, 1998). An even more unexpected discovery is that of the hydrophilid species *Coelostoma hispanicum* in sample STO20. This is a Mediterranean species restricted, in western Europe, to

Spain, southern France and Italy. The identification of the fossil is based on its larger size compared with the more widespread *C. orbiculare*.

The larger number of species in these assemblages enable MCR estimates of the thermal climate to be made on eleven samples from this Faunal Unit. These are shown in graphically on Fig. 3.

4.4. Faunal Unit SMi-4

The few species present in this Faunal Unit do not permit a satisfactory estimation of the thermal climate. However there were no cold-adapted species present and there is no reason to think that the climate was any colder than during the rest of the early Holocene.

4.5. Climatic synthesis

Fig. 3 shows a summary of the MCR estimates of the mean air temperatures of the warmest and coldest months. This diagram shows clearly that a sudden and intense climatic warming took place between samples STO2 and STO3. This change in temperature probably involved a rise in mean July figures of about 8 °C and a rise in the January/February figure of about 15 °C. The rise in the mean annual temperature was therefore about 11.5 °C. It has not been possible yet to estimate the rate of change involved because of inadequate geochronological sedimentological control, but the evidence suggests that it took place with dramatic suddenness.

According to Antoine et al. (2000), fluvial silts with a high calcareous contents are characteristic of Lateglacial

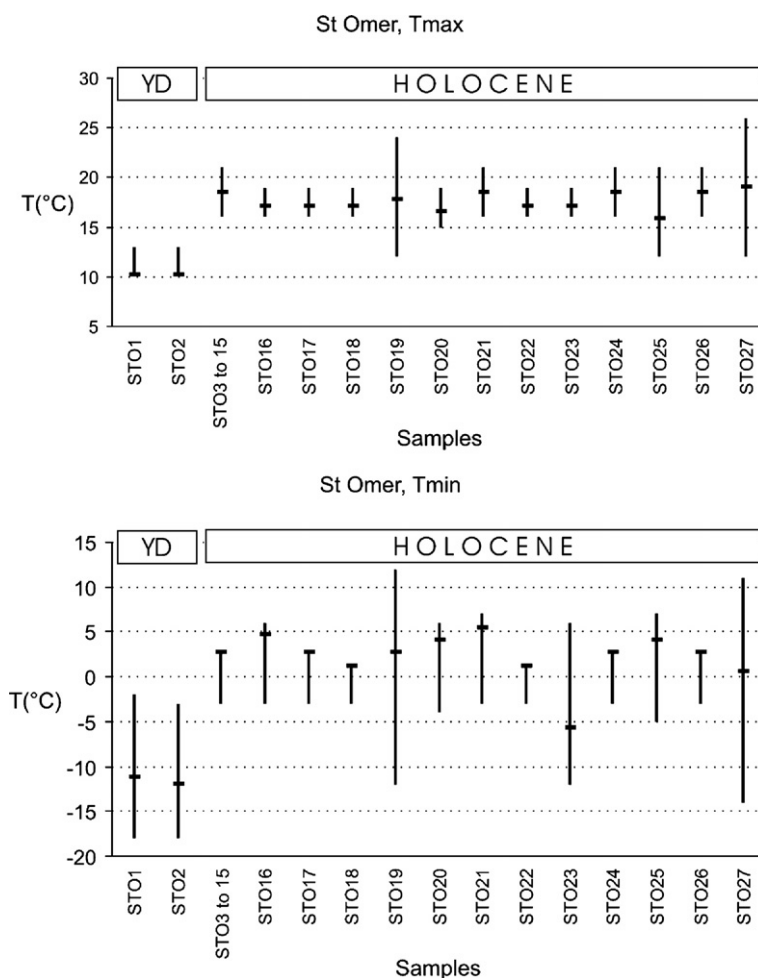


Fig. 3. Temperature reconstruction from Younger Dryas to Sub-Boreal at St-Momelin using the Mutual Climatic Range method. Vertical bars represent the mutual range of mean temperature of the warmest month (Tmax) and mean temperature of the coldest month (Tmin), reconstructed for each coleopteran assemblage. Horizontal lines on the bars indicate the most likely position for the actual mean temperature. Note, because of the sparseness of the faunas, the estimates from samples STO3 to STO15 have been amalgamated together.

cold periods (Oldest and Younger Dryas). Over much of NW Europe, where valleys cut through the chalk, calcareous muds were produced at this time by substrate gelification and accumulated in the valley bottoms (Ponel et al., 2005). In Belgium and Netherlands such fine and calcareous sand layers underlaying Pre-Boreal peat (Munaut and Paulissen, 1973; Berendsen and Stouthamer, 2000) have been dated to Younger Dryas. However, in some Lateglacial sequences minerogenic deposits, some of which have a high calcareous content, are associated with entirely temperate insect assemblages (e.g., Coope and Brophy, 1972; Coope, 1998). Thus minerogenic sedimentation alone should not necessarily be taken as an indicator of cold conditions, but independent evidence such as that derived from the Coleoptera assemblage should be sought as well.

On entomological grounds Faunal Unit SMi-1 is clearly indicative of cold conditions which, in this case, is in agreement with the sedimentary interpretation. At Holywell Coombe near Folkstone, Younger Dryas deposits which yielded a similar cold-adapted beetle fauna, are also followed by sudden warming, all within a minerogenic sequence (Coope, 1998). In the Netherlands, similar insect faunas of the same age were obtained from Notsel in the Mark Valley (Bohncke et al., 1987). On this evidence there can be little doubt that samples STO1 and STO2 date from the Younger Dryas period and that the sudden warming heralded the start of the Holocene.

Fig. 3 gives quantitative reconstructions of the thermal climate during the first half of the Holocene, namely from about 10,500 cal. BP to 4700 showing the mean air temperatures for the warmest and coldest months. The most likely Tmax figures fluctuate between 16 °C and 19 °C. Tmin figures are more difficult to summarise but they appear to range between 0 °C and 5 °C. It is too early yet to evaluate the regional significance of the relatively minor differences in temperatures shown by this figure but future investigations of Holocene insect assemblages will determine if they are temporarily consistent or merely reflect background noise in the system.

5. Relationship of the St Omer fauna to others in northern Europe

Lateglacial insect faunas have recently been described from Houdancourt and Conty in the Paris basin (Ponel et al., 2005). Unfortunately the Younger Dryas deposits at these sites did not yield any insect remains, so the insect record from the St Omer basin neatly fills this gap in the sequence enabling a complete climatic

history to be constructed for the Lateglacial of northern France. A summary of the major climatic events is shown on Fig. 4.

In general these climatic events are similar to those reconstructed from Lateglacial coleopteran assemblages from the British Isles (Coope and Brophy, 1972; Atkinson et al., 1987; Walker et al., 1993; Walker et al., 2003). In particular the Tmax values show that the warming at the beginning of the Bølling was intense, reaching figures similar to those of the present day. During the Allerød phase the climate was rather cooler but still warm enough to permit expansion of the forest cover. A moderate rise in temperature seems to have taken place towards the end of the Allerød. The presence in Britain at this time of numerous cold-adapted beetle species, some of which have exclusively arctic distributions, shows that the Younger Dryas cooling was intense with Tmax figures as low or lower than 10 °C and Tmin values even more depressed.

These figures for the thermal climate for the Younger Dryas are in agreement with climatic reconstructions based on beetle data from 77 sites across much of Northern Europe from Ireland to Poland (Coope et al., 1998) and also from the Netherlands (Bohncke et al., 1987; Van Geel et al., 1989), and with pollen data from Luxembourg (Guiot and Coûteaux, 1992). However, another large data set from Central and NW-Europe using climate indicator plant species (Isarin and Bohncke, 1999; Renssen and Isarin, 2001) suggests Younger Dryas Tmax estimates of about 13 °C. This is in contrast to the Tmax estimated for the Younger Dryas at St-Omer of 10 °C, based on the coleopteran fauna. These differences should stimulate further investigations into the Younger Dryas climate and in particular the transition to the Holocene using sedimentary sequences from many other sites across a broader geographical area and including analyses of a broad suite of palaeobotanical and physical environmental indicators.

Reconstructed Tmin temperatures from St-Omer are largely in agreement with coleopteran data from the British Isles and the Netherlands (Bohncke et al., 1987; Coope, 1998), and with the multiproxy reconstructions carried out at similar latitudes by Isarin et al. (1998) and Renssen and Isarin (2001).

The sudden and intense climatic warming at the Younger Dryas-Holocene transition, at St-Omer is similar to that from sites of similar age from the British Isles and Sweden as reconstructed by Coope and Lemdahl (1995). The amplitude of this sudden climate amelioration inferred from the St-Omer coleopteran assemblages is also similar to that obtained from Britain (Atkinson et al., 1987; Coope, 1998), and from Luxembourg (Guiot and

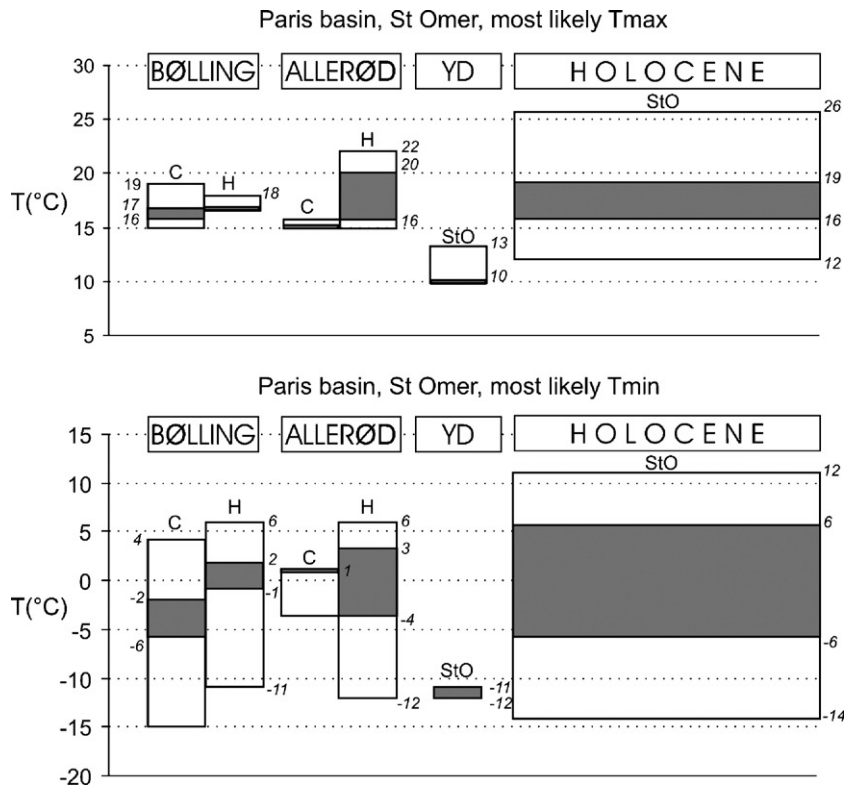


Fig. 4. Synthetic MCR beetle reconstruction from several sites in Paris Basin (Ponel et al., 2005), and St-Momelin data set. Shaded areas indicate most likely values for Tmax and Tmin. C = Conty, H = Houdancourt, StO = St-Omer.

Coûteaux, 1992), and, broadly, all over Central and NW-Europe (Renssen and Isarin, 2001; Davis et al., 2003).

From the start of the Holocene, insect assemblages from St-Omer suggest that climatic conditions at that time were about as warm as they are today. This is contrary to the view interpreted from pollen data that the beginning of the Holocene was characterised by a progressive rise in temperature (e.g., Davis et al., 2003). The Holocene Coleoptera from St Omer provide little evidence for any gradual improvement. However, the presence of warm-adapted species such as *Paracymus aeneus*, *Coelostoma hispanicum*, and *Dolichoderus quadripunctatus* in samples STO21 and STO22 suggests that by about 6,000 cal. BP the climate may have actually been warmer than the MCR figures indicate. This is because these southern taxa have not yet been incorporated in the MCR database which was primarily developed for the British Isles and Central and Northern Europe.

6. Impact of Holocene sea level fluctuations on beetle assemblages

Insects do not occur in fully marine conditions though several species are adapted to brackish habitats.

The influence of marine incursions near the estuary of the river are likely to have had effects further upstream in the increase of salt tolerant species of Coleoptera. At no level in the St-Omer sampled sequence is there any evidence for the presence of the truly salt marsh community. Two species, *Bembidion iricolor* and *Paracymus aeneus*, only found as rare individuals in Faunal Unit SMi-3, suggest the proximity of saline conditions probably reflecting marine incursions down stream from the study site. At this time salinity levels at St-Omer itself would have been extremely low at most indicative of brackish conditions.

From a lithological point of view, SMi-2 includes several types of clay silt and sand that are characteristic of marine environments. This sedimentary layer corresponds to the beginning of the Holocene/Flandrian transgression, regionally known as the Calais transgression (Dubois, 1924). According to Allen (2003), compact and micro-laminated clayey deposits are characteristic of marginal tidal palaeochannel deposits, whereas coarser deposits of sandy silt correspond to the central part of tidal channels. The marine deposits are interrupted by intercalated continental organic sediments which are rich in charophytes, organic silts and

gyttja. These organic sediments are interpreted as tidal palaeochannel infillings during periods of minor marine regression, caused by either hydro-isostatic readjustments, neotectonic processes and/or sediment consolidation as described in the North Sea coastal plain (e.g., Denys and Baeteman, 1995; Lambeck, 1997; Waller and Long, 2003). The beetle assemblages from the SMi-2b organic horizons suggest that these marine regressions may have involved a substantial retreat from the area and the development of an extensive *Phragmites* swamp near the St-Omer site. This marine regression need not have involved much altitudinal reduction since the gradient of the river Aa was probably low at this time.

During SMi-3, the Late-Atlantic/Sub-Boreal marine regression (Jelgersma, 1961) was associated with a great diversification of habitats throughout the Aa river floodplain (Gandouin et al., 2005). The insect record shows that the environment at that time consisted of a mosaic of biotopes, including both running water and standing water, open firm and marshy ground, shaded river banks and mature trees. During SMi-3a, the isolated finds of the halophilous ground beetle *Bembidion iricolor* and of the water beetles *Noterus clavicornis* and *Paracymus aeneus* are probably the result of accidental occurrences from more distant habitats and/or reflecting short marine pulsations downstream. The sudden increase in number and variety of running water beetles and rise in the larvae of the caddisfly *Hydropsyche* in SMi-3b indicates an increase of flowing water and appears to be indicative of an increased river gradient and thus a lowering of sea level.

Little can be inferred from the sparse insect assemblage of Faunal Unit SMi-4. It resembles an inadequate sample of the fauna from SMi-3 implying the availability of similar habitats. The sudden disappearance of the running water beetles might imply a reduction in the river's gradient associated with the Dunkirk marine transgression (Gandouin, 2003).

7. Conclusion

A continuous sequence of insect assemblages spanning the transition from the Younger Dryas cold interval to the Holocene has been analysed on borehole cores from the valley of the river Aa near St-Omer in Northern France. This is the first investigation of this period at sea level in continental Europe. The fauna shows a complex of palaeoecological developments leading up to the establishment of a forest beside a mature river meandering across a floodplain not far from the contemporary shoreline. The marine influence on the

fauna is enigmatic primarily because insects have almost never become adapted to the fully marine environment. Although there are a few scarce beetle species in these fossil assemblages that indicate saline habitats, none of the faunas are typical of the salt marsh community. Whereas transgressions are not associated with any positive evidence of marine influences, the Sub-Boreal marine regression, on the other hand, is associated with a spectacular increase in taxonomic diversity and strong evidence for the increased rate of flow of the river Aa.

Mutual Climatic Range estimates on the palaeotemperature of the Younger Dryas period in Northern France indicate that mean July values were near to 10 °C and associated with cold, rather continental winters. The transition to the Holocene was abrupt and intense with the immediate establishment of mean July temperatures of about 16 °C, that is equivalent to present day summer warmth. These figures for the thermal climatic history of Northern France complement those already obtained for the Lateglacial interstadial MCR figures from beetle assemblages in the Paris Basin. The climatic history for Northern France has here been extended into the middle Holocene.

It has not been possible yet to quantify the rate at which climatic warming took place at the transition from the Lateglacial to the Holocene, apart from recognising that it was very sudden and intense. Because the deposition of the sedimentary sequence has been rapid, the St-Omer basin should provide an opportunity for a more detailed investigation into its sedimentology and biostratigraphy and a resolution to the important problem of how fast the European climate can change.

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References

- Allen, J.R.L., 2003. An eclectic morphostratigraphic model for the sedimentary response to Holocene sea-level rise in northwest Europe. *Sediment. Geol.* 161, 31-54.
- Andrieu, V., Field, M.H., Ponel, P., Guiot, J., Guenet, P., de Beaulieu, J.-L., Reille, M., Morzadec-Kerfourn, M.-T., 1997. Middle Pleistocene temperate deposits at Dingé, Ille-et-Vilaine, northwest France: pollen, plant and insect macrofossil analysis. *J. Quat. Sci.* 12, 309-331.
- Antoine, P., Lautridou, J.-P., Laurent, M., 2000. Long-term fluvial archives in NW France: response of the Seine and Somme rivers to

- tectonic movements, climatic variations and sea-level changes. *Geomorphology* 33, 183-207.
- Ashworth, A.C., 1972. A Late-Glacial insect fauna from Red Moss, Lancashire, England. *Ent. Scand.* 3, 211-224.
- Atkinson, T.C., Briffa, K.R., Coope, G.R., 1987. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* 325, 587-592.
- Baeteman, C., De Gans, W., 1993. Quaternary shorelines in Belgium and the Netherlands. International union for quaternary research subcommission on shorelines in Europe. Fieldmeeting 1993, Belgian Geological Survey-Geological Survey of the Netherlands-Earth Technology Institute.
- Bell, M., Walker, M.J.C., 1992. Late Quaternary Environmental Change—Physical and Human Perspectives. Longman, Harlow.
- Berendsen, H.J.A., Stouthamer, E., 2000. Late Weichselian and Holocene palaeogeography of the Rhine-Meuse delta, The Netherlands. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 161, 311-335.
- Bernard, F., 1968. Les fourmis d'Europe occidentale et septentrionale. Faune de l'Europe et du Bassin méditerranéen, vol. 3. Masson, Paris.
- Bohncke, S., Vanderberghe, J., Coope, G.R., Reiling, R., 1987. Geomorphology and palaeoecology of the Mark valley (southern Netherlands): palaeoecology, palaeohydrology and climate during the Weichselian Late Glacial. *Boreas* 16, 69-85.
- Buckland, P.C., 1979. Thorne Moors: a palaeoecological study of a Bronze Age site (a contribution to the history of the British insect fauna). Department of Geography Occasional Publication, vol. 8. Univ. Birmingham.
- Buckland, P.L., 2003. Bugs MCR Climate Reconstruction Software [version Beta 1.52a]. Downloaded: 21 Nov. 2005.
- Buckland, P.C., Dinnin, M.J., 1993. Holocene woodlands: the fossil insect evidence. In: Kirby, K., Drake, C.M. (Eds.), *Dead Wood Matters: the Ecology and Conservation of Saproxylous Invertebrates in Britain*. English Nature Science, vol. 7. English Nature, Peterborough, pp. 6-20.
- Collingwood, C., 1979. The Formicidae (Hymenoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, vol. 8. E.J. Brill, Leiden.
- Coope, G.R., 1977. Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Philos. Trans. R. Soc. Lond., B* 280, 313-337.
- Coope, G.R., 1986. Coleoptera analysis. In: Berglund, B.E. (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. Wiley & Sons, Chichester, pp. 703-713.
- Coope, G.R., 1998. Insects. In: Preece, R.C., Bridgland, D.R. (Eds.), *Late Quaternary Environment Change in North-west Europe: Excavations at Holywell Coombe, South-east England*. Chapman & Hall, London, pp. 213-233.
- Coope, G.R., Brophy, J.A., 1972. Late Glacial environmental changes indicated by a coleopteran succession from North Wales. *Boreas* 1, 97-142.
- Coope, G.R., Lemdahl, G., 1995. Regional differences in the Lateglacial climate of northern Europe based on Coleopteran analysis. *J. Quat. Sci.* 10, 391-395.
- Coope, G.R., Lemdahl, G., Lowe, J.J., Walkling, A., 1998. Temperature gradients in northern Europe during the last glacial-Holocene transition (14-9 ¹⁴C kyr BP) interpreted from coleopteran assemblages. *J. Quat. Sci.* 13, 419-433.
- Davis, B.A.S., Brewer, S., Stevenson, A.C., Guiot, J., 2003. The temperature of Europe during the Holocene reconstructed from pollen data. *Quat. Sci. Rev.* 22, 1701-1716.
- Delpy, D., 2000. À propos du *Psammoporus sabuleti* Panzer (Coleoptera Scarabaeoidea Aegialiidae). *Le Coléoptériste* 38, 17-18.
- Denys, L., Baeteman, C., 1995. Holocene evolution of relative sea level and local mean high water spring tides in Belgium — a first assessment. *Mar. Geol.* 124, 1-19.
- Dinnin, M., 1997. Holocene Beetle Assemblages from the Lower Trent Floodplain at Bole Ings, Nottinghamshire, U.K. *Quat. Proc.* 5, 83-104.
- Dubois, G., 1924. Recherches sur les terrains quaternaires du nord de la France. *Mém. Soc. Géol. Nord* 8, 356 p.
- Emontspohl, A.-M., 1995. The northwest European vegetation at the beginning of the Weichselian glacial (Brørup and Odderade interstadials)— new data from northern France. *Rev. Palaeobot. Palynol.* 85, 231-242.
- Field, M.H., de Beaulieu, J.-L., Guiot, J., Ponel, P., 2000. Middle Pleistocene deposits at La Côte, Val-de-Lans, Isère department, France: plant macrofossil, palynological and fossil insect investigations. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 159, 53-83.
- Gandouin, E., 2003. Enregistrement paléoclimatique interdisciplinaire de la transgression Holocène. Signature paléo-environnementale des Chironomidae (Diptères) du bassin de Saint-Omer (France). Ph.D. Thesis, Univ. Sciences et Techniques de Lille, France.
- Gandouin, E., Franquet, E., Van Vliet-Lanoë, B., 2005. Chironomids (Diptera) in river floodplains: their status and potential use for palaeoenvironmental reconstruction purposes. *Arch. Hydrobiol.* 162, 511-534.
- Gandouin, E., Maasri, A., Van Vliet-Lanoë, B., Franquet, E., 2006. Chironomid (Insecta: Diptera) assemblages from a gradient of lotic and lentic waterbodies in river floodplains of France: a methodological tool for palaeoecological applications. *J. Paleolimnol.* 35, 149-166.
- Gandouin, E., Ponel, P., Franquet, E., Van Vliet-Lanoë, B., Andrieu-Ponel, V., Keen, D.H., Brocandel, M., Brulhet, J., in press. Chironomid responses (Insect: Diptera) to Younger Dryas and Holocene environmental changes in a river floodplain from northern France (St-Momelin, St-Omer basin).
- Gehu, J.M., 1970. Carte de la végétation de la France. Lille, vol. 4. CNRS, Paris.
- Gibbard, P.L., 1995. The formation of the Strait of Dover. In: Preece, R.C. (Ed.), *Island Britain: a Quaternary Perspective*. Geological Society Special Publication, vol. 96. The Geological Society, London, pp. 3-13.
- Guiot, J., Coûteaux, M., 1992. Quantitative climate reconstruction from pollen data in the Grand Duchy of Luxembourg since 15 000 yr BP. *J. Quat. Sci.* 7, 303-309.
- Hansen, M., 1987. The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, vol. 18. E.J. Brill, Leiden.
- Hebauer, F., Klausnitzer, B., 1998. Insecta: Coleoptera: Hydrophiloidea: Georissidae, Spercheidae, Hydrochidae, Hydrophilidae (exkl. Helophorus). *Süßwasserfauna von Mitteleuropa* 20/7, 8, 9, 10-1, Fischer, Stuttgart.
- Hickin, N.E., 1963. *The Insect Factor in Wood Decay*. Hutchinson, London.
- Holmen, M., 1987. The Aquatic Adaphaga (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, vol. 20. E.J. Brill, Leiden.
- Isarin, R.F.B., Bohncke, S.J.P., 1999. Mean July Temperatures during the Younger Dryas in Northwestern and Central Europe as Inferred from Climate Indicator Plant Species. *Quat. Res.* 51, 158-173.
- Isarin, R.F.B., Renssen, H., Vandenberghe, J., 1998. The impact of the North Atlantic Ocean on the Younger Dryas climate in northwestern and central Europe. *J. Quat. Sci.* 13, 447-453.

- Jelgersma, S., 1961. Holocene Sea Level Changes in the Netherlands. Medelingen van de Geologische Stichting, Leiden.
- Jones, R.L., O'Brien, C.E., Coope, G.R., 2004. Palaeoenvironmental reconstruction of the Younger Dryas in Jersey, UK, Channel Islands, based on plant and insect fossils. *Proc. Geol. Assoc.* 115, 43-53.
- Koch, K., 1989-1992. Die Käfer Mitteleuropas, Ökologie 1, 2, 3. Goecke and Evers, Krefeld.
- Lambeck, K., 1997. Sea-level change along the French Atlantic and Channel coasts since the time of the Last Glacial Maximum. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 129, 1-22.
- Lindroth, C.H., 1974. Coleoptera, Carabidae. Handbooks for the identification of British Insects, vol. 4(2). Royal Entomological Society, London.
- Lindroth, C.H., 1985-1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, vol. 15 (1 and 2). E.J. Brill, Leiden.
- Lucht, W.H., 1987. Die Käfer Mitteleuropas, Katalog. Goecke and Evers, Krefeld.
- Luff, M., 1998. Provisional Atlas of the Ground Beetles (Coleoptera, Carabidae) of Britain. Biological Records Centre, Huntingdon.
- Mangerud, J., Andersen, S.T., Berglund, B.E., Donner, J.J., 1974. Quaternary stratigraphy of Norden, a proposal for terminology and classification. *Boreas* 3, 109-127.
- Mansy, J.L., Manby, G.M., Averbuch, O., Everaerts, M., Bergerat, F., Van Vliet-Lanoë, B., Lamarche, J., Vanduycke, S., 2003. Dynamics and inversion of the Mesozoic Basin of the Weald-Boulonnais area: role of basement reactivation. *Tectonophysics* 373, 161-179.
- Meurisse, M., Van Vliet-Lanoë, B., Talon, B., Recourt, P., 2005. Complexes dunaires et tourbeux holocènes du littoral du Nord de la France. *C. R. Geosci.* 337, 675-684.
- Moretti, G., 1983. Tricoterri (Trichoptera). Guide per il riconoscimento delle specie animali delle acque interne italiane, vol. 19. Consiglio Nazionale delle Ricerche, Roma.
- Munaut, A.-V., Paulissen, E., 1973. Evolution et paléo-écologie de la vallée de la petite Nèthe au cours du Post-Würm (Belgique). *Ann. Soc. Geol. Belg.* 96, 301-348.
- Muona, J., 1993. Review of the phylogeny, classification and biology of the Family Eucnemidae (Coleoptera). *Ent. Scand. (Supplement 44)*.
- Nérat, T., 2005. Présence de *Mycetina cruciata* (Schaller, 1783) en Île-de-France (Coleoptera, Endomychidae). *Le Coléoptériste* 8, 43-44.
- Palm, T., 1948. *Svensk Insektfauna. Skallbaggar Coleoptera*, vol. 9. Entomologiska Föreningen, Stockholm.
- Ponel, P., 1995. Rissian, Eemian and Würmian Coleoptera assemblages from la Grande Pile. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 114, 1-41.
- Ponel, P., Coope, G.R., 1990. Lateglacial and Early Flandrian Coleoptera from La Taphanel, Massif Central, France: Climatic and Ecological Implications. *J. Quat. Sci.* 5, 235-249.
- Ponel, P., de Beaulieu, J.-L., Tobolski, K., 1992. Holocene palaeoenvironments at the timberline in the Taillefer Massif, French Alps: a study of pollen, plant macrofossils and fossil insects. *Holocene* 2, 117-130.
- Ponel, P., Andrieu-Ponel, V., Parchoux, F., Juhasz, I., de Beaulieu, J.-L., 2001. Late-glacial and Holocene high-altitude environmental changes in Vallée des Merveilles (Alpes-Maritimes, France): insect evidence. *J. Quat. Sci.* 16, 795-812.
- Ponel, P., Coope, G.R., Antoine, P., Limondin-Lozouet, N., Leroyer, C., Munaut, A.-V., Pastre, J.-F., Guiter, F., 2005. Lateglacial Palaeoenvironments and Palaeoclimates from Conty and Houdancourt, Northern France, reconstructed from Beetle remains. *Quat. Sci. Rev.* 24, 2449-2465.
- Renssen, H., Isarin, R.F.B., 2001. The two major warming phases of the last deglaciation at ~14.7 and ~11.5 ka cal BP in Europe: climate reconstructions and AGCM experiments. *Glob. Planet. Change* 30, 117-153.
- Robinson, M.A., 1991. The Neolithic and Bronze Age insect assemblage. In: Needham, S. (Ed.), *Excavation and Salvage at Runnymede Bridge, 1978: the Late Bronze Age Waterfront Site*. British Museum, London, pp. 277-326.
- Seifert, B., 1996. Ameisen: beobachten, bestimmen. Naturbuch-Verlag, Augsburg.
- Shennan, I., Horton, B., 2002. Holocene land-and sea-level changes in Great Britain. *J. Quat. Sci.* 17, 511-526.
- Smith, D.N., 2000. Disappearance of elm 'riffle beetles' from lowland river systems- the impact of alluviation. In: Nicholson, R.A., O'Connor, T.P. (Eds.), *People as an Agent of Environmental Change*. Oxbow Books, Oxford, pp. 75-80.
- Sommé, J., Munaut, A.V., Emontspohl, A.F., Limondin, N., Lefèvre, D., Cunat-Bogé, N., Mouthon, J., Gilot, E., 1994. The Watten boring- an Early Weichselian and Holocene climatic and palaeoecological record from the French North Sea coastal plain. *Boreas* 23, 231-243.
- Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, G., Van der Plicht, J., Spurk, M., 1998. INTCAL98 Radiocarbon Age Calibration, 24,000 to 0 cal BP. *Radiocarbon* 40, 1041-1083.
- Tachet, H., 2000. Invertébrés d'eau douce. Systématique, biologie, écologie. CNRS, Paris.
- Van der Woude, J.D., Roeleveld, W., 1985. Paleoeological evolution of an interior coastal zone: the case of the northern France coastal plain. *Bull. Assoc. Fr. Etude Quat.* 1, 31-39.
- Van Geel, B., Coope, G.R., Van der Hammen, T., 1989. Palaeoecology and stratigraphy of the Lateglacial type section at Usselo (The Netherlands). *Rev. Palaeobot. Palynol.* 60, 25-129.
- Walker, M.J.C., Coope, G.R., Lowe, J.J., 1993. The Devensian (Weichselian) Lateglacial Palaeoenvironmental Record from Gransmoor, East Yorkshire, England. *Quat. Sci. Rev.* 12, 659-680.
- Walker, M.J.C., Coope, G.R., Sheldrick, C., Turney, C.S.M., Lowe, J.J., Blockley, S.E.P., Harkness, D.D., 2003. Devensian Lateglacial environmental changes in Britain: a multi-proxi environmental record from Llanilid, South Wales, UK. *Quat. Sci. Rev.* 22, 475-520.
- Waller, M.P., Long, A.J., 2003. Holocene coastal evolution and sea-level change on the southern coast of England: a review. *J. Quat. Sci.* 18, 351-359.
- Zanetti, A., 1987. Coleoptera Omaliinae. *Fauna d'Italia*, vol. 25. Calderini, Bologna.