Changes in Life Conditions on Earth During the Past One Million Years

By THOMAS VAN DER HAMMEN

A J. C. Jacobsen Memorial Lecture

Det Kongelige Danske Videnskabernes Selskab
Biologiske Skrifter **22**:6

Kommissionær: Munksgaard
København 1979

DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB
udgiver følgende publikationsrækker:

THE ROYAL DANISH ACADEMY OF SCIENCES AND LETTERS
issues the following series of publications:

	Bibliographical Abbreviation
Oversigt over Selskabets Virksomhed (8°) *(Annual in Danish)*	Overs. Dan. Vid. Selsk.
Historisk-filosofiske Meddelelser (8°)	Hist. Filos. Medd. Dan. Vid. Selsk.
Historisk-filosofiske Skrifter (4°) *(History, Philology, Philosophy, Archaeology, Art History)*	Hist. Filos. Skr. Dan. Vid. Selsk.
Matematisk-fysiske Meddelelser (8°) *(Mathematics, Physics, Chemistry, Astronomy, Geology)*	Mat. Fys. Medd. Dan. Vid. Selsk.
Biologiske Skrifter (4°) *(Botany, Zoology, General Biology)*	Biol. Skr. Dan. Vid. Selsk.

Selskabets sekretariat og postadresse
The address of the Academy is:

Det Kongelige Danske Videnskabernes Selskab,
Dantes Plads 5,
DK-1556 Copenhagen V.
Denmark.

Selskabets kommissionær
The publications are sold by the agent of the Academy:

MUNKSGAARDS BOGHANDEL,
6, Nörregade,
DK-1165 Copenhagen K.
Denmark.

Changes in Life Conditions on Earth During the Past One Million Years

By THOMAS VAN DER HAMMEN

A J. C. Jacobsen Memorial Lecture

Det Kongelige Danske Videnskabernes Selskab
Biologiske Skrifter **22**:6

Kommissionær: Munksgaard
København 1979

A grant from The Carlsberg Bequest to the Memory of Brewer J. C. Jacobsen has made it possible to arrange and print a series of public J. C. Jacobsen Memorial Lectures, for which the Academy expresses its sincere gratitude.

Synopsis

In recent years, our knowledge of the environmental history of the past one million years of the earth has increased rapidly. The analysis of microfossils, such as pollen and foraminifera, in deep sections of lake sediments and oceans has greatly contributed to this knowledge, as also has the analysis of isotopes, including absolute dating, and indirect dating by the paleomagnetic method.

In this lecture some of the more relevant studies are discussed, first from Europe, then from tropical areas and finally from the oceans. A sequence of many cold, warm, dry or wet periods may be recognised and dated.

At the end some more general conclusions are drawn, and the importance of the new data, the cause of climatic change and possible future developments are shortly discussed.

THOMAS VAN DER HAMMEN
Department for Palynology and Palaeoecology
Hugo de Vries-Laboratorium
University of Amsterdam
NL-1018 BX Amsterdam
Netherlands

Printed in Denmark by Bianco Lunos Bogtrykkeri A/S. ISSN 0366-3612. ISBN 87-7304-087-8.

Introduction

About 18,000 years ago the aspect of our earth was quite different from now. Huge masses of land-ice, up to several kilometres thick, covered the northern part of Europe and North America. South of the ice-border, Europe was covered by polar deserts, tundra or cold steppes, and apparently no trees were growing north of the Alps. Some 13,000 years ago, at the beginning of the Late-Glacial, the ice started to melt away rapidly, and the ice-border retreated northwardly. One after another, arborescent species migrated into areas formerly covered by tundras and steppes. About 10,000 years before the present, central and western Europe was covered by birch and pine forests which in the next few thousand years developed into deciduous oak, lime and elm forests. If Man would not have deforested Europe, the present situation to-day would have remained very much the same.

To obtain a better idea of the magnitude of this type of climatic change, one should imagine what would happen here if ice-age conditions would return: cities like New York, Oslo, Stockholm and Copenhagen would be stripped off the surface of the earth by the slowly advancing glaciers. Nobody of our generation will see this happen. Is it at all possible that ice-age conditions will return at some time in the next thousands of years or so? We shall deal with this problem later on, after having discussed the changes in life conditions on earth during the last million years. It will be tried to answer first of all such questions as how many times were the northern continents partly covered with continental ice-sheets? – how many glacials and interglacials have been recognised? – how was the rest of the world affected? – and what do we know about the tropics and the oceans? Much we have learned of such matters during the last few years, and we are coming very close already to a more complete picture in space and time of the ice-age world.

The main contributions to this picture were provided by the palynological analysis of lake sediments and by the study of sediments on the ocean floor. Plants produce pollen grains. Pollen grains of different families or genera of plants can be recognised with the aid of a good research microscope. Pollen grains are often released in the atmosphere, and may eventually return to the surface of the earth as "pollen rain". The pollen rain may give a more or less distorted picture of the stands of vegetation that produced it. When the vegetation in an area changes, the pollen rain also changes. When the pollen rain falls into a lake or peatbog, it is conserved in the sediment. From series of such sediments we can take successive samples and extract the remains of the pollen grains from them. After studying and counting the latter with the aid of the microscope, the results can be represented in a so-called pollen diagram, which illustrates the changing pollen deposition in time in a certain place. A pollen diagram may be translated into vegetational history, and indirectly into a history of the general environment.

In much the same way the history of the oceanic environment may be deduced from the study of Foraminifera (and of other micro-organisms) in the sediment on the ocean floors. The isotopic oxygen composition of the calcareous tests of these animals yields data concerning the volume of ice accumulated on the continents. Different dating-techniques (including indirect ones such as paleomagnetism) allow for correlation between the records from the ocean and those from the continents.

In order to draw up a first draft of prevailing world-wide conditions one must in the first place consider what, in broad lines, is known from Europe and the Mediterranean area. Subsequently tropical South America, and later, more concisely, tropical Africa and Australia will successively be treated. Finally the recent results of paleo-oceanographic research and the computer simulation of the global glacial climate will be discussed. Some time ago another source of information became available, *viz.*, thick layers of inland ice accumulated in Greenland and in Antarctica. It was the Danish scientist W. Dansgaard who did pioneer work in this field. The isotopic oxygen composition of these ice masses yields data relating to the atmospheric temperatures of former times.

Europe

The natural vegetation cover of Europe has largely been destroyed by Man, but on the basis of what is left (mainly secondary vegetation) it is not difficult to reconstruct the principal original vegetation zones (Fig. 4: above). Along the arctic ocean there was a strip of tundra followed to the south by a zone of subarctic birch (*Betula*) forests becoming gradually denser southwards. The next zones consisted of pine (*Pinus*) and finally spruce (*Picea*) forests together indicated on the map as the zone of "Boreal Coniferous forest". Farther southward lay the zone of Central-European deciduous forests, with oak (*Quercus*) and beech (*Fagus*) as the most common trees, elm (*Ulmus*), ash (*Fraxinus*), lime (*Tilia*), hornbeam (*Carpinus*), and hazel (*Corylus*) occurring regularly where soil and ground water conditions were favourable for their growth. South of the Pyrenees and the Alps lay the zone of the warm and mediterranean oak forest, where also evergreen species of oak occurred. This latitudinal zonation was and still is largely determinated by the prevailing temperature ranges. Towards the east, the climate becomes more continental and a wedgelike zone of steppes and semi-deserts, broadening from the Donaudelta towards the east, is present. At the same time the zone of deciduous forest narrows towards the east, and finally disappears, so that, very generally speaking, there is a north-south (latitudinal) gradient of temperature and a west-east (longitudinal) gradient of precipitation.

Let us see what the pollen diagrams from the last 130.000 years can tell us of the changes in life conditions in that period (Fig. 1). The width of the diagrams represents the pollen total (trees and "dry" herbs). The percentages of a number of abundant genera or ecological groups of genera are indicated cumulatively in such a way that the forest elements are at the left and the elements of the open vegetation at the right. The history can thus be read from the base (the older part) to the top (the younger part).

The diagram at the right (from the Grande Pile, in the Vosges, Northern France) is the only continuous diagram we have from Western Europe. The diagram is drawn in a very simple way so as to show clearly the most important changes, namely the proportional changes of forest elements and of elements of the open vegetation types. At the base, the elements of open vegetation, representing a tundra-like vegetation, predominate, so that this part represents the end of what is probably the penultimate glaciation. Later the forest takes over, and the pollen spectra leave no doubt that the surroundings of the bog were now densely forested. This period characterised by dense woodland, mainly of the Central European mixed deciduous forest type, persisted for a long time, but was twice interrupted by relatively short periods with 'cold', open vegetation. The long tripartite forest period might in its entirity be considered to be an interglacial, but most probably only the lowest part corresponds with the typical Eemian interglacial (see below). The next interval of the diagram is one characterised by the predominance of open, 'cold' vegetation, and the period is only interrupted by

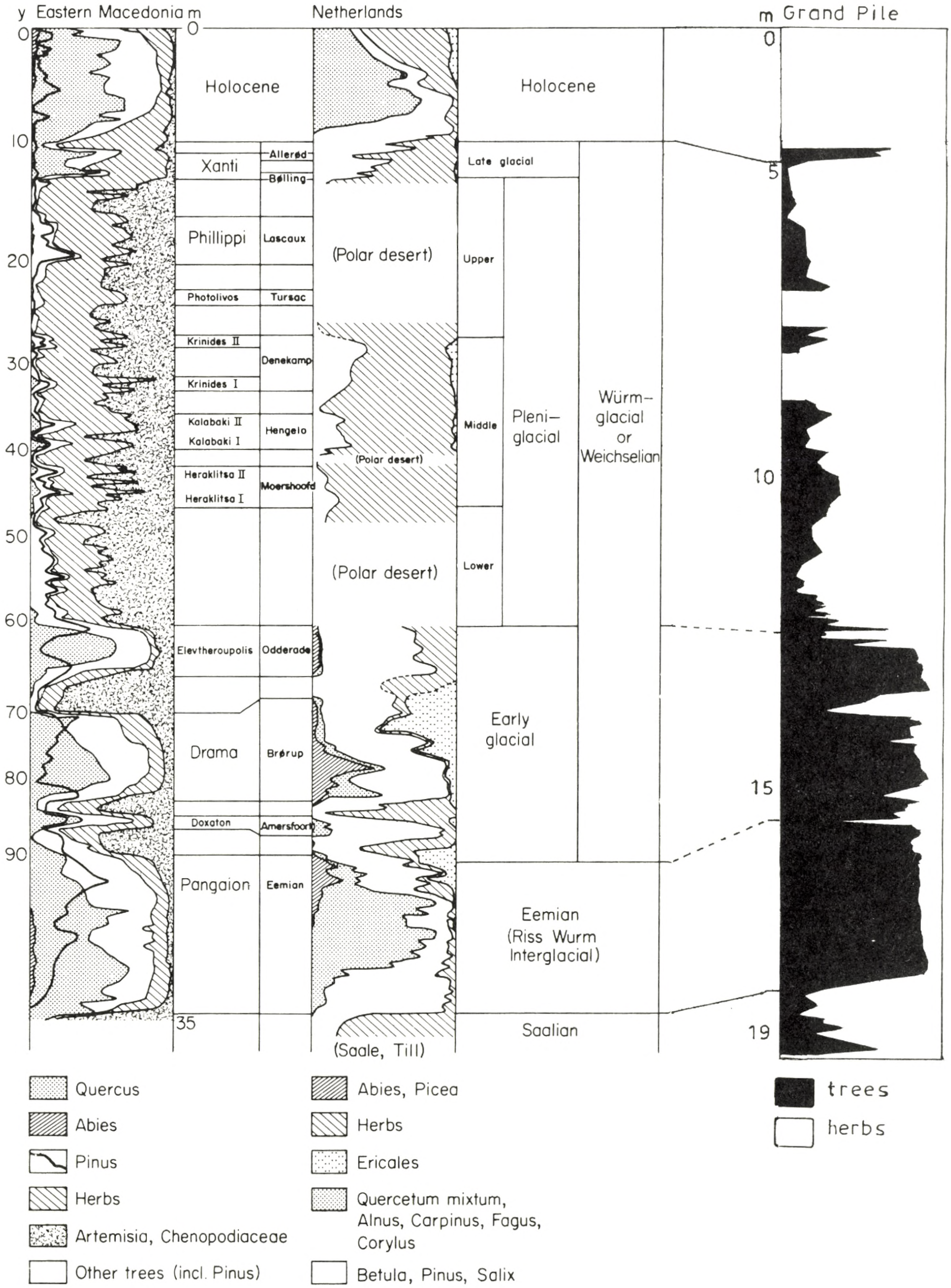


Fig. 1.
Pollen diagrams of the last 130,000 years, representing the last Interglacial (Eemian), the last Glacial (Weichselian) and the Holocene, from Eastern Macedonia (Philippi), the Netherlands and Northern France (Grande Pile). Redrawn from Van der Hammen et al., 1971, and Woillard, 1978).

minor increases of forest elements. ^{14}C Dates from the upper part of this interval, indicate ages of 30,000 years and younger, and there is no doubt that this whole "tundra period" corresponds with the Last Glacial (the Weichselian). The uppermost part of the diagram, representing the last 10,000 years, our present period, the Holocene, is once more a forest phase.

The diagram in the middle of Fig. 1 is from the Netherlands. It is a composite diagram compiled from a number of diagrams from different sites that could be placed in the right order by means of stratigraphical correlation and ^{14}C dating. The lower part again represents open tundra-like vegetation of the end of the penultimate glacial: the glacial till lies immediately below it. A forest period, corresponding with the typical Eemian (considered to be the last interglacial), follows. First there is a phase of birch and pine forest (as now found in the zone south of the tundra in Northern Europe), but from here it leads directly to deciduous forest of oak, elm, lime, etc. Later hornbeam enters and also fir and spruce. Heather (Ericaceae) increases and pine and birch take over again to become finally replaced by open, 'cold' vegetation. This interglacial sequence is primarily caused by the increase and subsequent decrease of the average temperature (and by the resulting displacements of vegetation belts), but also by the time required by different plants to migrate, and by the development (maturation, or degradation, as the case may be) of soils.

The cold period immediately following the Eemian did not last very long. A period followed with fluctuatung conditions, sometimes warmer (the Amersfoort, Brørup and Odderade "interstadials"), but sometimes colder (the "stadials" between them).

This period will here be called the "Early Glacial" of the Weichselian; during this period the climate apparently never became as mild as in an interglacial one. After this Early Glacial the climate became extremely cold (the Lower Pleniglacial). There is no pollen record available from that interval, but it can be recognised from the unmistakable signs left by the heavy action of frost upon the sediments of that time. There must have been a very scanty vegetation cover and the landscape is probably best described by the term "polar desert".

During the next interval (the Middle Pleniglacial) different conditions prevailed. There is ample evidence of tundra vegetation and of fluviatile sediments. The climate was cold and humid. There are three short intervals during which shrub tundra vegetation developed, with abundant dwarf birch, ^{14}C-dated as about 45,000, 38,000 and 30,000 years B.P.: the Moershoofd, Hengelo and Denekamp interstadials, respectively. The climate improved slightly during these phases which correspond more or less with the southernmost tundra zone.

After about 29,000 B.P. the climate deteriorated again (the Upper Pleniglacial), and the presence of frost-wedge polygons and other frost phenomena in the sediments indicate a very severe climate with permafrost and very little vegetation. The climate was very cold and dry, causing a polar desert. This Upper Pleniglacial, lasting till about 13,000 B.P., corresponds with the main cold period of the last glacial, the maximum extension of landice being reached by about 20,000–18,000 B.P.

After about 14,000 B.P., but in any case after about 12,600 B.P., the climate ameliorated notably (this marks the beginning of the Late Glacial), and although trees had not yet arrived, herbs requiring relatively high July temperatures immigrated or extended their ranges. Around 12,400 B.P. the first birches arrived and formed a kind of park landscape (the Bølling "interstadial").

During a short period of a few hundred years (Earlier Dryas time) the trees disappeared again, possibly because of severe continental climatic conditions, but they re-appeared soon already at the beginning of the Allerød-interstadial (c. 11,800 B.P.). Soon the Netherlands became covered by dense birch forest and a few centuries later pine immigrated and soon became an important element of the forest. Once again this forest disappeared partly, namely during the Late Dryas time (10,900–10,150 years B.P.) when the inland ice extended to the central Swedish endmoraines, to close more definitely at the beginning of the Holocene. The Holocene began with a period of birch and subsequently pine forest (Preboreal), followed by a pine-hazel period when thermophilous trees such as oak, elm and lime gradually took over (the Boreal) and a humid and warm oak-lime period with alder extending considerably (the Atlantic). The partly drier Subboreal follows with elm declining and beech immigrating, and the somewhat cooler and more humid Subatlantic (when beech and hornbeam extended strongly) when Man, after his first agricultural activities in the late Atlantic and Subboreal, finally destroyed the forest almost completely.

Let us now turn to the diagram at the left of Fig. 1. It is a continuous diagram, and reflects the vegetational changes in northeastern Greece (Philippi); we know, however, that a more or less similar succession took place in other parts of the northern Mediterranean (in Italy and in Spain), and the diagram from Greece, therefore, gives a good idea of what happened in this part of the world.

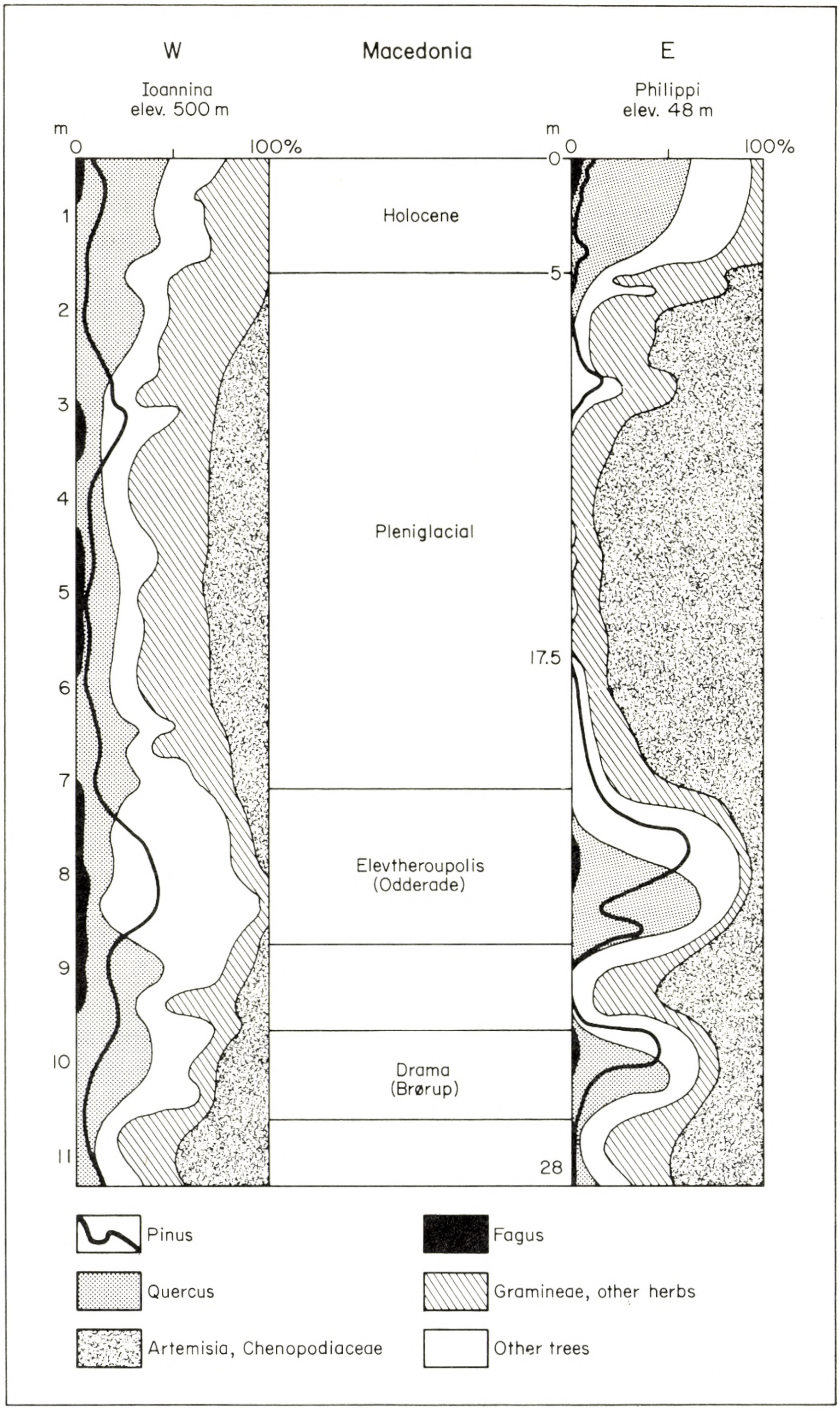
The changes registered are likewise alternations of forests and open vegetation. However, in this case the open vegetation types contained so much more *Artemisia* and Chenopodiaceae that we have to consider it to have been a cool steppe vegetation type and not a tundra, while it could be established that the forest contained, at least during certain intervals, typical mediterranean species such as evergreen oaks, *Pistacia*, *Olea*, etc. Once this has been established, it is easy to subdivide the diagram (above the lowermost records with steppe elements) into three major parts: at the base an extended tripartite forest period followed by a steppe period of appreciable duration, and a final forest period. ^{14}C dates from the upper half of the diagram indicate that the extended steppe period is contemporaneous with the last Glacial, and the upper woodland part of the diagram corresponds with the Holocene. It is, therefore, most likely that the lower forest zone corresponds with the last interglacial. The similarity with the Grande Pile diagram is striking, and a correlation of this entire tripartite interval with the Eemian and the Early Glacial is conceivable but not certain.

During the long "glacial" steppe period, the annual rainfall must have been very low, because, as will be pointed out below, it could not have been the temperature that prevented tree growth. During short intervals the effective rainfall must have increased slightly, because pine or oak could locally extend their distributional areas, and, asfar as could be established by ^{14}C dating, these intervals correspond with interstadials in the north. The Late-Glacial changes of climate also seem to be represented.

The obvious conclusion is, therefore, that steppes, and locally steppe forests, dominated the landscape in Eastern Macedonia (and the north Mediterranean lowlands in general) during the main part of the last Glacial, and it seems logical to accept that at that time the East European and Central Asiatic steppe zone extended much father to the west, and the climate in the north Mediterranean was much more continental with a very low rainfall.

Now that a picture of the last glacial period of a cold and treeless northern and central Europe is emerging, one may wonder where the thermophilous trees of the present central European deciduous forest may have survived. The answer to this question may be found by a perusal of other diagrams from the Balkan mountains. In Fig. 2 a diagram from an altitude of 500 m in Western Macedonia (Ioannina) is shown at the left, and at the right the corresponding part of the Philippi diagram just discussed (elev. c. 50 m). The lower forest-period does not show special features, but there are significant differences between the two diagrams concerning the last glacial steppe interval. While all trees seem to have disappeared in the lowland Philippi-site, the percentage of steppe ele-

Fig. 2.
Pollen diagrams representing the last 80,000 years in Western Macedonia (Ioannina, altitude c. 500 m) and Eastern Macedonia (Philippi, altitude c. 50 m). (From Van der Hammen et al., 1971; redrawn, after Bottema and Wijmstra).



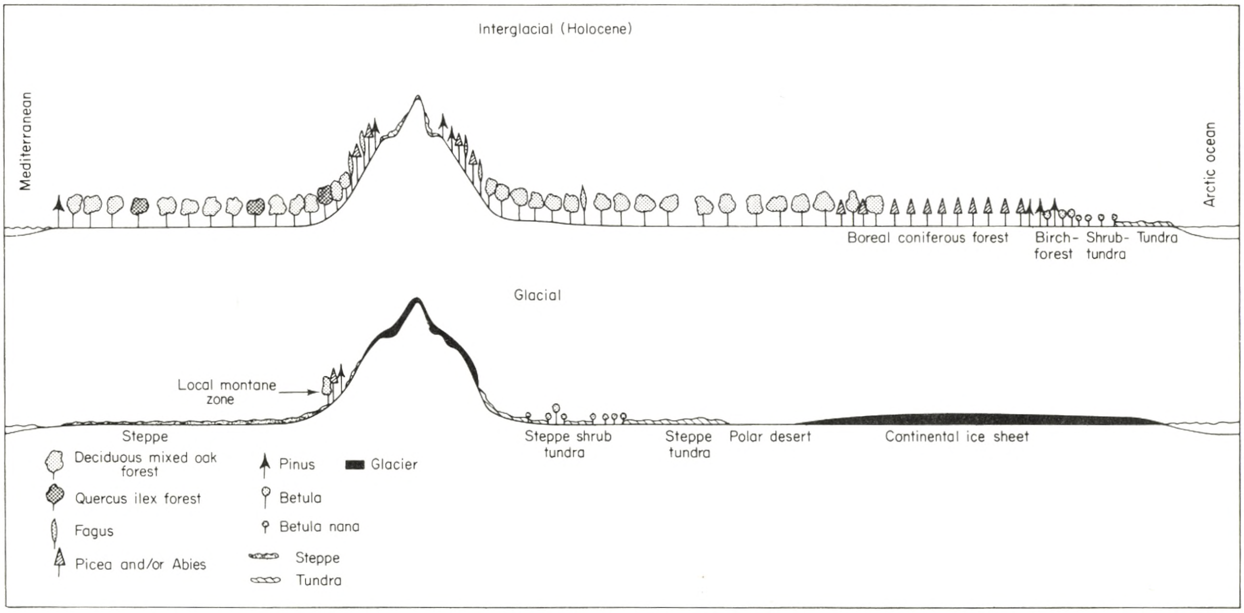


Fig. 3.
Schematic representation of the floral formations during an interglacial and during a glacial, in a south-north section through Europe. (From Van der Hammen et al., 1971).

ments was considerably lower at the mountain site, and there is a continuous presence of pollen of oaks (*Quercus*) and beech (*Fagus*). This fact strongly suggests the presence, at least locally, of a more humid montane zone at about 500 m altitude in the Balkan mountains, where trees could take refuge. Situations in which a relatively narrow belt of montane forest lies between dry steppe and cold "alpine" vegetation, or between cool and cold steppe vegetation types, occur at present in such widely separated regions as the Central Asian Highlands (*e.g.*, Pamir), Peru, and the southwestern United States.

In Figs. 3 and 4 a diagrammatic and partly tentative representation is given of the present situation (an interglacial) and the situation prevailing 18,000 years ago (during a glacial). They are based on the evidence from the pollen diagrams discussed here and from many other ones, and on additional (geological) data.

Fig. 3 shows a diagrammatic section through Europe, from the Arctic Ocean to the Mediterranean sea, demonstrating the profound changes that took place, and indicating the position of the local more humid montane forest zone in the south.

In Fig. 4 the local montane forest zone could not be indicated, but it is even more impressive than Fig. 3. Forest disappeared almost completely from Europe, in the north primarily because of the lowered temperature, and in the south primarily owing to the low effective precipitation. It follows that vegetation zones moved from north to south and from east to west, polar desert and tundra covering northern Europe (south of the continental ice sheet) and steppe vegetations southern Europe.

So far we have been discussing the changes in life conditions of the last 130,000 years in rather relative terms. One may wonder whether it is possible to procure more exact data, *e.g.*, in terms of degrees Celsius and millimetres of precipitation. The present climatic conditions prevailing in certain vegetation zones and zone-boundaries may serve as a yard-stick for former climatic data. This has been done for the Netherlands, and the results pertaining to the last interglacial-glacial cycle are shown in Fig. 5, in terms of the mean July temperature, a 5°C limit being taken as indicative of

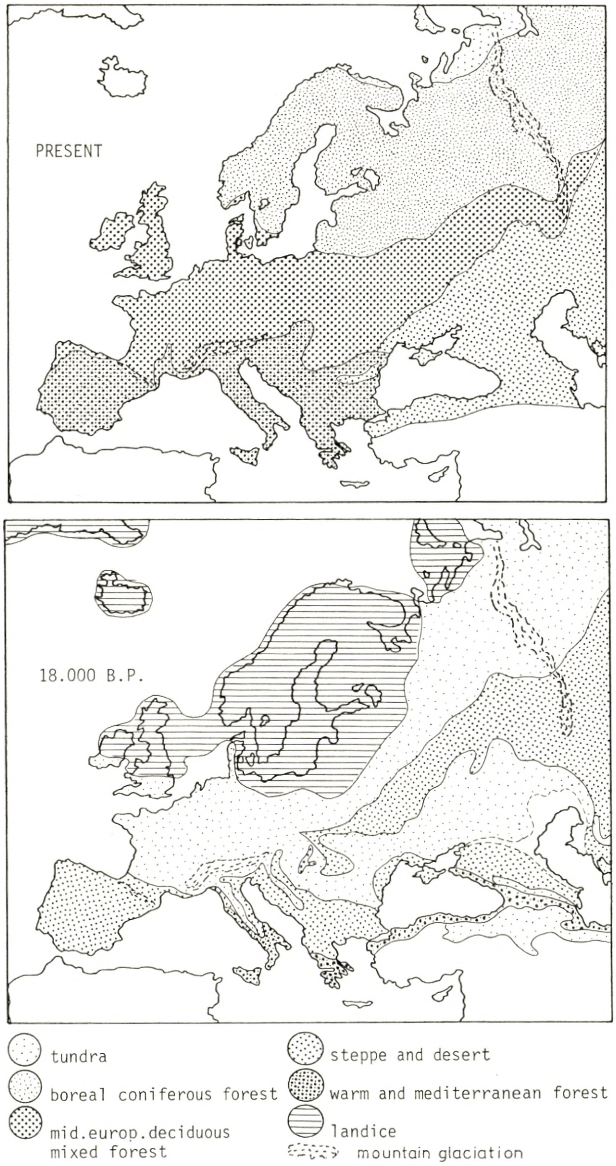


Fig. 4.
Principal vegetation (formation) zones of Europe to-day (Holocene) and during the maximum of the last Glacial (18,000 yrs. B. P.). (The last map, simplified and adapted from Frenzel, 1967, is only tentative). The local montane forest zone in the Mediterranean mountains could not be indicated on this scale.

the boundary polar desert-tundra, a 10° C limit for the boundary (shrub-)tundra-forest, etc.

Certain boundaries do not depend (or do not depend only) on the mean July temperature, however, but also on other ecological factors such as the winter temperatures, the amount of effective precipitation, and the distribution and thickness of the snow cover during the winter season. This renders a more exact estimate rather difficult. The best procedure seems to be the compilation of all available ecological information relating to the plant formations found and to the autecology of the individual plant species represented by pollen or by seeds. This approach is not always easy, however, since plants now growing at high latitudes in the arctic zone, may have different limiting boundary conditions when growing at lower latitudes (because both the quantity of the solar radiation received by the plants and its distribution throughout the year – such as day-length – are different).

As far as those plants growing in the arctic and at higher elevations in the Alps, or in other mountains at lower latitudes, are concerned, this problem may conceivably be solved in principle, but this does not hold for those growing only in the arctic. These and similar problems were discussed already by the great Danish master of paleoecology Johannes Iversen.

Anyhow, new advances are being made along the lines indicated above, and somewhat more reliable results may be expected in a not too distant future. As far as we ascertain, it seems that during certain intervals the average July temperature may have been somewhat higher than estimated before, while wintertemperatures may have been very much lower.

Once our present paleoclimatic knowledge of the last 130,000 years has been compiled, one may wonder what can be said about the preceding geological period. Much relevant evidence has been gathered in the last few years. The beginning of the Quaternary, *i.e.*, of the period of strong climatic changes known as glacials and interglacials, may be placed as far back as three million years. It has

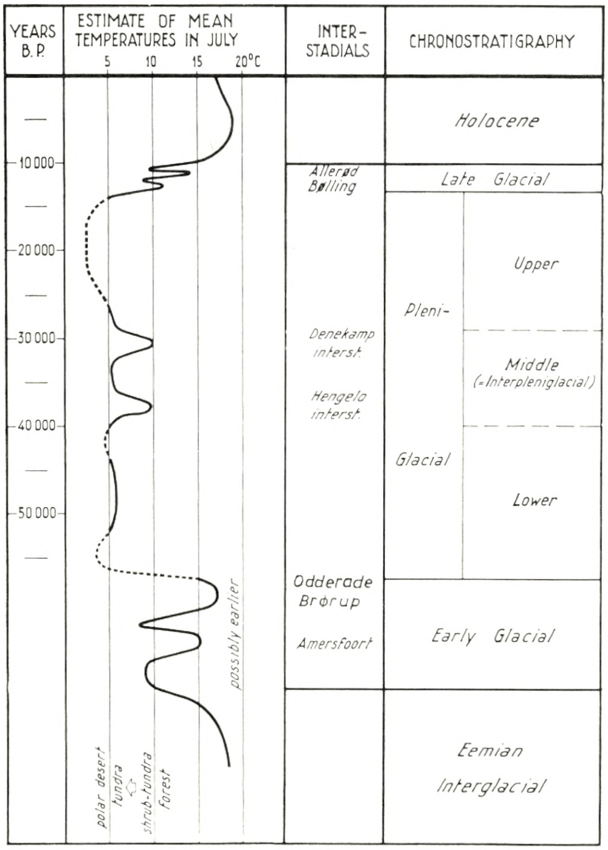


Fig. 5.
Climatic curve (average July temperatures) for the last Glacial in the Netherlands. The curve is based on the climatic evaluation of vegetational changes and of periglacial phenomena, and partly still tentative. (After Van der Hammen et al., 1967).

also become known, that there were many more glacial and interglacial periods, probably more than 20, of which most are older than the classic four alpine glacials. Previous to the Quaternary there was a very rich flora of East-Asiatic affinity that disappeared from Europe little by little on account of the local extinction of elements caused by the repeated glaciation of northern Europe and the central European mountains (the Asiatic elements survived in East Asia because a southward migration to warmer climatic belts was possible throughout).

There is no continuous section from northern and western Europe in which all or many of the glacials and interglacials are represented, and the present state of our knowledge has been built up in a cumbersome way from several isolated fragments. It is still a question whether all the major glacials and interglacials are known already, and the correlation between and the stratigraphic position of certain glacial and interglacial deposits are not always established beyond reasonable doubt.

In the Mediterranean area on the other hand, thick lake and peat deposits are present in certain "basins" and provided rather extended, continuous pollen diagrams. The best and longest of these is from Eastern Macedonia (Philippi), the continuation of the section discussed above. So far about 120 m of this more than 300 m thick, continuous deposit has been analysed, and the remainder has already been sampled. In the near future we may expect to have at our disposal a continuous pollen diagram covering most of the Quaternary sequence. At the moment only the pollen diagram of the upper 120 metres is available corresponding with a time-span covering the last 600,000 years. A general, diagrammatic representation of this unique diagram is shown in Fig. 6. The upper 35 metres correspond with the last interglacial-glacial cycle and the Holocene, and has already been discussed above. Downwards the same kind of intermittent change continues cyclically, and at least 5 or 6 major steppe periods can be recognised apart from several minor ones, all alternating with woodland periods. Altogether there may have been about 7 interglacial-glacial cycles. Some of the warmer interglacials (or groups of interglacials) have been given local names, so as to facilitate the discussion concerning their possible correlation with certain interglacials recorded from Northern Europe. The correlation is still very tentative, but one may trust that with the aid of paleomagnetic data for correlation and indirect dating, these problems will be solved in due time.

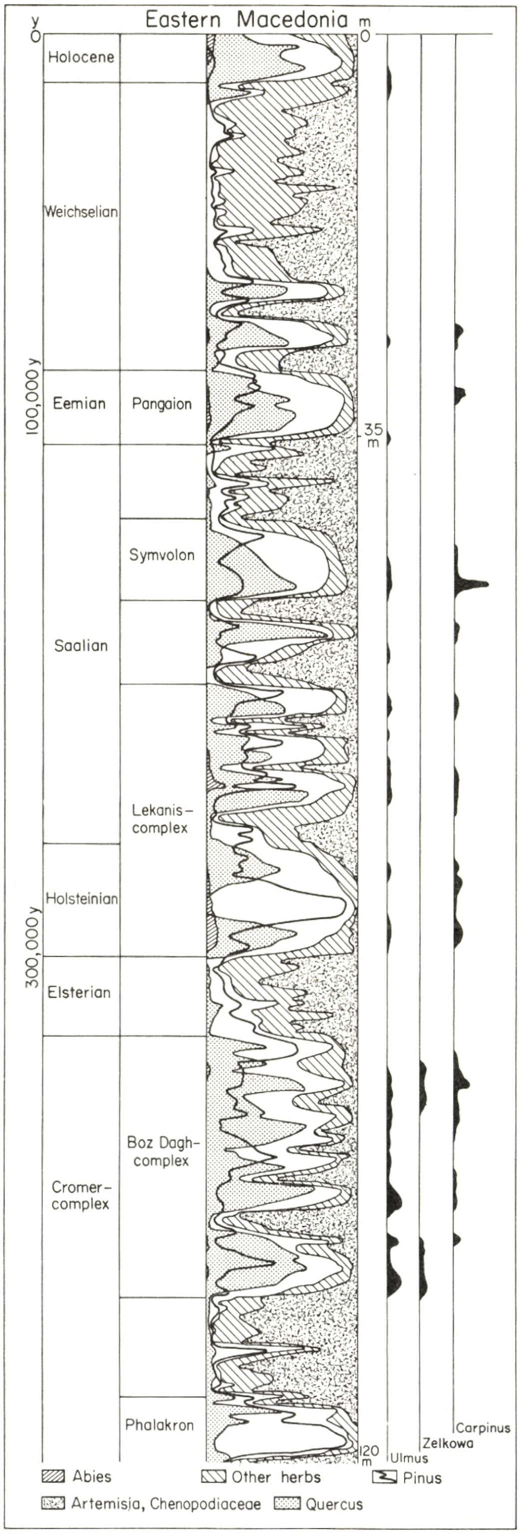


Fig. 6.
Pollen diagram of 120 m of lake sediments and peat, representing the last 600,000 years, from Eastern Macedonia (Philippi). (After Wijmstra in Van der Hammen et al, 1967).

The South American Tropics

After having noted the profound changes in life conditions which have taken place in what at present are the cold and temperate zones, one may well ask what happened meanwhile in the tropics.

In order to arrive at an answer to that question, one may first follow the events in the South American tropics, primarily in the tropical northern Andes. In these mountains there is manifest altitudinal differentiation of the ecological conditions, as in any other comparable mountain range elsewhere in the world. There is, however, one paramount difference between high mountains in the tropics and those in temperate zones: the tropical ones have no termal seasonality but a diurnal climatic cycle. Every day the temperature becomes relatively high, and there may be frost almost every night. This has one great advantage for the paleoecologist: one does not have to take different summer and winter temperatures into account, but only the average annual temperature.

The principal vegetation belts of the northern Andes are shown diagrammatical in a W-E section through the Colombian Cordillera Oriental (Fig. 8: left).

The lower tropical forest belt, very rich in species, extends from the lowlands to about 1000 m altitude. Where the climate exhibits a pronounced seasonality in the rainfall (and where the total amount of precipitation is lower), savannahs and dry tropical woodlands may be present, or even xerophytic vegetation.

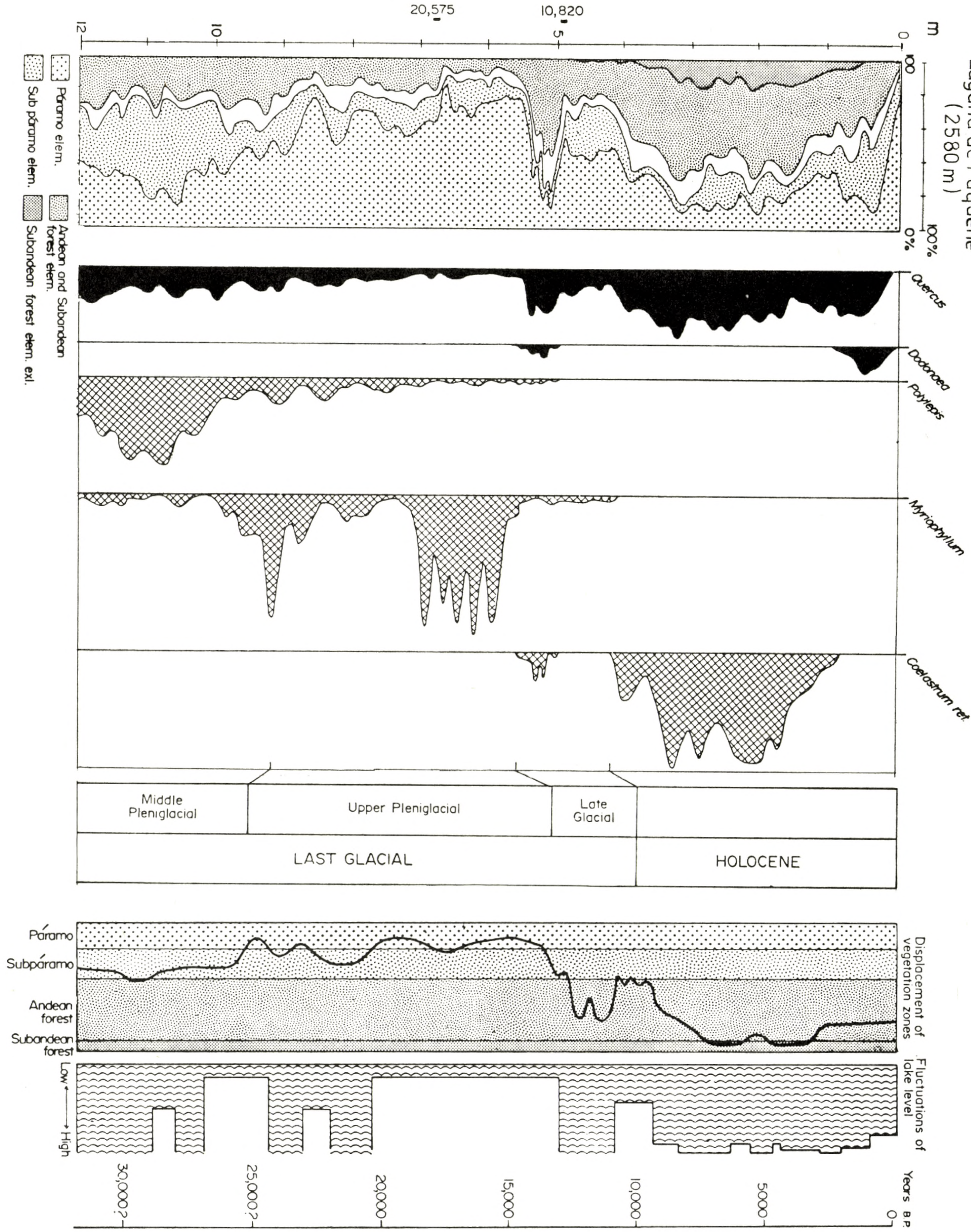
The belt of Subandean forest lies between 1000 m and 2300 m, and is followed between 2300 and about 3500 m, by the Andean forest. The floristic and quantitative composition differs from belt to belt. The limit between the Subandean and Andean forest seems to correspond approximately with the elevation above which night frost may occur. While the proportion of elements with a tropical origin is still very high in the Subandean forest, in the Andean forest there is a considerable proportion of elements with a southern (austral-antarctic) or northern (holarctic) origin. An example of the first-mentioned group is the genus *Weinmannia* and of the second oaks (*Quercus*) and alders (*Alnus*). In the Subandean belt, and more particularly in the Andean belt, cloud forests occur on the wet outer slopes; these forests lie in zones with a very high atmospheric humidity and generally with a high precipitation and are extremely rich in bryophytes and vascular epiphytes. On the inner slopes often drier forest types occur, and in the deeper longitudinal valleys, or otherwise in the rain shadow, xerophytic vegetation may occur. The upper limit of the Andean forest corresponds approximately with the altitudinal forest limit. Above it lies the so-called Páramo zone. There may, however, be a low forest with *Polylepis*, *Escallonia* and/or certain Compositae and Ericaceae locally attaining altitudes up to 4000 m.

The Páramo belt can be divided in three subzones, *viz.*, (1) the Subpáramo, where low shrubs of Compositae, *Miconia*, *Hypericum*, *Arcytophyllum* and many other taxa are still abundant in the otherwise open stands of vegetation; (2) the proper Grass páramo, where bunch grasses or small bamboos dominate together with the highly characteristic stem-borne rosettes ("caulirossula") of the Espeletiinae; and (3) the Superpáramo where the vegetation cover is incomplete and the soil freezes and thaws every night and day. The following or nival zone extends from about 4800 m upwards; the most elevated areas are usually covered with permanent snow and ice.

The altitudinal position of these belts depends principally on the average annual temperature, although the humidity also exerts some influence. The average annual temperatures of the lower tropical belt range from about 30° to 24° C, of the sub-Andean belt from 24° to 15° C, of the Andean belt from 15° to 8° C, and of the Páramo belt from 8°–0° C.

The pollen diagrams shown here are from the high plains in the Cordillera Oriental, at an elevation of about 2600 m (indicated diagrammatically in Fig. 8). The first diagram (Fig. 7) is from a layer of about 12 m of sediments from lake Fúquene, representing the last 30,000 years. The diagram is made in the same way as the European ones: at the left are the forest elements, at the right the elements of low, open vegetation. The pollen types are arranged in groups corresponding with the vegetation belts; some of these types are from plants exclusively occurring in only one of the belts, and other ones being principally restricted in their occurrence to a belt or appear to be dominant in that belt. The grasses and typical Páramo plants belong to the group of Páramo-elements, Compositae, *Hypericum* and some other taxa to the Sub-páramo group, *Weinmannia*, *Quercus*, etc. to the Andean and Subandean group, and *Cecropia*, *Acalypha* and *Alchornea* to the Subandean group. These groups are placed from right to left in this order. At the right of the main diagram some separate curves of important elements are drawn.

The diagram starts from the 30,000 B.P. level, with a phase characterised by dominating Subpáramo elements (to-day occurring at a 1000 m higher altitude). In this case the indicator is *Polylepis*, a typical high Andean tree of the rose family, which apparently formed a dense and relatively broad zone above the zone of Andean forest proper. A few millennia later, the Sub-páramo species gradually disappeared to become replaced by Grass páramo elements, and the lake became completely surrounded by open Páramo vegetation. At the same time the aquatic plant *Myriophyllum*, to-day very common along the shores of Páramo lakes, extended considerably. About 20,000 years ago apparently the maximum of cold seemed to have been attained and the lake level dropped appreciably as indicated by the marked increase of pollen from plants of the hygrosere and also by the type (facies) of sediment. Some 13,000 years ago a sudden rise of lake level occurred, Andean forest elements invaded the area, and a pioneer of eroded


Laguna de Fuquene
(2580 m)
m
0
5
10
12
20,575
10,820
100
0%
100%
Páramo elem.
Sub páramo elem.
Andean and Subandean forest elem.
Subandean forest elem. exl.
Quercus
Dodonaea
Polylepis
Myriophyllum
Coelastrum ret.
Middle Pleniglacial
Upper Pleniglacial
Late Glacial
LAST GLACIAL
HOLOCENE
Páramo
Subpáramo
Andean forest
Subandean forest
Displacement of vegetation zones
Low
High
Fluctuations of lake level
Years B.P.
30,000?
25,000?
20,000
15,000
10,000
5000
0

← Fig. 7.
Pollen diagram from Laguna de Fúquene at 2580 m alt. in the Cordillera Oriental, Colombia, representing the last 30,000 years. At the right the corresponding curves of displacement of the vegetation zones and fluctuations of the lake level. Some ^{14}C dates are indicated at the extreme left. (From Van der Hammen, 1974, adapted; after an original diagram of Van Geel & Van der Hammen).

soils, *Dodonaea*, extended its area temporarily. Shortly after 11,000 B.P. the forest disappeared temporarily to be replaced by Sub-páramo vegetation, but shortly after 10,000 B.P. the Andean forest re-invaded the area and, somewhat later even Sub-andean elements appeared, which indicates that the temperature must have been slightly higher than it is at present. Later, however, probably about 3000 years ago, these forest elements disappeared gradually again. Human influence began and, since the arrival of the Spaniards, the forest in the area was completely destroyed (stimulating an increase of the Páramo group of elements, here only represented by grasses), and *Dodonaea* colonized the eroded soils.

The curves at the right side of Fig. 7 indicate the movements of vegetational belts and the fluctuations of the lake level, both as deduced from the pollen diagram. The form of the first curve is strikingly similar to the corresponding European temperature curve.

The vertical displacement of vegetation zones during the coldest phase must have been of the order of 1200–1500 m; at the same time the aridity was high. Taking these factors into account, the average annual temperature may have been 8° C (and in any case at least 6°–7° C) lower than it is to-day, and the annual rainfall may not have exceeded 100–400 mm, what is less than half of the present value of about 890 mm. Another dated pollen diagram, from 2000 m alt. and not shown here, shows Grass páramo vegetation prior to c. 12,000 B.P., which also points to a lowering of the forest limit by at least 1300 (probably 1500) m as compared with its present position. Even taking a greater aridity into account, this would likewise indicate a lowering of the temperature by 6°–7° C.

In Fig. 8 (right side) the situation of the vegetational belts during the last glacial maximum has been indicated and is to be compared with the present situation. As we know from other sources that the temperature at sea-level cannot have decreased as much as it did in the high Andes, and possibly was only by about 3° C lower, the temperature gradient must have been steeper in glacial times, and the lower vegetation zones were compressed. It is also noteworthy that the surface occupied by Páramo vegetation increased considerably, and many now isolated Páramo "islands" were connected at that time. This is an important phenomenon from the point of view of phytogeography and evolution, especially so because this process of disruption and rejoining of areas of distribution was repeated several times.

Let us now turn to the longer sequences. As there were large lakes, some of them persisting for millions of years, on the high plains of the Cordillera Oriental, unique archives are available in the form of hundreds of metres of sediments deposited in these lakes. The outlines of three diagrams, two of them still unpublished, are presented here (Fig. 9). The diagram at the right is also from Fuquene, but represents 40 m of sediments and some 100,000 years of vegetational history. The curve of *Polylepis* is shown separately at the right. Although the details in the upper 12 m are not so clear as in the diagram of Fig. 7, the maximum of Páramo-elements and of *Polylepis* assists in the correlation of the diagrams; apparently the sediments of the last 30,000 years are almost of the same thickness. The Grass páramo elements attain very high percentages below the *Polylepis* maximum, but below this maximum there is a long sequence of alternating forest and (Sub) Páramo intervals. Only the lowermost two forest intervals indeed reflect warmer periods of an interglacial character, with an abundance of *Weinmannia*, and they clearly represent the last interglacial "complex"; it is striking how much the short and violent Páramo-maximum at about 33 m resembles similar phenomena in the last interglacial complex of Europe (compare Fig. 1).

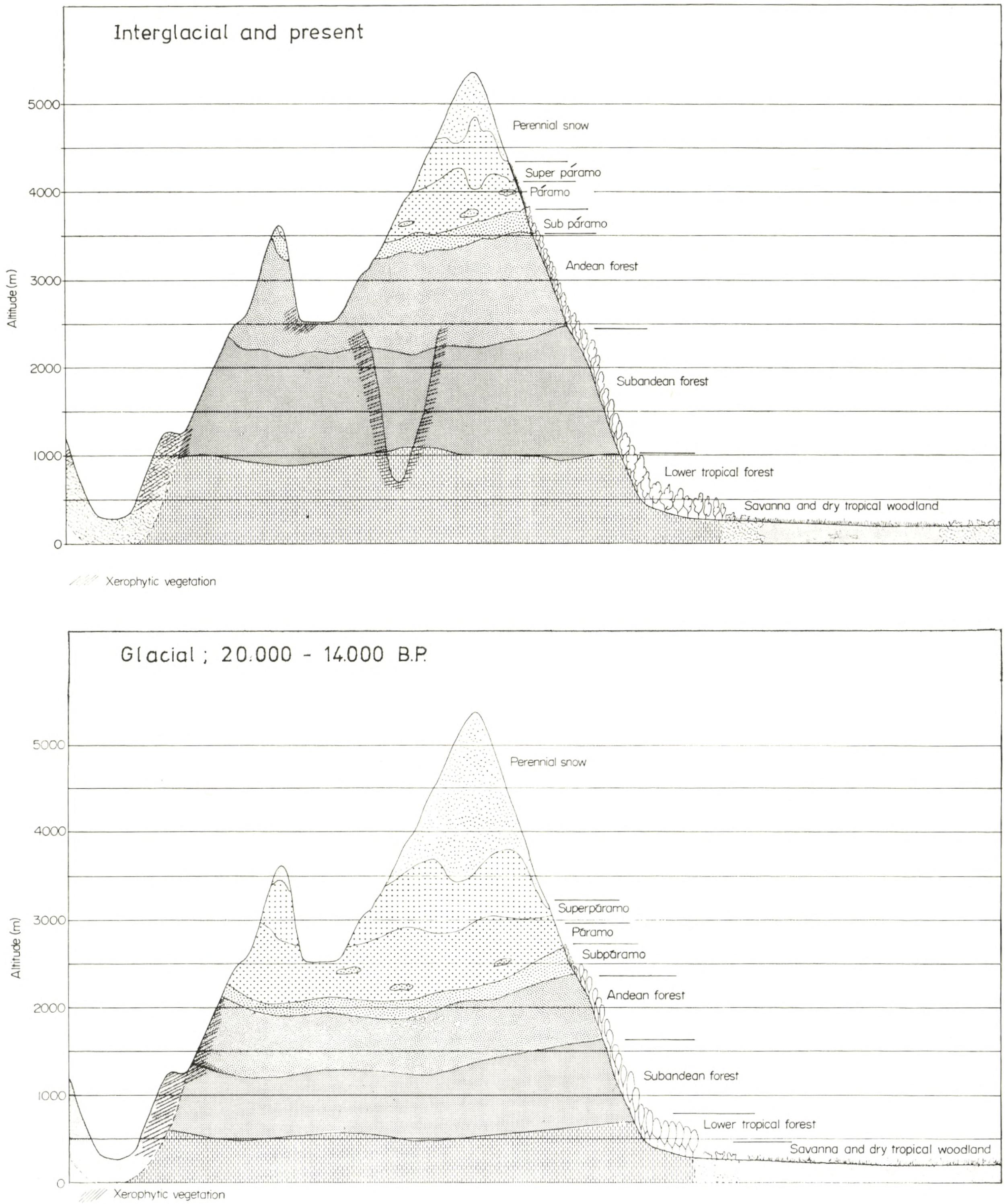


Fig. 8.
Diagrammatic representation of the vegetation belts in the Colombian Cordillera Oriental, as they are at present (above: interglacial situation) and as they were during the Last Glacial maximum of 20,000–14,000 years ago (below: glacial situation). (From van der Hammen, 1974).

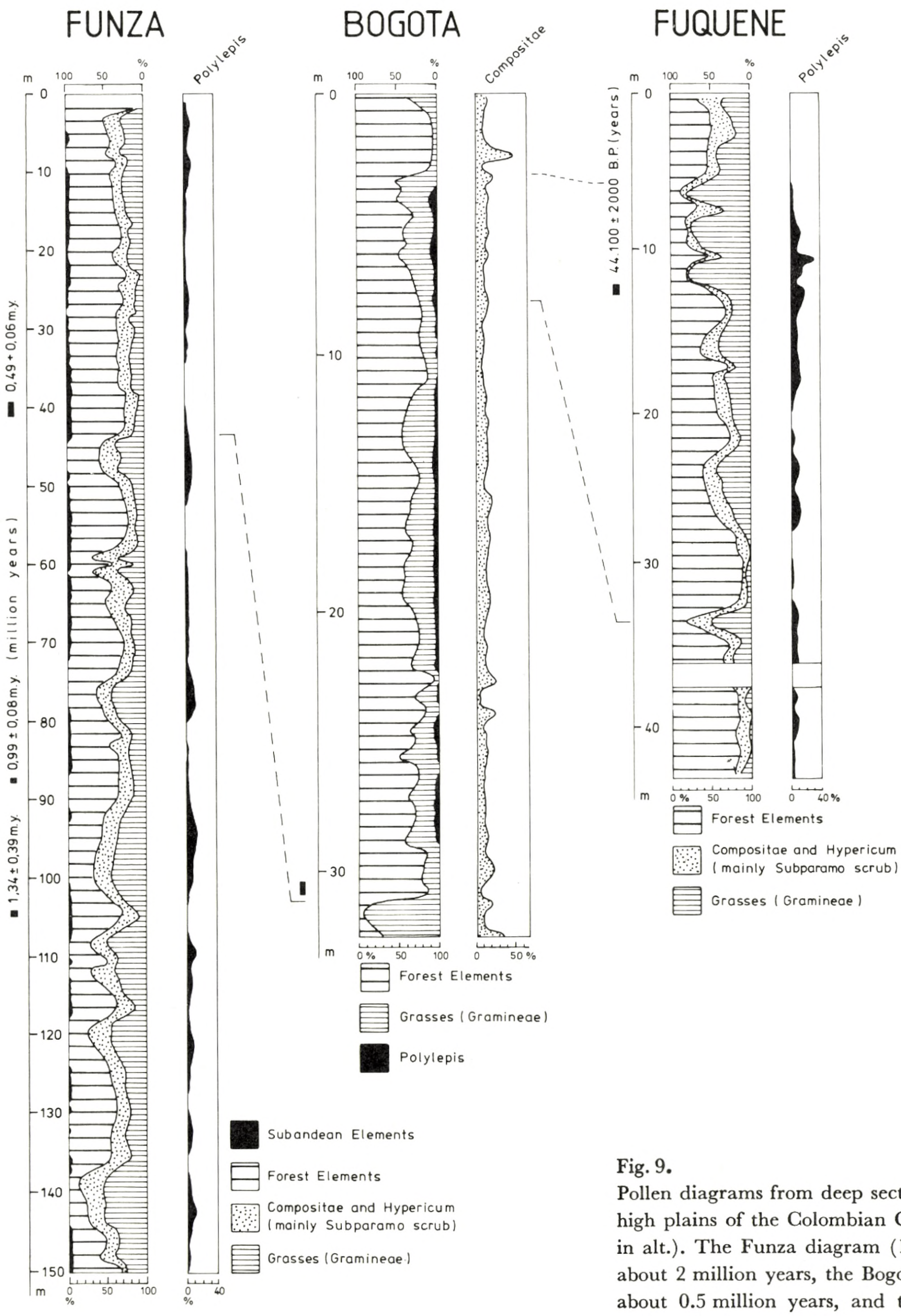


Fig. 9.
Pollen diagrams from deep sections of lake deposits from the high plains of the Colombian Cordillera Oriental (c. 2580 m in alt.). The Funza diagram (150 m of sediment) represents about 2 million years, the Bogotá section (c. 30 m sediment) about 0.5 million years, and the Fúquene section (c. 40 m sediment) about 100,000 years. The lines between the diagrams connect contemporaneous levels. (Based on unpublished Funza and Fúquene diagrams, and on Van der Hammen & Gonzalez, 1960).

The diagram in the middle of Fig. 9 is from Bogotá. It represents 30 m and about 500,000 years, and the sedimentation rate must have been much slower than it was in Fúquene. The lake of Bogotá dried up some 30,000 years ago, at a level of approximately – 3 m in the section, the entire Upper Pleniglacial being represented by a soil with a very high percentage of Páramo elements. This was later covered over by Late-Glacial and Holocene river clays. The interval between 3 m and 11 m represents (the remainder of) the whole, ultimate interglacial-glacial cycle, and downwards something like four glacials and three interglacials are evident. The lowermost (at c. 30 m) contains layers of volcanic ash also present in the corresponding interglacial interval at about – 40 m in section Funza (Fig, 9, left), where the ashes were dated as 0.49 ± 0.06 million years old (by fission-track dating). It thus becomes possible to follow the sequence downwards in this 150 m of section, with at least 7 interglacial-glacial cycles. On the base of data provided by other intercalated ash layers the age of the level at about – 87 m (interglacial) could be dated as 0.99 ± 0.08 million years, and another at – 104 m (interglacial) as 1.35 ± 0.39 million years. Other sections from the high plain of Bogotá, not shown here, indicate that several additional and similar cycles are found downward, at least down to a level of something like 3 million years old.

Let us now turn to the tropical lowland (between 0 and 400 m alt.). The fact that the tropical forest did not become replaced by subtropical forest of the sub-Andean type indicates that the lowering of the temperature cannot have been more than, say, 5° C. For an estimation the surface water temperatures of the southern Caribbean Sea, which at present has a temperature corresponding with the average annual temperature, may serve as a yard-stick. As we know from analysis of deep-sea sediments that 18,000 years ago the temperature was something like 2,5° lower than it is to-day, it seems reasonable to estimate a lowering by about 3° C for the tropical lowlands of South America.

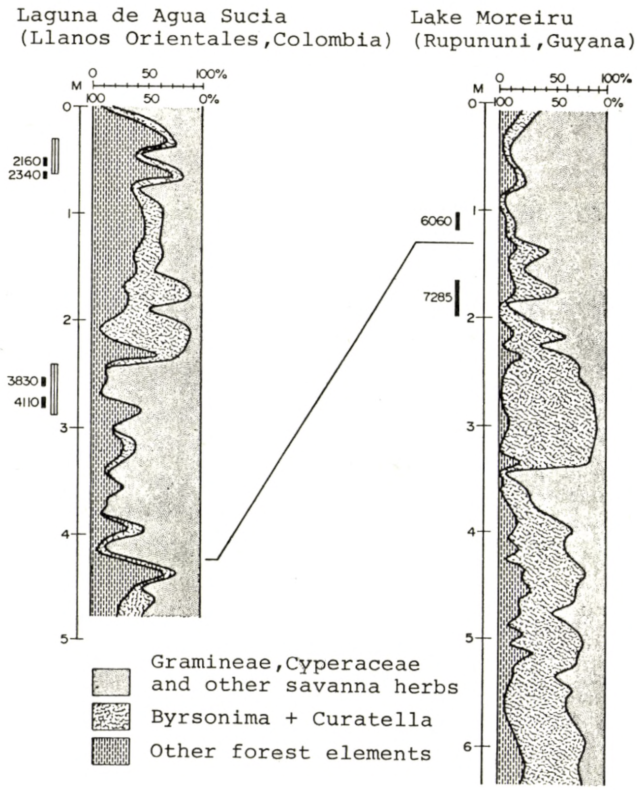


Fig. 10.
Pollen diagrams from tropical savannah areas. The one at the left from lake Agua Sucia (Colombian Llanos Orientales), the one at the right from the lake Moreiru (Rupununi Savannahs, Guiana). ^{14}C ages in years are indicated at the left in the diagrams. The diagrams represent c. 6000 and probably > 12,000 years respectively. (Van der Hammen, 1974; adapted from Wijmstra & Van der Hammen, 1966).

Although we cannot directly deduce any changes of temperature from the pollen diagrams of the tropical lowlands, there were significant vegetational changes.

Fig. 10 shows two pollen diagrams from present-day tropical savannah areas: the Colombian Llanos Orientales (left) and the Rupununi Savannah of Guiana (right). The first, from Lake Agua Sucia, is from an area at present covered for 90% with grass savannah and the rest with forest, mainly along small streams. The upper spectrum of the pollen diagram shows a similar proportional representation in the pollen rain. In the grass savannahs small trees or shrubs of *Byrsonima* and *Curatella* are typical elements and it is known that *Byrsonima* may form a type of savannah woodland in other places as soon as the circumstances are favourable.

Three groups have been used to draw up the pollen diagrams: one (at the right) representing open grass savannah elements, one *Byrsonima* and *Curatella* (middle), and one the other forest elements (left; gallery forest and marsh forest elements). The diagram at the left represents about 6000 years of vegetational history. After a short phase characterised by a high percentage of forest elements, elements of the open savannah became dominant (in about the same proportion as to-day). Apparently, this represents a dry time, because, finally, between 4000 and 3800 ^{14}C years ago, the level of the lake fell, and peat was formed. When the lake level rose again, there was a local and short-lived maximum of marsh forest elements, but subsequently the open savannah was almost completely replaced by *Byrsonima* woodland. Somewhat later the ratio between marsh forest and open savannah elements increased again, and between 2400 and 2000 years ago the lake level became so low again that the area became covered with marsh forest once more and again peat was formed.

After c. 2000 B.P. the lake level rose again and the local marsh forest disappeared but now human influence (mainly through the burning of woody vegetation) increasingly becomes stronger until the present situation with a dominating grass savannah became established.

The diagram at the right in Fig. 10 (Lake Moreiru, Guiana), is also from an area dominated at present by a grass savannah. From a depth of 2 metres a ^{14}C date of c. 7300 B.P. is available and probably the lower part of the section is of last-glacial age. Between -6 and -4 metres *Byrsonima* woodland dominated, but between 3,5 and 4 meters there was a very high maximum of open savannah elements. At the same time the lake level became very low (it almost completely dried up) and the rate of sedimentation was probably slow. Immediately afterwards the lake level began to rise again, and a closed *Byrsonima* woodland dominated the area.

From about 8000 B.P. onwards the representation of grass savannah elements increased again, with several fluctuations until they finally became dominant after 6000 B.P. No direct dating of the savannah period of $-3{,}5$ m is available, but it might be older than 10,000 B.P. At any rate the two diagrams show that considerable vegetational change took place in the tropical savannahs, principally from grass savannah to savannah woodland, or vice versa.

The contemporaneous fluctuations of the lake level show that the grass savannah phases correspond with intervals characterised by a lower effective precipitation. The dry phases between 5000 and 3800 B.P. and between 2400 and 2000 B.P. are also known from the Andean highlands, and possibly the very dry period at $-3{,}5$ m in Lake Moreiru equally corresponds with a very dry phase in the Andes, *e.g.*, with the dry period between 20,000 and 13,000 B.P. From other diagrams (from the coast of Guiana and Surinam), we know that during the last glacial with a low sea level, these areas were covered with grass savannahs, which is probably indicative of increased seasonality in, and a decrease in the annual amount of rainfall.

The supposition that many tropical lowlands were drier during glacial times was first brought forward by geomorphologists and biogeographers. Locally dunes were found underlying tropical rain forest, and sometimes indications of a former type of erosion and accumulation indicating a great instability of the soils. The distribution of species and subspecies of birds, reptiles, plants, etc. in, *e.g.*, the Amazon rain forest, had already induced biogeographers to postulate dry past periods when rain forest was restricted to large "islands" (refugia) surrounded by savannahs, where evolution in isolation could take place. The first pollen diagrams from the Amazon basin suggest that this indeed may have been the case, at least locally. The diagrams (Fig. 11) are from Rondonia, situated in

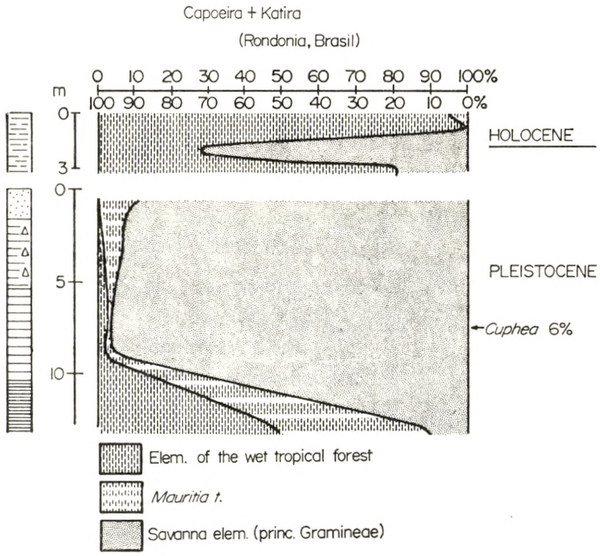


Fig. 11.
Pollen diagrams from the Southern part of the Amazon Basin (Capoeira and Katira, Rondonia, Brazil). The upper part represents the Holocene, the middle and lower portion parts of the Pleistocene. (From Van der Hammen, 1974).

the southern part of the basin. The area is nowadays covered with rain forest, and the upper diagram shows the presence of 100 % of tropical forest elements. Further down, a temporary increase of grass pollen is apparent. In the lower diagram, tropical rain- and marsh forest elements dominate at the base, but they are gradually replaced by elements of grass savannahs, while in the sediment there are signs of soil instability in the vicinity. Although we have no ^{14}C dates from this site, the sediments are most probably of Pleistocene age, and the afore-going considerations render a correspondence with some very dry part of a glacial period very probable.

In Fig. 12 the map at the left indicates the present distribution of the major vegetation formations in northern South America, and the one at the right indicates the situation during certain intervals of the Pleistocene as reconstructed by biogeographers. To prove or to disprove the details of this map additional studies will be required, but there can hardly be any doubt that part of the tropical rain forest was at least locally replaced by savannahs during the driest phases of the glacial periods.

Tropical Africa and Australia

It will now be attempted to complete the picture of the continental changes of life condition by mentioning some evidence from other continents, so as to demonstrate the universality of some of the phenomena.

The first example is from the East-African high mountains. The main vegetation belts on one of them, Mount Kenya, are shown in Fig. 13. At the base of the mountain, at approximately 1000 m alt., there are savannahs and cultivated land. On the southern slopes, montane forest is present from 2000 m alt. upward, but on the northern side forest is not found below about 3000 m alt. *Podocarpus* is an important element in this forest. Between about 2700 m and 3000/3200 m alt. lies the bamboo zone (which may be considered to be the upper part of the montane forest belt). A narrow belt of *Hagenia* forest with *Hypericum* follows (3100–3300 m). *Hagenia*, like the Andean *Polylepis*, is a member of the rose family, and resembles the latter strikingly both in appearance and habitat preference. A belt of Ericaceae follows (up to c. 3500 m), in which arborescent representations such as *Erica arborea* and species of *Philippia* are common in more or less open stands with grasses. Then follows the proper "Alpine", open tussock grasslands, with first *Senecio brassica* and the famous *Lobelia*, higher up replaced by the larger *Senecio keniodendron* with stem-rosettes. These ecological forms and as a consequence the physiognomy of the landscape, are very similar to the high Andean ones; they are apparently life forms adapted to the diurnal climate of tropical high mountains. Still higher up (c. 4500 m) the vegetation cover becomes sparser and sparser, and ultimately, permanent snow and glaciers are found. In Fig. 14 (left), a pollen diagram from Sacred Lake, at an elevation of 2400 m on Mount Kenya, is shown.

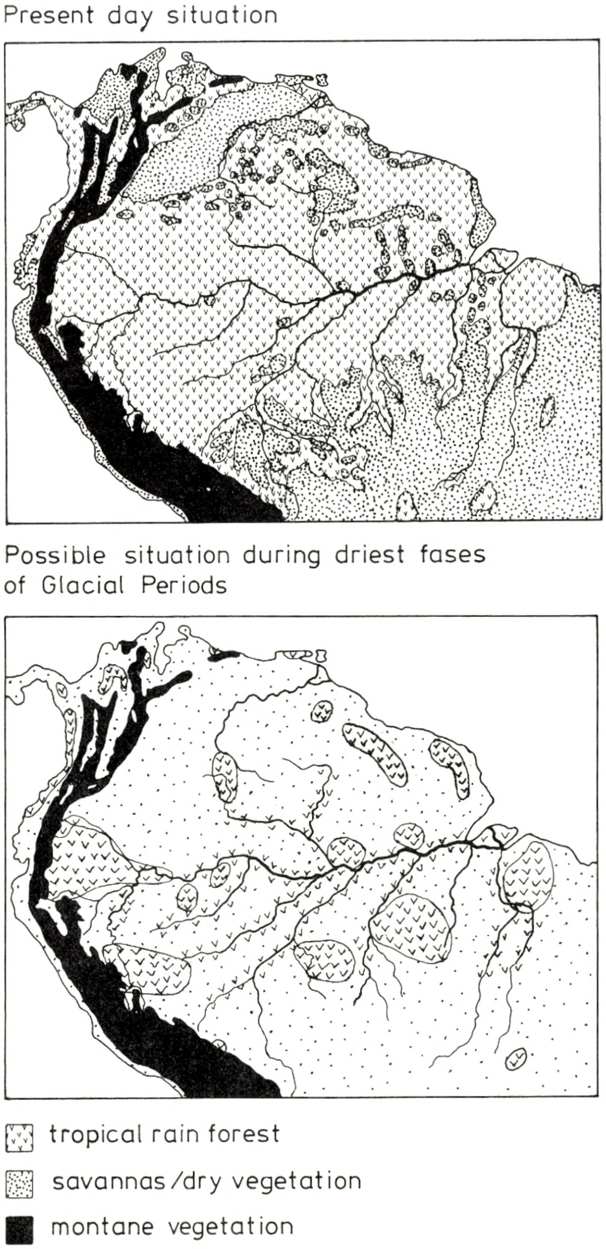
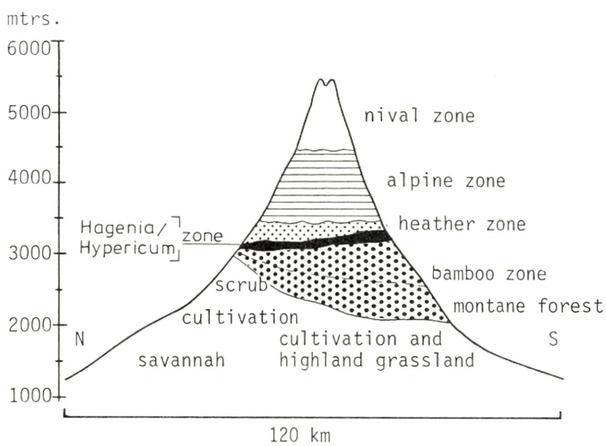


Fig. 12.
Maps of Northern South America, with present distribution of major vegetation units (above), and with a tentative reconstruction of the situation during the driest phases of glacial periods, with forest refuges (below). (After Haffer, 1977, Prance and others; adapted).

It is based on about 11 m of sediment and, according to the ^{14}C dates, represents 33,000 years of vegetational history. At the base of the diagram, open vegetation of the "Alpine" belt dominated, but around 30,000 B.P. a marked advance of the montane forest, indicating a rise of the forest limit, occurred. The local stands of vegetation remained open, however. An extended period of dominating, open alpine vegetation, followed and persisted till the Late Glacial, when the site lay within the *Hagenia* zone of the upper forest belt. After the beginning of the Holocene the climate ameliorated gradually and finally the montane forest occupied the site. From the complete palynological data (not shown here), tentative curves of the average annual temperature and humidity could be estimated (Fig. 14: right); they are drawn on the basis of a linear time scale. A calculation indicates that the mean annual temperature was at least 5° C lower than it is at present. Moreover, it was established that during the intervals corresponding with the Upper Pleniglacial and with the Late Glacial, the climate was relatively dry. At lowland sites, relevant data are provided by the fluctuations of the levels of the great East-African lakes, of which records of two of them, *viz.*, of Lake Victoria and

Fig. 13.
Diagrammatic representation of the vegetation belts on Mount Kenya (Kenya). (After Coe, 1967).



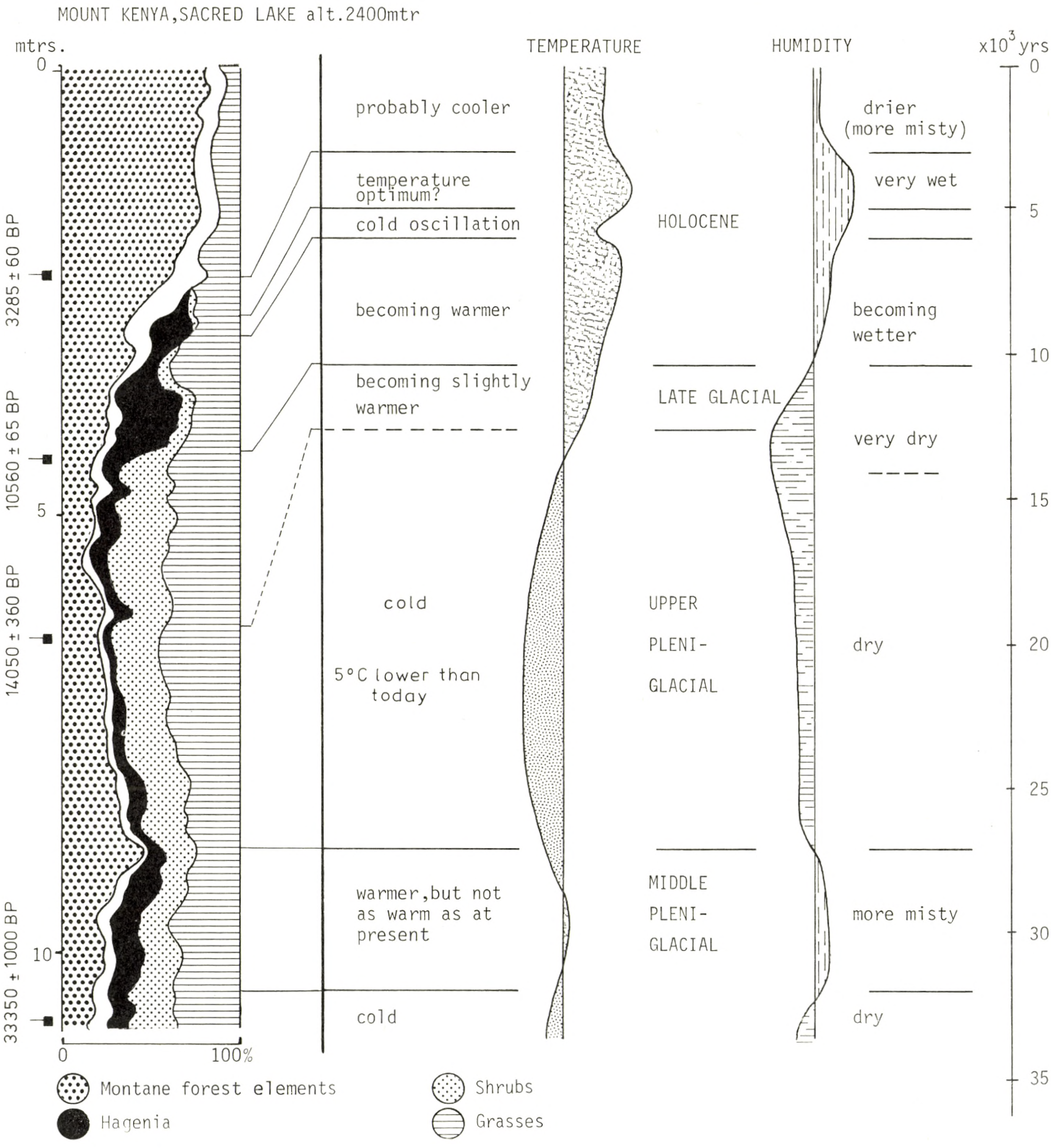


Fig. 14.
Pollen diagram from Sacred Lake (alt. 2400 m, Mount Kenya), representing the last 33,000 years (left), and the climatic interpretation (relative curves for temperature and humidity on a linear time scale) (right). Left of the pollen diagram the ^{14}C dates are indicated. (After Coetzee, 1967; adapted).

Lake Nakuru, are shown here. From Lake Victoria (alt. 1134 m) a pollen diagram and a lake level curve are available. Only the last is shown here, together with a table of the vegetation changes deduced from the pollen diagram (Fig. 15: left). Today the area is covered with semi-deciduous forest. Before 12,500 B.P. (and possibly back to 20,000 B.P.) the level of Lake Victoria was very low; it even had no outlet, so that the salinity of the water was higher. At the same time open grassland must have dominated in the area. Both facts point to a climate considerably drier than it is to-day, while an increase of *Podocarpus* pollen strongly suggests a lowering of the montane forest belt, and hence lower annual temperatures. About 12,500 years ago a sudden and considerable rise of the lake level established the outlet to the Nile again, and the water salinity became normal. Forest with abundant Oleaceae invaded the former grasslands. There was a short dry period before 10,000 B.P. when the lake level fell temporarily, which resulted in an extention of open grassland, but after that time the lake level became very high again, and the presence of an evergreen forest indicates a climate more humid than to-day. The last 6000 years show a slightly falling lake level, the vegetation cover gradually changing to its present type of semi-deciduous forest.

Data from Lake Nakuru (alt. 1763 m) are quite concurrent (Fig. 15: right): a low lake level, no outlet and high salinity before 12,500 B.P., a very high lake level and an outlet after 10,000 B.P., and later a falling of lake level leading to the present situation with a higher salinity.

These results from equatorial Africa agree rather closely with those obtained from the study of sediments of, *e.g.*, Lake Fúquene in equatorial South America (compare the curves in Fig. 7) and this permits the conclusion that very similar climatic trends prevailed in both areas in the last 20,000 years. An additional curve from Africa is available from a site situated farther to the N.W., namely in the area of Lake Tchad (13°–18° Northern Latitude), based on the history of sedimentation in the area (Fig. 16). It is a relative curve: at the right of the vertical line are the lake-phases, at the left the phases of more arid climatic conditions with, *e.g.*, dune formation. The curve points to a dry climate between c. 12,000 B.P. and 20,000 B.P. The lake level became high in the period corresponding with the Late Glacial and Early Holocene to fall again to its present position. Ample evidence from the Saharan area reveals that lakes existed in the area between 12,500 B.P. and about 6000 B.P., which is clearly indicative of a wetter climate with a denser vegetation cover than is found nowadays.

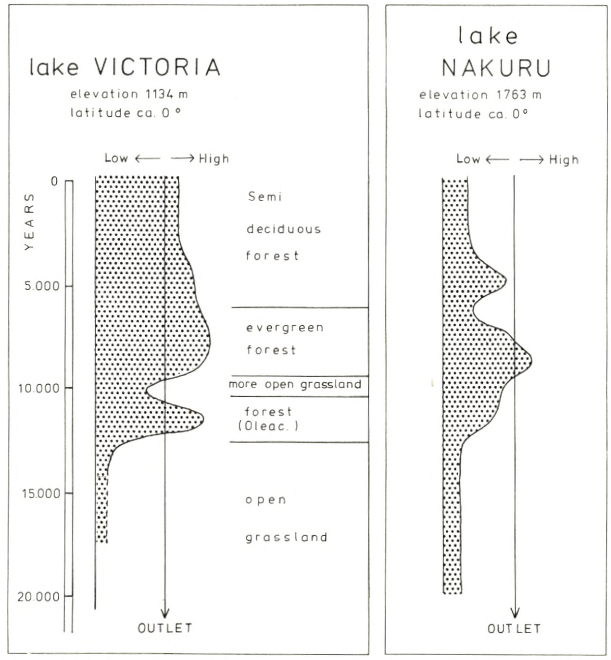
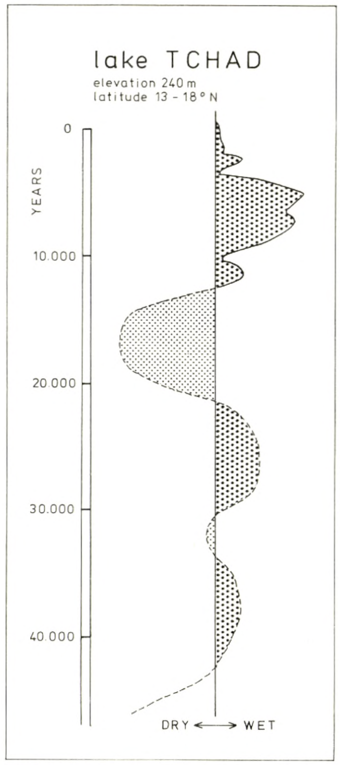


Fig. 15.
Fluctuations of the levels of some East African lakes during the last 20,000 years and their relation to the vegetational history. The minimum level of the outlet is indicated by a line. The vegetational history is reconstructed on the basis of the pollen diagram of Lake Victoria. (After Kendall, 1969 and others; adapted).

New data have recently become available from New Guinea and Australia. Only one example is given here, *viz.*, a pollen diagram from Lynch's Crater, in N.E. Queensland, Australia (Fig. 17). The site is in the area of (sub)tropical broad-leaved

Fig. 16.
Relative curve for the humidity in the area of Lake Tchad. (After Servant & Servant, 1970; adapted).

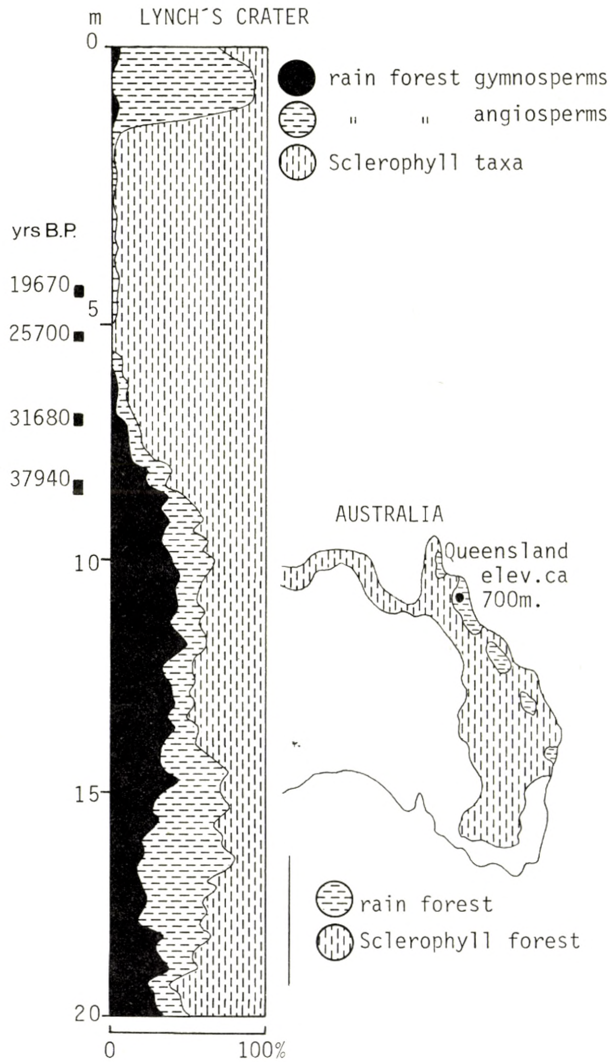


rain forest. Towards the west this forest changes into a sclerophyll forest with *Eucalyptus* trees. The diagram is partly ^{14}C dated, and represents a time-span of probably more than 60,000 years. From that time onward to about 38,000 B.P. subtropical rain forest with abundant stands of *Araucaria* existed, and the annual rainfall may have been about half of the present amount. This forest was gradually replaced by sclerophyll vegetation between 38,000 B.P. and 27,000 B.P., which is indicative of a considerable decrease in precipitation. After 10,000 years B.P. rain forest Angiosperms started to dominate, and the present situation was attained. The arid phase between 27,000 B.P. and the beginning of the Holocene is the most striking feature.

Although there are minor differences in the history of life conditions in the various tropical areas discussed, the close correspondence of the major trends is remarkable. There is also a clear relation with the paleoclimatic events in the northern temperate zone, especially as regards the temperature fluctuations, but there is often also a coincidence of the principal dry phases.

The most important conclusions are that the principal trends in climatic changes during the last 30,000 years were global, and that there was also

Fig. 17.
Pollen diagram of 20 m of sediment from Lynch's Crater (N. E. Queensland, Australia), representing 60,000 years. Radiocarbon ages in years B.P. are indicated. (From Kershaw, 1967; adapted).



a correspondence in the sequence of intermittent glacial and interglacial periods during the last one million years (or conceivably even during a longer time-span). This points very strongly to a common cause that effected the conditions for life throughout the world, albeit that the local effect may to some extent have differed from place to place, Fig. 18 shows a world map on which reliable information from a number of sites is indicated concerning the question whether 18,000 years ago, during the maximum of the Last Glacial, the climate was drier or wetter than it is to-day. It is clear that most parts of the earth were arid or at least drier than they are to-day, notwithstanding the lower annual temperatures (which must have kept the rate of evaporation low). The Southwestern United States, now lying in an arid zone, must have been exceptional in that there was at that time a higher effective precipitation. The world-wide incidence of a greater aridity during a period of maximum glaciation is not surprising, if one takes into consideration the overall lower temperatures of the ocean water (see below) and a lowering of the sea level by about 80 m (*i.e.*, a minimum total surface area of the seas and oceans), which in conjunction must have been the cause of a reduced evaporation from the oceans, and hence of a smaller quantity of water in circulation.

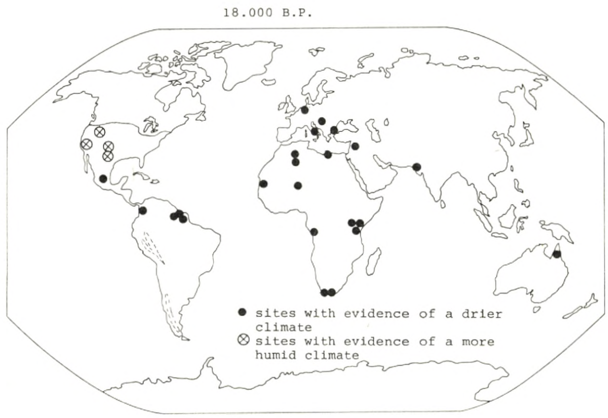


Fig. 18.
The world 18,000 years ago: sites with good evidence of a relatively arid climate (mostly drier than at present) or a relatively humid climate (mostly more humid than at present).

The history of life conditions in the oceans

The other major environment for life, that of the oceans, also became subjected to changes. It is interesting to ascertain whether the changes in the conditions for life are correlated with the continental record.

Huge quantities of small organisms, such as foraminifera, radiolaria, diatoms, coccoliths, etc. live in the oceans. Many of them live planktonically in the superficial water of the ocean, and make calcareous or siliceous tests or skeletons. When these organisms die, their skeletons sink to the bottom of the ocean, where they are deposited, partly together with mineral particles. These deep sea sediments are as valuable a source of information as the lake sediments on the continents. In recent years considerable numbers of cores from deep sea sediments have been collected in all the oceans. Quantitative analyses of the organisms in these cores, more or less along the lines of pollen analysis, in conjunction with direct or indirect dating, have produced an incredible quantity of new information regarding the history of life in the oceans and the concomitant changes in, for instance, the mean seawater temperature and the salinity. There is still another approach to the study of these cores which has yielded a wealth of information, *viz.*, the analysis of changes in the $^{16}O/^{18}O$ ratios in the calcareous tests of foraminifera. It reflects the isotopic composition of the water (and to a minor extent the temperature of the water). When water evaporates from the oceans and is not returned because of the increasing accumulation of ice on the continents, in other words: when the sea level drops, the proportion of ^{18}O in the seawater increases. An analysis of the $^{16}O/^{18}O$ ratio in the tests of foraminifera from different levels of sea cores, therefore, basically yields an ice-volume curve. This curve must be the same for every part of the oceans and this renders it a most valuable tool for correlation.

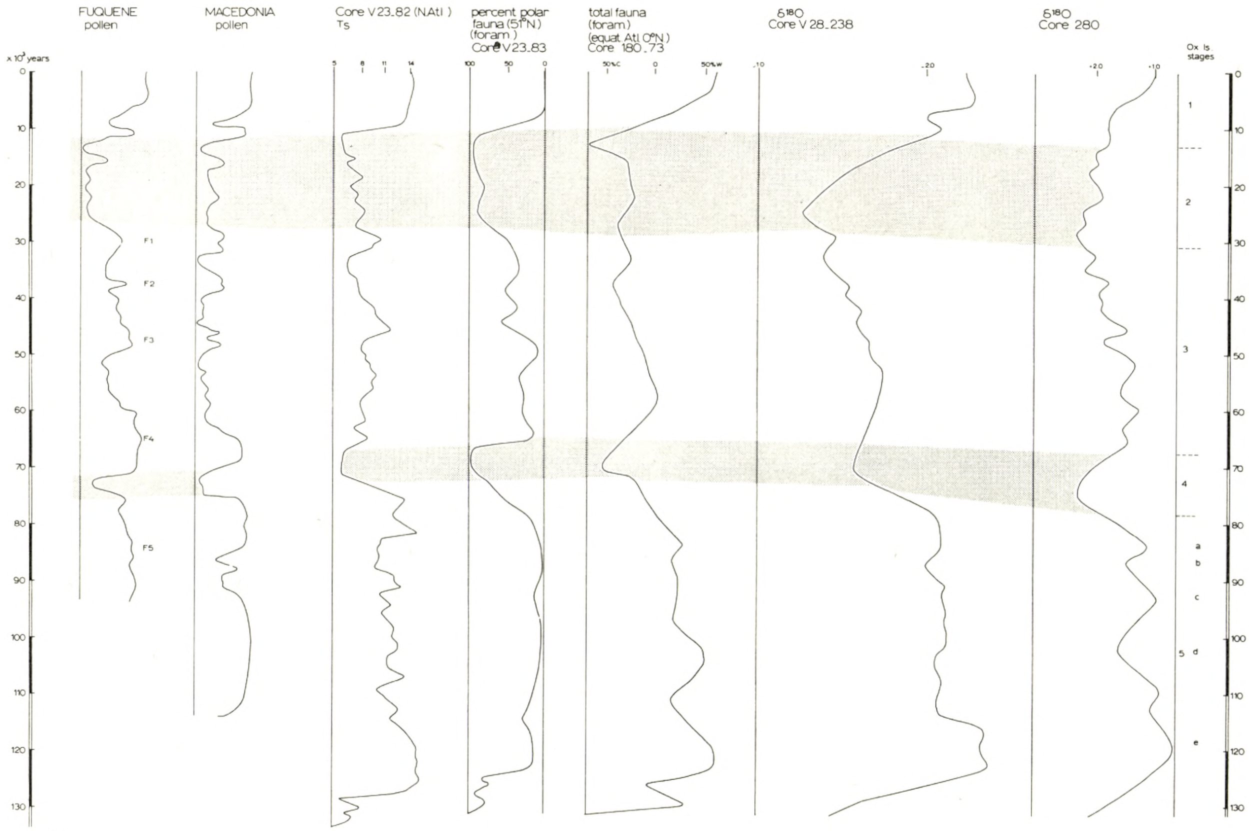


Fig. 19.
Correlation of curves of factors related to climatic conditions prevailing the last 130,000 years. From left to right: Relative changes of altitudinal forest limit, Fúquene (Cordillera Oriental, Colombia; Wijmstra & Van der Hammen, 1974). Relative changes in the proportion of forest and steppe vegetation, Philippi (Eastern Macedonia, Greece; based on Wijmstra, 1969). Changes of summer temperature of surface ocean water, based on associations of foraminifera in the North Atlantic deep sea core V23–82 (Sancetta, Imbrie & Kipp, 1974). Changes of percent polar fauna (foraminifera) in North Atlantic deep sea core V23–83 and in Atlantic Core 180–73 (McIntyre et al., 1972); Oxygen isotope curves for two deep sea cores (Shaekleton & Opdyke, 1973; Emiliani, 1958; Emiliani & Shackleton, 1974).

In Fig. 19 (middle) two curves are shown, one representing the summer temperature of superficial ocean water (based on foraminiferal associations) during the last 130,000 years and the other simply recording the percentage of polar fauna in respect of the total foraminiferal associations. They are based on two North Atlantic cores from different localities. The dating is based on ^{14}C analyses and on other radioactive dating methods, and estimated by inter- and extrapolation. Taking the relativily much larger sample distance (and hence less detail) in the ocean curves into account, there is a satisfactory agreement in the general course of the curves and those from the continents (Fúquene and Macedonia; Fig. 19: left). The salient features are the extended and possibly "tripartite" interglacial complex, the short very cold phase at the beginning and the longer one at the end of the last glacial, and an intermediate part with somewhat higher temperatures, and the warmer Holocene. Although the general correlation seems to be quite reliable, several minor points must be cleared up, especially as regards the correlation with the N.W. European Early Glacial interstadials in this general scheme.

If the ^{14}C dates of 56,000–c. 60,000 for these interstadials and the indirect dating of the lower part of the ocean curves is correct, they must be younger than the first temperature minimum (date 70,000 B.P. in the deep sea cores). If this is so the upper two phases of the "interglacial complex" are unknown in N.W. Europe (the first being the Eemian). However, this problem will certainly be solved in the near future.

In Fig. 20 (left) a diagram of foraminiferal associations is shown of a long core from the North Atlantic Ocean. The Polar association is on the right side of this diagram, then follow towards the left, the warmer ones: the Subpolar and Transitional + Subtropical associations. The whole sequence represents some 600,000 years and shows seven complete warm-cold cycles for the superficial ocean waters, doubtlessly representing the same glacial-interglacial cycles we know from the continents. A correlation with the long Macedonian pollen diagram (Fig. 20: right), covering the same time interval, appears to be possible. Although there may be some doubts concerning minor details, the overall similarity of the two diagrams, based on different environment, is striking.

In Fig. 21 another tentative correlation of data from the continents and the oceans is shown. The long Macedonian curve and the long one from Bogotá are mutually compared and also compared with two oxygen isotope curves from the Pacific and the Atlantic Ocean, respectively. The stage numbers given to the phases of the oxygen isotope curves are added, and an attempt is made to correlate them with the interglacials as known from Europe. The correlation of the four curves, all apparently primarily determined by temperature, is certainly possible as soon as absolute datings or an adequate paleomagnetic stratigraphy become available.

A paleomagnetic stratigraphy of the two ocean curves is already available, and recently one of the Macedonian core was worked out. The Bogotá core has been dated directly by fission-track datings of volcanic ashes. Although further and more pre-

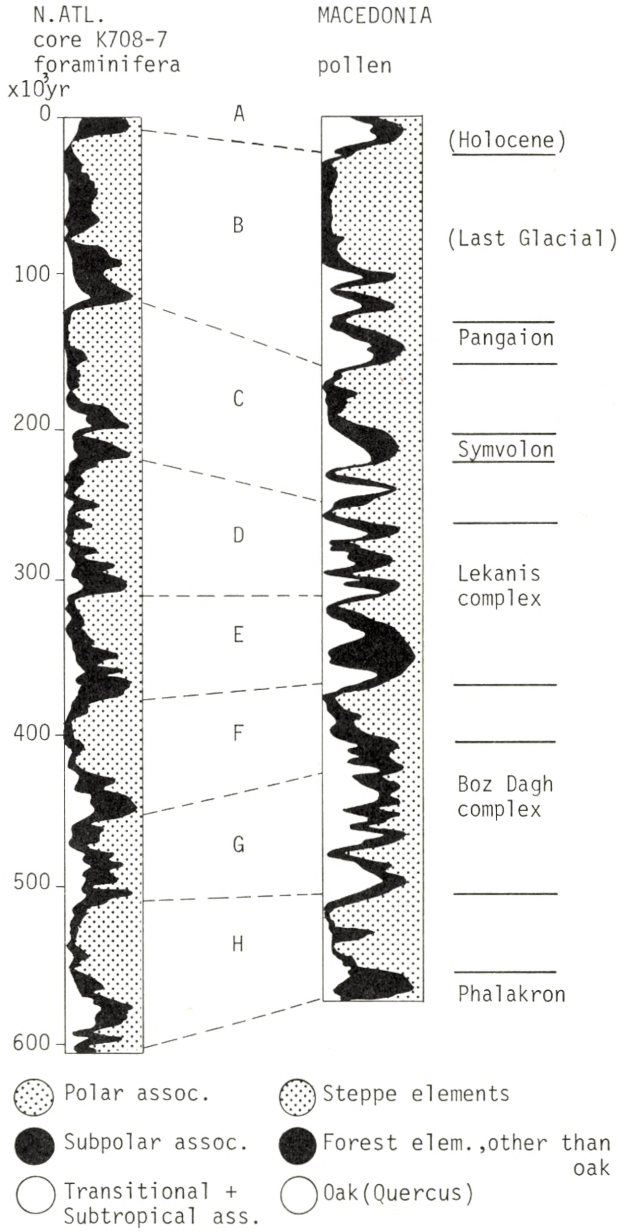


Fig. 20.
Proportional changes of ecological groups of foraminifera in North Atlantic deep sea core K 708-7 during the last 600,000 years (left); from right to left: polar, subpolar and transitional to subtropical ecological groups. Correlation is proposed with the long pollen diagram from Macedonia of Fig. 6 (right). (After Ruddiman & McIntyre, 1976; adapted).

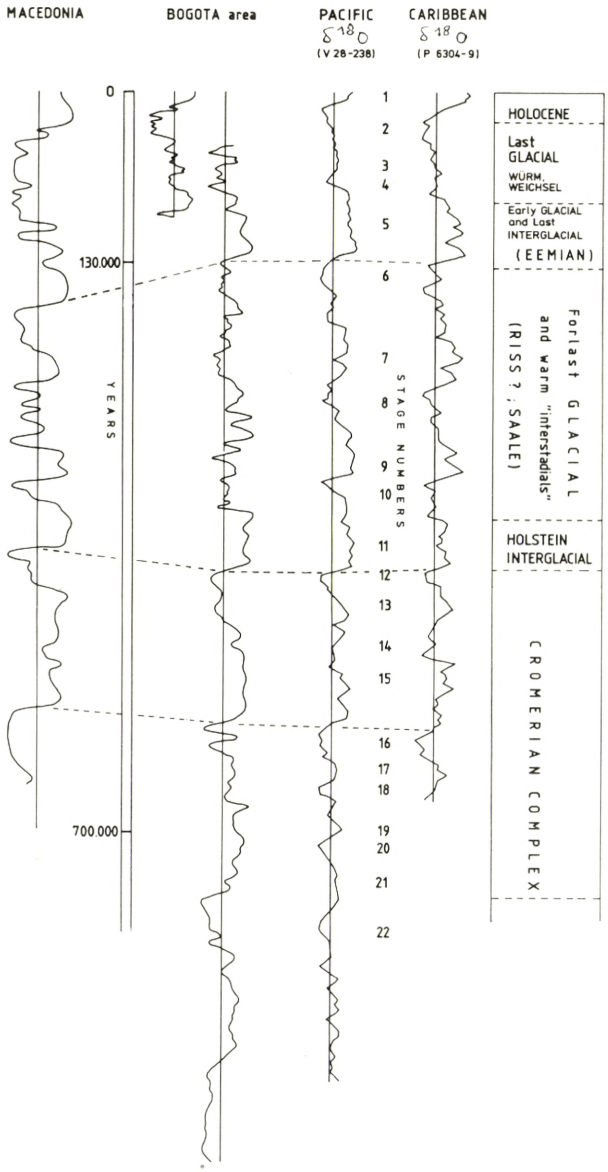


Fig. 21.
Tentative correlation of long continental and oceanic records: Macedonia (relation forest elements/steppe elements), Bogotá area (relation forest elements/páramo elements); Pacific deep sea core V28-238 (Delta ^{18}O) and Caribbean deep sea core P 6304-9 (Delta ^{18}O). Oxygen isotope stage numbers and possible European equivalent interglacials at right. (After, respectively: Wijmstra in Van der Hammen et al., 1971; Van der Hammen, unpublished; Shackleton & Opdyke, 1973, and Emiliani & Shackleton, 1974).

cise datings will be necessary to render the correlation more reliable, also in this case the general conclusion can be drawn that such a correlation of long sequences derived from oceans and continents is now possible, at least in principle. This will greatly assist us with the reconstruction of the history of life conditions during the last two or three million years, and to explain the causes and mechanisms of these climatic cycles.

During the last few years the collaborators of the CLIMAP organization (Climate Long Range Investigations, Mapping And Prediction) have done a great deal of analytical work on deepsea cores and on the reconstruction of past ocean surface temperatures. A major effort of CLIMAP was to produce temperature maps of the oceans as they were 18,000 years ago, to be used in conjunction with other data (such as the extension and thickness of the continental icesheets, the tracing of shorelines, and albedo) for the computer simulation of the ice age climate. Fig. 22 shows such a map, in a simplified form, of the northern Atlantic Ocean summer of 18,000 B.P., based on the analysis and dating of a large number of deep sea cores. At the left is the map of the present-day situation. The northernmost part of the ocean was bordered by continental ice and blocked by pack-ice, and the 10° C isotherm ran to Spain instead of to Iceland as it does to-day. The temperature differences were smaller in the tropical zone, so that there must have been a steep temperature gradient at the latitudes between Spain and Northern Africa, from 10° to 22° C. Fig. 23 shows the temperature differences between the August sea-surface temperatures of 18,000 years ago and the corresponding present-day values, for the entire world. The greatest differences are in the middle and high northern and southern latitudes. In the tropics and some other places, the temperature differences were often much smaller or even nil.

By means of this and additional basic material CLIMAP produced a computer simulation of the ice age climate. This is their first and not yet concluded experiment, but it is interesting to show

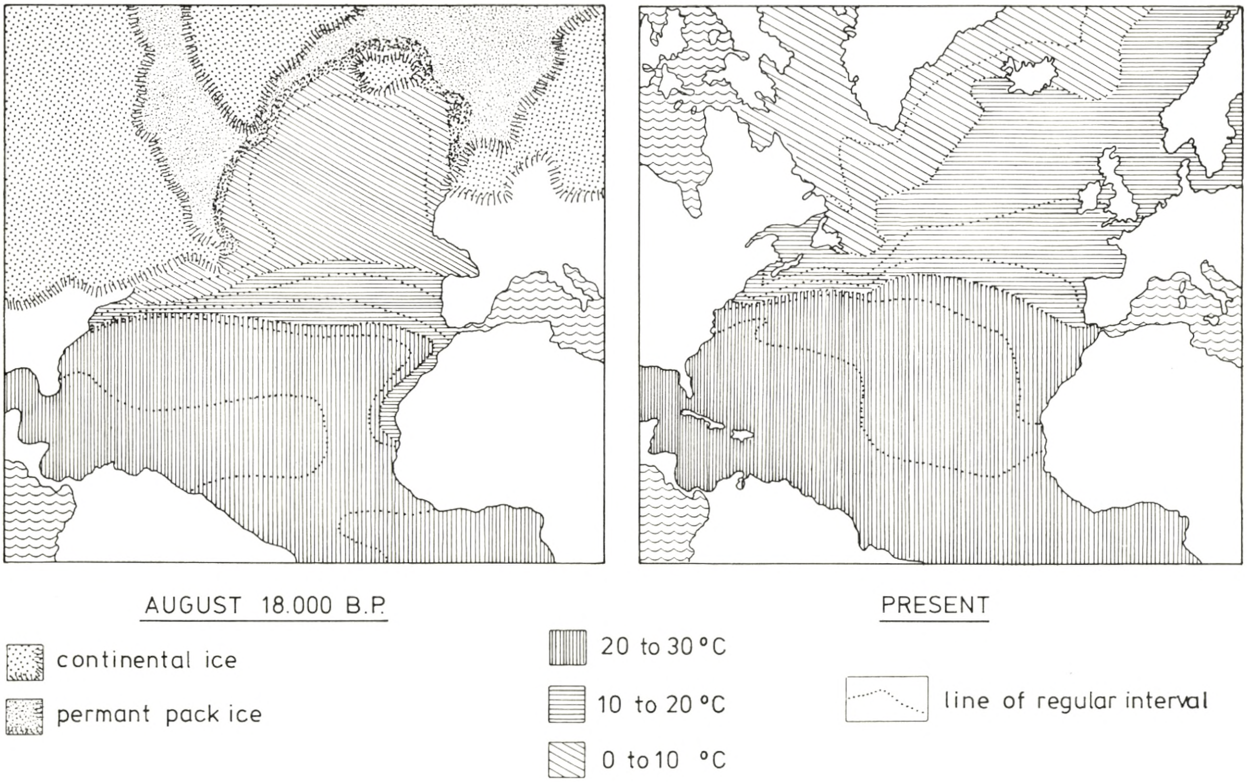


Fig. 22.
Temperature of North Atlantic surface water, at present and conditions of 18,000 years ago. A CLIMAP-reconstruction. (After McIntyre et al., 1976; adapted).

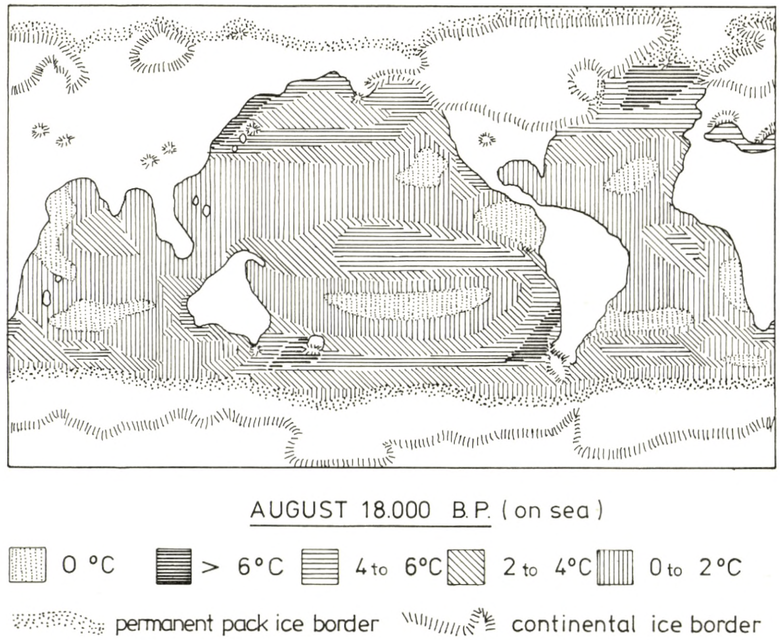
here, as an example of what has already been acomplished, the simulated differences (present values minus ice age values) of the July surface air temperature of 18,000 years ago. The lowest temperatures, (*i.e.*, the largest differences) are found on the northern hemisphere, where the continental glaciation was extensive, and particularly in Central Asia. The most striking result is the erstwhile occurrence in an ice-free area in northern Siberia of temperatures higher than at present. These kind of maps will have to be verified against the historical data from the continents (such as the map of the humidity of Fig. 18). A preliminary comparison with available data (such as the lowering of the temperature by 8° C in Bogotá, and by 5° C on Mount Kenya) shows a reasonably satisfactory agreement. An attempt is now being made to compile all available information concerning the paleotemperatures and humidity of 18,000 years ago in world maps. If these data are in agreement with the ultimate computer simulation, we may consider the results to be sufficiently trustworthy, and we can proceed to simulate the climate of other periods. Such an approach may ultimately yield a better understanding of the mechanism of climatic changes. (Fig. 24).

Discussion

The recent advances in science summarized above seem to permit the drawing of several more general conclusions.

Life conditions on earth changed profoundly and repeatedly during the last one million years, which resulted in approximately ten glacial periods alternating with interglacials. A glacial-interglacial

Fig. 23.
World map showing difference between August sea surface temperatures 18,000 years ago and at present (present minus ice-age). A CLIMAP-reconstruction. (After CLIMAP project members, 1976; adapted).



cycle apparently has an average duration of 100,000 years. There are, however, many more such cycles in the interval between three and one million years B.P., some apparently with somewhat smaller temperature amplitudes.

Changes in the life conditions effected the entire earth. While glaciers extended on the northern continents and in the mountains all over the earth, the sea level dropped by at least 80 metres, thus exposing large areas of the continental platforms. The air temperatures on the continents and the temperatures of the ocean water were considerably lower than they are to-day in most places. Since the exposed surface of the seas and oceans became smaller and the temperatures lower, the rate of evaporation was lower than it is to-day, and the total amount of precipitation on the continents was lower.

Owing to the lower temperatures in the north, and a lower rate of precipitation in, for instance, the Mediterranean area and the tropics, the areas covered by forest vegetation became drastically reduced in many parts of the earth, and were replaced by tundras, steppes or savannahs depending on the locally prevailing condition. Forest elements could survive the most severe phases of glacial periods in smaller or larger forest refuges, from where they could migrate again at the beginning of a following interglacial period.

Only the major changes of life conditions could be considered here. There are, however, many additional, minor changes, often apparently cyclic with a duration between a few thousand years and a few decades. More detailed studies of the shorter cycles are now in progress. After more knowledge of the short cycles has accumulated, the prediction of climate in the near and more distant future may be attempted.

This again raises the question, whether a future glacial period may be predicted. The computer simulation of former climates will certainly help us to acquire a better understanding of the changing global climatic system. It is also crucial to detect the *causes* of climatic changes. There can hardly be any doubt that there are many causes and not just a single one. In some of the minor cycles fluctuations of solar radiation, of the type of the well-known sun spot cycles, might very well be prima-

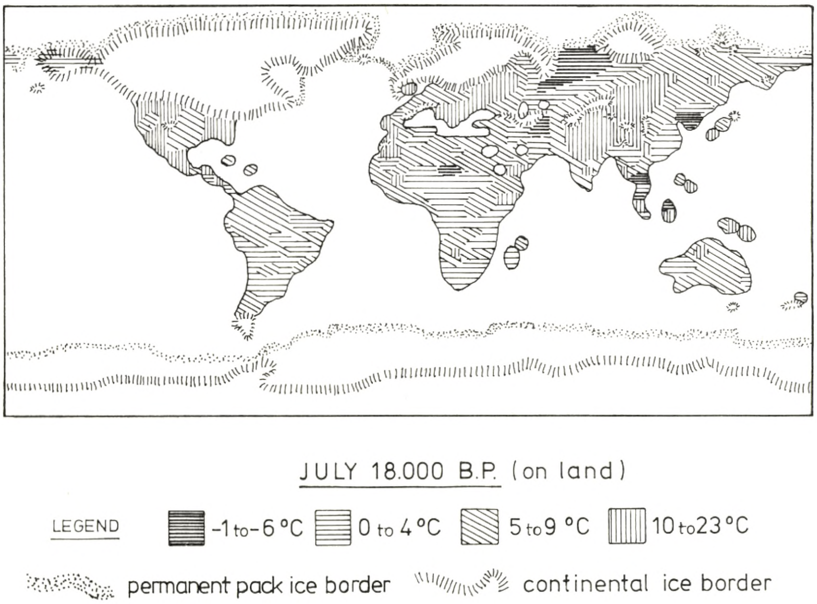


Fig. 24.
World map showing simulated differences (present minus ice-age) of July surface air temperatures 18,000 years ago. (After Gates, 1976; adapted).

rily involved. However, recently Hays, Imbry and Shackleton proved rather convincingly that changes in the earth's orbital geometry, mainly the obliquity of the earth's axis and the orbital eccentricity, indeed form the fundamental cause of the succession of Quaternary ice-ages. They estimated that 50% of the variance found in the climatic curves from the deep sea cores they analysed is attributable to the last-mentioned factor, with a period of approximately 100,000 years. Finally, they concluded that a model of future climate based on the observed orbital climate relationships predicts that the long-term trend over the next several thousand years is towards an extensive Northern Hemisphere glaciation. However, one must bear in mind that climatic oscillations of higher frequencies which are not dependent on the components of orbital geometry may temporarily change this trend, and that anthropogenic influences such as the burning of fossil fuels may also have an as yet not well-established effect. Although an extensive glaciation is certainly not an immediate threat, periods of long cold winters in Canada, and periods of extended drought in the tropical and subtropical areas (such as the Sahel and N.W. Brasil) may have most serious consequences for the world's food supply. For that reason the scientific advances of the last years are of great importance.

One may expect that continued research, including the study of the minor changes of the life conditions on earth, will provide the clues to predict the future climatic trend in greater detail, so that timely measures could be taken to avoid a disastrous shortage of food supplies. May this serve as an illustration of the benefits to humanity of studies orginally initiated for purely scientific reasons but at a later stage yielding unexpected results of considerable importance to well-being of the population of the world.

References and some other relevant publications

CLIMAP project members, 1976: The Surface of the Ice Age Earth. – Science 191: 1131–1137.

Coe, M. J., 1967: The Ecology of the Alpine Zone of Mount Kenya. – The Hague.

Coetzee, J. A., 1967: Pollen Analytical Studies in East and Southern Africa. – In: E. M. van Zinderen Bakker (editor), Palaeoecology of Africa, Vol. 3: 1–146. – Cape Town.

Emiliani, C., 1958: Paleotemperature Analysis of Core 280 and Pleistocene Correlations. – The Journal of Geology, Vol. 66(3): 264–275.

Emiliani, C. & N. J. Shackleton, 1974: The Brunhes Epoch. Paleotemperatures and isotopic geochronology. – Science, vol. 183: 511–514.

Frenzel, B., 1967: Die Klimaschwankungen des Eiszeitalters. – Brunswick.

Gates, W. L., 1976: Modeling the Ice-age Climate. – Science 191: 1138–1144.

Geel, B. van & E. Kolstrup, 1978: Tentative Explanation of the Late Glacial and Early Holocene Climatic Changes in North-Western Europe. – Geologie en Mijnbouw, Vol. 57 (1): 87–89.

Haffer, J., 1977: Pleistocene Speciation in Amazonian Birds. – Amazoniana 6 (2): 161–191.

Hammen, T. van der, 1974: The Pleistocene Changes of Vegetation and Climate in Tropical South America. – Journal of Biogeography 3: 3–26.

Hammen, T. van der & E. Gonzalez, 1960: Upper Pleistocene and Holocene Climate and Vegetation of the "Sabana de Bogotá" (Colombia, South America). – Leidse Geol. Meded., Vol. 25: 261–315.

Hammen, T. van der, T. A. Wijmstra & W. H. Zagwijn, 1971: The Floral Record of the Late Cenozoic of Europe. – In: K. K. Turekian (editor). The Late Cenozoic Glacial Ages. New Haven & London, Yale University Press.

Hays, J. D., J. Imbrie & N. J. Shackleton, 1976: Variations in the Earth's Orbit: Pacemaker of the Ice Ages.– Science 194: 1121–1131.

Iversen, J., 1973: The Development of Denmarks Nature since the last Glacial. – Geology of Denmark III, Danmarks Geol. Unders. V, 7-C.

Kendall, R. L., 1969: An Ecological History of the Lake Victoria Basin. – Ecol. Monogr. 29: 121–176.

Kershaw, A. P., 1976: A Late Pleistocene and Holocene Pollen Diagram from Lynch's Crater, North-eastern Queensland, Australia. – New Phytol. 77: 469–498.

Kolstrup, E. & T. A. Wijmstra, 1977: A Palynological Investigation of the Moershoofd, Hengelo and Denekamp Interstadials in the Netherlands. – Geol. en Mijnbouw, Vol. 56 (2): 85–102.

Livingstone, D. A. & T. van der Hammen, 1978: Palaeogeography and Palaeoclimatology. – In: Tropical Forest Ecossystems, a State-of-Knowledge Report prepared by UNESCO/UNEP/FAO: 61–90. Paris, UNESCO.

McIntyre, A., W. F. Ruddiman & R. Jantzen, 1972: Southward Penetrations of the North Atlantic Polar Front: Faunal and Floral Evidence of Largescale Surface Water Mass Movements over the Last 225,000 Years. – Deep-Sea Research 19: 61–77.

McIntyre, A., N. G. Kipp, A. Bé, T. Crowley, T. Kellog, J. V. Gardner, W. Prell & W. F. Ruddiman, 1976: Glacial North Atlantic 18,000 Years Ago: a CLIMAP-reconstruction. – Geol. Soc. Amer. Mem. 145: 43–76.

Ruddiman, W. F. & A. McIntyre, 1976: Northeast Atlantic Paleoclimatic Changes over the Past 600,000 Years. – Geol. Soc. Amer. Mem. 145: 111–146.

Sancetta, C., J. Imbrie & N. G. Kipp, 1974: Climatic Record of the Past 130,000 Years in North Atlantic Deep-Sea Core V23–82: Correlation with the Terrestrial Record. – Climatic Research Unit (Norwich), R.P. 2: 62–65.

Servant, M. & S. Servant, 1970: Les Formations Lacustres et les Diatomées du Quaternaire Récent du Fond de la Cuvette Tchadienne. – Rev. Geogr. Phys. et Geol. Dynam. 12: 63–76.

Shackleton, N. J. & N. D. Opdyke, 1973: Oxygen Isotope and Palaeomagnetic Stratigraphy of Equatorial Pacific Core V28–238: Oxygen Isotope Temperatures and Ice Volumes on a 10^5 Year and 10^6 Year Scale. – Journal of Quaternary Research, Vol. 3 (1): 39–52.

Woillard, G. M., 1978: Grande Pile Peat Bog: a Continuous Pollen Record for the Last 140,000 Years. – Quaternary Research 9: 1–21.

Wijmstra, T. A., 1969: Palynology of the First 30 m of a 120 m Deep Section in Northern Greece. – Acta Botanica Neerl. 18 (4): 511–527.

Wijmstra, T. A. & T. van der Hammen, 1974: The Last Interglacial-glacial Cycle: State of Affairs of Correlation Between Data Obtained from the Land and from the Ocean. – Geologie en Mijnbouw 53: 386–392.

Indleveret til Selskabet marts 1979.
Færdig fra trykkeriet august 1979.

Biologiske Skrifter

Biol. Skr. Dan. Vid. Selsk.
Priser excl. moms

Vol. 17 (DKr. 330.-)

1. Degerbøl, Magnus, and Fredskild, Bent: The Urus (*Bos primigenius* Bojanus) and Neolithic Domesticated Cattle (*Bos taurus domesticus* Linné) in Denmark. With a Revision of *Bos*-Remains from the Kitchen Middens. Zoological and Palynological Investigations. 1970 ... 200.–
2. Hansen, Hans Jørgen: Electron-Microscopical Studies on the Ultrastructures of some Perforate Calcitic Radiate and Granulate Foraminifera. 1970 .... 50.–
3. Mathiesen, Fr. J.: Palaeobotanical Investigations into some Cormophytic Macrofossils from the Neogene Tertiary Lignites of Central Jutland. Part II: *Gymnosperms*. 1970 .... 80.–

Vol. 18 (DKr. 450.-)

1. Hansen, Georg Nørgaard: On the Structure and Vascularization of the Pituitary Gland in some Primitive Actinopterygians (*Acipenser, Polyodon, Calamoichthys, Polypterus, Lepisosteus* and *Amia*). 1971 ..... 70.–
2. Dyck, Jan: Structure and Spectral Reflectance of Green and Blue Feathers of the Rose-faced Lovebird (*Agapornis roseicollis*). 1971 .... 60.–
3. Perch-Nielsen, Katharina: Elektronenmikroskopische Untersuchungen an Coccolithen und verwandten Formen aus dem Eozän von Dänemark. 1971 ... 160.–
4. Böcher, Tyge W., and Lyshede, Ole B.: Anatomical Studies in Xerophytic Apophyllous Plants. II. Additional Species from South American Shrub-Steppes. 1972 .... 160.–

Vol. 19 (DKr. 410.-)

1. Humphreys, William F., and Lützen, Jørgen: Studies on Parasitic Gastropods from Echinoderms. I. On the Structure of the Parasitic Gastropod Megadenus cantharelloides n. sp., with Comparisons on Paramegadenus n. g. 1972 .... 30.–
2. Surlyk, Finn: Morphological Adaptations and Population Structures of the Danish Chalk Brachiopods (Maastrichtian, Upper Cretaceous). 1972 .... 60.–
3. Hammer, Marie: Tahiti. Investigation on the Oribatid Fauna of Tahiti, and on some Oribatids found on the Atoll Rangiroa. 1972 .... 80.–
4. Wingstrand, Karl Georg: Comparative Spermatology of a Pentastomid, *Raillietiella Hemidactyli*, and a Branchiuran Crustacean, *Argulus Foliaceus*, with a Discussion of Pentastomid Relationships. 1972 .... 80.–
5. Böcher, Tyge W., and Jørgensen, C. A.: Jyske dværgbuskheder. Eksperimentelle undersøgelser af forskellige kulturindgrebs indflydelse på vegetationen. With an English Summary. 1972 .... 50.–
6. Lützen, Jørgen: Studies on Parasitic Gastropods from Echinoderms. II. On *Stilifer* Broderip, with Special Reference to the Structure of the Sexual Apparatus and the Reproduction. 1972 .... 30.–
7. Rasmussen, H. Wienberg: Lower Tertiary Crinoidea, Crinoidea, Asteroidea and Ophiuroidea from Northern Europe and Greenland. 1972 .... 80.–

Vol. 20 (DKr. 490.-)

1. Blom, Lars: Ridge Pattern and Surface Ultrastructure of the Oviducal Mucosa of the Hen (*Gallus domesticus*). 1973 .... 30.–
2. Jensen, Poul Vagn: Structure and Metamorphosis of the Larval Heart of *Calliphora erythrocephala*. 1973 .. 30.–
3. Hammer, Marie: Oribatids from Tongatapu and Eua, the Tonga Islands, and from Upolu, Western Samoa. 1973 .... 80.–
4. Gooding, Richard U., and Lützen, Jørgen: Studies on Parasitic Gastropods from Echinoderms. III. A Description of *Robillardia Cernica* Smith 1889, Parasitic in the Sea Urchin *Echinometra* Meuschen, with Notes on its Biology. 1973 .... 30.–
5. Manton, I., and Leadbeater, B. S. C.: Fine-structural Observations on six Species of *Chrysochromulina* from Wild Danish Marine Nanoplankton, including a Description of *C. campanulifera* sp. nov. and a Preliminary Summary of the Nanoplankton as a Whole. 1974 .... 40.–

6. BIRKELUND, TOVE, and HANSEN, HANS JØRGEN: Shell Ultrastructures of some Maastrichtian Ammonoidea and Coleoidea and their Taxonomic Implications. 1974 .... 50.–
7. POULSEN, CHR.: Silurian Pelecypoda, Monoplacophora, and Gastropoda from the Reefy Facies of the Offley Island Formation of Washington Land and Offley Island (Northwest Greenland). 1974 .... 30.–
8. BÖCHER, TYGE W.: Structure of the Multinodal Photosynthetic Thorns in *Prosopis Kuntzei* Harms. 1975 .... 60.–
9. MATHIESEN, FR. J.: Palaeobotanical Investigations into some Cormophytic Macrofossils from the Neogene Tertiary Lignites of Central Jutland. Part III: Angiosperms. 1975 .... 80.–
10. BROMLEY, R. G., SCHULTZ, M.-G., and PEAKE, N. B.: Paramoudras: Giant Flints, Long Burrows and the Early Diagenesis of Chalks. 1975 .... 60.–

Vol. 21 (DKr. 650.–)

1. NYGAARD, GUNNAR: New or Interesting Plankton Algae. 1977 .... 150.–
2. PEEL, JOHN S.: Systematics and Palaeoecology of the Silurian Gastropods of the Arisaig Group, Nova Scotia. 1977 .... 150.–
3. VAN DER LAND, JACOB, and NØRREVANG, ARNE: Structure and Relationship of Lamellibrachia (Annelida, Vestimentifera). 1977 .... 200.–
4. HAMMER, MARIE: Investigations on the Oribatid Fauna of the North West Pakistan. 1977 .... 150.–

Vol. 22 (*uafsluttet/unfinished*)

1. WINGSTRAND, K. G.: Comparative Spermatology of the Crustacea Entomostraca 1. Subclass Branchiopoda. 1978 .... 150.–
2. ALEXANDERSEN, VERNER: Sūkās V. A Study of Teeth and Jaws from a Middle Bronze Age Collective Grave on Tall Sūkās. 1978. (Publications of the Carlsberg Expedition to Phoenicia 6. The other reports from this expedition are printed in the *Historisk-filosofiske Skrifter*, including no. 5, *Hist.-fil. Skr.* 10:1, with the report of the excavation in question: Henrik Thrane: Sūkās IV, 1978, 100 DKr.) 80.–
3. BÖCHER, TYGE W., and OLESEN, PETER: Structural and Ecophysiological Pattern in the Xero-Halophytic C_4 Grass, *Sporobolus rigens* (Tr.) Desv. 100.–
4. HAMMER, MARIE, and WALLWORK, JOHN A.: A Review of the World Distribution of Oribatid Mites (*Acari: Cryptostigmata*) in Relation to Continental Drift. 1979 50.–
5. JØRGENSEN, C. BARKER; LARSEN, LIS OLESEN, and LOFTS, BRIAN: Annual Cycles of Fat Bodies and Gonads in the Toad *Bufo Bufo Bufo (L.)*, Compared with Cycles in Other Temperate Zone Anurans. 1979 .... 40.–
6. VAN DER HAMMEN, THOMAS: Changes in Life Conditions on Earth during the past One Million Years. 1979 .... 40.–
7. THOM, RENÉ: Théorie des catastrophes et biologie: Plaidoyer pour une biologie théorique. 1979 ...... 30.–
8. BÖCHER, TYGE W.: Xeromorphic Leaf Types. Evolutionary Strategies and Tentative Semophyletic Sequences.
9. HAMMER, MARIE: Investigations on the Oribatid Fauna of Java.

Volume 23

1. NIELSEN, ANKER: A Comparative Study of the Genital Chamber in Female *Trichoptera*.

Printed in Denmark by Bianco Lunos Bogtrykkeri A/S. ISSN 0366-3612. ISBN 87-7304-087-8