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Fossil Coleopteran Assemblages as Sensitive Indicators of Climatic Changes During the Devensian (Last) Cold Stage [and Discussion]

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Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage

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[1 Pullout]

Coleoptera are abundant fossils in Quaternary deposits laid down under freshwater or terrestrial conditions. They display a remarkable degree of evolutionary stability and reasons are adduced for believing that this morphological constancy is associated with physiological constancy. Thus whole communities of species have been assembled in the past, drawn together by common ecological preferences, so that the species composition of fossil assemblages resembles that of modern faunas. Marked changes in the geographical distribution of Coleoptera during the last glacial–interglacial cycle conform to an orderly pattern of climatic fluctuations. The Coleoptera contribute most information about the Devensian climates during warmer interstadial periods because during the colder episodes conditions in Britain became more or less intolerable to insect life and the fossil content of the sediments approaches zero. The term interstadial is here used for an interlude of milder climate in an otherwise cold period which either does not attain temperatures equivalent to those of the present day or which attains temperatures as warm, or even warmer than those of today but which does not last long enough for floral and faunal equilibrium to become established.

During the Chelford Interstadial, at the limit of acceptable radiocarbon dating but possibly about 60000 years (a) ago, the climate in central Britain was rather cooler than now with a moderate degree of continentality.

The Upton Warren Interstadial complex, between about 45000 and 25000 a ago, reached its thermal maximum at about 43000 a before present when temperatures were rather higher than those of the present day and the climate was moderately oceanic. This episode may have been as short in duration as 1000 a. After this the interstadial is characterized by a period of much lower temperatures, with a greatly increased degree of climatic continentality, lasting for about 15000 a.

Few insect faunas are known from the period of maximum ice expansion but the scant evidence supports an interpretation of a climate of arctic severity.

During the closing phases of the Devensian cold period there is faunal evidence for only one major climatic oscillation – here called the Windermere Interstadial. The sharp rise in the thermal environment at its beginning took place rather before 13000 a ago but later than 14000 a ago. Thermal maximum was attained almost immediately with temperatures during the summer at or above their present day level. Moderate oceanicity of the climate at this time means that winter temperatures were not much lower than those of the present day. At least during the earliest parts of this interstadial a temperate insect fauna was associated with a flora almost entirely dominated by herbs. The decline of the Windermere Interstadial from its thermal maximum seems to have been more or less synchronous from southern to northern England and to have taken place at about 12200 a ago. A cool temperate phase then ensued for over one thousand years with summers about 3 °C cooler than during the thermal maximum. This episode corresponds in time to the Allerød oscillation.

The Loch Lomond Stadial between 11000 and 10000 a ago saw the return of arctic faunas to the British Isles even as far south as Cornwall. The presence of Asiatic species, though not abundant, suggests that the climate at this time may have been rather continental.

26-2

The timing and intensity of the climatic changes during deglaciation show close parallelism to the changes in oceanic circulation in the eastern Atlantic now being interpreted from cores of ocean bottom sediments.

1. Introduction

The Coleoptera are characterized by a number of features, which taken together, combine to make them one of the most valuable components of the terrestrial biota in the interpretation of Quaternary environments. They have for the most part robust exoskeletons that survive as excellent fossils that are complicated enough in their structural details to permit many of them to be identified specifically. The fossils are often abundant, so that several thousand specimens can be obtained from a few kilograms of organic silt. In terms of numbers of species the order Coleoptera is one of the largest of the insects (in Britain alone there are over 3800 named species). Because they are easily caught and need little other than drying for their preservation, they have been, and still are, avidly collected, so that their taxonomy, geographical distributions and ecological preferences are relatively well known, particularly in the more inhabited parts of the northern hemisphere. From the point of view of the Quaternary palaeoecologist trying to reconstruct and understand past environments, this latter point is of the greatest importance since we are entirely dependent for our basic ecological data upon the skills of our neontological colleagues. It is thus both stimulating and humbling to read of the wealth of ecological information available and yet to realize how little we really know about the factors controlling the ecological fastidiousness of a species in its natural environment. For a particular species these environmental preferences are often quite narrow but, taken as a whole, the order Coleoptera contains species that are adapted to almost all terrestrial and freshwater habitats and trophic levels in the ecosystem.

The Quaternary fossil record of the Coleoptera has become extensive during the last two decades, especially in western Europe and North America. In spite of the fact that about 2000 species have been recognized, only one or two from the lower Pleistocene of Alaska (Matthews 1974) show any evidence of evolutionary change, and even in these cases the differences are of the same order of magnitude as we would expect today to differentiate geographical races of a single species. We have to look back into deposits that probably date from the late Miocene, namely the Beaufort formation in arctic Canada, before we see the first signs of evolution at the species level (Matthews 1976). Unfortunately the fossil evidence is restricted so far to temperate and polar regions of the northern hemisphere and we know very little of the fossil history of the Coleoptera in the tropics. However, it can be demonstrated that wherever fossils are available the Coleoptera show a remarkable degree of morphological stability throughout the Quaternary. Such is the precision of the preservation of these fossils that often exactly the same criteria can be used to differentiate between related species by both the modern coleopterist and the palaeontologist. It is not at all uncommon to find in Quaternary deposits the abdomens of beetles from which can be dissected the male genitalia which can be shown to match their modern counterparts, even to the intricacies of their internal sclerites. There can thus be little doubt that our Quaternary fossil Coleoptera represent exactly the same species as defined by present-day coleopterists.

However, although morphological constancy can be demonstrated directly, physiological constancy can not. Since the physiological make-up of a species determines its ecological tolerances or preferences, it is important to know to what extent physiological evolution might

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

have taken place without any associated morphological change. Fortunately this is not as intractable a problem as it might seem at first sight. There is a substantial and growing body of evidence to show that the communities of species that occurred in the past are similar to those that can be found today. In other words species of beetle to a large extent kept the same company in the past as they do today. Furthermore, when it is possible to find independent evidence of the local environment or climate, such as for example the presence of a particular host plant represented by its macrofossils or the presence of ice-wedge casts indicating permafrost conditions formed contemporaneously with the insect bearing horizon, the species of beetles that occur as associated fossils are the same as those that would be expected under similar circumstances today. Certainly ecologically 'mixed' assemblages do occur occasionally, but they are relatively rare and usually represent transitional faunas characteristic of periods of rapid environmental change. If gradual physiological evolution had taken place on a large scale hidden under the mantle of morphological stability, it might have been expected that, with increasing age, our fossil assemblages should have included increasingly bizarre assortments of species of contrasting environmental requirements and climatic tolerances. In fact no such progressive deviation from present-day population structures is found in our fossil assemblages even as far back as the Cromerian interglacial. This suggests that, for the most part, species of Coleoptera have remained as physiologically stable as their morphological constancy should have led us to expect.

There are, however, a few species that appear to be exceptions to this general pattern of ecological conformity; that is they persistently occur in our fossil assemblages in company with others with which they have not been found living today. Such species require special consideration. Of course these strange associations might be construed as indicating environmental conditions for which no analogue exists at the present day, but since these odd species make up such a small proportion of the total fauna (almost always less than 5 %) and since it is usually the same few species that offend against ecological conformity, it is more probable that the oddness of their associations is a property of the species concerned rather than of the environment in which they lived. It is not intended here to give the impression that all Quaternary environments have equivalent conditions to be found somewhere on the Earth today, since in a large number of cases this is almost certainly not true, but merely to emphasize that the occurrence of these few nonconformist species in our fossil assemblages is inadequate grounds for this sort of environmental special pleading.

Two examples of these misfit species will be given here. In the latter half of the Upton Warren (Mid-Devensian) Interstadial *Timarcha goettingensis* (L.) occurs at a number of localities in association with many species that are today characteristic of tundra environments. This species is widely distributed in Europe south of latitude 60° N and although it is a plant-feeding species it is unlikely that this northern limit is determined by the availability of some preferred host plant since the species is polyphagous. The second example comes from the Windermere (Late-glacial) Interstadial (see p. 326). *Hypnoidus rivularis* Gyll. is a circumpolar boreal species that in Europe has its southern limit of continuous distribution across Fennoscandia at about 60° N. This northern species has been found as a fossil at a number of sites but always in company with a suite of other species of more temperate preferences. It seems likely that species such as these have either changed their environmental requirements since the Devensian by physiological evolution, or else their present-day geographical range does not include the whole area potentially available to the species. Alternatively it is possible that, in the past, a gene pool

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

of greater diversity was available to the species, only part of which has survived to be handed down to their present-day representatives. Whichever explanation eventually accounts satisfactorily for these anomalously occurring species, their existence highlights the danger of using a limited number of indicator species as important clues to the determination of Quaternary environments. Since evolutionary stability seems to characterize the vast majority of species of Coleoptera during the Quaternary, it is the fossil assemblage viewed as a whole that provides the best evidence upon which to base our palaeoecological interpretations.

The remarkable degree of evolutionary stability shown by the Coleoptera during the Quaternary might at first sight seem unexpected in the light of the instability of the Quaternary environment. It might have been expected that successive ice advances and recessions with their associated climatic effects well south of the glacial limits, would have reduced population sizes, isolated them in restricted refuges and imposed upon them intense selection pressures – a certain recipe for rapid speciation. Yet in the northern latitudes most influenced by the vicissitudes of the ice age climates, rapid speciation evidently did not occur. There must, therefore, be something wrong with our view of the effects of the climatic oscillations on the fauna; some essential ingredient missing from our recipe. The fossil record provides abundant evidence that the geographical ranges of even the most sedentary species have changed on an enormous scale even within the last glacial/interglacial cycle. These rates of population movement were clearly adequate to enable species to keep pace with the changes in the location of suitable living conditions, so that the actual environment in which a species lived remained constant in spite of the drastic changes in the Quaternary climate that took place at any fixed geographical location. Thus the fact that insect species have remained stable during the Quaternary requires no special reconciliation with these environmental fluctuations.

It is of course possible that many species actually owe their constancy to the instability of the Quaternary environment. The hypothesis runs as follows. Many low temperature stenothermic species, that were widespread in Europe during the Last Glacial period, have today very disjunct distributions, being found in high latitudes in a zone of more or less continuous distribution down to sea level and also as isolated populations at high altitudes in the mountains of central Europe. This boreo-montane distribution pattern is largely due to the restriction of acceptable thermal environments during the climatic amelioration of the Post-glacial period. The northern and southern populations must have been isolated from one another for at least 10000 a, that is since the Loch Lomond Stadial (Younger Dryas times) which was the most recent period when such species were widespread throughout the lowlands of western Europe, and they may well have been isolated for much longer than this. It is evident that mere geographical isolation for this length of time has not led to any apparent speciation in spite of the fact that many of these isolated populations must be relatively small. However, large-scale climatic oscillations whose period is measured in a few tens of thousands of years, mean that these mountain top or high latitude evolutionary traps are easily escaped from, if climatic deterioration takes place before the marooned populations have become genetically isolated from one another. Under such conditions geographical barriers to genetic mixing are continuously being broken down or reformed in different contexts. The large-scale movements of insect populations that are so characteristic a feature of the fluctuating Quaternary environment would have repeatedly caused the merging or fragmentation of subpopulations; deployments and regroupings that would have ensured that the gene pool was kept well stirred. Speciation under such effervescent circumstances must have been well nigh impossible. It was this ability of insect populations to move rapidly, and far, in response to changes in the environment that was left out of our initial consideration of the response of the fauna to the vicissitudes of the Quaternary climate (p. 316). Certainly this readiness to move and to track environmental changes across the surface of the Earth coupled with the frequency of major climatic oscillations must be an important factor in maintaining specific stability of insects during the Quaternary.

The hypothesis outlined above is most relevant for the species that occur on the continental masses in temperate or polar latitudes where the opportunities and need to move in response to climatic changes are most pronounced. Conversely it should be expected that those species which live in situations where the option of large-scale population movement is not available, such as for example on oceanic islands or in cave systems, should show tendencies for more rapid evolution. There is of course abundant evidence that this is so. Similarly in those parts of the world where climatic changes associated with glacial/interglacial cycles would be expected to be minimal, namely in tropical latitudes, the necessity for population movement was no doubt correspondingly diminished with the consequent less frequent disruption of geographical barriers to genetic mixing. Under these circumstances evolution might have been more rapid than in the middle and polar latitudes. Paradoxically, therefore, it appears that Quaternary climatic instability could be the cause of evolutionary stability of insects during this period and conversely for the species of continental masses, long periods of climatic stability might be expected to lead to relatively rapid evolution.

2. The climatic significance of Quaternary coleopteran assemblages

The evolutionary stability of the Coleoptera during the Quaternary both in their morphology and their physiology means that the properties of present-day species can be used directly in the interpretation of fossil assemblages. This actualistic approach can be justified on the grounds that, in almost all cases, fossil assemblages when treated in this way make ecological sense; the best possible justification for a hypothesis, namely that it works.

All modern ecologists stress the fundamental rôle that climate plays in determining the geographical range, and often also the abundance, of insect species. Thus we find in that valuable compendium of papers on insect abundance published by the Royal Entomological Society (Southwood 1968), in discussing the processes that modify the size of insect populations Richards & Southwood (1968) state, 'First there is climate which sets the arena in which everything else interacts.' Later in the same volume Henson (1968) points out 'From the earliest stages in the development of our interest in insect populations, there has been a continued awareness that climate and its short-term expression which we call weather, have profound impact on the numbers of insects present at any one time'. This paper gives a useful account of reviews of biometeorological works. Finally Wilson (1968) states 'no one would doubt that climate is a major factor in determining limits of distribution'. Statements such as these serve to emphasize the importance that almost all insect ecologists attach to climate as one, if not the most potent, arbiter of insect distribution.

There are, of course, many factors other than climate that play important parts in the control of abundance and distribution, but these vary in their significance from species to species and place to place. They do not possess that all-pervasive quality that typifies the effects of climate. Thus in the central parts of the range of a species where environmental conditions are most favourable to its survival, population control is achieved largely by biotic factors such as

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

competition for food or living space or by predation and parasitism (figure 1). Factors such as these are almost always density dependent in their effectiveness. Even under these more or less favourable conditions, variations in the physical environment may often exert a limiting influence on the population which may also be density dependent since refuges from adverse circumstances may be limited and easily filled to capacity. Also climate may control food supply and thus indirectly influence density dependent processes. On the other hand at the fringes of the range of a species conditions become increasingly unfavourable and the physical environment, chiefly in the form of climate, begins to exert a limiting influence that becomes increasingly independent of density. Fringe populations are characterized by being transitory; subject to successive eliminations by hostile climatic events and recolonizations from the main body of the population. Climatic factors can thus be expected to be among the most important controlling influences on the limits of the geographical ranges of insect species.

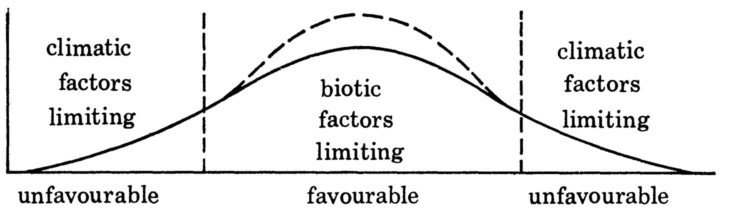


Figure 1. Hypothetical relation between the major regulating factors on a species throughout its geographical range (from Price 1975).

In the interpretation of the climatic significance of fossil insect assemblages, greatest attention is thus paid to the limits of the modern geographical distributions of the species of which it is composed. Some measure of the ancient climate can then be gained by comparing the ranges of a large number of species and the general 'fashion' of distribution determined. From some sites over 200 named species of fossil Coleoptera have been used in the interpretation of the climatic regime of a single time horizon. At localities where thick successions of fossiliferous deposits occur, spanning a considerable period of time, a sequence of insect faunas may be obtained. The varying fortunes of each species can then be plotted against time on a graph akin to those produced by palynologists. In the interpretation of the climatic significance of such diagrams, greater attention is paid to the simple presence of a species rather than to its abundance. This is because abundance is largely a reflection of the local environmental conditions and may well be determined by biotic factors, while the range of a species in time, just as it is in space, is likely to be governed chiefly by climatic factors. In this respect, therefore, beetle diagrams are dealt with rather differently from pollen diagrams.

The climatic factors governing insect distributions are chiefly those of the thermal environment and of moisture. Although these factors are known to interact, purely for convenience they will be dealt with here as separate entities.

The part played by moisture in determining the composition of fossil insect assemblages is difficult to assess beyond the immediately local environment. Most of our fossiliferous deposits were laid down in water, accumulating in shallow ponds or peat bogs, and the sediment has usually remained waterlogged throughout the year. Many of the fossil insect assemblages are thus dominated by aquatic or semi-aquatic species. The existence of these shallow ponds, that must have survived for much of the summer and never dried out completely, suggests that for much of the time during the Devensian glaciation adequate precipitation was available to maintain them. This precipitation need not have fallen in the summer since for much of the time winter temperatures were well below freezing and thus any precipitation would fall as snow and accumulate. The whole year's precipitation would then be available for biological and physical processes during the summer as the accumulated winter snows melted. There is ample evidence from fossil insect assemblages that, away from the marshy hollows, much of the country was dry with a patchy vegetation cover and well drained soils. There is almost no evidence of the steppe species that we might expect had these areas been truly arid during this period.

The appropriateness of the thermal environment is of fundamental importance in determining the suitability of habitats for poikilothermic animals. This may be viewed in two ways. Thermal intensity, measured as temperature, will set existence limits within which a species can survive. Furthermore, animals exhibit decided temperature preferences, well within existence limits, that determine behaviour patterns such as breeding and feeding, essential for the survival of the population. The availability of adequate heat, measured in day degrees, is also of great importance, contributing to the survival limits of a species as well as, for instance, to the rate of development and thus duration of life cycle and the rate at which a hibernating animal consumes its fat reserves, a factor that may be of importance to the survival of insect species in areas of oceanic climate where winters are relatively warm and thermally unstable. These examples are quoted in order to indicate the intricacy of the controls exerted by the thermal environment upon insect populations; they are in no way intended to be comprehensive but merely to hint at the complexity of the subject. Andrewartha & Birch (1954) and Price (1975) provide numerous case-histories and detailed discussions based upon data from both laboratory and field experiments.

When dealing with the vast majority of modern insect species, however, it must be admitted that we do not know the actual factors governing their distributions or abundance. In practice therefore we must fall back upon the simple expedient of investigating the modern geographical ranges of the species that make up our fossil assemblages and interpreting these in terms of the known environmental parameters that circumscribe these ranges. Usually these environmental parameters are expressed in terms of average figures of temperatures or rainfall and it must thus be emphasized that these are not the actual factors experienced by the organisms and influencing their population dynamics. They are, however, valuable as approximations that enable environments to be compared objectively.

In the interpretation of the climatic significance of a Quaternary insect assemblage, greatest attention is paid to the limits of the present-day geographical distributions of its component species. Assuming that the limits of these ranges are governed, in most cases, by climatic factors, and the justification for this assumption has been outlined above, species whose ranges are restricted to narrow climatic zones are considered to be stenothermic, while those with widespread distributions are interpreted as eurytherms. Naturally, in making climatic inferences, greatest attention must be given to the stenothermic species. In those cases where the range of a species is not governed by climate the use of this assumption should pick them out as recurring misfits in the overall distributional style of the bulk of the fauna.

This procedure does seem empirically justifiable. At least in Europe, where both the distributions of insects and climatic parameters are fairly well known, it can be shown that for many species their ranges do in fact correspond to well known climatic zones. This correspondence can well be illustrated by comparing the distributional limits of species of Coleoptera in Fennoscandia (a region chosen solely because it is one of the few places for which detailed data are available) in the *Catalogus Coleopterorum Fennoscandiae et Daniae* (Lindroth, ed. 1960) and the climatic parameters for the same area obtainable from numerous standard atlases. Such a comparison shows that the most consistent correlation is between summer temperatures and the northern limits of the ranges of those species which, whilst occurring in the southern areas of Fennoscandia, do not extend into the far north. The southern limits of the more boreal species are rather more ragged, breaking up into isolated patches associated, no doubt, with colder local climates. Even in such cases, however, the main areas of distribution have limits that also correspond to a large extent with summer temperature parameters. It is thus apparent that in latitudes such as north and central Europe the Coleoptera are best equipped to provide information about the thermal environment of the summers. Species with restricted ranges in western Europe, or conversely in the east palaearctic region, may also imply oceanicity or continentality of climate respectively with the added implication of winter temperatures. In our palaeoclimatic reconstructions we have used the July average temperatures of the regions that would best suit each fossil assemblage if they were living today. The July average temperature in this context is only intended to be used as a crude assessment of summer warmth.

3. Climatic changes during the Devensian cold stage

Numerous assemblages of fossil Coleoptera are now known that date from the various phases of the Devensian cold period and, though not all of them are fully investigated, over 50 fossiliferous localities have been discovered. Two recent reviews deal with the climatic changes during the Devensian as inferred from assemblages of fossil Coleoptera (Coope, Morgan & Osborne 1971; Coope 1975). Although this paper presents new information, particularly concerning the episodes of climatic amelioration during this period, there has not been any reason to alter the inferred curve for variations in the summer warmth (figure 2).

In the discussion that follows the term interstadial is used for an interlude of climatic amelioration which, either does not reach the degree of summer warmth characteristic of the present day, or for a period during which the intensity of summer warmth may have reached or even exceeded that of the present day but which did not last long enough for floral and faunal equilibrium to become established.

(*a*) *The Chelford Interstadial*

Sites that date from this period are still remarkably rare in spite of 20 years search since the discovery of the original locality at Chelford, Cheshire (Simpson & West 1958). Only one other deposit can be ascribed with certainty to this interstadial, namely the lens in the Four Ashes gravel pit that underlay the mid-Devensian horizons (Morgan 1973). A puzzling lens of organic silt at Wretton, Norfolk (locality of WG of West *et al.* 1974) has a pollen spectrum not unlike that of Chelford suggesting that woodland existed at that time. On the other hand an assemblage of Coleoptera from the same horizon suggests truly arctic conditions with an open treeless landscape (Coope 1974). This anomalous association has been further discussed (Coope 1975).

The only new information of the faunas of this interstadial arises from a re-evaluation of the original fossils from Chelford (Coope 1959) in the light of improved comparative material taxonomy and, by no means least, personal expertise. The emendations and additions to the original faunal list are as follows. *Bembidion harpaloides* Serv. was incorrectly named and is in fact *Trechus rivularis* Gyll. The numerous fossils of *Hydroporus*, many of them thought at the time to be unidentifiable, have been investigated by R. B. Angus. He reports that only three species can be named with certainty; *H. longicornis* Sharp, *H. melanarius* Sturm and *H. memnonius* Nic. These are all species of acid pools with *Sphagnum*, though *H. longicornis* seems to require trickles

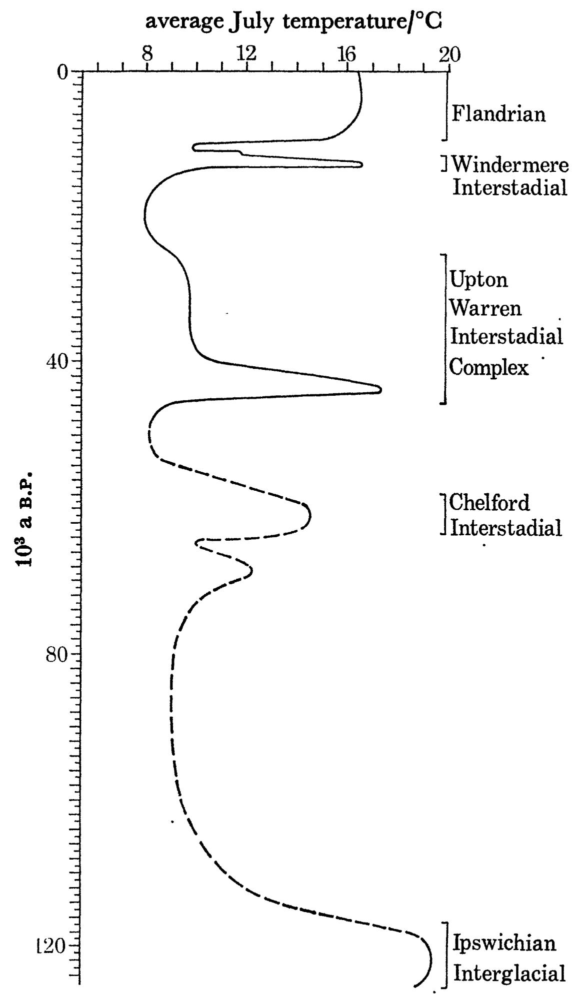


FIGURE 2. Variations in the average July temperatures in lowland areas of the southern and central British Isles since the Last (Ipswichian) Interglacial.

of water, such as those found at mossy flushes. Until its occurrence in this habitat was discovered (Foster 1968) the species was considered to be one of our rarest water beetles. The small staphylinid species *Boreaphilus henningianus* Sahlb. must be added to the Chelford faunal list. It is widespread in boreal Europe but absent from the present-day fauna of the British Isles. There are two emendations necessary among the moss feeding byrrhid beetles. *Simplocaria metallica* Sturm must be added. This is a very rare species today that is widely distributed in boreo-alpine parts of Europe but is absent from Britain. *Morychus aeneus* F. replaces *Cytilus* sp. This species is found all over Europe as far north as 65° N. The identification of two weevils also needs correcting; *Limnobaris pilistriata* Steph. must replace *L. t-album* L. and *Otiorrhynchus scaber* L. is almost certainly the correct identification for some badly preserved fossils originally named *O. ligneus* Oliv.

These alterations and additions to the original faunal list from Chelford do not alter the overall interpretation of the local environmental conditions. The climatic inferences are, however, considerably reinforced. Originally the fossil insect assemblage was interpreted as indicating a climatic regime similar to that in southern Finland between 60 and 65° N. The addition to the faunal list of two or more 'non-British' species, both of which live today in this part of Finland, gives added support to this interpretation. Furthermore, two out of the four species which in the original paper were pointed out as exceptions in that they did not live today in southern Finland, have now been recognized as misidentifications. The Chelford insect assemblage thus provides an internally consistent picture both of the local environmental conditions and of the climate of the times. What is more, this picture is remarkably similar to that derived from the botanical data by West (Simpson & West 1958). Clearly, for this interstadial at least, complete harmony of flora and fauna existed, suggesting that either the climatic changes had been slow enough, or adequate time had been available, for biotal equilibrium with the physical environment to have been achieved.

(*b*) *The Upton Warren Interstadial complex*

In contrast to the environmental harmony shown by both the flora and fauna from Chelford, the biota of the thermal maximum of the Upton Warren Interstadial (figure 3) suggest that equilibrium between its various components and the physical environment had not been reached during this period. This biotal disharmony may be summarized as follows. A thoroughly temperate insect fauna of considerable diversity and ecological complexity was associated with a flora completely lacking in trees and with an assemblage of herbs of contrasting distributional styles (Bell 1969). The fact that the older Chelford fauna is in such complete environmental accord with the flora suggests that the curious assemblage of flora and fauna from the thermal maximum of the Upton Warren Interstadial is not a matter of evolution in the tolerances of the species concerned. Nor is it possible to argue that the environment was so different from that of the present day that a totally different equilibrium biota could be maintained since it has been shown (Coope & Angus 1975) that the insect communities are entirely meaningful in terms of present-day conditions and require no environmental special pleading for their occurrence. It is not intended here to claim that the interstadial environments were exactly analogous to those of the present day but simply to indicate that deviation from modern environmental conditions is inadequate by itself to explain the degree of apparent disharmony between the flora and the fauna. The reasons for this curious concourse of species must, I believe, be sought for in the historical context of this interstadial; that is in the sequence of environmental changes that came both immediately before and after its thermal maximum.

The climatic changes of the Mid-Devensian (Weichselian) in western Europe inferred from fossil coleopteran assemblages have recently been revised (Coope 1975) and only a brief summary will be given here. The Upton Warren Interstadial complex spans about 20000 a between 45000 and 25000 B.P. (figure 3). Before the thermal maximum of the interstadial, the insect fauna was dominated by boreal or boreo-montane species, many of which (about 20 % of the fauna) do not now live in the British Isles. There can be little doubt that the climate at this time was of arctic severity but the absence of any exclusively eastern species from the faunas of this period may indicate that the climate was not markedly continental though the winters were no doubt severe.

The thermal maximum of the interstadial apparently follows this phase of arctic climate with dramatic suddenness. Thus in a stratigraphical sequence at Tattershall, Lincolnshire (Girling 1974) a temperate insect assemblage replaces the boreal fauna within a few centimetres of organic silt. Furthermore, the radiocarbon dates for these horizons emphasize their proximity

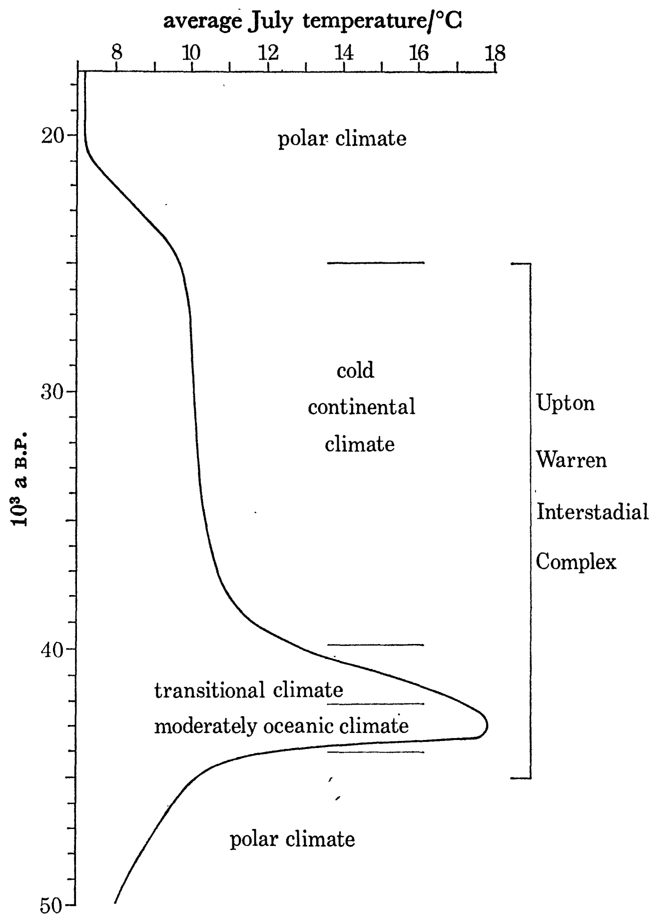


FIGURE 3. Climatic changes in lowland central England during the Middle Devensian.

in time; 44300 ± 1600 B.P. (Birm-408) for the stratum with the boreal fauna and 43000 ± 1200 B.P. (Birm-341) for the layer above with the temperate insect assemblage. Some idea of the intensity of this episode of climatic amelioration may be gained from the ecological study of a similar temperate insect assemblage to that from Tattershall, obtained from the flood plain terrace of the Thames at Isleworth (Coope & Angus 1975). This deposit gave an almost precisely comparable radiocarbon date to that from Tattershall, namely 43140 ± 1400 B.P. (Birm-319). Out of a total of 248 named species, only one has a northern geographical distribution today and it, *Deronectes griseostriatus* DeG., ranges as far south as the northern parts of the British Isles. None of the boreal species that were so important an element of the preceding faunas survive into this episode and in their place there are a large number of species that are widespread in central and southern Europe but which barely reach the extreme south of

England. The bulk of the Isleworth fauna (95 %) can be found today in north central Europe; say in the region of the north German plain. The insect fauna thus indicates that at its thermal maximum the summer temperatures were somewhat *warmer* than those of the present day in southern England. The absence of the far eastern species that characterize the next phase of the interstadial and the presence of exclusively west European species suggests that the climate of this period was moderately oceanic with winter temperatures only a little below those in southern Britain today.

The deterioration in the climate following the thermal maximum of the interstadial seems to have been more gradual than the amelioration at its beginning. Several of the faunas from Four Ashes (Anne Morgan 1973) appear to represent this transition. Though they contain a number of temperate species, they lack all the extreme thermophilous species that were so conspicuous an element in the faunas at Isleworth and Tattershall, and a number of moderately northern species were present. The insect assemblage described from Upton Warren (Coope, Shotton & Strachan 1961) shows still further deterioration and also contains a number of exclusively eastern species the ranges of which do not at the present time extend as far westwards as Europe. Two climatic inferences may be drawn from these transitional faunas. First, though the summers were evidently less warm than they were at the thermal maximum of the interstadial, they were by no means arctic since all the extreme boreal species, soon to become such an important component of the British insect fauna, were absent at this time. Secondly, the occurrence of east European and Asiatic species, often represented by large numbers of individuals, is strongly suggestive of increased continentality. Thus, though the summer temperatures fell by two or three degrees, the winters may have become relatively colder, but it is difficult to quantify this.

Numerous insect faunas are now known from middle Devensian deposits that post-date the temperate episode of the Upton Warren Interstadial complex (Coope *et al.* 1971). Collectively their radiocarbon dates span almost all the time between 40000 and 25000 B.P. and at the moment there does not seem to be any evidence to justify any major climatic oscillations during this period. The insect assemblages from all these sites are characterized by almost total lack of the relatively thermophilous species and in their place there are a large number of exclusively boreal, or boreo-montane, species and a number of eastern asiatic species that are often numerically abundant. The faunas as a whole would today be most characteristic of the Lower Alpine zone in the Scandinavian mountains or its equivalent near the forest limit in the Siberian arctic. Average July temperatures must thus have been at or just below 10 °C. The abundance, in these fossil assemblages, of east palaearctic species may be indicative of exceedingly cold winters with average February temperatures below −20 °C.

(*c*) *The Devensian ice maximum*

Very little evidence is available from the British Isles of the flora and fauna at the time when the ice front reached its most southerly extent, that is from the northwest of Norfolk in the east, across the English Midlands to south Wales in the west. A restricted insect fauna was obtained from a mossy silt beneath about 30 m of Devensian till on the Holderness coast of East Yorkshire (Penny, Coope & Catt 1969). Radiocarbon dates on the moss 18500 ± 400 B.P. (I-3372) and 18240 ± 250 B.P. (Birm-108) indicate that the insect fauna must have only just pre-dated the phase of maximum ice advance. Unfortunately, only a few species are represented but they indicate a harsh climate with summer temperatures probably several degrees below 10 °C.

Though arguing from absence of evidence is precarious, and doubly so in this case because of the smallness of the fauna, the lack of the exclusively Asiatic species, that were so common in the latter parts of the Upton Warren Interstadial complex, may indicate that the climate was less continental than it was at that time. If this is so, increased precipitation may have been largely responsible for the advance of the ice sheets into lowland Britain at this time, rather than a deterioration in the thermal environment. Certainly, for the 15000 years that followed the thermal maximum of the interstadial, the temperatures in the English Midlands would seem to have been adequate to sustain lowland ice sheets, yet throughout this period they were evidently absent.

(*d*) *The closing phases of the Devensian*

The disappearance of the ice sheets from the British Isles, after their maximum extent between 17000 and 18000 radiocarbon years ago, must have occurred with great rapidity. The whole process may well have taken place within 5000 years (Sissons & Walker 1974). Evidently the climatic amelioration was not constant or gradual but was characterized by relatively sudden changes reflected in the response of the flora and fauna as well as in geomorphological evidence of the readvance of the ice sheets. In so far as the evidence from the British Isles is concerned there is information to support only one large scale climatic oscillation towards the close of the Devensian period. During the thermal maximum of this oscillation it is possible that the ice sheets disappeared totally from Britain to be regenerated anew in the Western Highlands of Scotland (Sissons 1974) and to build corrie glaciers in the mountains further south as the climate subsequently deteriorated. This ice advance is called the Loch Lomond Readvance and the colder episode should be termed the Loch Lomond Stadial. It is approximately equivalent in time to Pollen Zone III and to Younger Dryas times of continental authors.

Before discussing the insect faunas of this period it is necessary to comment upon the naming of the episode of milder climate that immediately preceded the Loch Lomond Stadial. Much of this period falls within the time that has been rather loosely allocated to the Late-glacial and the period of climatic amelioration has been informally referred to as the Late-glacial Interstadial. However, regardless of the utility of these terms, they have strictly no validity according to the internationally accepted rules of stratigraphical classification. These rules require the establishment of stratotypes, i.e. standard sections wherein the lower boundary of the stratigraphical unit can be defined. In the British Isles the Late-glacial Interstadial has most frequently been equated with the Allerød oscillation which has its type section in Denmark and with which a great many continental sequences have been correlated. At first little evidence was found in Britain for the earlier Bølling Interstadial, also with its type section in Denmark, but recently abundant evidence has been recognized (Pennington & Bonny 1970; Pennington 1975) for a marked climatic warming more than a thousand years before the generally accepted date for the beginning of the Allerød. Numerous coleopteran assemblages provide independent evidence for this early warming and indicate that the climate was as warm during the summers as it is today, even before the conventional beginning of the Bølling oscillation (Vogel & Zagwin 1967), and apparently earlier than the date selected for the beginning of the Bølling chronozone in Fennoscandia, namely 13000 B.P. (Mangerud, Anderson, Berglund & Donner 1974). The Late-glacial Interstadial of the British Isles cannot, therefore, be satisfactorily equated with either the Allerød or Bølling interstadials as at present interpreted by continental authors, nor can it be accommodated in a combination of both.

It thus seems desirable that a stratotype should be selected to represent the deposits of the Late-glacial Interstadial in the British Isles.† Since we are concerned with the stratigraphical expression of a climatic event it is necessary to choose either a terrestrial or freshwater deposit. Three sedimentary environments are available, peat bog accumulations, kettle hole or small pond infillings and lake bottom sediments. Peat bogs with their unique biota and likelihood of breaks in sedimentation are, for these reasons, unsuitable as representative sections. Kettle hole sequences, though often extremely rich in flora and fauna, suffer from the complications inherent in the hydroseral development of all shallow ponds and also they may have the added complication of spasmodic melting out of buried ice. Limnic deposits, on the other hand, are much more likely to occur as continuous sedimentary sequences and those that accumulate near the lake margins are likely to reflect the terrestrial environment as well as that of the lake itself. As sources of fossil coleopteran assemblages, however, lake sediments are far from ideal since most of the beetles must have been incorporated in the deposit by accidental derivation from the surrounding land surface and are therefore sparsely distributed in the sediment. Representative faunas can thus be obtained only from relatively large samples. To some extent this problem can be overcome if limnic deposits are investigated in the vicinity of incurrent streams that are likely to carry terrestrial plant and animal macrofossils into the lake.

As a result of discussions with a number of workers in the field and particularly with Dr Pennington, it is suggested that the stratotype for the Late-glacial Interstadial in Britain should be selected from the deposits in Windermere (see Discussion). Perhaps the best locality is Low Wray Bay at the north end of the lake where minor streams have brought in much terrigenous material. This is also the site of numerous detailed investigations of both the lithostratigraphy and biostratigraphy carried out during the past 30 years.

In the account that follows of the climatic implications of coleopteran assemblages during the closing phases of the Devensian, the faunas will be considered under three headings; pre-interstadial, the Windermere Interstadial and the Loch Lomond Stadial.

(i) *Pre-interstadial*

No fossils have yet been found in the lower laminated clays in Windermere that predate the interstadial sediments. Four other sites in the British Isles have, however, yielded insect faunas that can be ascribed to the period immediately before the Interstadial.

The Late-glacial deposits at Hawks Tor on Bodmin Moor, Cornwall, have for long been the object of biostratigraphical investigations (Connolly, Godwin & Megaw 1950). Recently a reinvestigation of the stratigraphy and palynology of the site has been carried out by Brown (1977) during which he discovered a sequence of organic silts and gravels whose stratigraphy suggested that they predated the interstadial sequence. From samples of this deposit (section No. 4 of Brown's account) a sparse insect fauna of 17 taxa was obtained which contained a number of boreal species such as *Helophorus sibiricus* Mtsch., *Pycnoglypta lurida* Gyll., *Boreaphilus henningianus* Sahlb. and *Olophrum boreale* Payk., none of which live in the British Isles today. There can be little doubt that the climate at this time was very cold and probably too cold for the growth of trees. Unfortunately the sequence is extensively penetrated by roots from the overlying Flandrian deposits, so any radiocarbon date for this horizon would be unreliable.

At Glanllynnau 4.5 km west of Criccieth, North Wales, a sequence of Late-glacial deposits are immediately underlain by fossil-bearing grey silty clays and are exposed on the coast. The

† See discussion by Coope & Pennington, pp. 337–339.

insect fauna from this site has been described by Coope & Brophy (1972). The assemblage of Coleoptera from the pre-interstadial horizons is sparse but characterized by a variety of low temperature stenothermic species: these include *Bembidion fellmanni* Mnh., *Bembidion hasti* Sahlb., *Amara alpina* Payk., *Deronectes griseostriatus* DeG., *Helophorus sibiricus* Mtsch., *Helophorus obscurellus* Popp., *Helophorus splendidus* Sahlb., *Boreaphilus henningianus* Sahlb., *Simplocaria metallica* Sturm, *Syncalypta cyclolepidia* Munst. and *Phytonomus obovatus* Cki. This is by far the richest arctic assemblage known from pre-interstadial deposits and indicates very open country with no trees and an extremely cold and probably continental climate. A ^{14}C date of 14468 ± 300 B.P. (Birm-212) was obtained from a moss rich band at the base of the succession. Above this dated horizon were 120 cm of silty clay containing throughout the arctic–alpine assemblage of Coleoptera described above. A second radiocarbon date was obtained from seeds of terrestrial plants washed out of a detritus mud with a temperate insect fauna, that lay 20 cm above the highest stratum that contained arctic beetles. This upper date was 12556 ± 230 B.P. (Birm-176). The type of material dated precludes the possibility of 'hard water error' and prolonged pre-treatment of the sample was carried out to remove any possibility of contamination by modern humate. These two dates set time limits for the age of the arctic–alpine fauna from below the interstadial deposits of Glanllynnau.

At Glen Ballyre near Kirkmichael, on the northwest coast of the Isle of Man, a sediment filled kettle hole is exposed in section at the top of the cliff (Mitchell 1965; Dickson, Dickson & Mitchell 1970). Gravelly silts and clays underlie organic deposits that can be correlated with the Windermere Interstadial. From the lowest 30 cm of these deposits (that is well below the samples analysed by Dickson *et al.* 1970) an assemblage of northern Coleoptera was obtained that included *Bembidion hasti* Sahlb., *Bembidion lapponicum* Zett., *Agabus arcticus* Payk. and *Syncalypta cyclolepidia* Munst. One of the most abundant of the water beetles was *Coelambus mongolicus* Jak. that today is restricted to eastern Asia. A moss layer (chiefly *Drepanocladus*) at the base of this sequence gave radiocarbon dates of 18900 ± 280 B.P. (Birm-213) and 18700 ± 500 B.P. (Birm-270). A detritus mud with temperate insects about 5 cm above the topmost strata that contained the northern species gave a radiocarbon date of 12645 ± 280 B.P. (Birm-412). Here again the two radiocarbon dates set limits for the age of the pre-interstadial fauna from Glen Ballyre.

A rather enigmatic assemblage of fossil coleoptera from Colney Heath, Hertfordshire, has been described by Pearson (1962) from a peat erratic embedded in gravels stratigraphically below the level of a pollen bearing sequence characteristic of the Allerød climatic oscillation. A radiocarbon age of 13560 ± 210 B.P. (Q-385) was obtained from wood contained within the erratic. The assemblage of Coleoptera contains a curious assortment of relatively northern and southern species but since the fossils were not preserved it has not been possible to verify their determinations. However, the unmistakable *Diacheila arctica* Gyll., *Miscodera arctica* Payk. and large numbers of *Notaris aethiops* F., indicate that the climate must have been considerably colder than it is at the present time. However, the presence of relatively southern species, ranging barely north of 60° N, such as *Carabus monilis* F., *Bembidion minimum* F., *Aphodius plagiatus* L. and *Dorytomus longimanus* Forst., suggest a climate not much colder than the present day. It is an intriguing possibility that this peat erratic spanned the period of abrupt change from arctic to temperate climatic conditions that must have occurred at about the same time as the radio-carbon date from the Colney Heath erratic.

A single sample from the base of a deep depression beneath the Late-glacial and Flandrian deposits at Stafford (Morgan, A.V. 1973, Fig. 30) provided an insect fauna that included

Helophorus obscurellus Popp., and was indicative of a climate of arctic severity (Anne Morgan 1970). A radio-carbon date of 13490 ± 375 B.P. (Birm-150) was obtained from this sample which, since it was obtained from about 15.5 m depth, is unlikely to be influenced by modern humate. This is the most recent date obtained for a pre-interstadial arctic–alpine insect fauna.

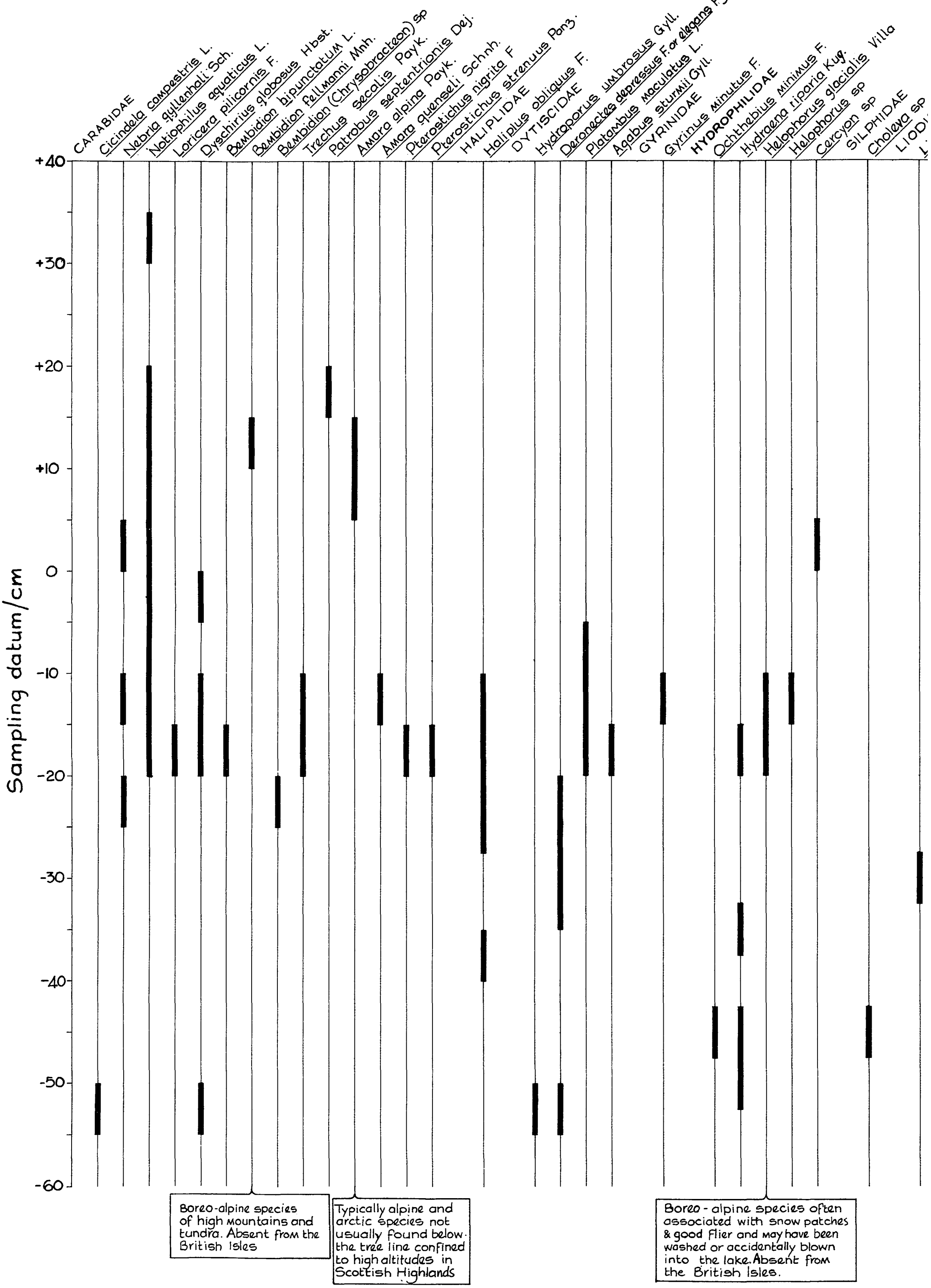
(ii) *The Windermere Interstadial*

The occurrences of various species of Coleoptera through the interstadial sediments at Low Wray Bay, Windermere, are given in figure 4. Sampling datum O is taken at the base of the upper laminated clay, a level that may be correlated with the beginning of the Loch Lomond Stadial (= Pollen Zone III or Younger Dryas times). Direct comparison may therefore be made between the pollen spectrum (Pennington 1977) and the Coleoptera diagram. No effort has been made to indicate the abundance of species because of the smallness of the fossil assemblage. Enough evidence is, however, available to permit this spectrum to be compared profitably with other more completely sampled sequences and also to provide information on the climatic changes during the Windermere Interstadial.

Even at the base of the interstadial deposits there are none of the obligate arctic–alpine species that were so characteristic an element of the pre-interstadial faunas. In their place is a suite of species that would be quite at home in the Windermere area today and which includes a number of species that are either absent from the more northerly parts of Europe or else very rare there. Such species are indicated at the foot of figure 4. These relatively southern species are not present in the upper part of the interstadial sequence and in their place we have the first incoming of the more northern species heralding the truly arctic faunas of the ensuing Loch Lomond Stadial. The faunal change within the latter part of the interstadial seems to correspond with the layer of clay with rock fragments that occurred at about 15–20 cm below sampling datum 0. The change in the fauna and lithology suggest a sharp decline in the thermal environment at this time, but after it there is little evidence of any climatic recovery and conditions must have remained very much colder than during the early part of the interstadial.

The pattern of climatic events inferred from the interstadial Coleoptera from Windermere has now been recognized at a number of widely scattered localities in the British Isles (Coope 1975). The rapidity with which an entirely temperate assemblage of beetles replaced the arctic–alpine fauna at the start of the interstadial at both Glanllynnau and Glen Ballyre, where sedimentation throughout this time seems to have been complete, suggests that the initial climatic amelioration must have been sudden and intense. The precise dating of this event is, however, difficult because of the largely inorganic nature of the associated sediments. Even where the deposits are organic the plant debris is frequently the remains of aquatic plants, notably of *Chara*, with the consequent risk of 'hard water error'. In a Late-glacial context in North Jutland radiocarbon dates based on bulk samples of pond bottom detritus were greater by 1700 a than those obtained from twigs at the same stratigraphical position (Shotton 1972). Only two dates on early interstadial temperate faunas so far seem free of the imputation of 'hard water error'. At Hawks Tor section No. 3 (Brown 1977) where the Late-glacial sediments rest on bedrock a date of 13088 ± 300 B.P. (Q-979) was obtained and, though this was from a bulk sample of a water lain deposit, it is unlikely to be afflicted with 'hard water error' for two reasons. First, the site is in a hollow on the Bodmin Moor granite providing a thoroughly acid substrate, and second, there are no calcareous drifts as far south as this in the British Isles and thus no possibility of a base rich veneer over the granite. The second date 12940 ± 250 (Q-643) was obtained

OW WRAY BAY, WINDERMERE (COLEOPTERA) 1975



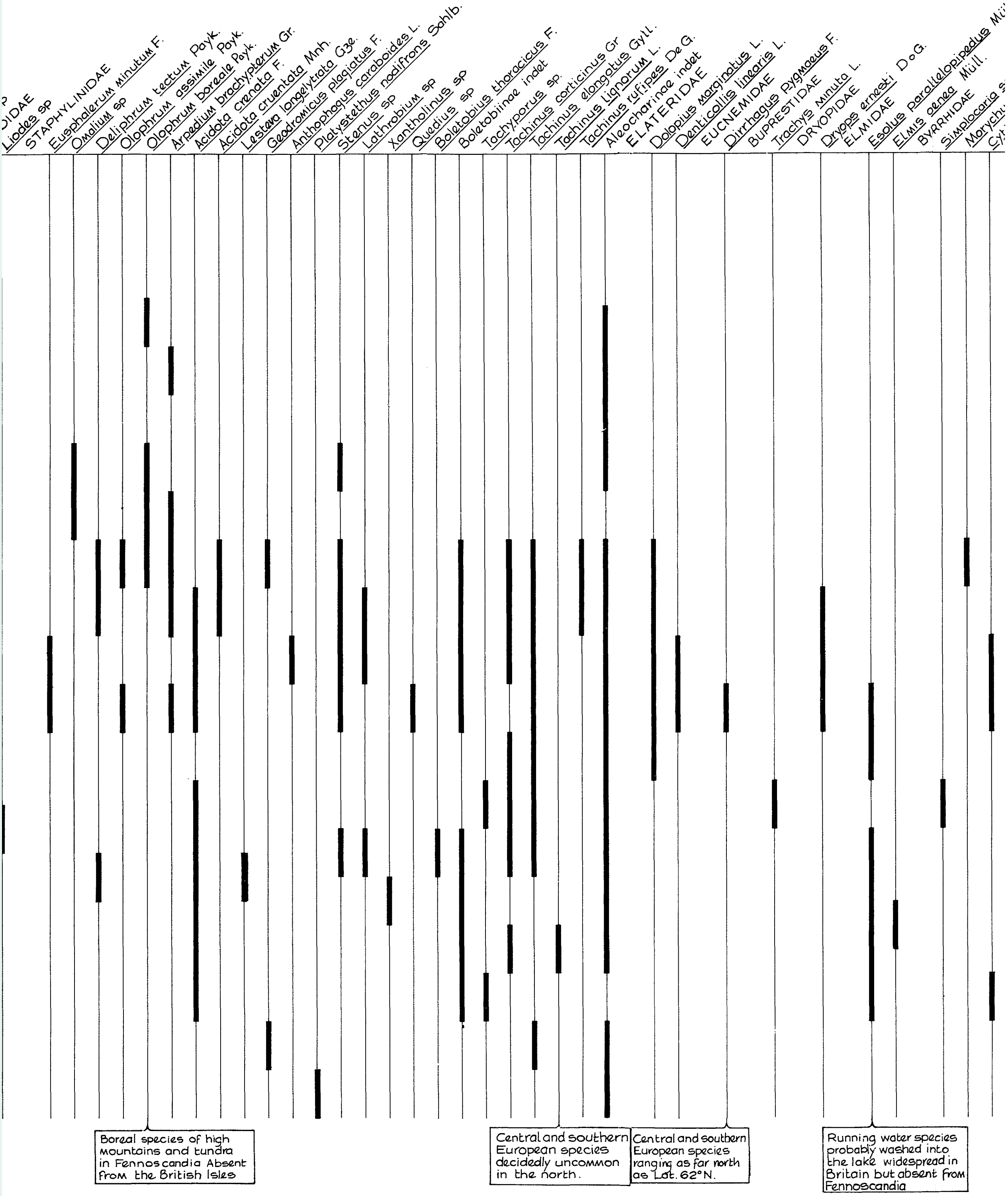
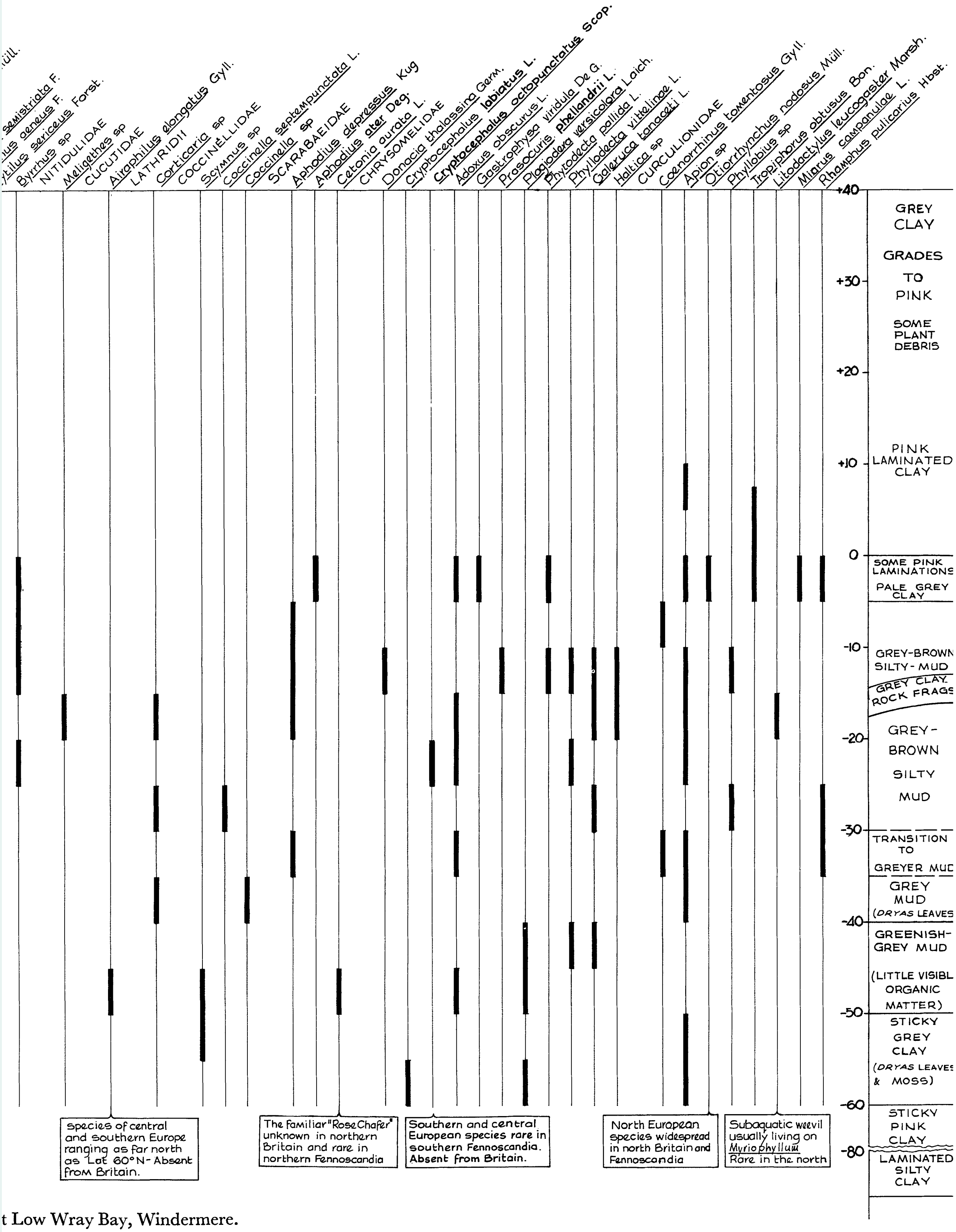


FIGURE 4. The occurrence of species of Coleoptera in the Late Devensian deposits at
Sampling datum 0 is the same as that used by Pennington



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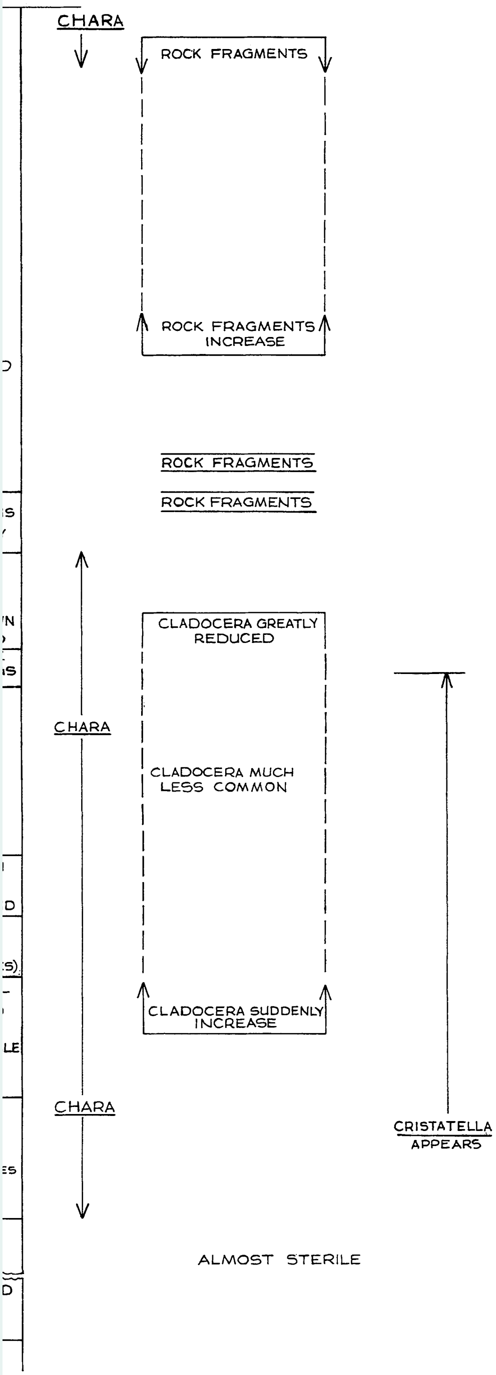
CHARA
ROCK FRAGMENTS
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CLADOCERA GREATLY REDUCED
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CLADOCERA MUCH LESS COMMON
CLADOCERA SUDDENLY INCREASE
CHARA
CRISTATELLA APPEARS
ALMOST STERILE

from wood out of a Late-glacial sequence at Roberthill, near Lockerbie, Dumfriesshire (Bishop & Coope 1977). In both these cases temperate conditions were evidently already established for sufficient time for the relatively thermophilous insect species to have spread as far west as Cornwall and as far north as southwest Scotland. It is likely therefore that the climatic amelioration at the start of the Windermere Interstadial took place somewhat earlier than 13000 B.P. but probably not much earlier than 13500 B.P. if the Stafford date is reliable.

The decline from the thermal maximum of the interstadial seems also to have been sudden and on the evidence of the assemblages of fossil Coleoptera, there would seem to have been a diminution of about 3 °C in the average July temperatures compared with those of the thermal maximum. At Hawks Tor, though no dates actually were measured at the change in fauna, the best fit by intercalation between known dates is about 12300 B.P. At Church Stretton this event can be dated at 12135 ± 200 B.P. (Birm-158). At Red Moss near Harwich, Lancashire (Ashworth 1972) the thermophilous Coleoptera had been replaced by 'colder' species by 12160 ± 140 B.P. (Birm-127). In the Glen Ballyre section this same faunal change can be dated at about 12150 B.P. (GRO. 1616) (Joachim 1974). A reinvestigation of the Coleoptera from St Bees, Cumbria, also shows a sudden change from a rich, temperate fauna to an assemblage of thoroughly northern affinities, slightly before 12200 B.P., after adjustments had been made for 'hard water error' (Williams & Johnson 1976). In the interstadial deposits of Windermere the loss of the thermophilous element from the fauna and the incoming of northern species took place sometime shortly before 12000 B.P. In southwest Scotland a cool temperate insect fauna had already replaced the more temperate assemblage by 12290 ± 250 (Q-816) at Redkirk Point (Bishop & Coope 1977). There thus seems to be abundant evidence from radiocarbon dates and from changes in the beetle fauna that there was a marked deterioration in the thermal environment about two centuries before the date 12000 B.P. selected for the upper limit of the Bølling chronozone in Norden (Mangerud *et al.* 1974). In spite of this minor discrepancy in timing, it seems likely that this climatic deterioration is the same as that ascribed to the Older Dryas period of continental authors.

If the episode of climatic cooling mentioned above is to be equated with the Older Dryas period, there is very little evidence from the Coleoptera to support an inference of a period of climatic warning after this, that would be equated with the Allerød Interstadial. In general the assemblages of Coleoptera that date from between 12200 and 11000 B.P. are monotonously similar and suggest a cool temperate climate throughout. There is evidence now accumulating to suggest that during this period the gradient in average July temperatures from the Midland Valley of Scotland to the south of England was about 4 °C. Three faunal sequences suggest that this climatic plateau may not have been entirely flat but may have had a minor episode of slightly warmer conditions. The Church Stretton fauna (Osborne 1972) shows a small-scale increase in the proportion of temperate species shortly after 12000 B.P., but one of the important indications of this change was the southern species *Berosus affinis* Brulle that has now been redetermined as *Berosus luridus* L. (Osborne, personal communication), a species that ranges today as far north as Lapland. Even before this adjustment to the faunal list Osborne had commented (1972, p. 351) 'Despite a rise in the thermophile graph ... it seems unlikely that a marked rise in summer temperatures occurred'. At Red Moss (Ashworth 1972) there is a diminution in the northern element in the fauna but no evidence of the return of temperate species at about the time normally attributed to the Allerød oscillation. Finally, in the Windermere sequence, there is evidence from the sedimentology and entomology that the period of sudden

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

climatic deterioration shortly before 12000 B.P. may have been rather colder than the period that immediately followed it. Against this evidence of a small-scale climatic oscillation, the Coleoptera from Glen Ballyre and St Bees show no significant changes in the climate between about 12000 and 11000 B.P. Preliminary work on Coleoptera of this period from Sproughton, Suffolk, also show no evidence of any significant oscillation during this period (M. Bryan, personal communication). Thus the Coleoptera provide scant evidence for a climatic oscillation equivalent in time to the Allerød and what evidence there is seems to be most marked in the northern half of the British Isles. In comparison to the total amplitude of the change in thermal environment during the Windermere Interstadial, the climatic oscillation during the equivalent time to the Allerød was very small indeed.

A brief comparison will be made here between the records of palynology and Coleoptera from the Windermere Interstadial. A taxonomically diverse insect fauna that indicates temperate conditions, with summer warmth at least equivalent to that of the present day, is characteristic of the earliest parts of this Interstadial. In these early stages this fauna is associated with herb-dominated pollen assemblage zones with Graminae, Cyperaceae and *Rumex* the chief groups present. The temperate fauna shows gradual increase in diversity throughout this period and there is no acceleration of this process to mark the incoming of *Juniperus* in the pollen diagrams. This relationship holds good for Hawks Tor, Church Stretton, Glanllynnau, Glen Ballyre, St Bees, Windermere and Roberthill, in fact for all localities where pollen and beetle data are available. In general the pollen assemblage zone dominated by *Betula*, that occurs during the second part of the Windermere Interstadial at many localities in England and southern Scotland, is accompanied by a beetle assemblage that lacks all the more southern species that were so characteristic a feature of the faunas from the early part of the Interstadial. Complimentarily a number of boreal species are present that were absent from faunas of the first half of the Interstadial. When interstadial conditions came to an end, the fall in the proportion of *Betula* pollen and the associated increase in curves for open country herbaceous plants is accompanied by a great increase in the numbers of northern beetle species as well as in their specific abundance. Radiocarbon dates for these floral and faunal changes marking the termination of the Windermere Interstadial tend to cluster around 11000 B.P.

(iii) *The Loch Lomond Stadial*

The assemblages of Coleoptera from this period are remarkably consistent and include a large number of boreal or boreomontane species. Even the most southerly site, known so far, Hawks Tor, has yielded a thoroughly northern fauna from this period including such species as *Olophrum boreale* Payk., *Acidota quadrata* Zett. and *Boreaphilus henningianus* Sahlb. This fauna was obtained from section No. 2 (Brown 1977) midway between two samples dated 10884 ± 210 B.P. (Q-1016) and 9654 ± 190 B.P. (Q-1017). Osborne (1971) reports a thoroughly arctic beetle assemblage from the Croydon area, that was associated with wood fragments that gave a radiocarbon date of 10130 ± 120 B.P. (Birm-101). A similar insect fauna has recently been obtained at Sproughton, Suffolk, associated with a radiocarbon date of 10880 ± 250 B.P. (Birm-779). These three faunas serve to illustrate the degree to which arctic species extended their ranges to the southernmost part of England during the period of the Loch Lomond Stadial. Numerous arctic assemblages are now known from localities in the English Midlands, the North of England, North Wales, the Isle of Man and Ireland but so far only one locality in Scotland has yielded an assemblage of Coleoptera that dates from this period. At Bigholm Burn, Dumfriesshire, a small fauna dominated by *Olophrum boreale* was extracted from a peaty lens in gravels overlying peats of Windermere Interstadial age. This is the most northerly insect assemblage that can be dated to the Loch Lomond Stadial and suggests that conditions approaching polar desert must have existed in Scotland at this time (Bishop & Coope 1977).

A curious feature of these faunas is the presence in the British Isles at this time of species that have since become apparently extinct in Europe. Thus *Pterostichus magus* Mnh. is a Siberian species that occurred as a fossil in the low terrace of the Thames at Farmoor near Oxford, in deposits that gave a radiocarbon date of 10600 ± 240 B.P. (Birm-590). *Helophorus jacutus* Popp. has been recovered from 'Pollen Zone III' deposits at Comberton near Ludlow. Its range today is exclusively east Siberian. Finally *Tachinus jacuticus* Popp. occurs as a fossil in the upper parts of the Late-glacial deposits of the Isle of Man. This is an eastern Asiatic and North American species that today lives no nearer to the British Isles than 7000 km. The occurrence of these species suggests that the climate of the times was continental but because this eastern element in the fauna is less, both in terms of numbers of species and their abundance, than in the faunas from the colder parts of the Upton Warren Interstadial, it is probable that the climatic continentality was less extreme during the Loch Lomond Stadial.

(iv) *Summary of climatic changes during the closing phases of the Devensian*

Figure 5 is an attempt to show the pattern of change in summer warmth for various latitudes in the British Isles during the closing phases of the Devensian. It is based on assemblages of Coleoptera from over 25 widely scattered localities that cover most of the British Isles with the

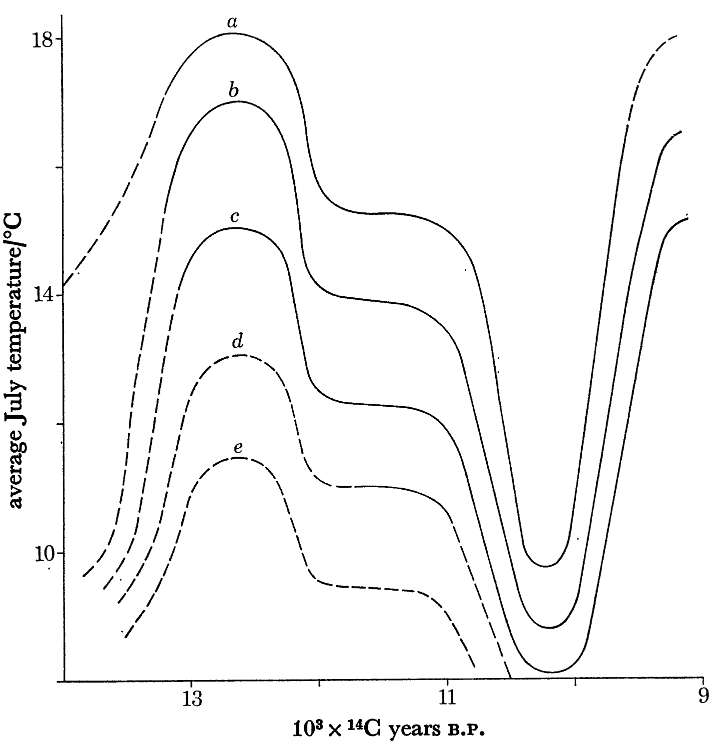

FIGURE 5. Variations in the average July temperatures, near sea level, during the closing phases of the Devensian (Last) cold stage (*a*) for southern England, (*b*) for central England and north Wales, (*c*) for northern England and southwest Scotland, (*d*) for central Scotland and (*e*) a hypothetical extrapolation for the north of Scotland. Dashed lines are used where these are conjectural.

exception of Scotland north of the Midland Valley. The estimates of the average July temperatures are based wherever possible on sites near to present-day sea level. For localities at higher altitudes a normal lapse rate of 6 °C per 1000 m has been assumed.

It is evident that during the period under consideration there is only one large-scale climatic oscillation. The initial amelioration seems to have been somewhat earlier in the south of England than in the Midlands and North. The thermal maximum seems to have been reached sometime shortly before 13000 B.P. and probably lasted for about 1000 radiocarbon years. The decline from the thermal maximum seems to have taken place in two steps. The first of these, a drop of almost 3 °C in the average July temperature, took place almost synchronously at all latitudes. The second step in the climatic deterioration must have taken place at about 11000 B.P. and may have involved a decrease of over 4 °C in the average July temperature. At all localities in the British Isles, where insect faunas of Loch Lomond Stadial age are known, they suggest a climatic régime over the whole area equivalent, at its thermal minimum, to that of the arctic tundra today. The recovery from glacial conditions was apparently very sudden and by 9500 B.P. the thermal environment of the British Isles was fully as warm as it is at the present time.

4. General discussion

(a) *Microclimate versus macroclimate*

The interpretation of ancient climates on the basis of assemblages of fossil Coleoptera has been criticized on the grounds that the beetles actually live in microenvironments whose parameters differ markedly from those measured at meteorological stations. Changes in beetle faunas might thus be merely a reflection of change in microclimate. This argument is most frequently encountered in those contexts where temperate assemblages of Coleoptera are found in situations hitherto believed to have had climates similar to those of the present-day tundra or the alpine zones of the mountains. Of course this criticism can be applied to climatic inference based on any biological data but the arguments for its rebuttal will here be based on information about the Coleoptera and may not be applicable to other sorts of fossils such as plants, molluscs or terrestrial vertebrates.

The discussion here will be restricted to two problem periods; the thermal maxima of the Upton Warren Interstadial complex and of the Windermere Interstadial. In both these cases entirely temperate and rich assemblages of Coleoptera are found in association with herbaceous vegetation and with an apparent absence of trees, or in the case of the Windermere deposits, a marked scarcity of trees. There are three main reasons why peculiarities of microclimate are an inadequate explanation for the existence of an exclusively temperate insect fauna in what appears to be a fully glacial environment. Firstly, the faunal changes, particularly at the beginning of the interstadials, are characterized by the sudden substitution of temperate for arctic–alpine species and on either side of this boundary the local environments were apparently identical; namely open treeless country with a scant vegetation cover (Coope & Brophy 1972). In such exposed habitats, peculiar microclimates would indeed have been expected but they would have been common to the living conditions both below and above the level of the change from an arctic to a temperate fauna. Secondly, a number of diverse and fairly sizeable ecological communities are present at these times and all of them include numerous thermophilous species (species intolerant of colder summers than those of the present day). Peculiar microclimates would have had to be almost universal, in all ecological contexts, everywhere hostile to arctic–

alpine species and permissive to thermophilous species. Thirdly, and lastly, if the presence of the numerous thermophilous Coleoptera is to be accounted for by invoking the peculiar qualities of the arctic style microclimate, which can indeed involve high temperatures (Corbet 1972), these same species would be present in the arctic today and conversely, modern arctic species would be expected in these interstadial faunas. In fact neither of these conditions is fulfilled.

Special pleading that the Coleoptera are merely indicative of microclimates, is thus unconvincing. It is certainly true that microclimates will frequently determine the local distribution of a species but the occurrence of acceptable microclimates is ultimately dependent on suitable macroclimates. For this reason gross geographical ranges have been used in this climatic interpretation. We are left with the inescapable, if rather commonplace, conclusion that a temperate European style fossil fauna implies a temperate European style climate.

(*b*) *Patterns of climatic change during the Devensian*

A number of features that are common to all the climatic changes outlined above, emerge from this study. Thus the amplitude of the oscillations in summer warmth is similar in the two interstadials that are adequately known; the Upton Warren and Windermere Interstadials. At its beginning each interstadial is characterized by a sudden increase in warmth to an early thermal maximum, after which the deterioration seems to have been more gradual. The duration of the period of thermal maximum seems to have been relatively short, of the order of a thousand years or so, but in spite of this a rich and thoroughly temperate insect fauna was able to colonize at least the southern half of the British Isles. At the thermal maxima of both interstadials the average degree of summer warmth was as high or even slightly higher than it is in central and southern Britain today.

The incoming of eastern Asiatic species, often specifically in great abundance, seems to be a feature of the colder phases, particularly the long period of more or less arctic conditions that followed the thermal maximum of the Upton Warren Interstadial. During this period and also during the time of the Loch Lomond Stadial, the insect faunas were rich in arctic–alpine species suggesting that the average July temperature was at or below 10 °C. The diversity of these faunas and the abundance of some species, however, is strongly suggestive of temperatures not much below this level. In this context the eastern Asiatic species are of particular interest. They are well adapted to surviving winters of extreme harshness, and though many can tolerate high summer temperatures they are usually species that have ranges that include the Siberian arctic or the high cold steppes further south. Thus, though they can tolerate high summer temperatures they are also able to accept much lower levels of summer warmth. Furthermore, their arctic–alpine companions in these fossil faunas preclude the possibility of persistent high summer temperatures at this time.

An attempt is made in figure 6 to illustrate the likely seasonal variation in mean monthly temperatures for the three main climatic types found in the interstadials of the Devensian. The figures are estimates for central England. Little need be added to what has already been said about the interludes of temperate climate (figure 6*c*). So far only two short intervals are known from the Devensian that have climatic régimes of this type; the thermal maxima of the Upton Warren and the Windermere interstadials. If the deposits at Chelford represent the thermal maximum of that interstadial, then this phase was somewhat cooler than the other two interstadials. The climate was also rather more continental with greater difference in seasonal temperatures (figure 6*b*). The more continental style climates (figure 6*a*) probably characterized much of the Middle Devensian, the phase immediately before the Windermere Interstadial and also the period of the Loch Lomond Stadial. During these periods the strong seasonal variation in temperature may have been associated with fairly large diurnal temperature range distinguishing our glacial climate from that of arctic Siberia at the present day.

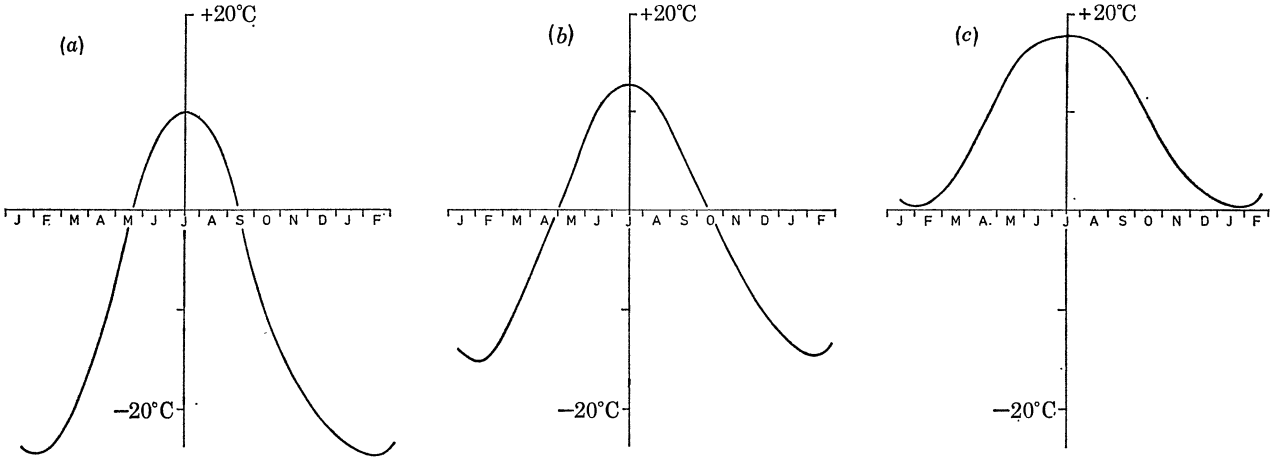

FIGURE 6. Annual fluctuations in the average monthly temperature for the main interstadial climatic regimes in the British Isles. (*a*) During the latter part of the Upton Warren Interstadial complex, (*b*) during the Chelford Interstadial, (*c*) during the thermal maxima of the Upton Warren and Windermere interstadials. Note: The climate in much of England during the Loch Lomond Stadial probably resembled (*a*).

Support for this interpretation of a continental style climate in the British Isles during the colder episodes of the Devensian comes from an entirely independent quarter. Deposits that date from the long cold tail of the Upton Warren Interstadial, that is between about 40000 and 25000 B.P., are often riven by thermal contraction cracks now represented either by ice-wedge casts or by sand wedges. Similar structures can be found penetrating deposits that can be dated with certainty to the Loch Lomond Stadial, 11000–10000 B.P., almost at sea level in the Isle of Man. These cracks are one of the few recognized features that indicate the existence of permafrost at the time of their formation (French 1976, p. 136). Furthermore, these cracks are frequently developed in gravels (including those from the Isle of Man) suggesting that average annual temperatures must have been below −6 to −8 °C (Williams 1975). If these cracks were formed more or less at the same time as the insect-bearing deposits, it is possible to associate these average annual temperatures with the figure of about 10 °C for the average July temperature inferred from the Coleoptera. Though precise contemporaneity cannot be established with certainty there can be little doubt that some of the cracks cannot have been far removed in time from the insect faunas with their abundant continental species. If some of these wedges are indeed sand wedges, and some of them certainly resemble these rather than ice-wedge casts, there is evidence that the cold period that characterized much of the mid-Devensian was arid as well.

No thermal contraction cracks have yet been found that suggest contemporaneity with the thermal maxima of the interstadials. What is more some deposits that yield temperate insect faunas also contain large molluscs, such as *Anodonta* indicating that at such times, precipitation was adequate to maintain shallow ponds not only throughout the whole year but for several years in succession. At least during the thermal maxima of the Upton Warren and Windermere interstadials the climate appears to have been moderately oceanic and not much different from that of northwest Europe of the present time.

The rapid switches in the terrestrial climate of the British Isles from cold-continental conditions on the one hand to temperate-oceanic conditions on the other may be a reflection of the changes in the north Atlantic circulation described by Ruddiman & McIntyre (1973). Certainly with respect to the Windermere Interstadial both the timing and intensity of the climatic change on land resemble the changes in the temperature of the ocean waters of the west coast of Britain. Similarly the return of polar water to the western coasts of Britain corresponds with the timing of the ice advances of the Loch Lomond Stadial (W. F. Ruddiman, personal communication). If this relation between the climate of the British Isles and the circulatory régime of the adjacent ocean is a general one, we might expect a northward excursion of the polar front in the eastern Atlantic around 43000 B.P. and corresponding to the thermal maximum of the Upton Warren Interstadial. Such is the shortness of this episode that it may be close to the resolving power of ocean core analysis.

In spite of the intensity of the thermal maximum of the Upton Warren Interstadial it is seemingly short and hemmed in on either side by climates of near arctic severity. It is unlikely, therefore, to be reflected by a return to present-day figures either in the sea-level changes or isotopic fluctuations in ocean water that are both indications of gross ice volume. A short sharp interstadial is unlikely to inflict the same damage on the world's ice sheets as a cooler but much longer interstadial interval.

There can be little doubt therefore that the rapid and intense climatic changes in western Europe, and particularly in the British Isles where they are likely to be at their most extreme, are dependent on the interaction of the oceanic and terrestrial geometry upon the circulatory patterns of the hydrosphere and atmosphere in this particular area. It is not to be expected that, in their intensity, timing and duration, those climatic changes have necessarily any hemisphere wide or global equivalents.

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Discussion

By G. R. Coope and Winifred Pennington.

The Windermere Interstadial of the Late Devensian

We propose to use the Windermere section as a standard reference section because:

(i) A large lake has several favourable characteristics, the most important being the *continuity* of the sedimentary sequence,

(ii) Lake sediments reflect the terrestrial as well as the lacustrine environment,

Table 1. Correlation table for the lithostratigraphy, biostratigraphy and chronostratigraphy of the Late Devensian Deposits at Low Wray Bay, Windermere

lithology	fossils: plants	fossils: animals: Coleoptera	fossils: animals: others	^{14}C dates	interpretation: environment	interpretation: climate	duration of interstadial climate: W.P.	duration of interstadial climate: G.R.C.
rock fragments increase; upper laminated clay	*Artemisia* p.a.z.; pollen very sparse	sparse fauna with characteristic arctic–alpine species		(11000)	seasonal melt from mountain glaciers in Lake District corries	very cold		
becoming less organic; organic detritus silt (maximum carbon)	Cyperaceae; *Betula–Juniperus* p.a.z.; tree birch macroscopics	woodland species present; fauna less rich, without 'southern' species	Cladocera decline to 0	SRR-669 11344 ±90	increased snowfall, declining temperatures; increased soil erosion / re-establishment of *Betula–Juniperus* woods	cool temperate becoming colder towards the top		
paler silt with rock fragments	*Betula–Rumex* p.a.z.	*Helophorus glacialis*		SRR-670 12213 ±150	increased soil erosion woodland reduced	sudden cooling		
organic detritus silt (maximum carbon)	*Betula* p.a.z.; *Juniperus* p.a.z.	sparse fauna at base, becoming richer towards the top, species present that are absent from arctic Europe	Cladocera reduced; Trichoptera larvae; Chironomidae larvae; *Cristatella* statoblasts	SRR-672 12112 ±125; SRR-673 12517 ±150; SRR-675 12441 ±82; SRR-676 12913 ±120; (13000)	maximum environmental diversity of Windermere Interstadial (woodlands established)	temperate throughout		
somewhat organic silt; carbon content increasing	*Rumex*–Gramineae p.a.z. (tree birches present)		Cladocera suddenly increase	SRR-677 13185 ±170; SRR-679 13938† ±210; SRR-680 13863† ±270	phase of pioneering flora and fauna, vegetation rich in herbs, including species which do not grow in the arctic today, although tree birches are present, no development of woodland	plant evidence inconclusive on temperature, but some factor unfavourable to trees / temperate throughout on insect evidence		
slightly organic silt	*Salix herbacea*–Cyperaceae–*Lycopodium selago* p.a.z.; moss stems	very sparse fauna, no alpine species		SRR-681 14557 ±280; SRR-682 14623 ±360	on plants, compare with Middle Alpine zone of NW Europe / insect fauna lacks any alpine species and suggests early pioneer fauna	plant evidence suggests alpine conditions / insects inconclusive but no evidence to support alpine conditions		
clay	no plant fossils							
lower laminated clay					seasonal melt from mountain glaciers	very cold		

† ^{14}C dates with evidence of 'hard-water error'.

(iii) The position of Windermere is central in the British Isles, and the lake received glacial drainage, both in the closing phases of the main Devensian glaciation and during the period between 11000 and 10000 ^{14}C a B.P. which is correlated with the Loch Lomond Readvance of Sissons (1974),

(iv) The interstadial sequence, most fully developed in the marginal parts of the lake (Pennington 1943), is best known from Low Wray Bay, where the sediments contain both pollen and the macroscopic remains of plants and animals which have been washed into the lake by small streams.

Detailed analyses of this section, the results of which are presented in our papers, show that the lower boundary of interstadial sediments may be drawn at different horizons, depending on the criteria that are adopted, whether they be lithostratigraphic, palaeoentomological, or palaeobotanical. Table 1 indicates the position of the lower boundary of the Windermere Interstadial on each criterion. If the notion of interstadial is based on a climatic interpretation, two alternative views (those of W.P. and G. R. C.) are given on the right-hand side of the table.

Description of stratotype

1. *Lithostratigraphy*

We interpret the upper boundary of the Lower Laminated Clay (Pennington 1943) as representative of the termination of the main Devensian glaciation of northwest England, and the commencement of interstadial sedimentation. 'Interstadial' is here used in its lithostratigraphic sense, and the climatic change represented is from a glacial to a non-glacial environment.

Above the Lower Laminated Clay the lowest sediments are almost entirely minerogenic with extremely sparse fragments of plant and animal tissue. The change to biogenic sediment is very gradual and there is no clearly discernible boundary between clay and organic silt. At its most organic the silt contains *ca.* 5 % carbon. At about 15 cm below the top of the organic silt is a persistent horizon of grey silt containing rock fragments. The base of the Upper Laminated Clay (Pennington 1943) defines the commencement of Loch Lomond Stadial sedimentation in this area.

2. *Biostratigraphy*

The biostratigraphy is summarized in table 1. The environmental interpretation based on both floral and faunal biostratigraphy yields a consistent ecological picture throughout most of the time represented by non-glacial sediments.

On the palaeobotanical definition of 'interstadial' – namely an environment capable of supporting a vegetation of woody plants (trees and shrubs), only part of these non-glacial sediments can be described as interstadial – see table 1. The usefulness of the palaeobotanical definition is that comparison between British sites indicates the presence of a generally distinctive vegetation of woody plants between the ^{14}C dates which delimit the woodland biozone in Windermere, so the particular environment required by a vegetation of woody plants appears to have been restricted to the period between *ca.* 13000 and 11000 ^{14}C a B.P.

Below this woodland biozone the plant remains define two botanical subzones within a herbaceous biozone. Pollen data equate the lower of these with present alpine vegetation in northern Europe. In the upper zone the assemblage of herbs identified includes species which do not grow in the Arctic today, and both pollen and macroscopic evidence shows that tree birches were present but did not expand into woodland. This is interpreted as indicative of conditions not generally favourable to trees.

Only within the herbaceous biozone is there any discrepancy between the interpretations based on botanical and entomological data. Throughout the two divisions of the herbaceous biozone the fauna shows a continuous development, but even at the base no obligate alpine species are present. A number of insect species occur which, though widespread in Europe today, are absent from arctic regions and the alpine zones of the mountains, suggesting that, at least during the *Rumex*–Gramineae pollen zone, temperate climatic conditions prevailed. Comparable temperate insect assemblages, often much richer than that from Windermere, are now known from a number of localities in Britain always in the same palynological context – namely well before the commencement of the woodland biozone. Whatever factor was unsuitable for trees during the herbaceous biozone, it did not inhibit the development of an ecologically complex temperate insect fauna.

No contemporary biota match the fossil assemblage of plants and insects from these lower zones. Both pollen and insect data suggest primarily pioneer communities. This may be an important reason why it is difficult to match these phases of colonization with existing biota which are in equilibrium with contemporary climates.

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G. F. Mitchell, F.R.S. and R. G. West, F.R.S. It is important to provide a defined lower boundary for the proposed Windermere Interstadial. The difficulty is that such a boundary may be defined either lithostratigraphically or biostratigraphically, and if biostratigraphically on the basis of pollen or beetles. There is the usual difficulty of definition which confronts the Pleistocene stratigrapher when there is a plethora of information. One solution is to draw an arbitrary line at a radiocarbon age, say 14000 B.P., a time when pollen content increases and *Betula* and *Juniperus* increase their representation (see Tutin, this volume, p. 337). Alternatively, a pollen-based interstadial could be defined as beginning at 13000 B.P. at the base of the *Juniperus* pollen frequency rise, or a beetle-based interstadial could be defined as beginning earlier than 14000 B.P. (see Coope, (this volume, p. 337).

The decision to place the definition of the base of the interstadial must be an arbitrary imposition on the observed lithostratigraphical–biostratigraphical sequence. We suggest 14000 B.P. is a position which has some significance for the evolution of the climate in the late-Devensian, with observed changes in pollen and beetles in the Windermere sequence, and that this age should mark the base of the Windermere Interstadial. We note that this level corresponds closely with the boundary between the *Salix herbacea*-Cyperaceae and *Rumex*-Gramineae-Rubiaceae-*Artemisia* pollen assemblage biozones at Windermere (Tutin, this volume, p. 255).

In Ireland the corresponding Woodgrange Interstadial opens at about 14000 B.P. at the base of the Irish *Rumex*-Gramineae pollen assemblage biozone (see Mitchell 1976, pp. 68–73).

A. V. Morgan (*Department of Earth Sciences, University of Waterloo, Waterloo, Ontario, Canada*). Dr Coope has shown a number of remarkable shifts in the distribution of beetle species from their known fossil localities in the British Isles to their present ranges in northern, central or southern Europe, and even beyond, into Asia. I would like to point out that changes of similar magnitude have taken place in North America. Dr Anne Morgan, working on beetle faunas from Toronto, has shown that many of the species found in Early Wisconsin deposits at Scarborough occur today along the northern treeline of Canada. Several of these species now live in the extreme northwest of the continent, e.g. *Diacheila polita* (one of the species mentioned in Dr Coope's lecture) is present in Alaska and occurs at its closest point (as far as is known) in the Mackenzie Delta some 4000 km from the fossil locality. *Helophorus sibiricus* has a similar distribution except that its present occurrence seems centred on the west coast of Alaska over 4800 km from Scarborough. Unfortunately one is faced with the dilemma of poor collecting records in areas nearer Ontario (northern Ungava/Labrador for example), absence of readily available collections (there are no easily accessible Victorian collections in Canada) and a dearth of knowledge about the present ecology of the much larger North American fauna. Distributions of other species of Coleoptera, *Asaphidian yukonense* and *Carphorborus andersoni*, indicate that these northwestern species occupied sites in southern Ontario and Wisconsin until about 10000 a B.P.

The distribution of relict permafrost features in North America does not appear to have the same widespread areal extent as those described in western and central Europe. Permafrost features believed to have been formed contemporaneously with the maximum Wisconsin ice advance (or with the retreating ice) have been described from Washington, Montana, North Dakota, Wisconsin, Illinois, Indiana and possibly the New England States in the United States, and from southwestern Ontario, Quebec, Nova Scotia and Newfoundland in Canada. The permafrost indicators are usually ice-wedge casts, although associated polygonal ground has been found in North Dakota, Indiana and southwestern Ontario. The patchy nature of the relict structures suggests that permafrost was present in restricted areas, possibly due to localized climatic conditions or to favourable lithologic and hydrologic regimes. The disappearance of permafrost in southern Ontario (43° N) is roughly coincident with that in the central English Midlands (53° N) about 13500 a B.P. Permafrost conditions prevailed later in Gaspé, Quebec, and in southwestern Newfoundland, apparently disappearing about 10000–10500 a B.P.

J. D. PEACOCK (*Institute of Geological Sciences, Murchison House, West Mains Road, Edinburgh*). At the Institute of Geological Sciences we have been examining the late-glacial raised marine deposits in the Clyde area, and have now obtained radiocarbon-dated, overlapping sections for the interval from a little before 12000 B.P. to 10000 B.P. It is clear from the lithological and faunal data that water temperatures were generally much lower than at present in the area, and that conditions were arctic during the Younger Dryas period (*ca.* 11000–10000 B.P.). However, there is evidence for a short-lived amelioration about 11000 B.P. when low-boreal Mollusca and foraminifera immigrated into the district, though winter temperatures probably remained low. Similar temperature variations can be inferred from the records of a poorly dated borehole from the Sea of the Hebrides (Binns, Harland & Hughes 1974), and from undated late-glacial sections described 100 a ago near Greenock. Since these temperature changes appear to have been general, it is unlikely that they were influenced by any relict cover of glacier ice in the Highlands. The form of our temperature curve thus differs from that of Dr Coope, and one wonders if there is any evidence from deposits on land for a more temperate interval at 11000 B.P.

Reference

Binns, P. E., Harland, R. & Hughes, M. J. 1974 Glacial and post-glacial sedimentation in the Sea of the Hebrides. *Nature, Lond.* **248**, 751–754.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

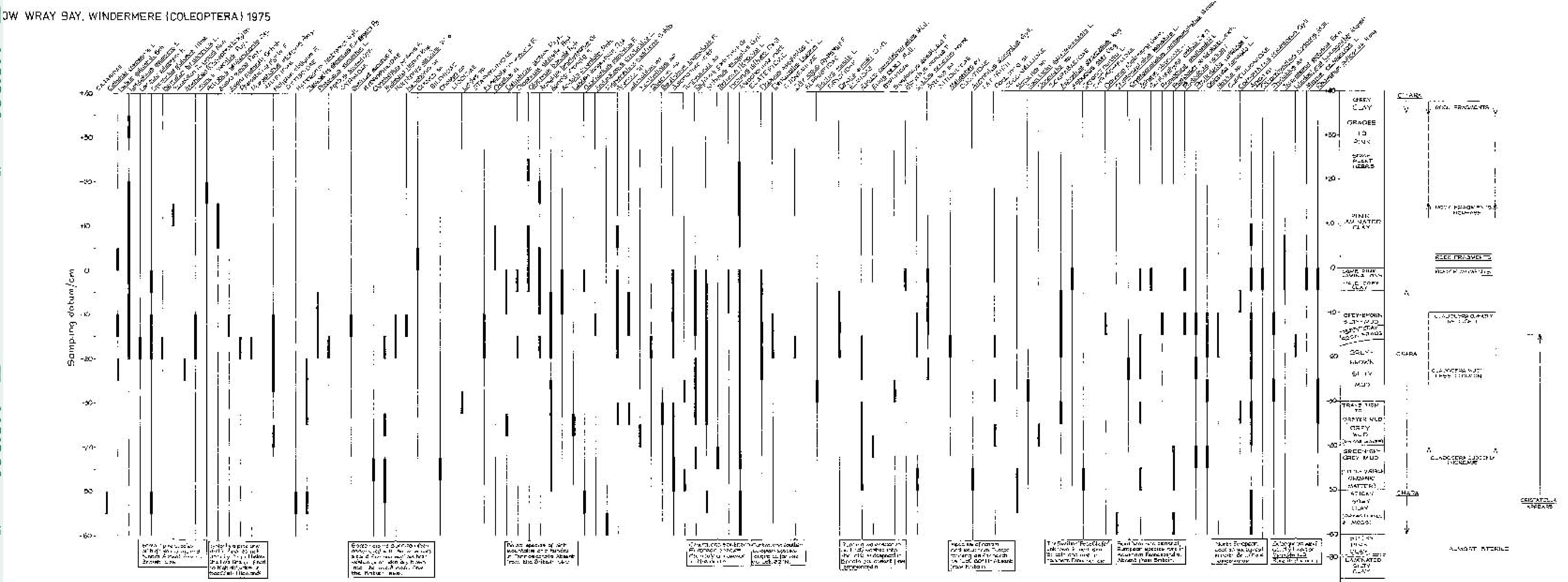

FIGURE 1. The occurrence of species of Coleoptera in the Late Devensian deposits at Low Wray Bay, Windermere. Sampling datum 0 is the same as that used by Pennington (1976).