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The climatic significance of coleopteran assemblages from the Eemian deposits in southern England

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Abstract

Assemblages of fossil coleoptera (beetles) have been obtained from eight sites in southern England that date from the early phase (*Pinus – Quercetum mixtum – Corylus* pollen assemblage zone) of the Eemian (Ipswichian) interglacial Stage. Altogether 294 different species have been identified from these sites. They represent a wide spectrum of habitat requirements; terrestrial, aquatic, carnivorous and phytophagous species and many more with subtle dependences of specialist biotopes. Almost all of them live today in central and southern Europe and some are restricted to regions well south of the British Isles.

By using mutual climatic range methods, the thermal climate of the early phase of the Eemian Interglacial has been estimated quantitatively, showing that mean July temperatures were about 4 °C above those of southern England today. Mean winter temperatures were not much different from those nowadays. This phase was probably the thermal maximum of the Eemian Interglacial. Precipitation levels are difficult to quantify but were adequate to maintain flowing rivers in England throughout the year. These results are in agreement with the presence of other fossils, both plants and animals, in the same deposits.

Keywords: climate, coleoptera, Eemian, England, interglacial, mutual climatic range (MCR), palaeotemperatures, precipitation

Introduction

The climate of the Eemian (= Ipswichian) Interglacial is, on the basis of numerous physical and biological criteria, generally believed to have been warmer than that of the present day. It is important to understand the nature of this geologically recent episode, the warm climate of which cannot be attributed to any human activity, before we can understand any future global warming for which we may be responsible. In order to discuss possible causes and their effects, it is essential to quantify parameters of the thermal climate; in other words, to put figures on our subjective estimates.

One of the most useful indicators of the Quaternary terrestrial thermal environments are assemblages of Coleoptera (beetles). They are abundant in all manner of sediments that have remained in a reducing condition since deposition. Oxidation and pedological processes rapidly destroy all subfossil insect remains. Although it is most frequently believed that coleoptera are best preserved in peats (*sensu lato*), in practice the most productive sediments are fine sands and silts with scattered organic matter, the sort of deposit that accumulates in fairly shallow ponds or the margins of lakes where input from the surrounding landscape comes from inflowing streams. Under such conditions, insect remains can often be extraordinarily common. Amongst these, the coleoptera are usually the most conspicuous.

The value of the Coleoptera as palaeoenvironmental indicators depends on a number of factors:

- their exoskeleton is composed of chitin and sclerotin, much of which is very resistant to decomposition, provided that the sediment has remained in an anoxic and waterlogged condition since deposition; most limnic and swamp sediments fall into this category;
- the fossils present a wide variety of characters, which are constant at a range of taxonomic levels; since adequate collections of modern Coleoptera are preserved in most major museums it has been possible to compare the fossil remains with well-determined modern material so that it is often possible to identify fossils to the level of the species, each of which has often precise environmental preferences;
- species of Coleoptera show a remarkable degree of morphological constancy throughout the Quaternary; although it cannot be demonstrated objectively, it seems most likely that the species maintained a similar degree of stability in the past in their environmental preferences, since their past assemblages resemble those of the present day and demonstrate ecologically consistent pictures of the past environments;
- Coleoptera are abundant and diverse (more than a quarter of the known species of animals and plants on Earth are beetles); they are found in a wide spectrum of terrestrial and fresh-water environments, occupying almost all possible niches with the exception of the fully marine;
- they are physiologically very sensitive to factors of the thermal environment, particularly to aspects of temperature; as climates change, so the species of Coleoptera adjust their geographical ranges to track the whereabouts of acceptable thermal conditions; their mobility (many can fly) means that they can respond with great promptness to rapid and often intense climatic changes;
- a computer-based programme has now been devised with which coleopteran assemblages can be employed for the quantification of thermal conditions.

Earlier attempts to use Quaternary Coleoptera as palaeoenvironmental indicators were limited by two major problems. Firstly, an inadequate knowledge of stratigraphy meant that the occurrences of coleopteran fossils were attributed to such periods as pre-glacial, glacial and post-glacial with little other geochronological detail. Secondly, there was a general belief that Quaternary fossil insects were remains of extinct animals and thus deserving new names (Scudder, 1895; Mjöberg, 1915), albeit with some prefix or suffix indicating that the species was an ancestral form of one living today. If the species were different from those of the present day, their environmental requirements might also be different, thus depriving them of any useful environmental significance. There were, obviously, significant exceptions to these limitations, such as the pioneer work on the Quaternary insects of Boryslav and Starunia by Lomnicki (1894, 1914), Henriksen's monumental research on the Quaternary insects from Denmark and Scania (1933) and Lindroth's account of the interglacial (actually interstadial) beetle faunas from central Sweden (1948).

More recently there has been a renewal of interest in Quaternary entomology not only in Europe but also in North America and Russia (see Elias, 1994, for a summary.) Much of the research into the Quaternary Coleoptera was initiated in the British Isles (Coope, 1959) and was subsequently concentrated on the fossil assemblages from interstadial and full-glacial sediments and particularly on climatic reconstructions of the Weichselian Late Glacial (e.g., Coope et al., 1998). Expansion of this work has progressed into an archaeological context where it has enabled detailed environmental reconstructions of human living conditions (Buckland & Coope, 1991). Interglacial Coleoptera have been investigated with the threefold object of stratigraphical correlation, ecological interpretation, and quantification of past climate. The present contribution concentrates on this latter aspect, and more specifically on the question: how warm was the Eemian Interglacial? Since adequate Eemian coleopteran assemblages are so far only available from southern England, this question will be focused on this region. It should, however, be emphasised that similar assemblages of interglacial beetles are no doubt awaiting attention in other parts of continental Europe.

Study area

Altogether eight coleopteran assemblages will be considered here (Fig. 1). These are all of early Eemian age and can, wherever pollen analysis has been carried out, be correlated with the *Pinus – Quercetum mixtum – Corylus* biozone (see table 1 in Aalbersberg & Litt, 1998). They are thus equivalent to pollen zone Ip II of the classical British equivalent of the Eemian stage at Bobbitshole, Ipswich (West, 1957). The reasons for limiting this enquiry to the early phase of the Eemian are threefold. Firstly, there is no doubt about the stratigraphical position of this part of the Eemian at the selected sites: they are all from low down in the valleys of present-day rivers in southeastern England and lie close to, or slightly below, the '0' datum for the present-day sea level. Secondly, these sites are characterised by the presence of a similar suite of fossil ver-

Fig. 1. The locations in southeastern England of the early Eemian sites.

tebrates, insects and mollusca which facilitates their stratigraphical recognition. Thirdly, it now seems probable that these sites may date from the thermal maximum of the Eemian in spite of the fact that they come from such an early part of the interglacial.

At the present time it is not possible to attribute with certainty any localities in Britain that purport to date from the later phases of the Eemian (Ipswichian). Difficulties arise because several localities in Britain that are of allegedly later Eemian age, have very similar pollen spectra to those from other sites that have demonstrably older stratigraphical positions (see Green et al., 1984; De Rouffignac et al., 1995). Without a consensus of opinion as to the stratigraphical position of these localities, it is prudent to omit them from this analysis at this stage.

The eight localities included here as acceptable Eemian sites are:

1. Bobbitshole, Ipswich, Suffolk (West, 1957; Coope, 1974),
2. Deeping St James, Spalding, Lincolnshire (Keen et al., 1999),
3. Elsing borehole, Norwich, Norfolk (Taylor & Coope, 1985),
4. Itteringham, Norwich, Norfolk (Beesley, 1988),
5. Maxey, Peterborough, Cambridgeshire (Coope *in:* Davey et al., 1991),
6. Shropham, Attleborough, Norfolk (Walkling, 1996),
7. Trafalgar Square, central London (Franks et al., 1958; Gibbard, 1985),
8. Woolpack Farm, Fenstanton, Cambridgeshire (Gao et al., 2000).

The coleopteran assemblages from all these sites are remarkably similar. Altogether 294 species have been recognised, a figure that does not include specimens that can only be identified at the generic level. All these species have representatives living currently in Europe. Many of them have exclusively southern geographical ranges, being widespread in central and southern Europe, including the Mediterranean region. No coleopteran species from Eemian deposits in Britain have distributions that are exclusively northern in Europe, though many eurytherm species have present-day ranges that are widespread over the whole of Europe including high latitudes. Such species capable of tolerating both high and low temperatures are of little value as climatic indicators.

Amongst the exotic beetle species recovered from these Eemian deposits, two can be identified only to the generic level but have so far defied all attempts at more precise identification, though each is very distinctive. They may well be of importance as climatic indicators.

Firstly, a species of the genus *Drepanocerus* was found in both the Trafalgar Square and the Woolpack Farm deposits. This genus does not live anywhere in Europe at the present day. It is found in the Ethiopian region (27 species) and in oriental regions (9 species) (Balthasar, 1963: 61). Little is known about its ecological requirements though it has been obtained by sifting through decomposing vegetable debris. The modern specimens that most closely resemble the fossils belong to an undescribed species in the collection of the Natural History Museum in London. They were obtained in Nepal in the valley bottoms and not on the mountains.

Secondly, a species of dung-beetle of the genus *Heptaulacus* was found as fragments of several individuals in the deposits at Deeping St James. Though this genus is represented in Europe by a number of species, these fossils appear to differ from any species yet described. They resemble, however, the species *H. pirazzolii* (Fairmaire) from North Africa, i.e. from Tunisia and Libya (Baraud, 1985). The fossils differ slightly from this species in that they lack the subsidiary stria on the elytra between normal striae 7 and 8 that *H. pirazzolii* possesses. If close similarity between these fossils and their two closest living relatives can be used as evidence of close similarity in their thermal tolerances, they suggest that the Eemian climate was substantially warmer than that of southern England at the present day.

The remaining identified species from these Eemian coleopteran assemblages are all members of the present-day European fauna. It would be out of place here to list them all, but selected species will be discussed to highlight some of the more climatically significant species.

Climatically significant species

The relatively southern geographical ranges at the present day of the climatically significant species found in the Eemian deposits of southern England may be taken as indicative of their thermophilous requirements. It is important, however, to recognise that these thermophilous species include species of very diverse ecological preferences; terrestrial and aquatic species, generalist carnivores and scavengers, phytophagous species (restricted to particular hosts or not), specialist dead wood borers, and a great array of dung feeders. Thus, their presence in these coleopteran assemblages cannot be attributed to the prevalence of some particular narrow ecological niche, i.e. they are not merely facies faunas. Rather they should be seen as indicative of climatic conditions over a wide spectrum of available habitats. In the brief discussion of these significant species, the nomenclature and taxonomic order will follow that employed in Lucht (1987).

Bembidion elongatum Dej.

This small carnivorous species is a frequent member of Eemian assemblages. The details of its habits are not well known. Its geographical distribution is, however, well documented. It is not living in Britain today but is widespread throughout southern Europe and Asia Minor, and in the warmer parts of central Europe (Fig. 2).

Bembidion octomaculatum (Goeze)

This very small carnivorous species is frequent as a fossil in all warm temperate coleopteran assemblages. It lives in the margins of very small ponds that often dry up in the summer. It is extremely rare today in the southeast of England where it does not seem to be able to establish long term breeding colonies, though it manages to cross the Channel. It is interesting to note that it was widespread as a fossil in northern England during the thermal maximum of the Weichselian Late Glacial interstadial (13-12.5 ka BP) when it lived and presumably bred, just as in the Eemian, in considerable numbers well to the north of its present-day geographical limit. In the context of the early Eemian faunas, it was particularly abundant in the Deeping St James site.

Oodes gracilis Villa

This species lives in eutrophic swamps with rich reedy vegetation. In the northern parts of its range, it lives exclusively in places that become strongly warmed up in the summer. Lindroth (1986) points out that this species is a true thermophile constantly seeking high-

Fig. 2. Present-day geographical range of *Bembidion elongatum* Dej.

er temperatures than its relative *O. helopioides,* with which it is almost always associated in interglacial assemblages.

Rhysodes sulcatus (Fab.)

This is a species that lives in decaying wood of both deciduous and coniferous trees, mainly in fallen trunks in moist places (Silfverberg *in:* Lindroth, 1986). Its geographical range today extends only as far north as southernmost Sweden, where it is extremely rare. It does not occur in Britain. In southern Europe, where it is rare everywhere, it has a patchy distribution reminiscent of a relict distribution associated with the old primordial forest. The climatic significance of species of this type is always rather enigmatic but again it would seem likely that some climatic factor, such as low temperatures, is prohibiting their spread into central and northern Fennoscandia.

Cybister lateralimarginalis (Geer)

This large and conspicuous carnivorous water-beetle inhabits vegetation-rich pools. It is widespread across central and southern Europe but its occurrence in Britain is very sporadic, having been recorded only on three occasions, each time from south Essex (Balfour Browne, 1950). It does not seem to have established itself in Britain as a breeding species. As a fossil it is a frequent component of almost all early Eemian assemblages and was clearly established at the time as a breeding species at least as far north as central England.

Hydrophilus caraboides (L.)

There has for long been some confusion over the generic name of this species. In much of the literature, the genus is given as *Hydrous* or *Hydrochara*, whereas the name *Hydrophilus* is frequently used for the following species (Balfour Browne, 1958). There can, however, be no confusion between the two animals (see Hansen, 1987: plate 4). *H. caraboides* is a species of eutrophic ponds with muddy or grassy bottoms. It is widespread in central and southern Europe, today reaching only as far north as the English Midlands (Guest, 1996) and southern Fennoscandia. As a fossil it is common in most of the early Eemian sites in England.

Hydrous piceus (L.)

This large and conspicuous water beetle (up to 48 mm in length) is unlikely to be overlooked, yet it is a species notoriously rare near to its northern limit in southern England and southernmost Fennoscandia. It lives in “stagnant rather eutrophic and well vegetated, clear fresh water with a muddy bottom, mainly in rather sunny ponds” (Hansen, 1987: 218). The species has larvae that are entirely carnivorous, feeding predominantly on snails (mainly *Lymnaea*). The adults are rather omnivorous but feed largely on vegetation just below the surface (among others *Lemna*). Because of its large size, this species easily breaks up under the usual extraction techniques and is therefore very fragmentary in fossil assemblages. It is therefore difficult to know exactly how common it was. There are recent fossil records as far north as Yorkshire (Dinnin, 1991). The fragments are common, however, in most early Eemian deposits in England, suggesting that the species was in fact abundant. Its occurrence thus gives the distinct impression that the climate at the time was well within the existence limits of the species.

Dryopidae (Elminthidae)

The large numbers of these ‘riffle beetles’ which are present in many early Eemian deposits include many species which are extremely rare today and rather southern in their geographical ranges (e.g., *Stenelmis canaliculatus* (Gyll.), *S. consobrinus* Duft. and *Macronychus quadrituberculatus* Müll.) Caution must, however, be exercised in using these species as climatic indicators, because their habitats in naturally flowing rivers may have been drastically curtailed by recent human activity, and their present-day distribution may have been similarly restricted.

Pelochares versicolor (Waltl) and *Limnichus pygmaeus* (Sturm)

Although related to the moss-feeding byrrhid beetles, these species are, in contrast, algae feeders. They live on sandy or muddy banks that have been overgrown by algae. *P. versicolor* is a central and southern European species that does not range as far north as Britain or Fennoscandia. *L. pygmaeus* reaches as far north as southern England. Both species are very common in early Eemian deposits in England.

Scarabaeidae

One of the most outstanding features of all early Eemian coleopteran assemblages is the array of exotic dung beetles, in both the number of different species and their abundance. These species include **Oniticellus fulvus* (Goeze,), *Copris lunaris* (L.), **Caccobius* *schreberi* (L.),★*Caccobius histeroides* (Menetr.), †*Onthophagus taurus* (Schreb.), *Onthophagus verticicornis* (Laich.), *Onthophagus joannae* Goljan, ★*Onthophagus furcatus* (F.), †*Onthophagus nuchicornis* (L.), *Onthophagus vacca* (L.), ★*Onthophagus gibbulus* (Pall.), ★*Onthophagus massai* Barr. and ★*Aphodius carpetanus* Grav. (in this list ★ indicates species that do not reach as far north as the British Isles at the present day; species indicated by † are now probably extinct in Britain since no recent records of their presence exist: they must be seen as having recently relinquished their rather tenuous hold on areas at the northern extremity of their ranges).

Scolytus koenigi Schew

This is a bark beetle that attacks a variety of *Acer* species, excavating elaborate galleries in the cambium layer up to 12 cm long. It is a widespread but very rare species in central and southern Europe extending as far east as Turkmenia and as far south as Morocco and Algeria (Fig. 3). It is not found anywhere in northern Europe at the present day (Balachowski, 1950). It is unlikely that this restriction to southern regions is due to limited availability of its host tree since the distribution of *Acer* extends much further to the north than does the distribution of *S. koenigi*. Here again, it seems likely that some climatic factor today is imposing a limit on its northward extension and, conversely, warmer climates than now must have prevailed in southern England at this early phase of the Eemian.

Platypus cylindrus (F.)

This species drills galleries into stumps of fallen timber of various species of deciduous trees, particularly of *Quercus*, *Fagus* and *Fraxinus*. It is a southern species with the northern limit of its geographical range reaching southern England and the extreme south of Sweden.

Climatic implications

It is evident that the climates of the early part of the Eemian were well within the tolerance limits of all the above species, as testified by both their ubiquity and their abundance. Had such assemblages represented communities of species living close to their climatic tolerance limits, it is very unlikely that such an elaborate group of species would have been found together in one place. Most of these species are nowadays extremely rare along the northern limits of their geographical ranges, where they are probably associated with locally warmer localities than their overall surroundings. For these rich assemblages to have existed in such widespread profusion in southern England during the early Eemian, these exceptional circumstances would have had to be almost ubiquitous in southern England at the time; an implausible conclu-

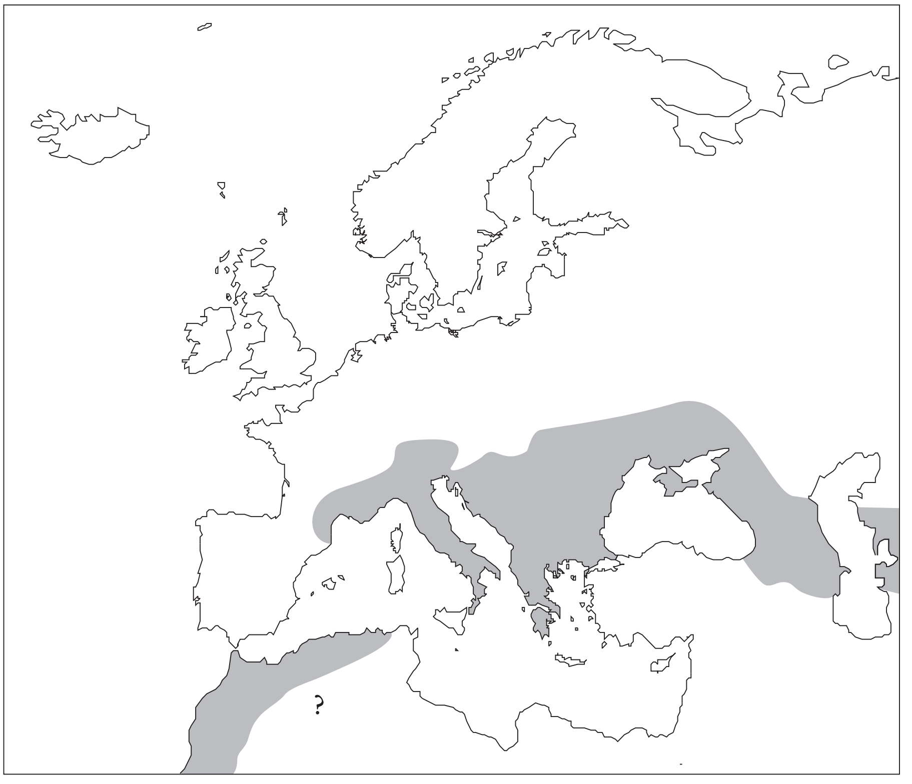

Fig. 3. Present-day geographical range of *Scolytus koenigi* Schew.

sion that carries within it its own contradictions. To illustrate this point, the coleopteran assemblage from Trafalgar Square included at least 8 individuals of *Oniticellus fulvus*, 5 individuals of *Copris lunaris*, 43 individuals of *Caccobius schreberi*, 6 individuals of *Onthophagus taurus*, 6 individuals of *Onthophagus furcatus*, 5 individuals of *Onthophagus nuchicornis* and at least 49 individuals of *Onthophagus massai* (the latter species is apparently restricted today to the Island of Sicily). It is probable that these figures are actually underestimates of their real abundance, since they represent the minimum numbers of individuals in the sample, estimated on the maximum number of any identifiable skeletal element. An assemblage of this sort could only be found today in a climatic regime equivalent to that in central and southern Europe.
Rhyssemus germanus (L.) and *Pleurophorus caesus* (Creutz.) are both widespread in central and southern Europe, but reach their northern limit in the extreme south of Sweden. In Britain they are known only from old records from southern regions and they are now presumed to be extinct in Britain (Hodge & Jones, 1995). Since both these species are characteristic of sandy places where they live amongst vegetable debris, there seems no ecological reason why these species should have been so restricted near the northern limits of their ranges. The most likely explanation for their rarity is that they were near to the northern limit of their climatic tolerance.

This review of selected species from the early phase of the Eemian Interglacial was designed to illustrate that relatively southern geographical ranges are characteristic of a wide spectrum of species with different ecological preferences. There were no species in these assemblages (out of a total of 294 named species) that have modern geographic ranges that are exclusively north of southern England. There can be little doubt that the climate was substantially warmer during the early phase of the Eemian than it is today. By reference to the northern limits of the species involved and recognising that many species were so abundant in the fossil assemblages that they were probably living well within their temperature tolerance limits, it is most likely that the climate was at least as warm as central France or Germany at the present day.

Quantitative estimates of palaeotemperatures – the mutual climatic range

Quantitative estimates can be made of the thermal climate using the existence limits of various species inferred from the boundaries of their geographical distributions. By looking for the area where the present-day geographical ranges of most species in a fossil assemblage overlap, palaeoclimatic inferences can be adduced from the overlap area. Although this method has been extensively used in the past, and it still is occasionally, there are a number of important problems associated with it:

- in order for the geographical overlap method to work, the complete geographical range for each species must be known; since many of the species involved are small, they can easily be overlooked; furthermore, since species are often in a state of dynamic flux, this requirement may not be realistic especially where small numbers of species are involved;
- species may live under similar thermal conditions but in different geographical locations; an obvious example is illustrated by the boreal species that could live in the mountainous areas further south: the fact that they do not is often a matter of the random accidents of space and time that dictated their biogeography; conversely, southern montane species may find in theory arctic locations equally acceptable had their geographical opportunities been different;
- the actual geographical range that can be culled from the literature and from entomological collections is often vague and it is often impossible to construct precise geographical distribution maps on that basis (what is one meant to do with labels such as 'central Italy' or 'Transbaikalia'?);
- geographical distributions are frequently very patchy due to the local availability, or otherwise, of acceptable habitats; the gaps between these patches do not necessarily define areas of unsuitable climatic conditions;
- geographical areas of overlap often contain localities of contrasting relief with contrasting thermal climates.

All these difficulties show that climatic interpretation based on the simple overlapping geographical distributions is not as easy as they might appear at first sight. In order to remedy some of these problems, or at least minimise their importance, the distributions of species have been plotted in 'climate space' rather than on geographical space. This method was pioneered by Iversen (1944) and later by Gruchek (1969) using selected species of plants. An adaptation of this method, called 'mutual climatic range' (MCR) was initially applied to coleopteran assemblages from Pleniglacial and Late Glacial deposits in Britain by Coope (1986) and by Atkinson et al. (1987). MCR reconstructions were compared in detail with the palynological succession of a high-resolution Late Glacial succession from Gransmoor, East Yorkshire (Walker et al., 1993). More recently, MCR methods were used in the climatic interpretation of early Weichselian stadial and interstadial insect faunas from Germany (Walkling & Coope, 1996).

The advantages of the MCR method over simply overlapping geographical ranges are as follows. It is not necessary to know the entire geographical range of a species in order to plot the range of a species on climate space. All that is required is that the species reaches its climatic limits in enough places for a climatic envelope to be constructed. Further additional localities, though they may increase the geographical range of a species, may – and often do – fall within the limits of the climatic envelope itself and therefore do not extend its limits. This aspect alone reduces many of the problems encountered in the simple geographical overlapping method mentioned above. In practice, many ragged geographical ranges condense into neat envelopes when plotted on climate space (Coope, 1986b: figs. 5 and 6). The climatic envelopes for each species can then conveniently be stored in a database. The drawing up of the climatic envelopes is the time-consuming part of the procedure. Our database currently contains envelopes for 433 species of coleoptera, but many significant species still remain to be added.

In order to avoid any suggestion that beetles, being animals, must rely on plants as the ultimate source of energy and therefore merely reflect the vegetational picture, only carnivorous or general scavenging species were utilised in the MCR climatic reconstructions. In such cases, their food chains can be traced back ultimately through smaller and smaller soil arthropods, worms etc. which in turn feed upon decomposing plant debris, algae, fungi and lichens. Coleopteran species were thus used that are as far as possible removed from specific aspects of the macrophyte vegetation. The climatic inferences are thus as independent as possible from those based on the palaeobotanical record. The term 'mutual climatic range' arises from the procedure in which the climatic envelopes for the species in a fossil assemblage that are also in the database, can be overlapped and the climatic parameters determined of the climate space of the area where the envelopes of most species overlap, i.e., their mutual climatic ranges. Usually the overlap involves 100% of the species involved in the analysis. The axes of the envelopes were originally chosen as T_{max} (the mean temperature of the warmest month) and T_{range} (the difference between the mean temperature of the warmest month and the mean temperature of the coldest month) because an analysis of the modern meteorological records suggested that most thermal climatic variables were subsumed by these factors. It is, of course, a simple matter to arrive at figures for T_{min} (the mean temperature of the coldest month). Assuming a sinusoidal curve for the seasonal fluctuations of mean monthly temperatures, it is a simple matter to reconstruct mean figures for each month of the year.

The MCR method of reconstructing palaeotemperatures operates on the basis only of presence or absence of a species and does not take into consideration its abundance. This is because of the intricate mosaic of local habitats that make up the terrestrial/ fresh-water environment. Since the fossil assemblages of Coleoptera are drawn from relatively small sampling areas, the effect of this heterogeneity can be significant; under these conditions, species abundance is likely to have varied greatly from place to place. Species that are common in a fossil assemblage were almost certainly common in the neighbourhood in which they were buried. On the other hand, species that are rare in a fossil assemblage could have been either actually rare in the original neighbourhood or else living abundantly at some considerable distance from the site of sedimentation. Species rarity in a fossil assemblage is therefore often difficult to interpret. In the list of selected Eemian species given above, most of them were chosen because they were either abundant in fossil assemblages or else occurred at several sites, thus indicating that they were thoroughly at home in the early Eemian climate of the British Isles.

It is possible to check the validity of the MCR method of reconstructing Quaternary palaeoclimates by carrying out MCR analyses on present-day assemblages of Coleoptera that live close to meteorological stations (but not utilising the species that had been used in the establishment of the initial database) and then checking the degree of correspondence of the MCR-reconstructed temperatures with those actually measured at the nearby meteorological stations. Although there is close agreement between the two sets of figures, there were minor but persistent discrepancies between the MCR figures and those of the meteorological stations. In summary, the MCR figures are always conservative estimates: the warmth was not warm enough and the cold not cold enough. A regression equation was therefore calculated to provide a possible correction factor for the raw figures (Atkinson et al., 1987). This procedure has been discussed recently and an improved regression equation has been calculated (Coope et al., 1998: 420).

In any quantitative reconstruction of interglacial palaeoclimates, the MCR method must be used in conjunction with specific entomological knowledge. For example, it is probable that entomological factors may well have influenced the sizes of each species envelope. This is because the occurrence of a species is much more likely to be recorded by entomologists at the margins of its range – where it is unexpected and 'out of place' – rather than in the central part of its range where it is too commonplace to excite attention. This bias in recording species at the extreme limits of their ranges leads to species climatic envelopes that are more expansive than their more normal range. It may account for the persistent discrepancy between the MCR estimates and actual measured temperatures mentioned above. It is plain from the abundance of many of the thermophilous species that lived in southern England during the early Eemian well to the north of their present day ranges, that they were evidently living well within the existence limits shown by their climatic envelopes. It is difficult to quantify this effect. The regression equation, used as a correction factor for the raw MCR data, may be the nearest that can be attained at the moment.

Conclusions

The remarkable uniformity of the early Eemian coleopteran assemblages from southeast England, in combination with the fact that thermophilous species occur abundantly in all of them, means that the MCR palaeotemperature figures are equally uniform. From the point of view of the present synthesis, the site at Shropham, Norfolk, which has been climatically analysed in detail by Walkling (1996), can be taken as representative. Raw MCR temperature figures for the early phase of the Eemian are as follows:

- T_{max} (mean temperature of the warmest month): 18 to 24 °C;
- T_{min} (mean temperature of the coldest month): -6 to +6 °C.

It must be emphasised that these figures mean that T_{max} and T_{min} lay somewhere between the limits given and not that temperature ranged between these limits.

When the data was subject to the regression correction factor mentioned above, the most likely palaeotemperature figures were as follows:

- T_{max} = 21°C;
- T_{min} = 4 °C.

These figures are not out of keeping with the rest of the palaeontological data from this phase of the Eemian in the British Isles. Amongst the vertebrates, the well known abundance of *Hippopotamus amphibius* bones in many river gravels and cave deposits of this age as far north as Middlesborough on Teesside (Stuart, 1982) testifies to the widespread climatic suitability for this species throughout most of southern Britain at the time. Bones of the straight-tusked elephant *Palaeoloxodon antiquus* and of the narrow-nosed rhinoceros *Dicerorhinus hemitoechus* are also frequent. Bones of the central and southern European pond-tortoise *Emys orbicularis* have also been recovered from deposits of this age (Stuart, 1979). Amongst the molluscs, the presence of the the southern European terrestrial gastropod *Clausilia pumila*, the fresh-water snail *Belgrandia marginata* and the southern pearl mussel *Margaretifera auricularia* all support the interpretation of warm temperatures at the time. Amongst the plant fossils, the presence of the water chestnut *Trapa natans*, with its predominantly southern European distribution, is also significant. Wherever these fossils have been located with adequate precision, they have been found in association with coleopteran assemblages characterised by the presence of the suite of thermophilous species described here. They all seem to relate to the thermal maximum of the Eemian.

The evidence presented above indicates that the thermal maximum of the Eemian occurred during its early phase, namely in the pollen zone characterised by *Pinus – Quercetum mixtum – Corylus* (see table 1 in Aalbersberg & Litt, 1998, for biostratigraphical correlations with previous subdivisions of the Eemian). The Coleoptera show that, at this time, the thermal climate in southern England was considerably warmer than it is today and that mean July temperatures were about 4 °C higher than those of the present day. Winter temperatures, on the other hand, were probably not much different from those of the present day.

Although it is not yet possible to quantify interglacial precipitation levels, the presence in these early Eemian sites of many species of Coleoptera such as the riffle-beetles and of other animals such as the large bivalve molluscs, require water to be present in the river channels all the year round. Since the mean temperatures of the coldest month were not sufficiently low for much of the winter precipitation to fall as snow, the English river systems were probably sustained at this phase of the Eemian by monthly precipitation levels that were sufficiently high and continuous to maintain the flow throughout the year.

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