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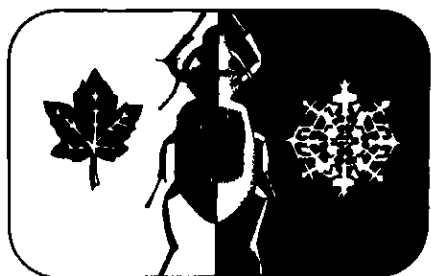
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Résumé de l'article

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Beetle Bits— The Science of Paleoentomology

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Summary

Several Quaternary sequences in North America have been analysed for fossil insects. Most of the insect remains are from beetles, and these are rapidly becoming recognised as very reliable indicators of climatic and vegetational changes. Like pollen they are present in most Quaternary deposits, but unlike most pollen grains they can be identified specifically. Also, beetles appear to respond rapidly to climatic change illustrating thermal variations which are often not detected by other conventional indicators. This paper briefly summarises some of the techniques and results of work in Canada, parts of the United States and England.

Introduction

Whenever one talks about the subject of paleoentomology, even in academia, one is met with blank stares and a faintly bemused expression. Further elaboration of the topic signifying that it is the study of fossil insects (or, in the case of our own studies, fossil beetles) elicits comments which usually revolve around the four from Liverpool. It would appear that, to most geologists, beetles rank in familiarity way down a scale descending from dinosaurs and trilobites, through ammonites and lesser known molluscs to a level which, sad though it seems, probably is equivalent to a sophomore's knowledge of conodonts. Everyone has seen a beetle – the active field geologist perhaps under rocks or logs somewhere in the Rockies or Arctic; more sedentary types may have observed them squashed on sidewalks; either way beetles are all around us in practically every environment except the extreme high Arctic and in the oceans of the world. Beetles, or more scientifically,

Coleoptera, come in a bewildering variety of shapes, sizes, colours and numbers. One in five living things is an insect, and well over a third of all insect species are Coleoptera, or, put in another way, of the over 1,250,000 described species on the planet, nearly one quarter are beetles.

The longest beetle, *Xyloryctes satyrus*, is over 1000 times the length of the smallest member of the family Trichopterygidae. Individuals of this latter family would probably have a hard time in a confrontation with some small protozoans, since many of the unicellular organisms are larger than the beetles themselves.

Beetles have a reasonable pedigree in the geological column, being first recorded in the Permian. Thus they have not yet reached the longevity of the class Trilobita, but they have outlived the last dinosaurs by about 60 million years and have a 50 million year head start on the mammals.

Despite their immense diversity, fossil beetles have received little study to date. The reason for the lack of interest is fairly clear. Insect remains are not particularly common in the fossil record with the exception of well-known localities such as Florissant, the Green River Shales, some Tertiary deposits in Montana and British Columbia, and various amber deposits in Europe and North America. The vast majority of fossil remains (except for the amber deposits) consist of compressed and sometimes carbonized impressions of fragments or, more rarely, whole insects. Morphological details are poorly preserved and colour patterns obscured or non-existent in these fossil arthropods. In addition the phylogeny of many mid-Tertiary and older insect groups is poorly understood.

The formidable problems associated with the study of older insect remains are somewhat reduced in the examination of Quaternary insects. The latter consist of the original chitinous parts, thus colour patterns, hairs and scales can be well-preserved, even on specimens which date back two million years.

Almost any non-marine sediment containing organic debris is likely to preserve insect remains. The nature of the preservation depends upon the rapidity with which the organism was buried, the depth of burial, post-depositional changes in the sediment and the position of the modern water table in respect to the stratigraphic position of the site. Probably the two most important factors are oxidation of the organic horizon and the degree of compression undergone by the sequence. Insect fragments are remarkably resilient to chemical attack, but they are relatively brittle, and stresses caused by overburden

pressures or cyclic wetting and drying tend to fragment specimens to the point where they become almost unidentifiable.

Materials which are known to preserve arthropod remains include silts and organic horizons within littoral facies of lacustrine sequences, organic lenses in fluvial deposits, and peat bogs or swamps. Abundant and well preserved insects have also been found in the well-known tar seeps of southern California, Peru and Eastern Europe. Drier environments do not preclude the preservation of arthropods since the chitinous exoskeleton remains unaltered, and insect fossils have been described from wood rat middens in cave deposits in the arid southwestern United States (Ashworth, 1973), and equally well-preserved remains have been recovered from organic horizons in permafrost of the Arctic (Matthews, 1968). Human influences have also provided numerous environments favorable for preservation in such features as hand dug wells and ditches, refuse pits, grave sites and even granaries (Kenward, 1976).

Although sites with potential for paleoentomological research are quite common, it is surprising that relatively few workers have ventured into this field. The reasons for the apparent lack of enthusiasm are varied. Initially there appeared to be a widespread (but fallacious) belief that beetle, or other insect remains, could not be identified from disarticulated fragments. The nature of paleoentomological research is almost a deterrent in itself, being a blend of paleontology, stratigraphy, entomological taxonomy and zoogeography, so it is rare that any prospective researcher starts in this field fully qualified in all aspects. Other factors detrimental to beetle studies involve the tedium of sorting through large quantities of sediment to extract the fragments, lack of well-organised collections and taxonomic keys, and uncertainty about the ecology and zoogeography of many species.

In spite of the problems, small research groups have become established in Britain, Canada, the United States and the USSR; and paleoentomology, in terms of Quaternary studies, is becoming a more generally recognised subject.

Historical Development of Paleoentomology

The first references to fossil insects were made by the natural historians of the last century (see Fisher, 1863). These early records only served to alert readers to the occurrence of coleopterous fragments in peats. Those organic deposits, which we now know to be of Pleistocene or Recent age, were variously attributed to deposits of the Noachian flood, or later, the Ice Age

(Pengelly, 1870). About a century ago the high cliff sections along the north shore of Lake Ontario, east of Toronto, attracted geologists interested in recording fossil remains from the detrital peats of the Scarborough Bluffs. G. J. Hinde (1878) discovered fossil beetle fragments in these deposits, initiating a series of studies which progressed for almost 50 years under Chamberlain, Coleman and Scudder.

Samuel H. Scudder described insect fragments from the Scarborough Formation sent to him by Coleman (Scudder, 1895, 1900). He obviously had problems with the identification of many of the beetle fragments. In a series of papers he described the coleopterous fauna of the Scarborough deposits as consisting of seventy extinct, and two extant, species. The specific determinations are interesting; the names *Bembidium expletum*, *B. damnosum*, *Platynus delapidatus*, *Lathrobium frustum* and *Olophrum dejectum* presumably reflect the degree of frustration involved in matching the fossils with modern counterparts. One can certainly empathise with Scudder in his problems of specific identification; many of the over 30,000 species of beetles in North America were undescribed at the time of his work and, from our own experience, the preser-

vation of the Scarborough fossils is generally not good. However, our own work has shown that not only are the majority of Scudder's specific determinations incorrect, but unfortunately a number of the generic determinations are completely inaccurate. Examples of these major mis-identifications are given in Figure 1. Possibly part of Scudder's problems in specific determinations may have been because of the scientific logic of the day which postulated intense speciation during the 'Ice Ages'. We now know that this does not appear to have been the case at least in the Arctic and cool temperate zones of both Europe, North America and portions of the Soviet Union.

The first studies which identified Pleistocene fossil insects as extant forms on a faunal basis were written in Europe during the first half of this century. Foremost among these were papers by Bell (1922), Henriksen (1933), Zeuner (1934), Thor- kelsson (1935) and Lindroth (1942, 1948). Although the Scandinavian workers (principally Lindroth) retained an interest in the fossil insect studies, the next major research group to emerge was at the University of Birmingham, England in the late 1950s and early 1960s. G. R. Coope, P. J. Osborne and F. W. Shotton commenced a series of publications establishing insect

faunas as useful indices for a variety of Pleistocene and Holocene environmental conditions (Coope, 1959; Coope *et al.*, 1961; Coope, 1970). Not only have they shown the potential for climatic and ecological reconstruction using Pleistocene beetles, but Coope, his co-workers and students, have refined the climatic curves for the last interglacial-glacial cycle in Britain, with a remarkable degree of accuracy (Coope *et al.*, 1971; Morgan, 1973; Coope, 1977). In the late 1960s and early 1970s the first North American beetle papers appeared (Matthews, 1968; Coope, 1968a; Ashworth and Brophy, 1972; Morgan, 1972). A series of papers describing insect faunas recovered from the tar pits and other Tertiary and Quaternary deposits in California had been produced by W. D. Pierce during the 1940s and 1950s, but a large number of the identifications have recently been shown to be erroneous, and they have not been considered in this discussion.

Extraction Techniques

In the field, fossil insects may be observed on bedding planes in peat or within fine silts which have thin detrital organic horizons. If insects are observed they are sometimes worth isolating because associated fragments may be together on the

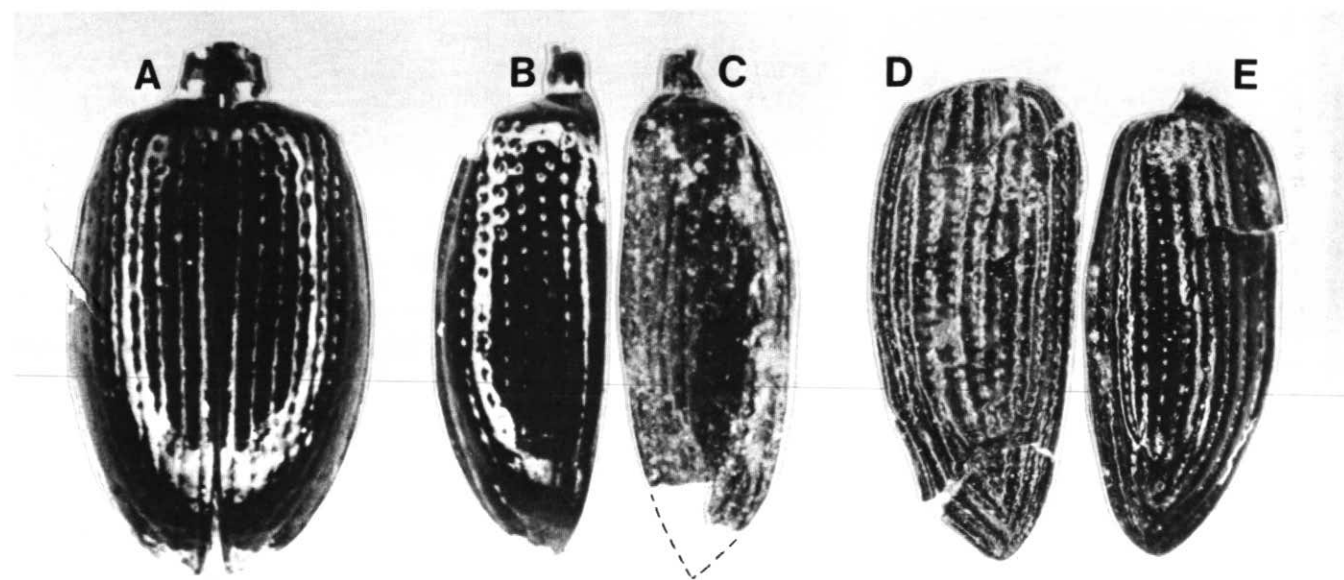


Figure 1

Comparison of fossil specimens identified by S. H. Scudder, with other fossil material.

- A) Partially fused elytra of *Dyschirius cf. globulosus* Say (Two Creeks, Wisconsin, about 12,000 yrs. B.P.)
 B) Single (left) elytron of *Dyschirius* also from Two Creeks, Wisconsin (Morgan and Morgan, 1979)

- C) Single (right) elytron identified by Scudder as "*Helophorus rigescens*!!". The specimen is hand labelled (by Scudder?) "Clay Beds near Cleveland Ohio" and numbered 14,505. Unfortunately the specimen is not an *Helophorus* species, indeed it does not even belong to the family Hydrophilidae. We believe that the specimen belongs to the family Carabidae and is a member of the genus *Dyschirius*.

- D) A left elytron, once again identified and labelled (by Scudder?) as "*Loricera? lutosal* (det. Sc.) *Scarboro*"; on a second label "Clay Beds Scarboro Ca." and numbered 14,559. Although this has been identified as a member of the family Carabidae, it is definitely a member of the Scarabaeidae, almost certainly of the genus *Aegialia* and probably *A. lacustris* LeC.
 E) Single (right) elytron of *Aegialia lacustris* from Two Creeks, Wisconsin.
 A, B, C (x32), D, E (x20)

stratum. Generally, splitting of organic debris is not conducted because it is time consuming and because the insects observed often are the largest and most brightly coloured, thus introducing a sampling bias. Rather, bulk samples (approximately 5–10 kg per 5 cm interval) are collected for laboratory treatment.

The standard technique for extracting fossil insect fragments has been described many times (Coope, 1968b; Morgan and Morgan, 1979). The basic procedure involves placing the field sample in a polythene bowl and washing the organic debris through a 300 micron (No. 50 or 52) mesh sieve. The fine silt and clay fraction passes through while organic material is retained. Organic debris trapped on the sieve is placed in a clean polythene bowl. Kerosene is added and kneaded into the sample, the excess decanted, and cold water added. The insect fragments tend to rise to the surface on the water/kerosene interface. This flotant is carefully decanted into a clean sieve, washed thoroughly with detergent, and rinsed in clean water until free of detergent. The sample is dehydrated and sorted in alcohol under the binocular microscope at 8 to 10x magnification. Insect fragments (and other associated fossils) can be picked out with fine forceps and stored in alcohol until they are mounted (Fig. 2). Heads, thoraxes and elytra are mounted

on standard (white background) micro-paleontological slides with water-soluble gum tragacanth. Semi-transparent specimens (thin elytra or thoraxes, caddis or dipteran remains) can be mounted in polyvinyl lactophenol mounting medium on glass microscope slides with a cover slip.

Identification

The identification of fossil fragments requires general familiarity with a wide spectrum of beetle families, a good systematic collection and sympathetic taxonomists. Modern taxonomic keys rely heavily upon features seen on articulated specimens; the disarticulated fossil material has to be looked at in an entirely different way, often utilising features which are obscured, or not readily apparent under the regular light microscope. In this respect the paleoentomologist can utilise shape and macro-ornamentation of various sclerites (Fig. 3), and by using the petrographic microscope, examine micro-ornamentation at magnifications of about 150x. This type of analysis is particularly useful when looking at carabid (ground) beetles. The genus *Bembidion*, for example, includes over 150 species in Canada and Alaska (probably over 400 species in North America) which can often be recognised to sub-generic level by gross morphological features, and then

narrowed considerably by the examination of micro-ornamentation (Fig. 4). One of the most powerful tools in this respect is the scanning electron microscope. The first SEM photographs of fossil beetles were taken at the University of Birmingham (Morgan, 1969, 1970). Detailed comparison of fossil and modern weevils of the same species revealed identical features at high magnifications (Fig. 5). Besides revealing details of beetle microsculpture, the SEM is also capable of illustrating the remarkable preservation of parts which remain articulated in fossil specimens



Figure 2
Beetle and other arthropod fragments photographed in alcohol under reflected light (x10). Identifications can be made to the generic level at this stage. The strongly punctate specimen (a) is a part of the right elytron of a sedge-eating

beetle, *Donacia* or *Plateumaris* (b) is a strongly striped elytral fragment of the diving beetle *Colymbetes*, and (c) is the right elytron of the ground beetle *Bembidion*. These specimens are from Lockport Gulf (northwestern New York State) and are about 11,000 years old.



Figure 3
Macro-ornamentation (eg. the 'mirror' areas illustrated as x on the elytra) provide diagnostic clues to help narrow the number of species during identification. These patterns, together with overall shape and punctae on the head and thorax, coupled with size, enable this specimen to be identified as *Asaphidion yukonense* Wickham (x38). The individual fragments can be put together to provide a picture of the whole beetle. The fossil is from Two Creeks, Wisconsin; modern specimens live no closer than the Nordegg area of Alberta and then range northward into Alaska.

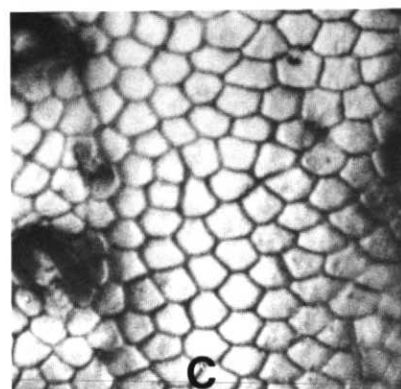
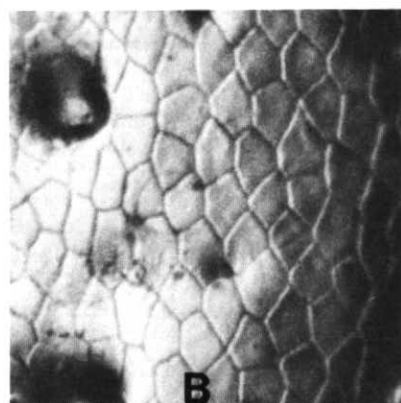
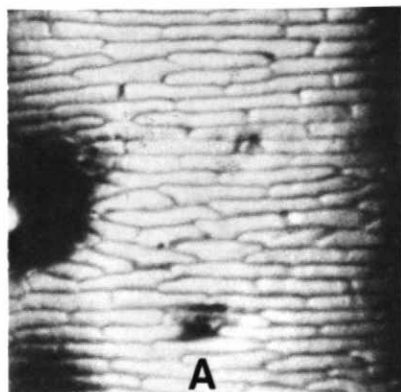


Figure 4
Micro-ornamentation in the carabid genus *Bembidion* photographed under polarised light.
A) *Bembidion nigripes* Kby. (x ca. 550)
B) *Bembidion concretum* Csy. (x ca. 550)
C) *Bembidion versicolor* LeC. (x ca. 550)
All the specimens are from Winter Gulf (south of Buffalo, N. Y.) dated at about 12,700 yrs. B.P. (Schwert and Morgan, 1980).

(Fig. 6). The SEM is still used today in illustrating specific fossil fragments, but it may damage rare specimens (eg. fragments tend to charge readily and often must be coated). Colour patterns cannot be seen under the SEM, and photomicrographs are difficult to compare to specimens photographed under the light microscope because of the detail revealed by the SEM. Undoubtedly innovations, such as environmental chambers and low KV operation, will allow more frequent use of this technique.

The key characters for a species, recognised by all modern taxonomists, are the beetle genitalia. All fossil abdomens are carefully dissected to see if they have retained the genitalia. Unfortunately this search is often unsuccessful; the specimen may be female, parthenogenetic, or the genitalia have been lost. Figure 7 illustrates one particularly well preserved example recovered from material in a borehole at Parkhill, Ontario, at a depth of 9 m. Associated organic detritus has been dated at 10870 ± 90 yrs. B.P. (Wat - 376). After comparison with modern specimens the aedeagus was identified as *Gyrinus bifarius* Fall, a species found in the southern boreal zone of North America.

Uses of Fossil Insects

The applied aspects of fossil insect research can be related to three major fields; archaeology, geology (incorporating paleoenvironmental and paleoclimatological reconstruction), and zoogeography. Of course there are areas of overlap between each of these disciplines, but we would like to give some examples of how each of these areas has incorporated the results of beetle research.



Figure 5
Scales of the weevil *Cryptorhynchidius lapathi* L. (x540). This SEM photomicrograph illustrates one of 3 different sets of diagnostic scales on the elytron of this curculionid. These can be matched exactly with scales on fossil counterparts of the same species (Morgan, 1970).



Figure 6
Detail on heads of fossil specimens illustrated by the SEM.

- A) Ventral view of a specimen of the genus *Heterocerus*. This is a fossil specimen recovered from the McKittrick tar seeps, California. The tar was dissolved and the specimen later cleansed in alcohol. The specimen is probably hundreds or possibly thousands of years old but still has hairs, articulated palps and antennae attached. The right eye can be seen at top left, the left eye at lower (centre) right. The scale bar is 300 microns.
- B) Dorsal view of *Otiorrhynchus nodus* Muell. (x62). The specimen is from Four Ashes, England (Morgan, 1973) from a sequence dated at 36,350 yrs. B.P. Note that the antennae of this weevil are still in their sockets. The left eye is at the lower right.



Figure 7
Aedeagus of *Gyrinus bifarius* Fall (x85 approx.)

Archaeology

Archaeological sites, especially in Britain, have been the subject of a number of papers describing associated insect faunas (Osborne, 1973). These include a Bronze Age ceremonial shaft near Wilsford, Wiltshire (Osborne, 1969), a Roman well at Barnsley Park, Gloucestershire (Coope and Osborne, 1967), a Viking-period site at York (Kenward, 1975) and a Medieval site, also at York (Buckland *et al.*, 1974). These fossil faunas associated with early occupation sites provide much interesting information, such as the type and extent of insect infestations in ancient granaries or on cultivated crops. To a lesser degree we can determine the directions of early trading systems, or even the distribution of disease-carrying organisms, such as bed bugs!

Deposits (not necessarily associated with archaeological sites) belonging to Mesolithic, Neolithic and younger periods (from about 10,000 yrs. B.P.) have been examined at a number of locations and show good evidence on the nature of the forest cover and agricultural practices (Kelly and Osborne, 1964; Osborne, 1965; Morgan, 1976). The examination of insect faunas associated with archaeological sites in North America has not been conducted on the scale seen in western Europe. Insect fragments recovered from the Lubbock site (Texas) are all contaminants, probably brought into the archaeological horizons by parasitic Hymenoptera (Morgan, unpublished data). At Parkhill, Ontario, deposits close to a Paleo-Indian locality are currently being processed for environmental data. Unfortunately this locality is approximately 400m from the human occupation site, but is believed to be of the same age, based upon stratigraphic interpretation.

Geology

Perhaps the most dramatic use of fossil insects has been in the reconstruction of paleoenvironments and paleoclimates during the Pleistocene Epoch. A series of increasingly severe climatic fluctuations during the Tertiary eventually culminated in major ice advances in both hemispheres during Quaternary time. The magnitude of most of these advances and retreats is unknown because of the complexity of the terrestrial record coupled with the poor preservation of many of the sequences. Insects have been utilised in examining deposits of earliest Pleistocene, Pliocene or possibly even Miocene sites in northern Canada and Alaska (Matthews, 1974, 1976; Morgan *et al.*, 1979). Other sites of Middle and Late Pleistocene age have been examined in Western Europe and various parts of North America (Coope, 1970, 1977), but most fossil insect work

has been concentrated on the time span involved in the last interglacial/glacial cycle. Much of our research has dealt with sites centred on southern Ontario but encompassing adjacent American states. In this way we hope to start reconstructing a climatic curve for a restricted geographic area, similar to the one developed by Coope and his co-workers in southern Britain. Before embarking on a précis of the uses of Coleoptera in the determination of climatic change we should discuss why these insects are believed to be so useful.

As Coope has frequently pointed out, a large number of beetle species are quite specific about their living requirements. For example, scolytids (the bark beetles) are often restricted to certain types of trees, frequently occupying specific locations on the tree under attack, e.g., the lower bole and root region or the mid portion of the bole, or the growing tips of branches. Certain scarabaeids (dung beetles) are confined to the dung of specific animals. Many carabid (ground) beetles have decided preferences for different types of substrates, often having modified sclerites to take advantage of differing lithologies. Finally many phytophagous (plant eating) beetles, representing a number of families, utilise specific host plants, although they frequently are not present over the whole range of the plant species, but often stop as though confined by certain climatic factors. There are, of course, many species of beetles whose ecological requirements are very poorly understood, and also large numbers which are eurythermic, extending in Europe from the Mediterranean coast to North Cape, and in North America from the Gulf of Mexico to the Tuktoyaktuk Peninsula. Nevertheless, two important principles have been established by an examination of a large number of fossil faunas: 1) Ecological assemblages have remained relatively constant through time with groups of genera and species apparently occupying the same niches for hundreds of thousands, or even millions of years; and 2) beetles appear to be rapid colonisers and are able to take advantage of their mobility and position in the food chain to move quickly into a region once conditions become suitable for life. For example, in recently deglaciated terrain, carnivorous beetles can prey upon spiders and flies, which in turn depend upon lichens or algae for sustenance. In this way they are not dependent upon higher plants which in turn are often restricted from moving into a region because of unsuitable substrate development.

Perhaps the most remarkable use of these principles has been in the English Midlands where a short-lived, but intense,

warmer episode punctuated the Siberian-like cold of the Middle Devensian (Middle Wisconsinan/Weichselian). One locality, a small gravel pit at Four Ashes near Wolverhampton, produced a number of organic lenses which revealed deposition from the last (Ipswichian/Sangamonian) interglacial through to the late Devensian (A. V. Morgan, 1973). More importantly, the Four Ashes sequence indicated the presence of a thermophilous insect fauna between faunas which contained Scandinavian and Siberian species (Morgan, 1970). Microhabitat and microclimatic differences could not be readily invoked, since the substrate was the same for all the sites, and since they were all deposited within an area of some 400 by 200m in relatively flat terrain (vertical amplitude less than 5m). This observation verified the results of a number of other sites of similar ages, but found in scattered geographic locations. These data, along with data from other areas, were incorporated in a paper on climatic reconstruction of Central England in Middle and Late Devensian times (Coope *et al.*, 1971). The preliminary climatic curve (Fig. 8) shown in this publication was modified by subsequent research (Coope, 1975, 1977). The beetles changed from arctic boreo-montane species, to thermophilous species largely representative of the North German plain (i.e., warmer than southern England), and then reverted once again to treeline/tundra species. Other remarkably rapid shifts in insect faunas have been recorded from Late-glacial (Late Wisconsinan) sites in many different parts of the British Isles (Coope, 1977), but our work in southern Ontario has not yet produced a similar continuity of the climatic record. Rather we have established isolated points for a climatic curve, and two such examples from Toronto are discussed below.

The first locality is the long-famous Sangamon site of the Don Valley Brickpit. For about a century the Don Formation has been examined for its warm climate flora and the fossils of beetles, which have remained both generically and specifically unidentified. Recently we have examined and identified a small fauna which shows that the insects reflect a climate which is almost identical to that of Toronto today. The presence of a diverse group of beetles and associated caddisflies (Williams and Morgan, 1977) indicates a mixed deciduous and coniferous woodland bordering a well-vegetated, slowly moving river flowing into a lake with a water level well above that of the present day Lake Ontario. The July average temperature would have been about 20°C.

The second locality, referred to earlier in the historical discussion, is at the Scarbo-

rough Bluffs. An insect fauna recovered from the lower part of the Bluffs indicates a vastly different climatic regime from that of the Don. The Scarborough Formation, of Early Wisconsinan age, rests on top of the Don Formation (Karrow, 1967; Karrow and Morgan, 1975). Insects collected from the deltaic Scarborough Sands and the lacustrine Scarborough Silts and Clays are typical of the northern boreal forest or open tundra, close to treeline. The habitat reflected by the insects appears to be a patchy spruce environment with open-ground areas. The July average temperature would have been about 12°C.

Although the thermal environments of the Don and Scarborough were, obviously, drastically different, we cannot interpret the rapidity of change which took place during the deposition of the two sequences since it lies beyond conventional radiocarbon dating. This is singularly unfortunate, since it would have been extremely interesting to see just how rapidly the last interglacial climate deteriorated – a prospect which may await us in the not so distant geological future. It is equally interesting to examine the poorly preserved insect faunas of the Wisconsinan and to contemplate the even more severe climates indicated by tundra insect assemblages in southern Ontario. The prospect of increasingly harsh climates,

the disappearance of deciduous trees, followed by conifers and the advent of a bleak tundra with active permafrost and a slowly advancing ice sheet is one which can only be welcomed by Alberta and OPEC!

Zoogeography

One of the most exciting facets of this research is that of zoogeography, although this subject would seem to be furthest removed from the geological applications of paleoentomology. Most people tend to regard beetles as being secretive and possibly somewhat lethargic, but anyone observing beetles on a warm summer day will quickly realise that large numbers of species can move extremely rapidly both on the ground and in the air. In the previous section we alluded to the fact that beetles were rapid colonisers and were well adapted to certain ecological niches. The climatic fluctuations of the Pleistocene forced beetles to move vast distances so that their present distribution is often quite dissimilar to their distributions during the Pleistocene. For example, the present Canadian insect fauna would only have been able to colonise most of Canada during the period following ice retreat. With the exception of the Yukon, parts of the Northwest Territories, possibly portions of the east coast of Labrador and some of the islands in the Gulf of St. Lawrence, ice retreat has taken place less than 15,000 years ago. Substantial portions of Quebec and smaller areas of the Northwest Territories were ice-covered as recently as 7,000 years ago. Figure 9 illustrates the distribution of four

beetle species which have moved considerable distances during the Pleistocene.

Diacheila polita (a ground beetle) is today confined to the extreme northwest of Canada, with a range expanding westward through Alaska, Kamchatka and eastern Siberia to central and western Siberia, eventually terminating on the east side of the Kola Peninsula. This beetle is flightless and usually inhabits open peaty soil on the tundra. It has been found in southern Ontario in the Scarborough Formation, and has been recorded from a number of sites in the English Midlands.

Helophorus arcticus (a water scavenger beetle) was first described in 1937 and is only known from three modern collecting localities (Brown, 1937), at Churchill (Manitoba), at Lake Harbour (Baffin Island) and at Hebron (Labrador). The habitat is poorly understood, but generally the beetle appears to be associated with littoral muddy substrates near large water bodies. In southern Ontario it has been found in the Scarborough Formation (Morgan, 1972) and in Early Wisconsinan deposits at Woodbridge (northwest of Toronto).

Anotylus gibbulus (formerly *Oxytelus gibbulus*), a rove beetle, was found in Sangamonian (last) Interglacial deposits at the Don Valley Brickpit (Toronto) in 1974. This species is of extreme interest to entomologists because it is not living in North America (or even Western Europe) at present. The core area of *Anotylus gibbulus* appears to be the Caucasus Mountains in Southern Russia. One other modern locality near Vladivostok has also been described (Hammond *et al.*,

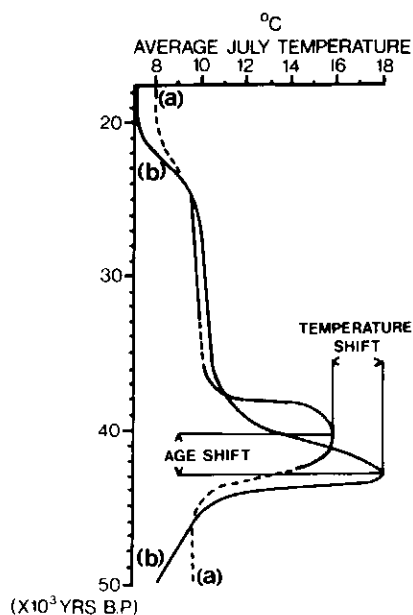


Figure 8
Paleotemperature curve for the Middle Devonian in Central England. The short lived climatic amelioration illustrated in curve (a) (Coope *et al.*, 1971) has been modified to curve (b) (Coope, 1977). The magnitude, longevity and timing in the peak of warmth has gradually been refined with research into additional sites.

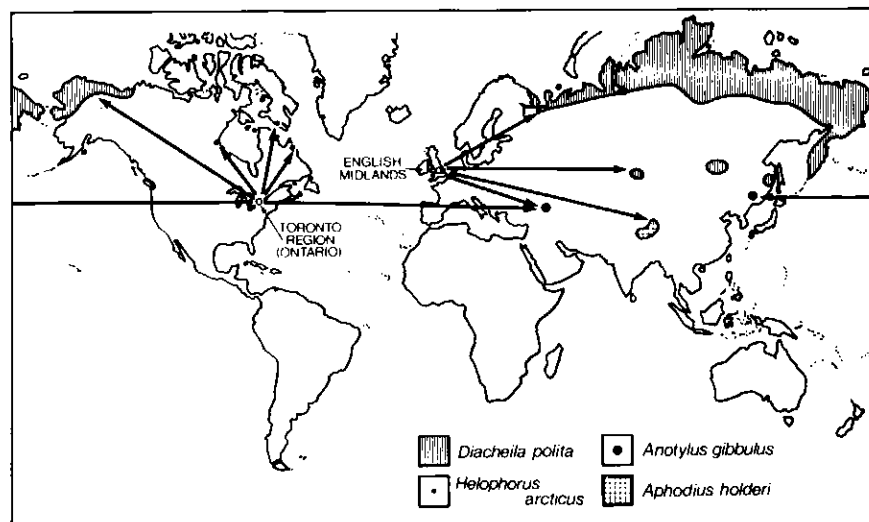


Figure 9
Changes in the geographic ranges of selected species. Modern distributions are shown and selected areas (Southern Ontario and Central England) illustrate regions where fossil specimens have been found.

1979). The reason for the contraction in range is not clear, because *A. gibbulus* was also present in Central England until approximately 35,000 years ago. It is possible that the range of this beetle (often associated with dung) may have been curtailed by the demise of the large mammals in latest Pleistocene time.

Aphodius holderi (a lamellicorn beetle) is another species which is now living far from fossil sites of Middle Wisconsinan age. This dung beetle is exceptionally common in certain deposits of Central England. In spite of an extremely distinctive morphology, the fossil specimens were not matched to living counterparts until the early seventies (Coope, 1973). The somewhat restricted distribution is shown in Figure 9 in the region of Tibet, north of the Himalayas.

Although we have only used four examples above, many more could be cited illustrating movements in distribution which amount to thousands of kilometres between fossil and modern locations, even for relatively recent Late Wisconsinan sites. We hope that, as this research area expands it should be possible to illustrate the movement of selected species, or even whole faunal assemblages, through time and reconstruct the shifts of beetle populations in front of the advancing and retreating Wisconsinan Ice-Sheet.

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