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The Record of the Cold Stages [and Discussion]

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The record of the cold stages

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Evidence for climatic conditions on the continents during the cold stages lies in a number of areas: glacial history, vegetational and faunal history, periglacial history, weathering horizons. Whereas glacial history provides evidence of periods of glacierization within cold stages, palaeontology provides evidence of a variety of climates within cold stages, as does the periglacial evidence, at times when glacierization was not extensive. The definition and history of cold stages is considered. The evidence for climatic change is reviewed, based on the occurrence of periglacial phenomena and fossil floras and faunas, and the problems of interpreting cold-stage climates are considered.

1. Introduction

With the advent and acceptance of the glacial theory in the last century the idea of a succession of glaciations formed the basis for the classification of Quaternary successions, implying the existence of interglacial events of climatic amelioration. Thus, the sequence of glacial deposits, the most obvious consequence of climatic change, was the measure of Quaternary stratigraphy, until it was later replaced by systems of alternating glacial and interglacial stages as knowledge of biostratigraphy accrued.

With the continued accession of terrestrial and marine evidence concerning Quaternary climates, this simple division is no longer sufficient for the classification and understanding of events. In northwest Europe, at least, a major division into temperate and cold stages is likely to be a useful basis for subdivision of the Quaternary sequence, with the temperate stages resulting from climatic amelioration to a state we see at the present day, to use one possible definition of the term interglacial. A summary of such a division in the later Pleistocene of northwest Europe is given in table 1.

It is also now clear that the cold stages are themselves complex, probably more so than the temperate stages, containing one or more periods of ice expansion and showing evidence for degrees of climatic change within them.

On the continents, phenomena related to physical conditions, such as permafrost, can be clearly used to interpret cold-stage climates and, as Dylik (1975) has pointed out, can be used more widely for climatic interpretation than the more locally developed glaciations. The biological evidence of climate is more difficult. Whereas we see in the development of the Flandrian (postglacial) a sequence of vegetation units or faunas which are recognizable to a large extent in living plant or animal communities, in the cold stages we are dealing with peculiar biota and environments largely outside our experience, even if they are now represented to some extent in cold regions. Interpretation of cold-stage biota and environments is a challenge, not least because with biota the present is by no means certainly the key to the

Table 1. Stage names in northwest Europe in the later Pleistocene

(Abbreviations: t, temperate stage; c, cold stage.)

Ireland[a]	Britain	continental northwest Europe	stage
Littletonian	Flandrian	(Holocene)	t
Midlandian	Devensian	Weichselian	last cold stage
Glenavian	Ipswichian	Eemian	t
Munsterian	Wolstonian	Saalian	c
Gortian	Hoxnian	Holsteinian	t
	Anglian	Elsterian	c

[a] From Mitchell (1986).

past. Present distributions, which might be used to interpret past environments, represent the organism's response to present climate, historical factors and competition. In cold stages, cold conditions reached to lower latitudes and the climates that occurred then are not necessarily similar to those of present cold regions. The response of identified organisms to such climates is not known.

The purpose of this discussion is to examine this complexity and the problems of interpretation in more detail in the area of northwest Europe.

2. Definition and occurrence

Cold stages are naturally not easy to define with any precision, because climatic variation is a continuous process. They are not synonymous with glacial periods, but include them. In northwest Europe, and in botanical terms, they are periods of time when climatic deterioration leads to the long-term prevalence of largely herbaceous vegetation with no thermophilous trees. As discussed below, there may be interruptions by short forested periods. Expansion of ice sheets and periods of permafrost occur from time to time, and there is evidence of lowered sea levels. Formally, it is desirable to define the lower limit of a stage; Zagwijn (1957) has suggested a definition based on the appearance of a subarctic vegetation type, when tree pollen is largely replaced by herbaceous pollen. The opposite change, with the subsequent development of a long period of temperate forest, is taken to indicate the beginning of a temperate stage and the end of a cold stage, by analogy with the changes seen at the beginning of the Flandrian (Holocene) temperate stage (Zagwijn 1957).

In the marine oxygen-isotope record cold stages are represented by periods of increased proportions of ^{18}O in foraminiferal tests compared with those of the present time and in the last temperate stage. The end of such periods may be marked by sharp terminations (Broecker & van Donk 1970), indicating rapid deglaciation. Such terminations appear to herald the beginning of a temperate stage, and there is evidence to link them to the beginning of the continental temperate stages. The beginnings of cold stages are more problematical, both in the oceans and on the continent, because they seem to be accompanied by more gradual and variable conditions, as will be discussed later. Shackleton (1986) discusses the problems of the subdivision of the isotope record.

Between temperate stage climates and the full expression of cold stage climates as seen in the so-called full-glacial or pleniglacial, there lies a variety of conditions, and it is periods with this variety that make for the difficulties of definition, particularly so when it seems possible that

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such periods may have occupied a larger fraction of Quaternary time than periods with more extreme climates.

The difficulties of definition make an assertion about the number of cold stages impossible. But in the Pacific cores V28-238 (Shackleton & Opdyke 1973) and V28-239 (Shackleton & Opdyke 1976) some ten cold stages were indicated in the past 800 ka and certainly there were earlier ones, as indicated by The Netherlands succession (Zagwijn 1985), with the Praetiglian cold stage at about 2.3 Ma BP. A similar age is suggested by Backman (1979) for evidence in the north Atlantic of the initial ice rafting and so extension of Northern Hemisphere ice sheets, and by the isotope record in the north Atlantic (Shackleton *et al.* 1984; Shackleton 1986), although there are signs of a slightly earlier refrigeration in the isotope record (Shackleton *et al.* 1984). There is little stratigraphical evidence for associating widespread ice advances in northwest Europe with these earliest cold stages, although indications are present from erratics in gravel trains arising in the Alps, Scandinavia and Britain. Elsterian and Anglian glacial deposits of the Middle Pleistocene thus appear to be the earliest extensive evidence of widespread glaciation, although there may be evidence for further earlier and less extensive development of ice sheets. The sequence of glacial deposits, starting with those of the Elsterian and Anglian, formed the original basis for the subdivision of the Quaternary in northwest Europe. Evidently in the Middle and Late Pleistocene extensive ice sheets were characteristic of cold stages in a way not so far discovered in the earlier Pleistocene.

In view of the difficulties of exact definition of cold stages (see the discussion by Shackleton (1986)), their length is consequently difficult to estimate. To judge by the course of the isotope curve, especially during at least the past 300 ka, cold stages in the Middle and Upper Pleistocene are considerably longer than the major recognized temperate stages. In the earlier Pleistocene this does not obviously seem to be so, except for the earliest very pronounced cold stage of the Pretiglian in The Netherlands. This implies rather different relations between cold and temperate stages in the Lower Pleistocene, also suggested by the evidence for glaciations discussed above.

Most information on length naturally comes from the most recent cold and temperate stages. Figure 1 outlines subdivisions and estimated ages for the past 130 ka in northwest Europe.

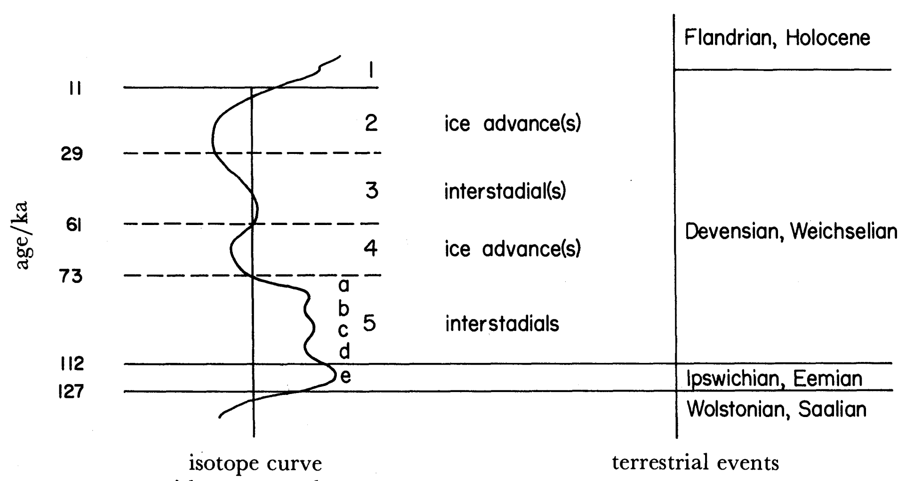

FIGURE 1. Generalized oxygen-isotope curve through the past 130 ka according to Shackleton (1969), using his and Emiliani's (1961) subdivisions, related to estimated ages (years B.P.) suggested by Woillard & Mook (1982), to major terrestrial events in northwest Europe, and to the latest Pleistocene stages.

Taking the length of the last temperate stage (Eemian, Ipswichian) as, say, 15 ka and the length so far of the present one as 10 ka, the intervening cold stage (Vistulian, Weichselian, Devensian) lasted some 102 ka. The complexity and instability of this period is indicated in figure 1, and is seen in both the marine and continental evidence. There must have been considerable climatic changes during the period, on a timescale not perhaps very different from those of a single temperate stage. The first part of the cold stage, as defined here, is some 40 ka in length. It is characterized by alternating so-called stadial and interstadial conditions, in The Netherlands (Staalduinen *et al.* 1979) by three periods of subarctic park or open landscape enclosing and following two periods with boreal forest. Further southeast, at Grande Pile (Woillard & Mook 1982), similar changes are expressed by short periods with herbaceous pollen increasing in frequency and by forest periods with temperate trees. The contrast is a result of degrees of climatic change and proximity of plant refuges, and exposes the difficulties of characterizing periods as interglacials or interstadials, and also of drawing the lower boundary of a cold stage. In this instance, should it be at 73 ka BP or 112 ka BP? I prefer the latter, and have used the latter, because the end of the preceding temperate stage can be clearly defined in palaeobotanical terms.

The remaining part of the cold stage, 63 ka in our estimate, is characterized by severer conditions, with clear evidence for permafrost, ice advances, polar desert in The Netherlands, and 'tundra' vegetation, with evidence for climatic amelioration from time to time. The details will be discussed in a later section.

The instability seen in the early part of the last cold stage also appears to have been present in the early part of the preceding cold stage, the Saalian, as expressed in The Netherlands sequence by the Hoogeveen and Bantega interstadials followed by the major Saalian ice advances (Zagwijn 1985). Even so there is no reason why the type of sequence seen in the last cold stage should be repeated in earlier cold stages; climatic changes and their causes are very complex. Indeed, it appears that certain pre-Weichselian cold stages have more than one extensive ice advance separated by an interval (e.g. the Saalian in northwest Germany (Grube *et al.* 1986)). Each major ice advance itself may result may result in a complex multiple till sequence, as in the Weichselian–Devensian cold stage.

Perhaps the only generalization that can currently be made about these matters in the Middle and Upper Pleistocene is that terminations and climatic amelioration lead to major and widely expressed temperate stages, which are followed by unstable periods expressed in different ways in different areas, in the end involving permafrost and ice expansion.

3. Evidence and expression

Evidence for climates of cold stages comes from several sources, as follows. Bradley (1985) considers these matters in much more detail.

(*a*) *Isotope curve*

Shackleton (1986) has discussed the complex relations between the isotope curve, global ice volume and sea levels. Ruddiman & MacIntyre (1981) and Mix & Ruddiman (1984) have investigated the possible relations between them, suggesting feedback mechanisms and lag effects. For the present purpose, we can note that the isotope curve is a form of record of global ice volumes at particular times in the cold stages. The details of more local expansion of ice sheets must come from the study of continental sequences. The contrast between the terminations and the instability of earlier parts of cold stages presumably reflects rapid widespread deglaciation on the one hand, and on the other hand the variable buildup of ice in the various Pleistocene ice sheets and the climatic changes associated with these ice-volume changes.

(*b*) *Geological evidence*

Geological evidence for cold-stage environments comes from the very variable lithology of the sediments. Historically, glacigenic sediments formed the basis for the designation of cold stages, but periglacial sediments are now seen to supply details of environmental changes not available from glacigenic deposits. The problem now is to place glacigenic sediments in their correct position in relation to the widespread deposition of fluviatile and aeolian sediments in periglacial sequences. Such sequences are divisible through periods of soil formation (see, for example, Kukla 1975) and organic deposition which occur within them. Each sediment type makes its own contribution to the interpretation of cold-stage environments: glacigenic sediments to the record of glaciation, fluviatile sands and gravels to the history of cold-stage rivers, cover sand and dunes to evidence for severe and often pleniglacial environments, loess

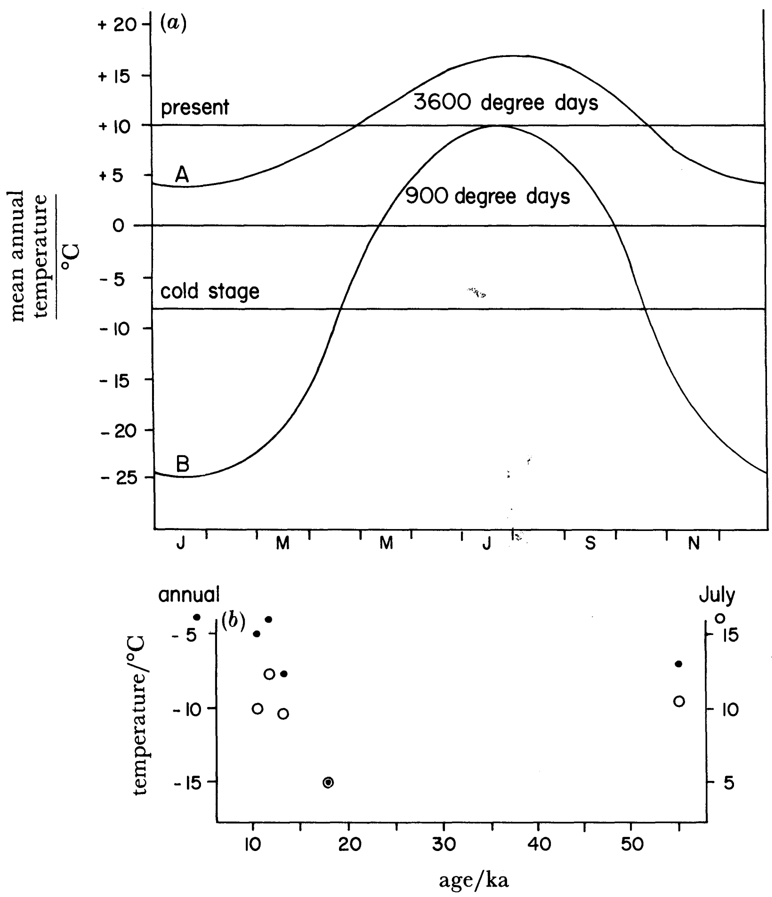

FIGURE 2 (*a*). Williams (1975) re-construction of monthly temperatures in central England at present (A) and in the coldest part of the last cold stage (B). (*b*). Watson's (1977) estimated mean air temperatures in the last cold stage.

to evidence for more continental environments, and solifluction sediments to periods of degradation of landscapes.

A very important component is the structural evidence for cold climates seen in periglacial phenomena, including involutions and features indicating permafrost, such as thermal contraction cracks. The observation that these latter occur at particular horizons within, for example, the last cold stage, underlines the climatic variability of cold stages, proving the presence of mean annual temperatures of at least *ca.* −5 °C at particular times. Thermal contraction cracks have been described from cold stages back to the Beestonian of East Anglia (West 1980*b*) and intra- or pre-Eburonian (?) in Normandy (Clet-Pellerin 1983).

Karte & Liedtke (1981) have discussed further the climatic interpretation of periglacial phenomena in some detail. They thus enlarge the point made by Dylik (1975), contrasting climatic evidence from the more local ice-sheet development in cool and oceanic areas with that from periglacial phenomena, expressed more widely and significant for drier and more continental climates. Williams (1975) has used periglacial phenomena of the last cold stage in

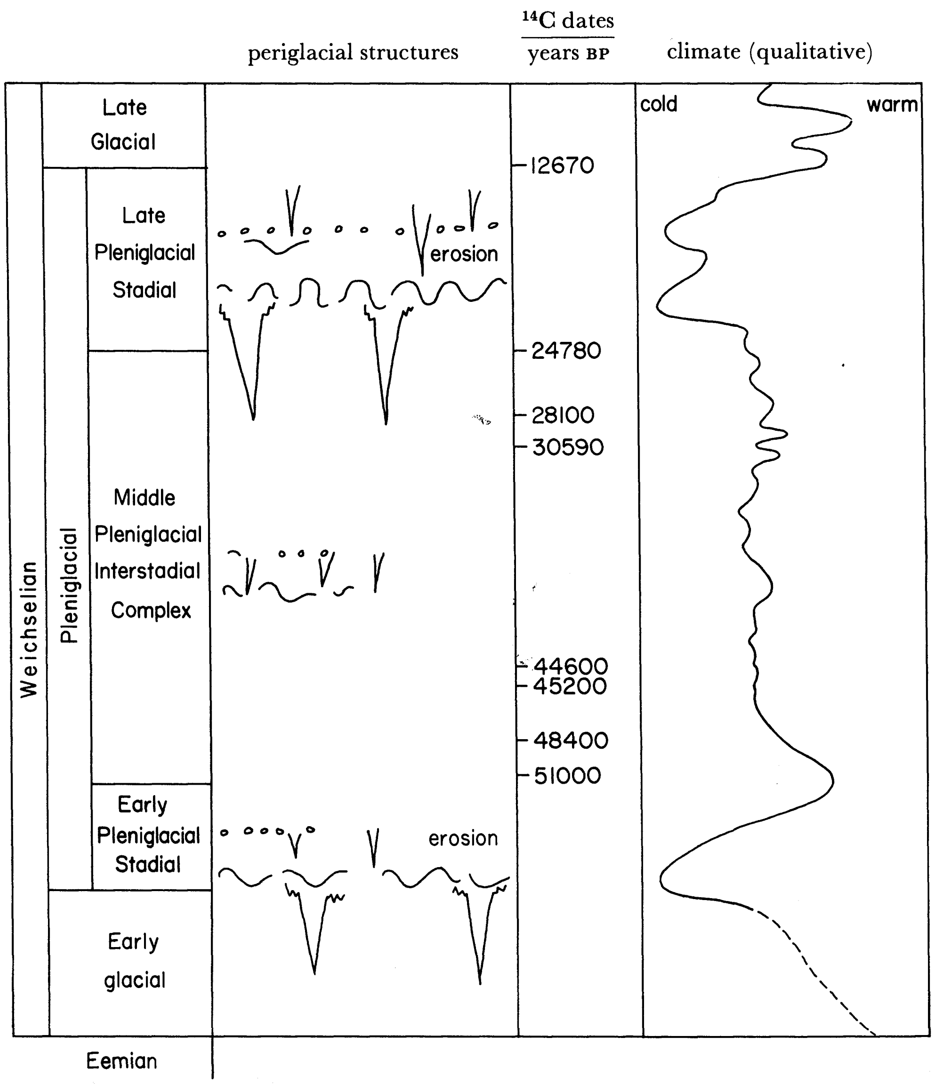

FIGURE 3. Outline of Vandenberghe's (1985) stratigraphy of the Weichselian in the southern Netherlands, showing periglacial structures and inferred climate. Sediments, mainly cover sands and loams, are omitted.

Britain to estimate mean annual temperature, monthly temperatures, rainfall and snowfall, and wind and pressure systems. Watson (1977) has considered the climatic significance of permafrost, continuous and discontinuous, in Britain, suggesting falls of mean annual air temperature of up to 25 °C and falls of July mean temperature of 5–10 °C. Figure 2 shows some of the suggested temperatures of Williams and of Watson. The opportunity offered by sediment and structure studies for reconstructing climates and environments of the last cold stage are excellent, as shown by studies of the Netherlands and Belgian periglacial sequences of the Weichselian by Vandenberghe (1985) (figure 3).

A further and different type of evidence for climatic change in cold stages derives from speleothem studies. Periods of low or no speleothem growth are thought to indicate cold and/or conditions of climate with warmer and wetter conditions resulting in greater growth (Ivanovich 1985). Cave sequences appear to yield information on climatic fluctuations in cold stages as well as between cold and temperates stages.

Glacioeustatic sea-level changes have already been mentioned above in relation to the isotope curve. From the stratigraphical point of view, they are important in our area as a factor (low sea level) in control of river development in cold stages and as a factor (high sea level) evident in the major widespread temperate stages.

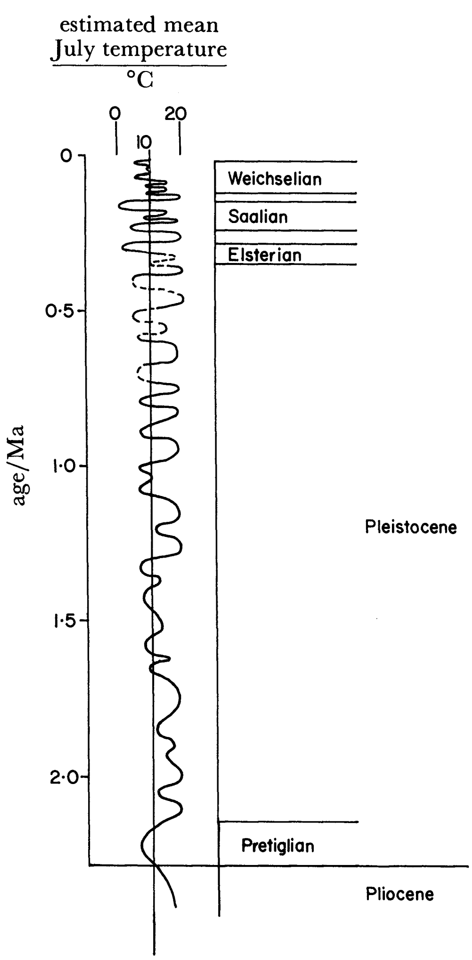

FIGURE 4. Zagwijn's (1985) climatic curve (estimated mean July temperature) for The Netherlands. Only the latest cold stages (which contain very extensive ice advances) and the earliest are named.

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(c) *Biological evidence*

Fossil evidence of cold-stage biota is abundant; pollen, plant macroscopic remains, vertebrates, molluscs, ostracods and Coleoptera have all provided bases for climatic interpretation, on the basis of present-day distribution of either species or of communities. Here I consider floras, Coleoptera and vertebrates.

The most complete temperature curve for northwest Europe is that for The Netherlands Quaternary described by Zagwijn (1985), based on climatic deteriorations indicated mainly by a paucity of trees (treeline taken to be related to 10 °C isotherm in the warmest month) and by the presence of evidence for polar desert (temperature lower than 5 °C). The curve (figure 4) shows the marked cold stage at 2.3 Ma BP, the later and lesser fluctuations of the earlier Pleistocene and the more marked cold stages of the later Pleistocene. A similarly based curve for the last cold stage is discussed later. The use of particular plant species for climatic deductions, based on their present day ecology, is exemplified by Kolstrup (1979, 1980) in her estimations of last cold stage climates in The Netherlands.

The detailed work of Coope (1977) on Coleoptera led to his reconstructions of an average July temperature curve for the last cold stage in southern and central British Isles and of average monthly temperatures for interstadial climatic regimes in the last cold stage in the British Isles (figure 5). Such reconstructions are based on the combined distributional evidence of species from dated assemblages, including arctic–alpine species and continental east Asian species. Massive changes in range and diversity are shown by some species in these assemblages.

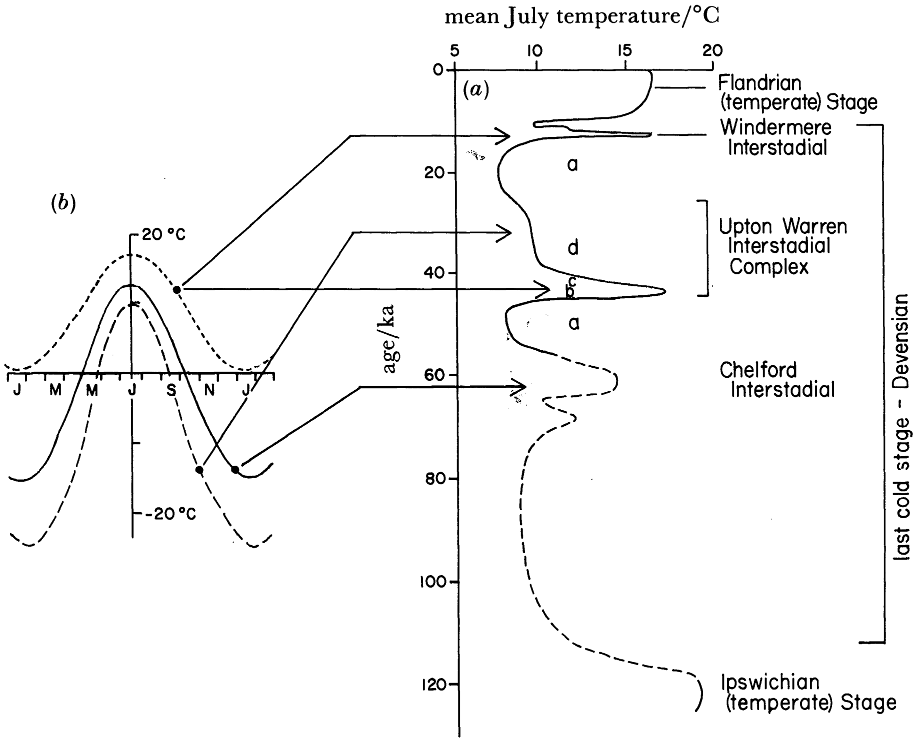

FIGURE 5. Coope's (1977) reconstruction of last cold stage climates from Coleopteran evidence. (*a*) Average July temperature in lowland areas of southern and central British Isles: a, polar climate; b, moderately oceanic climate; c, transitional; d, cold continental climate. (*b*) Average monthly temperatures for four interstadial climates in the British Isles.

On the basis of the plant assemblages, polar desert, tundra, 'steppe–tundra', and shrub tundra have all been described, again with mixtures of arctic–alpine and continental species (Bell 1969; Godwin 1975), with the occasional addition of halophytic species, a problematical group perhaps indicative of continental climate. Vertebrate faunas, although their taphonomy is more insecure, also show the presence of northern and continental species (Stuart 1977, 1982).

The question remains, however, how all this data can be used to determine palaeoclimates. The situation is far more complex than with ocean biota. The first problem is the relation today of the organism concerned to climate, with the additional effects of historical and competition factors now and then; the second is the unknown ecological tolerance of the organism at the present time, and the third is whether the organism at the time of the fossil occurrence was distributed according to an equilibrium with the climate (Prentice 1986; Webb 1986). Discrepancies in the evidence from different parts or the biota suggest that equilibrium was not always obtained by the plants, as discussed later with reference to the last cold stage.

4. The last cold stage

There is abounding evidence for last cold-stage environments in northwest Europe. In addition the chronology, relative in the earlier part and absolute in the later part, is also reasonably well established. The result is that we can survey the last cold stage as an example of the diversity of evidence for Pleistocene cold-stage climates. This is not to say that the course of each cold stage followed the same pattern, in terms of, say, glacial or permafrost events. Even though we have this evidence for an outline of environmental history and climatic change in the last cold stage, much is still conjectural or uncertain, as will be seen in the following discussion.

(a) *Geological evidence*

The till complex associated with the last cold stage in northwest Germany, Denmark, southern Sweden and southern Finland now appears to have resulted from ice advance and retreat (figure 6) in the later part of the last cold stage, although there is evidence for earlier advances further north. Radiocarbon evidence suggests the till complex was deposited in a period between 21 and 13 ka BP (Lagerlund 1983; Sjørring 1983; Ehlers 1983; Lundqvist 1986; Donner *et al.* 1986). The same appears to be true in eastern Britain (Penny *et al.* 1969), although, in Ulster, McCabe (in Bowen *et al.*, 1986) has suggested an early Midlandian ice advance. There is yet no certain evidence of extensive earlier ice advances into these areas in the last cold stage. Thus the period of greatest ice extension was short compared with the total length of the cold stage, although its effects on landscape through ice movement and glacigenic sedimentation were huge.

Outside the ice limit, the most complete record of the last cold stage has been found in The Netherlands, Belgium and northwest Germany, expressed as a sedimentary sequence of lacustrine, fluvial and aeolian deposits, interrupted by periglacial structures. A threefold division of early Weichselian, middle Weichselian or Pleniglacial, and late Weichselian has been established (figure 7). It should be noted that whereas the late Weichselian begins at *ca.* 13 ka BP, the late Devensian lower boundary has been placed at 26 ka BP (Mitchell *et al.* 1973).

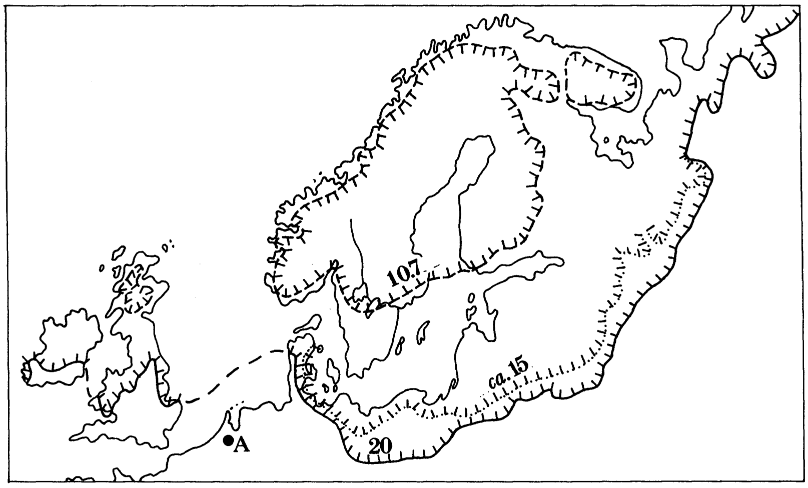

FIGURE 6. Major ice margins in northwest Europe in the last cold stage (Weichselian, Devensian) (after Starkel 1977). Point A marks the general area of the detailed Netherlands/Belgian Weichselian sequence (figures 3 and 7); figures refer to time (ka BP).

(*i*) *Early Weichselian*

A number of periods with climatic amelioration have been described from The Netherlands (Zagwijn 1961), Belgium (Woillard 1978), northwest Germany (Menke & Tynni 1984; Behre & Lade 1986) and Denmark (Andersen 1961) (figure 7). They are separated from the last temperate stage (Eemian) by a cold interlude. The Brørup and Odderade interstadials, with their correlatives at Grande Pile, St Germain I and II, are the firmest established of these, with the earlier Rodebaek and Amersfoort interstadials and later Keller interstadial of less certain status. Further south, at Les Echets, near Lyon, de Beaulieu & Reille (1984)have described a long pollen diagram which substantiates the evidence for these interstadials, as does the long sequence at Samerberg, Bavaria, described by Grüger (1979).

(ii) *Middle Weichselian or Pleniglacial*

Vandenberghe (1985) has described in detail the sediments and structures of this period. He proposes early and late Pleniglacial stades, characterized by permafrost features with thermal contraction cracks, and an intervening middle Pleniglacial interstadial complex with milder conditions. The age of the upper stade is *ca.* 18–25 ka BP., and the less certain age of the lower stade is *ca.* 60–70 ka BP. The upper stade thus bears a relation to the time of ice expansion. Climatic variation within the middle Pleniglacial interstadial has been much discussed. On the one hand there is the view that amelioration is associated with deposition of organic sediments within the sequence of cover-sands and fluvial sediments (see, for example, van der Hammen *et al.* 1967; Zagwijn & Paepe 1968; Zagwijn 1974), resulting in the formulation of the Moershoofd, Hengelo and Denekamp interstadials. On the other hand, Vandenberghe (1985) has pointed out that peat formation is not necessarily related to amelioration, but is controlled by geomorphology and hydrology. He has considered in detail, as has Maarleveld (1976), the climatic implications of periglacial structures and sediments in The Netherlands (see figure 3).

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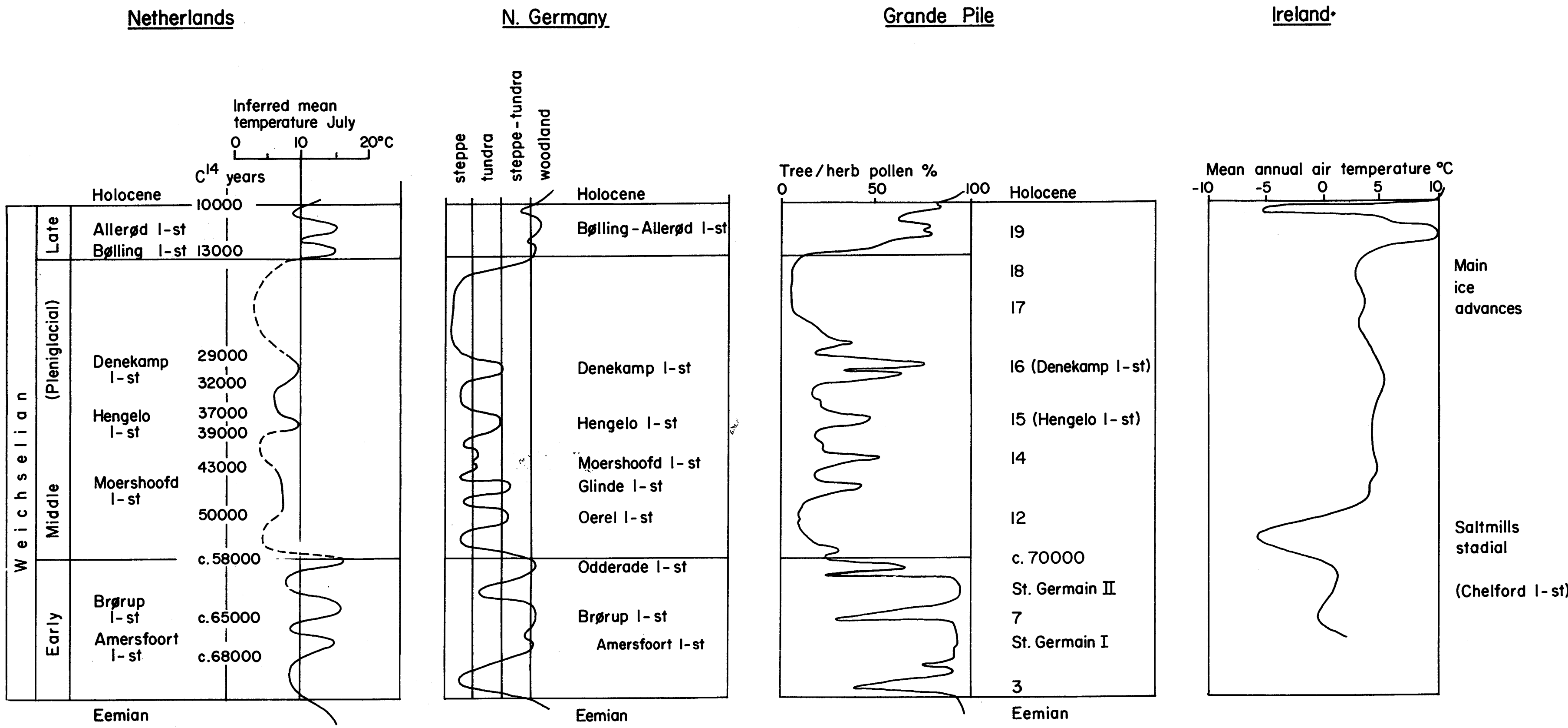

FIGURE 7. Climate curves from the last cold stage in various areas: The Netherlands, according to Staalduinen *et al.* (1979); north German lowland, according to Behre & Lade (1986); Grande Pile, according to Woillard & Mook (1982) (the numbers refer to Woillard's pollen zones); Ireland, according to Mitchell (1977).

(iii) *Late Weichselian*

The changes associated with this period are well known, and have a much more certain absolute chronology than the earlier periods. The climatic amelioration of the Bølling interstadial and the following readvance or standstill of the Scandinavian and British ice-caps is well documented in terms of ice limits, periglacial sequences and biota changes. Climatic curves are shown in figure 7. In addition there is information on changes in wind direction in this period, resulting from dune studies (Maarleveld 1960).

The geological evidence in our area so far discussed is summarized in figure 7, together with a curve for Ireland complied by Mitchell (1977). Elsewhere in Europe evidence for climatic change will not be necessarily conformable to the scheme in figure 7. For example, further east, in northwest Poland, Kozarski (1986) has described thermal contraction cracks believed to date from the time between the Brørup and Odderade interstadials; this observation suggests that permafrost was present to the east in the early part of the last cold stage.

(*b*) *Biological evidence*

The most continuous evidence for climatic change in the last cold stage is from vegetational history, particularly pollen diagrams. Figure 7 shows a curve for inferred mean July temperatures in The Netherlands drawn up by Staalduinen *et al.* (1979), and based mainly on vegetational history, on the principles described by Zagwijn (1985). In The Netherlands the pollen sequence is discontinuous but, as already mentioned, at other sites in northwest and southern Germany and in France there are continuous pollen diagrams from deep lake sites which give an excellene record over the last cold stage. They bear out the sequence described from The Netherlands and illustrate vegetation gradients south and east from The Netherlands. In particular, they show how forest with thermophilous trees extended in the early Weichselian interstadials in areas nearer to central Europe. Further away, the interstadials are represented by coniferous forest. The variation emphasizes the problem of disentangling the factors of climate, competition and migration in determining vegetational history (see West 1980*a*, p. 615).

The Middle Weichselian interstadial complex, with its scarcity of evidence for well-developed permafrost, has a vegetational record more difficult to analyse. The evidence for the Moershoofd, Hengelo and Denekamp interstadials relies, in northwest Europe, on the presence of organic sediments and on changes in *Betula* pollen percentages and also *Artemisia*. The ameliorations concern the change from polar desert to tundra (Moershoofd) or from tundra to shrub–tundra (Hengelo, Denekamp). Vandenberghe (1985) describes the Riel interstadial with subarctic vegetation at the beginning of the interstadial complex, suggesting a correlation with pollen zone 14 of the Grande Pile pollen diagram at 49 ka BP (Woillard & Mook 1982). Later than about 30 ka BP is the long period of severe climate leading to the upper permafrost episode.

The Late Weichselian begins at *ca.* 13 ka BP with a rise in *Artemisia* pollen percentages (van der Hammen 1951), a rise seen elsewhere in Europe at about the same time or earlier (e.g. Les Echets (Beaulieu & Reille 1984)) and which is taken to indicate a warming and drying of the climate. To the interpretation of July temperatures by Zagwijn (1985) we can add the conclusions of Kolstrup (1979, 1980) regarding mean January and July temperatures in the middle and late Weichselian, again based on vegetation history; these are shown in figure 8.

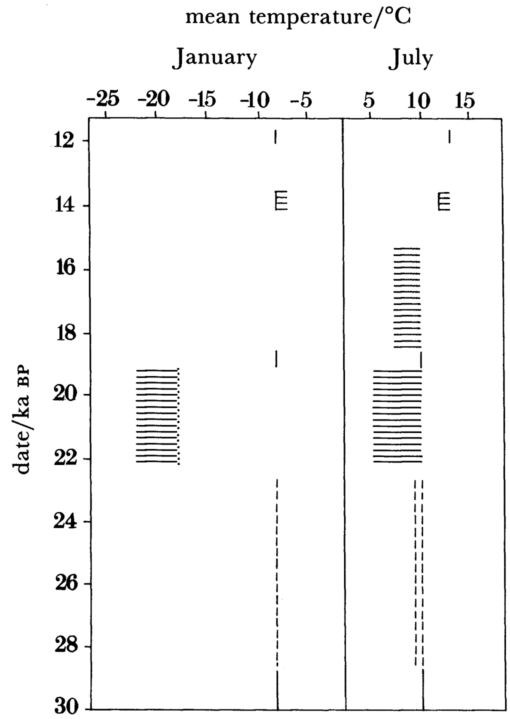

FIGURE 8. Kolstrup's (1980) reconstruction of January and July temperatures in the middle and late Weichselian in The Netherlands, based on vegetational history and periglacial phenomena. Solid line, temperature approximately as indicated; solid line with hatching, temperature possibly higher than indicated by line; horizontal lines, temperature estimated to fall between the limits; dotted line with hatching, temperature possibly lower than dotted line; single or double broken line, temperature approximately as shown, but age uncertain.

Turning now to further evidence of last cold-stage climates we must consider the extremely valuable evidence obtained by fossil Coleoptera by Coope (1977). He has made a detailed study of last cold stage faunas and has outlined curves for average July temperatures in lowland areas of the southern and central British Isles and for average monthly temperatures during the Chelford Interstadial, the thermal maxima of the Upton Warren and Windermere Interstadials, and the latter part of the Upton Warren interstadial complex. These are shown in figure 5, and portray striking changes in July temperatures and the coldness of winters. More recently Coope and his colleagues have extended the detailed interpretation of seasonal changes in the past 22 ka (Atkinson *et al.* 1987). The evidence for seasonal changes is particularly valuable. The warming at 13–14 ka BP compares with evidence for the same effect from pollen studies mentioned above. Similarly the evidence for warming in the Chelford Interstadial (Brørup Interstadial?) of the early Devensian compares well with the palaeobotanical evidence (Simpson & West 1958).

In the intervening middle Devensian, however, there is a strong contrast in the Upton Warren Interstadial between herbaceous pollen spectra of 'full-glacial' type (see, for example, Kerney *et al.* 1982), normally thought to indicate colder conditions, and beetle faunas indicating temperate conditions possibly warmer than those of the present day (Coope & Angus 1975). The origin of the contrast is fully discussed by Coope (1977). It may lie in rapid climatic change and the response times of different parts of the biota. The contrast poses fundamental questions about the interpretation of palaeoclimates from fossil biota. A second contrast is between the climate curve obtained from palaeobotanical evidence in The Netherlands, considered above, and that of Coope (1977). He identifies on convincing evidence a single temperate interstadial at *ca.* 43 ka BP, rather than the sequence of Middle Weichselian interstadial of The Netherlands. Again, the origin of the apparent discrepancy may lie in the variable behaviour of the plant and beetle responses to local environmental changes (related, for example, to hydrology (Vandenberghe 1985)) and to regional climatic changes.

The vertebrate faunas of the last cold stage in the British Isles and on the continent have been discussed by Stuart (1977, 1982). He records animals of the present day tundra, boreal forest and steppe, with southern and extinct species, associated with the herbaceous plant communities of the Early and Middle Devensian. An interesting point is the abundance of *Bison* bones in at certain times (e.g. Upton Warren Interstadial (Rackham 1978)), indicating productive vegetation supportive of a rich fauna. Detailed climatic interpretations from the vertebrate fauna seem difficult, partly because of taphonomic problems, partly because of difficulties of interpreting climatic controls of the living species.

5. Conclusions

The first clearly defined cold stage, the Praetiglian of The Netherlands, occurred at about 2.3 Ma BP, although the isotope record shows a slightly earlier similar event of the much shorter duration (Shackleton 1986). The Praetiglian cold stage brought to an end the long period in northwest Europe of Tertiary forests with their rich floristic diversity.

The cold stages show a great variety of geological events within glacial and periglacial régimes, accompanied by faunal and vegetational changes, all controlled by climatic change. The position of northwest Europe on the fringe of the continent is likely to result in a sensitivity to complex climatic changes, involving degrees of continentality–oceanicity (e.g. seasonal changes, snowfall) and mean annual temperatures and precipitation. The distance of refuges for temperate-stage species also complicates the biological evidence for climatic change.

Taking the last cold stage as an example, climatic change in terms of temperatures has been investigated through the geological and biological evidence. Variable precipitation and snowfall are less amenable to investigation, except generally through evidence for continentality and for ice-sheet growth. The identification of climatic change through the postulation of interstadials is problematical, because definitions vary, and the evidence from different parts of the biota is at first sight conflicting, indicating a complexity in the processes of climatic control and migration. Evidence from periglacial phenomena, especially permafrost, is more secure, with indications of two important times of permafrost development. The main ice advance appears to have taken place over a few thousand years in the later parts of the last cold stage. Nevertheless, the glacigenic sediments left behind show a complex development of the Scandinavian, British and Irish ice sheets, with sharp changes of direction of flow, a succession of ice margins and multiple tills.

The complexity seen in the last cold stage is likely to have occurred in the earlier cold stages, but not necessarily with the same organization in time and space. The extent of ice-sheet expansion in earlier cold stages in the Middle Pleistocene is approximately known, but much less is known of the timing within cold stages, or of periglacial sequences, both basic to the reconstruction of climate change within cold stages and necessary to understand the causes of climatic change.

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References

Andersen, S. T. 1961 Vegetation and its environment in Denmark in the Early Weichselian Glacial (Last Glacial). *Danm. geol. Unders.* ser. 2, no. 75.

Atkinson, T. C., Briffa, K. R. & Coope, G. R. 1987 Seasonal temperatures in Britain during the past 22000 years, reconstructed using beetle remains. *Nature, Lond.* **325**, 587–592.

Backman, J. 1979 Pliocene biostratigraphy of DSDP sites 111 and 116 from the North Atlantic ocean and the age of Northern Hemisphere glaciations. *Stockh. Contr. Geol.* **32**, 115–137.

de Beaulieu, J.-L. & Reille, M. 1984 A long Upper Pleistocene pollen record from Les Echets, near Lyon, France. *Boreas* **13**, 112–132.

Behre, K.-E. & Lade, U. 1986 Eine Folge von Eem und 4 Weichsel-Interstadialen in Oerel/Niedersachsen und ihr Vegetationsablauf. *Eiszeitalter Gegenw.* **36**, 11–36.

Bell, F. G. 1969 The occurrence of southern, steppe and halophyte elements in Weichselian (last glacial) floras from southern Britain. *New Phytol.* **68**, 913–922.

Bowen, D. Q., Rose, J., McCabe, A. M. & Sutherland, D. G. 1986 Correlation of Quaternary glaciations in England, Ireland, Scotland and Wales. *Quat. Sci. Rev.* **5**, 299–340.

Bradley, R. S. 1985 *Quaternary paleoclimatology*. Boston: Allen & Unwin.

Broecker, W. S. & van Donk, J. 1970 Insolation changes, ice volumes, and the ^{18}O record in deep see cores. *Rev. Geophys. Space Phys.* **8**, 169–198.

Clet-Pellerin, M. 1983 Le Plio-Pleistocene en Normandie: apports de la palynologie. Thesis, C.N.R.S., Caen.

Coope, G. R. 1977 Fossil Coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Phil. Trans. R. Soc. Lond.* B **280**, 313–340.

Coope, G. R. & Angus, R. B. 1975 An ecological study of a temperate interlude in the middle of the last glaciation, based on fossil Coleoptera from Isleworth, Middlesex. *J. Anim. Ecol.* **44**, 365–391.

Donner, J., Korpela, K. & Tynni, R. 1986 Veiksel-Jääkauden alajaotus Suomessa. *Terra* **98**, 240–247.

Dylik, J. 1975 The glacial complex in the notion of the Late Cenozoic cold ages. *Biul. peryglac.* **24**, 219–231.

Ehlers, J. 1983 The glacial history of north-west Germany. In *Glacial deposits in north-west Europe* (ed. J. Ehlers), pp. 229–247. Rotterdam: Balkema.

Emiliani, C. 1961 Cenozoic climatic changes as indicated by the stratigraphy and chronology of deep-sea cores of Globigerina-ooze facies. *Ann. N. Y. Acad. Sci.* **95**, 521–536.

Godwin, H. 1975 *History of the British flora*. 2nd edn. Cambridge University Press.

Grube, F., Christensen, S. & Vollmer, T. 1986 Glaciations in north west Germany. *Quat. Sci. Rev.* **5**, 347–358.

Grüger, E. 1979 Spätriss, Riss/Würm und Frühwürm am Samerberg in Oberbayern – ein vegetationsgeschichter Beitrag zur Gliederung des Jungpleistozäns. *Geol. Bavarica* **80**, 5–64.

van der Hammen, T. 1951 Late Glacial Flora and periglacial phenomena in the Netherlands. *Leidse geol. Meded.* **17**, 71–183.

van der Hammen, T., Maarleveld, G. C., Vogel, J. C. & Zagwijn, W. H. 1967 Stratigraphy, climatic succession and radiocarbon dating of the last glacial in the Netherlands. *Geologie Mijnb.* **46**, 79–95.

Ivanovich, M. 1985 Application of Uranium series dating to palaeoclimatic studies. *Mod. Geol.* **9**, 249–260.

Karte, J. & Liedtke, H. 1981 The theoretical and practical definition of the term 'periglacial' in its geographical and geological meaning. *Biul. peryglac.* **28**, 123–135.

Kerney, M. P., Gibbard, P. L., Hall, A. R. & Robinson, J. E. 1982 Middle Devensian river deposits beneath the 'Upper Floodplain' terrace of the River Thames at Isleworth, West London. *Proc. Geol. Ass.* **93**, 385–393.

Kolstrup, E. 1979 Herbs as July temperature indicators for parts of the Pleniglacial and Late-glacial in the Netherlands. *Geol. Mijnb.* **58**, 377–380.

Kolstrup, E. 1980 Climate and stratigraphy in northwestern Europe between 30000 B.P. and 13000 BP., with special reference to the Netherlands. *Meded. Rijks geol. Dienst* **32** (15), 181–253.

Kozarski, S. 1986 Early Vistulian permafrost occurrence in north-west Poland. *Biul. peryglac.* **31**, 163–170.

Kukla, G. J. 1975 Loess stratigraphy of central Europe. In *After the Australopithecines* (ed. K. W. Butzer & G. L. Isaac), pp. 99–188. The Hague: Mouton.

Lagerlund, E. 1983 The Pleistocene stratigraphy of Skane, southern Sweden. In *Glacial deposits in north-west Europe* (ed. J. Ehlers), pp. 155–159. Rotterdam: Balkema.

Lundqvist, J. 1986 Stratigraphy of the central area of the Scandinavian glaciation. *Quat. Sci. Rev.* **5**, 251–268.

Maarleveld, G. C. 1960 Wind directions and cover sands in the Netherlands. *Biul. peryglac.* **8**, 50–58.

Maarleveld, G. C. 1976 Periglacial phenomena and the mean annual temperature during the last glacial time in the Netherlands. *Biul. peryglac.* **26**, 37–78.

Mitchell, G. F. 1977 Periglacial Ireland. *Phil. Trans. R. Soc. Lond.* B **280**, 199–209.

Mitchell, G. F. 1986 *The Shell Guide to reading the Irish landscape*. Dublin: Country House.

Mitchell, G. F., Penny, L. F., Shotton, F. W. & West, R. G. 1973 A correlation of Quaternary deposits in the British Isles. *Geol. Soc. Lond. Spec. Rep.* no. 4, 99 pp.

Mix, A. C. & Ruddiman, W. F. 1984 Oxygen isotope analyses and Pleistocene ice volumes. *Quat. Res.* **21**, 1–20.

Penny, L. F., Coope, G. R. & Catt, J. A. 1969 Age and insect fauna of the Dimlington Silts, East Yorkshire. *Nature, Lond.* **224**, 65–67.

Prentice, I. C. 1986 Vegetation responses to past climatic variation. *Vegetatio* **67**, 131–141.
Rackham, D. J. 1978 Evidence for changing vertebrate communities in the Middle Devensian. *Quat. Newsl.* **25**, 1–3.
Ruddiman, W. F. & MacIntyre, A. 1981 The mode and mechanism of the last deglaciation: oceanic evidence. *Quat. Res.* **16**, 125–134.
Shackleton, N. J. 1969 The last interglacial in the marine and terrestrial records. *Proc. R. Soc. Lond.* B **174**, 135–154.
Shackleton, N. J. 1986 the Plio-Pleistocene ocean: stable isotope history. *Mesozoic and Cenozoic Oceans, Geodynamics Series*, **15**, 141–153.
Shackleton, N. J., Backman, J., Zimmerman, H. *et al.* 1984 Oxygen isotope calibration of the onset of ice rafting and history of glaciation in the North Atlantic region. *Nature, Lond.* **307**, 620–623.
Shackleton, N. J. & Opdyke, N. D. 1973 Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes on a 10^5 and 10^6 year scale. *Quat. Res.* **3**, 39–55.
Shackleton, N. J. & Opdyke, N. D. 1976 Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28-239, late Pliocene to latest Pleistocene. In *Investigation of late Quaternary paleoceanography and paleoclimatology* (ed. R. M. Cline & J. D. Hays), pp. 449–464. Geological Society of America Memoir no. 145.
Simpson, I. M. & West, R. G. 1958 On the stratigraphy and palaeobotany of a late Pleistocene organic deposit at Chelford, Cheshire. *New Phytol.* **57**, 239–250.
Sjørring, S. 1983 The glacial history of Denmark. In *Glacial deposits in north-west Europe* (ed. J. Ehlers), pp. 163–179. Rotterdam: Balkema.
van Staalduinen, C. J. *et al.* 1979 The geology of the Netherlands. *Meded. Rijks geol. Dienst* **31**, 9–49.
Starkel, L. 1977 The palaeogeography of mid- and east Europe during the last cold stage, with west European comparisons. *Phil. Trans. R. Soc. Lond.* B **280**, 351–372.
Stuart, A. J. 1977 The vertebrates of the Last Cold Stage in Britain and Ireland. *Phil. Trans. R. Soc. Lond.* B **280**, 295–312.
Stuart, A. J. 1982 *Pleistocene vertebrates of the British Isles*. London: Longman.
Vandenberghe, J. 1985 Paleoenvironment and stratigraphy during the Last Glacial in the Belgian–Dutch border region. *Quat. Res.* **24**, 23–38.
Watson, E. 1977 The periglacial environment of Great Britain during the Devensian. *Phil. Trans. R. Soc. Lond.* B **280**, 183–198.
Webb, T. 1986 Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* **67**, 75–91.
West, R. G. 1980*a* Pleistocene forest history in East Anglia. *New Phytol.* **85**, 571–622.
West, R. G. 1980*b* *The Pre-glacial pleistocene of the Norfolk and Suffolk coasts*. Cambridge University Press.
Williams, R. B. G. 1975 The British climate during the Last Glaciation: an interpretation based on periglacial phenomena. In *Ice ages: ancient and modern* (ed. A. E. Wright & F. Moseley), pp. 95–120. Liverpool: Seel House Press.
Woillard, G. M. 1978 Grande Pile peat bog: a continuous pollen record for the last 140000 years. *Quat. Res.* **9**, 1–21.
Woillard, G. M. & Mook, W. G. 1982 Carbon-14 dates at Grande Pile: correlation of land and sea chronologies. *Science, Wash.* **215**, 159–161.
Zagwijn, W. H. 1957 Vegetation, climate and time-correlations in the Early Pleistocene of Europe. *Geologie Mijnb.* **19**, 233–244.
Zagwijn, W. H. 1961 Vegetation, climate and radiocarbon datings in the Late Pleistocene of the Netherlands. I. Eemian and Early Weichselian. *Meded. geol. Sticht.* N.S. **14**, 15–45.
Zagwijn, W. H. 1974 Vegetation, climate and radiocarbon datings in the Late Pleistocene of the Netherlands. II. Middle Weichselian. *Meded. Rijks geol. Dienst* N.S. **25**, 101–110.
Zagwijn, W. H. 1985 An outline of the Quaternary stratigraphy of the Netherlands. *Geologie Mijnb.* **64**, 17–24.
Zagwijn, W. H. & Paepe, R. 1968 Die stratigraphie der weichselzeitlichen Ablagerungen der Niederlande und Belgiens. *Eiszeitalter Gegenw.* **19**, 129–146.

Discussion

J. Rose (*Department of Geography, Birkbeck College, University of London, U.K.*). One of the problems with the identification of cold stages is the differing levels of sensitivity of the types of evidence used to identify 'cold' conditions and in particular to identify stage boundaries. This is seen specifically in the Cromerian Interglacial Stage, to which Professor West made reference, where plant evidence in zone CrIVc suggests interglacial status, whereas soil evidence for the same episode, in the form of ice-wedge casts, suggested that permafrost was in existence and the environment was more typical of the conditions that are generally attributed to the Anglian Glacial Stage (West 1980*b*). Similar problems exist when sensitive and mobile insect faunas are used as a basis of climatostratigraphy in parallel with less sensitive arboreal plant assemblages, as is well understood for the middle and late Devensian. Should priority or a ranking be given to different types of evidence in order that a degree of consistency can be maintained in subdividing the Quaternary on a climatic basis and deriving generally acceptable stage and substage boundaries?

R. G. West. Of course, at present, permafrost underlies forest over large areas. There will always be a problem in devising boundaries where none exist in nature; the question of definitions will have to await agreement on the most useful and informative method of division. It will have to be realized that any division is artificial and should not obscure the variety of climatic change or overshadow the variety of evidence for such change. The problems revealed by the wealth of evidence for climatic change is one of the attractions of Quaternary research. Such problems must also exist further back in geological timescale, but cannot be revealed by the time resolution available.

P. Coxon (*Department of Geography, Trinity College, Dublin, Ireland*). The terrestrial record of the penultimate interglacial (Gortian–Hoxnian–Holsteinian) from Ireland is known from numerous sites around the country (Watts 1985); one common feature of these sites is that the interglacial cycle is abruptly truncated during its latter part. Recent detailed sampling at one Gortian site at Derrynadivva, County Mayo (P. Coxon, G. Hannon & P. J. Foss, unpublished results) has shown that the interglacial is terminated within a phase of heath (especially *Empetrum*), *Pinus*, *Abies* and *Picea* dominating the vegetation. The upper sedimentological units of the interglacial deposit at Derrynadivva record increased inwashing of inorganic sediment in discrete horizons and re-worked pollen (especially of *Alnus*) becomes increasingly frequent.

The Gortian sites appear to contain a record that is the western equivalent of the Hoxnian Interglacial except that the later stages of the Gortian Interglacial appear to be truncated or missing. Is it possible that the sudden end of the Gortian Interglacial was due to the more rapid onset of climatic deterioration in these western sites that was caused by their proximity to the polar front in the North Atlantic?

Reference

Watts, W. A. 1985 Quaternary vegetation cycles. In *The Quaternary history of Ireland* (ed. K. Edwards & W. P. Warren), pp. 155–185. London: Academic Press.

R. G. West. This idea could be a valuable starting point for realizing the variation of climates at the end of a temperate stage on a transect across Europe.

H. Osmaston (*Department of Geography, University of Bristol, U.K.*). Professor West has contrasted the apparently greater complexity of glacials as compared with interglacials, and Mr Rose has commented on the differing sensitivity of the various indicators we use. I suggest that many of the indicators, from glaciers to beetles, are generally more sensitive to 'equal' changes in the macroclimate (e.g. a change of 1 °C in mean temperature) of cold periods than to those of warm periods. This affects the apparent complexity of such periods and makes it necessary to distinguish between complexity of indicator behaviour and complexity of the underlying factors.

H. H. Lamb (*Climate Research Unit, University of East Anglia, Norwich, U.K.*). If there is anything relevant to this discussion to be learnt from studies of the last thousand years, it surely is that the year-to-year, decade-to-decade, and century-to-century variability increased greatly during the development of the colder phases. This also applies to the spatial variability. The colder phases and their onset are associated with blocking anticyclones, whose occurrence is bound up with the dynamics of the upper westerlies (which they distort and interrupt), and they characteristically turn up in different positions, especially different longitudes, from one year to the next.

This variation suggests that all through the long development of the Pleistocene cold stages, as long as there was no extensive ice-sheet present, there may have been considerable variability in where the coldest climates in Eurasia were found to be developing. But once an extensive ice-sheet had formed, it presumably introduced a greater stability of position. It is probably implied that, because the cold trough in the upper westerlies in the North American–western Atlantic sector would be to a great extent anchored in the lee of the Rocky Mountains–Laurentide ice-sheet massif, the spatial and temporal variability there should have been less than over Eurasia.

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