INTERGLACIAL VEGETATIONAL SUCCESSION AND LAKE DEVELOPMENT IN DENMARK

SVEND TH. ANDERSEN

Geological Survey of Denmark, Charlottenlund, Denmark

ABSTRACT

Deposits from three interglacial stages are now known in Denmark. The Eemian Interglacial is the youngest one and is known from marine as well as numerous fresh-water deposits. The Holsteinian Interglacial has been studied only in a marine deposit, whilst a still older interglacial is known from the fresh-water deposits of Harreskov, Ølgod and Starup.

The author has studied the forest succession of the Eemian in the lake deposits at Herning and Hollerup. 7 interglacial pollen zones are recognized. Light requiring plants were frequent in the early and the late stages of the succession, and acidophilous plants increase their frequencies in its later part. The lakes reflect a parallel development from basic to acid conditions, or from calcareous to non-calcareous deposition.

The interglacial vegetational succession represented in the deposits at Harreskov and Ølgod is divided into 6 pollen zones. It differs essentially from the Eemian succession. Nevertheless, the general features of the successions are very similar, and the lake development is parallel too.

The interglacial vegetational successions thus fall into a protocratic, a mesocratic and an oligocratic stage, the last stage being conditioned by soil evolution rather than by climatic change.

THE plant successions of the Quaternary interglacial stages in northern Europe have been sufficiently studied to prove their unique importance for the building of a Quaternary chronology in this area. Thus we know that the interglacial vegetational successions differed so much from each other that individual interglacials can be recognized and serve as corner stones in the Quaternary stratigraphy. In the present paper I shall emphasize not such differences in general vegetational development, but rather the possible common features or analogies of the interglacial successions studied by me. Indeed, the interglacial vegetational successions represent long and uninterrupted sequences of vegetational stages intercalated between periods of vegetational annihilation, and their possible fundamental principles may therefore be of interest.

Deposits from three interglacial stages are known in Denmark, the Eemian, the Holsteinian, and a still older one, which is probably of Cromerian age (ANDERSEN, 1963), however, the Holsteinian Interglacial is represented only by marine deposits at present. From the other two interglacial stages I have selected deposits that are lacustrine throughout and contain the complete interglacial plant succession as those best suited for pollen analysis.

Interglacial floras are of considerable age, and have been subjected to the hazards of migration during one or more glacial stages. We may therefore wonder whether evolutionary changes have occurred. The early Quaternary interglacial floras of northern Europe differ substantially from the present, but the middle and late Quaternary floras in this area are essentially similar to the flora of today, and the number of extinct species is limited. The vicissitudes of migration may have caused changes in the racial constitution of the species, however, as I have discussed at an earlier occasion (ANDERSEN, 1961), such evolutionary changes during migration need not have been inevitable. The whole biomass of a species may have migrated and survived glaciations without changes if the refugial areas offered sufficient variation of habitat. The credibility of conclusions about the character of the past environments does increase if supported by the parallel behaviour of several species or genera of common ecology today, but if a species behaves unexpectedly, one may be aware of the possibility that its ecology has changed. Thus the surprisingly late immigration of *Picea abies* from the east into northwestern Europe in the Eemian Interglacial and in the Postglacial was presumably caused by its failure to survive in western European refugia during the preceding glacials with the extinction of its oceanic biotypes as a consequence, and the explosive development of *Fagus silvatica* in the Postglacial was probably due to the formation of a new and aggressive race, as pointed out by Firbas (1951, 1958).

The pollen diagram shown in Fig. 1 is from the Eemian Interglacial site at Hollerup in north Jutland. The deposit, earlier described by Jessen & Milthers (1928), consists of lake marl and diatomite. The lake was about 300 m. across, and the pollen diagram comes from the deeper part of the deposit. The diagram shows curves for the most common trees and shrubs and for the total of herbaceous plant pollen. This short paper is not the place for a discussion of the fundamental principles of pollen analysis, but it may be emphasized, that pollen diagrams from lake sediments do express a general development, which is repeated in every similar deposit in a wide area. The present pollen diagram is based on the total pollen sum excluding only the aquatics, and the pollen analyses thus include pollen produced by the reed and swamp

vegetation which bordered the lake. However, the influence of such strictly local vegetation is indeed small. Thus the total of herbaceous plant pollen, which includes the pollen of possible reed vegetation, constitutes only one per cent of the pollen total at the time when the forest was most dense, and the *Alnus* curve, which includes pollen derived from the swamp forest, reaches only 10-20 per cent. Its constancy indicates indeed, that the strictly local vegetation belts did not expand their area substantially. It may thus be assumed that the lake had rather steep shores, and that no extensive swamp vegetation existed.

The pollen diagram from Hollerup is typical of the Eemian Interglacial in Denmark, and its curves are nearly identical to the curves in the pollen diagram from the site at Herning, which I have shown at an
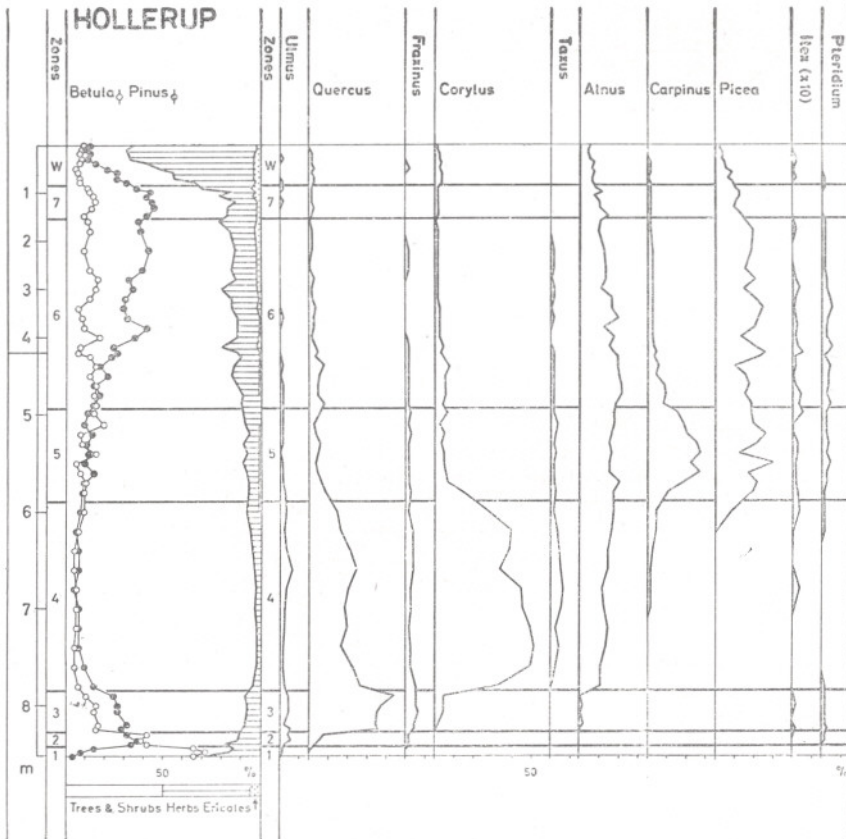
TEXT-FIG. 1 — Pollen diagram from the interglacial lake deposit at Hollerup, Denmark (Eemian Interglacial).

earlier occasion (ANDERSEN, 1964). The curves allow a subdivision of the interglacial succession into seven pollen zones, the details of which I shall omit mentioning here.

The pollen diagram indicates a long succession of forest stages. Thermophilous plants such as *Viscum*, *Hedera* and *Cladium* are recorded from the earliest zones, and we must assume that there was a rapid initial temperature increase, and that the climate quickly became warm and oceanic. Still, the trees and shrubs immigrated and spread with varying efficiency. *Betula* and *Pinus* expanded first, and *Ulmus*, *Quercus* and *Fraxinus* also immigrated and expanded rapidly. *Alnus*, *Corylus* and *Taxus* immigrated more slowly, and *Carpinus* and *Picea* appeared and spread at a late point of time. Numerous pollen diagrams from Denmark and north Germany show a similar sequence, and it seems that immigration opportunity and seed dispersal capacity were more important for the order of immigration than climate. There is indeed little indication of climatic change throughout the interglacial, and the climatic optimum extended into zone 6, where *Ilex* was frequent, and where such thermophilous plants as *Buxus*, *Viscum*, *Hedera*, *Lonicera periclymenum* and *Osmunda* are recorded. The temperature probably decreased at the transition to zone 7, and the interglacial forest succession ends with a very distinct rise of the herb pollen curve and decreases of *Pinus*, *Betula*, *Picea* and *Alnus*. The interglacial forest was here replaced by non-forest vegetation in a climate of glacial type.

A clearer picture of the vegetational changes may be obtained by summarizing the curves for plants of common ecological preferences. A similar method was used for the Herning site (ANDERSEN, 1964). Curve A in Fig. 2 is intended to show the competitively weak plants, which do not tolerate shade, curve B summarizes the plants indicative of raw humus or acid peats, and curve C summarizes the most important plants of the rich soils, and in addition, a curve for *Quercus*. The trends of the curves from Hollerup are indeed very similar to those from Herning. Curve A divides the interglacial succession into three phases, (I) with a decreasing curve, (II) with low values of curve A, and (III) with again increasing values of these plants. The first stage of the interglacial succession

was thus characterized by high values for the light-requiring plants. At that time the glacial drift was still raw and unleached. The light-requiring plants decreased due to the spreading of the shade-giving *Ulmus*, *Quercus*, *Taxus*, *Corylus* and *Alnus*. In stage II the forest reached maximum denseness. The plants of rich soils (curve C) reach maximum frequencies, and the vegetation was apparently in equilibrium for a considerable time. Mull soils presumably prevailed. In this state leaching of the soil salts to some extent is counteracted by the mixing activity of the soil fauna and the ability of the prevailing trees and shrubs to extract bases from the deeper soil layers and contribute them to the upper layers during the decomposition of their litter. However, a slow removal of calcium carbonate will bring the soils into a less stable state, where the equilibrium may more easily be disturbed.

The re-increase of the light-requiring plants (curve A) in stage III coincides with the increase of curve B, which is intended to summarize the plants characteristic of acid soils. *Picea abies* prevails in this group, and it may be superfluous to point out the tendency of this tree to promote an accumulation of acid organic material when it grows in regions with a humid climate. The simultaneous spreading of the light-requiring plants and the acidophilous plants and decrease of the plants of rich soil suggest soil deterioration due to the accumulation a mor layer. From the present day, Swedish soil investigators (LUNDBLAD, 1924; TAMM 1930; ROMELL 1935; LINNERMARK, 1961) have shown how easily grey-brown podsolic soils, which support *Quercus* or *Carpinus* forest, change into podsols at the introduction of *Picea*. The mechanism of this process may not be fully known, however, it seems that the tendency of *Picea* to form a flat root system and the unattractiveness of its needles to the soil mixing fauna and their resistance against decay may help to provoke accumulation of mor and subsequent podsolization (KRAUSS *et al.*, 1939; WITTICH, 1953). Only on soils flushed by calcareous seepage water does *Picea* not promote raw humus accumulation under humid climatic conditions (TAMM, 1930; GENSSLER, 1959).

The pollen curves in Fig. 2 thus suggest that the immigration and expansion of
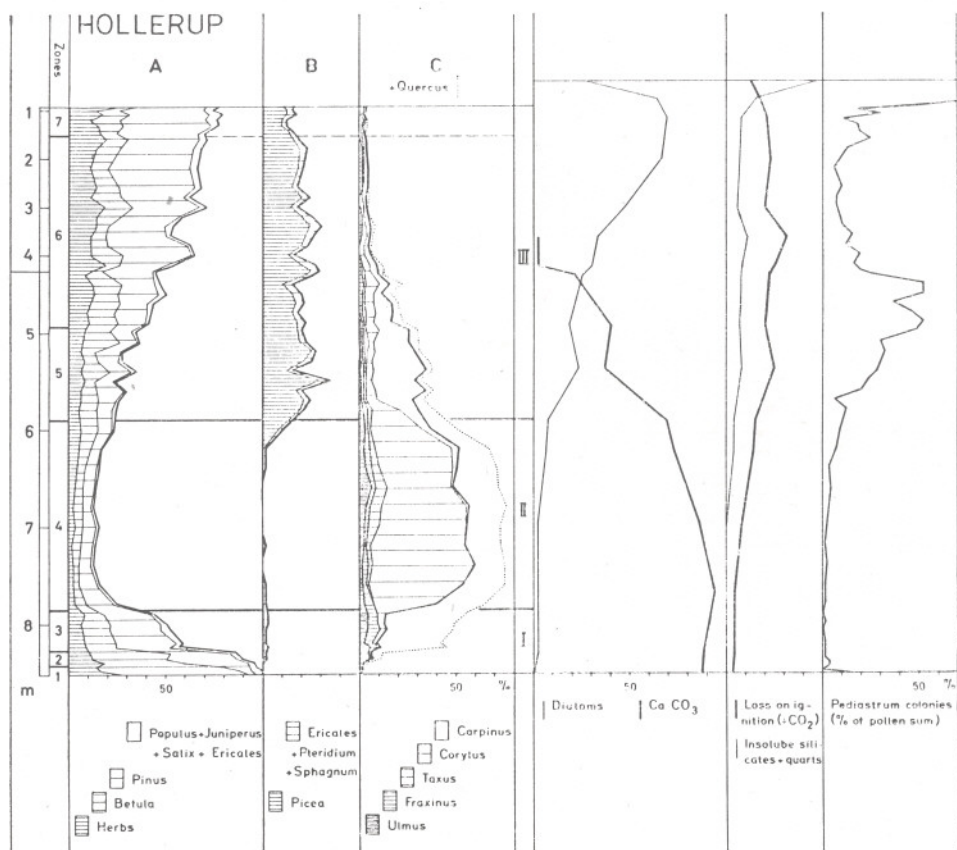
TEXT-FIG. 2 — Cumulative pollen curves for plants of various ecological categories (A, B and C, cp. text), and chemical composition of the lake sediments in the interglacial deposit at Hollerup, Denmark. I: protocratic stage II: mesocratic stage, III: oligocratic (and telocratic) stage.

Picea in the middle stage of the Eemian Interglacial in Denmark provoked podsolization with subsequent expansion of open heath forest at least on the better drained soils. The low lying soils presumably resisted the soil leaching better, however, as the seepage water became increasingly poor, even these habitats became impoverished, and the rich soil plants disappeared almost entirely.

The changes towards more oligotrophic conditions that I have described occurred in the climatic optimum of the Eemian Interglacial. Iversen has recently shown (1964) that a retrogressive succession from mull to mor type forest occurred on sandy soils in the Subboreal of the Danish Postglacial. In the Eemian Interglacial soil degradation and retrogressive succession probably began on the best drained soils too, however, it progressively affected all soils.

Conclusions about soil development based on the changes in the pollen content of lake sediments must of course remain speculative. It is unfortunately not possible to study the soils of the Eemian Interglacial in Denmark, as the interglacial surface was destroyed during the subsequent Weichselian Glacial. However, soil evolution may be reflected in lake ontogeny itself, as shown by Pearsall (1921), Lundquist (1927), Groschopf (1936), Pennington (1943), Hansen (1956) and Pearsall *et al.* (1960). In the interglacial lake at Herning, which was deficient in lime, I have shown a development from base-rich to base-poor water parallel to the deterioration of the upland soils (ANDERSEN, 1964).

The Hollerup site was surrounded by soils of initially high calcium carbonate content. Curves for the content of calcium carbonate, diatom silica, ignitable matter, and insoluble silicates + quartz in the lake sediments are shown in Fig. 2 together with a curve for the frequency of *Pediastrum* colonies in relation to the pollen sum. Initially, the carbonate content is extremely high. The lake received apparently strongly calcareous water from its surroundings, and the sedimentation of calcium carbonate overshadowed the sedimentation of other matter entirely. As the content of insoluble mineral matter is low, it may be concluded that the calcium carbonate was precipitated in the lake from dissolved bicarbonate adduced by seepage water, but it is difficult to say whether the lime was precipitated due to bilogic activity of aquatic organisms or to decrease of carbon dioxide pressure in the water by physical exchange. However, the low content of microorganisms and the low organic content do suggest a lake with low production. At any rate, large amounts of bicarbonate were transported into the lake and precipitated there. This strong leaching of calcium carbonate suggests highly calcareous soils, and a high biologic activity in the top soil layers, as CO_2 produced by the activity of roots and soil microorganisms is mainly responsible for the solution of calcium carbonate. The low biologic activity of the lake was presumably due to poorness of nutrients, as the leaching of soil minerals other than lime will be insignificant, until the calcium carbonate has been removed.

About half way up in the profile in Fig. 2, the calcium carbonate content of the sediments decreases, and diatom silica subsequently dominated the sedimentation entirely. The curve for calcium carbonate is remarkably similar to the curve C of the pollen diagram, which represents the plants of the richest soils. As these plants decreased, the carbonate leaching apparently decreased too. Whilst the leaching of calcium carbonate thus was strong under the mull soil conditions, this process ceased at the spreading of a mor layer, probably mostly because the subsequent shallowing of the soil profile induced the surplus water to run off superficially and not penetrate deeply into the soil. With the absence of calcium carbonate in the top soil, other minerals became leachable. This apparently caused an improved nutrient status in the lake, and rich planktonic and benthic communities developed, as shown by the rich diatom flora, the higher content of ignitable matter, and the high *Pediastrum* frequencies at the level where the calcium carbonate curve decreases.

The rigorous conditions at the end of the interglacial are reflected by an increase of the content of insoluble silicates + quartz in the lake sediment (FIG. 2). This increase in allochthonous mineral matter was no doubt due to increased surficial erosion. Curiously enough, the *Pediastrum* curve rises to very high values (maximally 520 per cent). Although this curve is calculated only relatively to the pollen precipitation and does not show absolute frequencies, the multiplication of the *Pediastrum* frequencies by about 50 suggests indeed a renewed productivity. Thus the erosion apparently caused improved nutrient status in the lake.

Fresh-water deposits from a still older interglacial are known in Denmark. This interglacial preceded the Holsteinian and is probably contemporaneous with the Cromerian. I have earlier shown a pollen diagram from Ølgod in western Jutland (ANDERSEN, 1964). The present diagram (FIG. 3) is from the site at Harreskov earlier described by Jessen and Milthers (1928). These lake deposits intercalated between clay layers represent the entire interglacial stage. The pollen curves from Harreskov are nearly the same as those at Ølgod, and the same six pollen zones can be distinguished. The earliest stage was a *Pinus-Betula* forest quickly superceded by deciduous forest. A major part is characterized by high values for *Quercus*, *Ulmus*, and *Taxus*. *Corylus* is not very prominent, and *Carpinus* is absent. Decreased temperature is indicated at the transition to zone 6, as all the tree curves decrease except *Pinus*, *Betula* and *Picea*. The herb pollen increases at the top of the diagram, indicating a transition to forestless vegetation.

Cumulative curves for ecological categories are shown in Fig. 4. Curve A shows the light-requiring and competitively weak plants, curve B shows the plants characteristic of acid humus or peat, and curve C the plants of rich soils, and *Quercus*. Three stages are suggested again, (I) with decreasing values of the light-plants, (II) with high values for the rich soil plants, and

TEXT-FIG. 3 — Pollen diagram from the interglacial lake deposit at Harreskov, Denmark (Harreskovian Interglacial).

(III) with increasing frequencies for the light-plants and the acidophilous plants. In this interglacial *Picea* was present in the earliest stage, and the light-plants and the acidophilous plants gradually expanded as calcium carbonate was leached and a mor layer formed. It may be noticed that the *Quercus* values do not decrease together with the rich soil plants. *Quercus* undoubtedly was a member of the rich soil vegetation, but the species probably persisted on the acid soil types, and the competition of *Picea* was apparently less pronounced than in the Eemian Interglacial.

The curves for calcium carbonate and diatom content of the lake sediments (FIG. 4) are very similar to those from the Hollerup site. The early stages have high calcium carbonate content and low diatom content, low loss on ignition and low *Pediastrum* frequencies. The carbonate content decreases markedly, parallel to curve C of the pollen diagram, and the diatom content and the *Pediastrum* frequencies increase at the same level. The lake development is thus strikingly similar to the development

at Hollerup and shows a similar dependance of upland vegetational and soil development, although the details of forest succession differ widely in the two interglacial stages.

At the top of the section at Harreskov insoluble silicates + quartz increase indicating strong erosion and transport of allochthonous matter in the approaching glacial stage.

I have shown pollen diagrams characteristic of two interglacial stages, and two similar diagrams have been mentioned at an earlier occasion. (ANDERSERN, 1964). In order to compare the trends of development of these four interglacial sites, I have calculated average frequencies for the various pollen zones (FIG. 5). The sites Herning and Hollerup represent the Eemian Interglacial, and the sites Ølgod and Harreskov the older interglacial, that we may tentatively call Cromerian or Harreskovian. The curves A, B and C designate the same categories as before, A being the competitively weak and light-requiring plants, B the plants of acid humus, and C the plants of rich soils including *Quercus*. Average
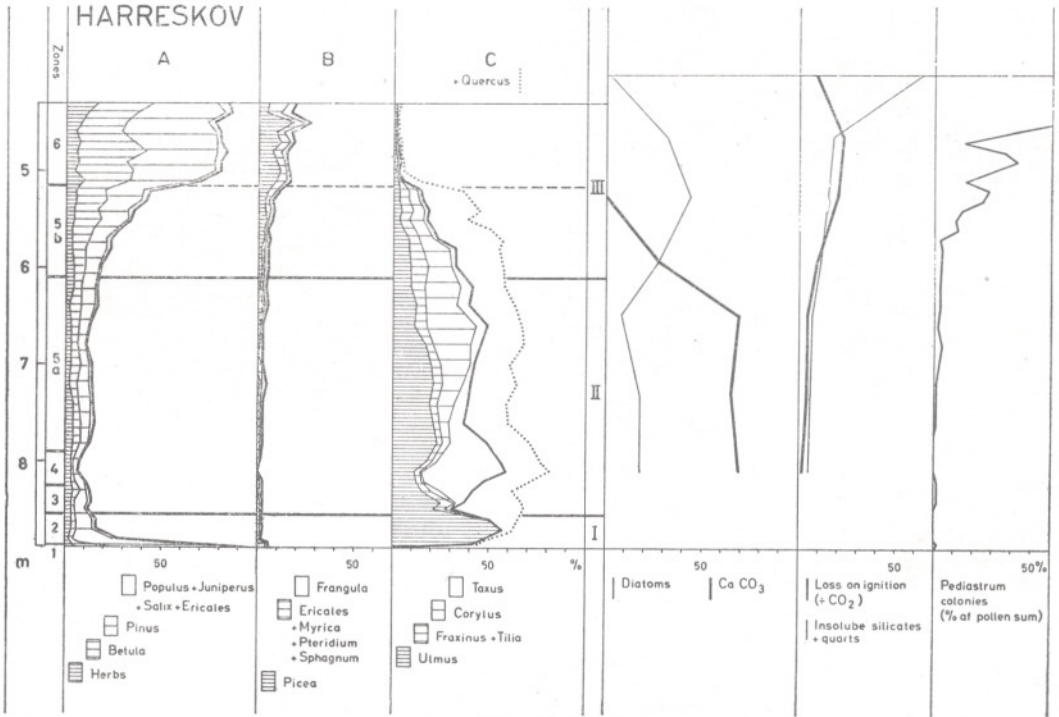
TEXT-FIG 4 — Cumulative pollen curves for plants of various ecological categories (A, B and C, cp. text), and chemical composition of the lake sediments from the interglacial deposit at Harreskov, Denmark. I: protocratic stage, II: mesocratic stage, III: oligocratic (and telocratic) stage.

frequencies for *Alnus*, *Ilex* and *Hedera* are also shown. The pollen frequencies have been calculated without corrections, and since we may wonder about the influence of differential pollen production and dispersal capacity on the curves, the curves have been re-calculated according to the method employed by Fægri & Iversen (1964) and shown in Fig. 6. It may be seen that the re-calculation causes little change in the trends of the curves, and it makes little difference whether we contemplate one figure or the other.

It can be seen from Figs. 5 and 6 that the curves A, B and C have very characteristic trends. It should be remembered that we contemplate sites from two interglacial stages, which differ greatly in the details of vegetational development, and two sites from each interglacial. Nevertheless, the curves are very much alike. The curves A are almost symmetrical, with maximum values in the lower and upper parts of the interglacials, the curves B all have maximum values in the upper part,

and the curves C are almost binomially distributed, with a maximum in the middle part of the interglacials. The curves may illustrate the response of undisturbed vegetational successions to the changes of the environment. The plants of curve A constituted pioneer forest of open type in the earliest parts of the interglacials, they became suppressed by the shade-giving and -tolerant trees and shrubs, and they re-expanded due to decreased competition pressure as a result of degeneration of the soils. The acidophilous plants shown in curve B were absent or insignificant on the immature soils of the early stage, but once the soils had matured, they expanded with the progress of soil degeneration, or may be, they expanded by means of soil degeneration. The plants of curve C, the plants of the dense climax forest, were slow to immigrate and establish themselves. Therefore they were absent from the earliest stage. Once established, they dominated the vegetation until they were forced back by the soil impoverishment.
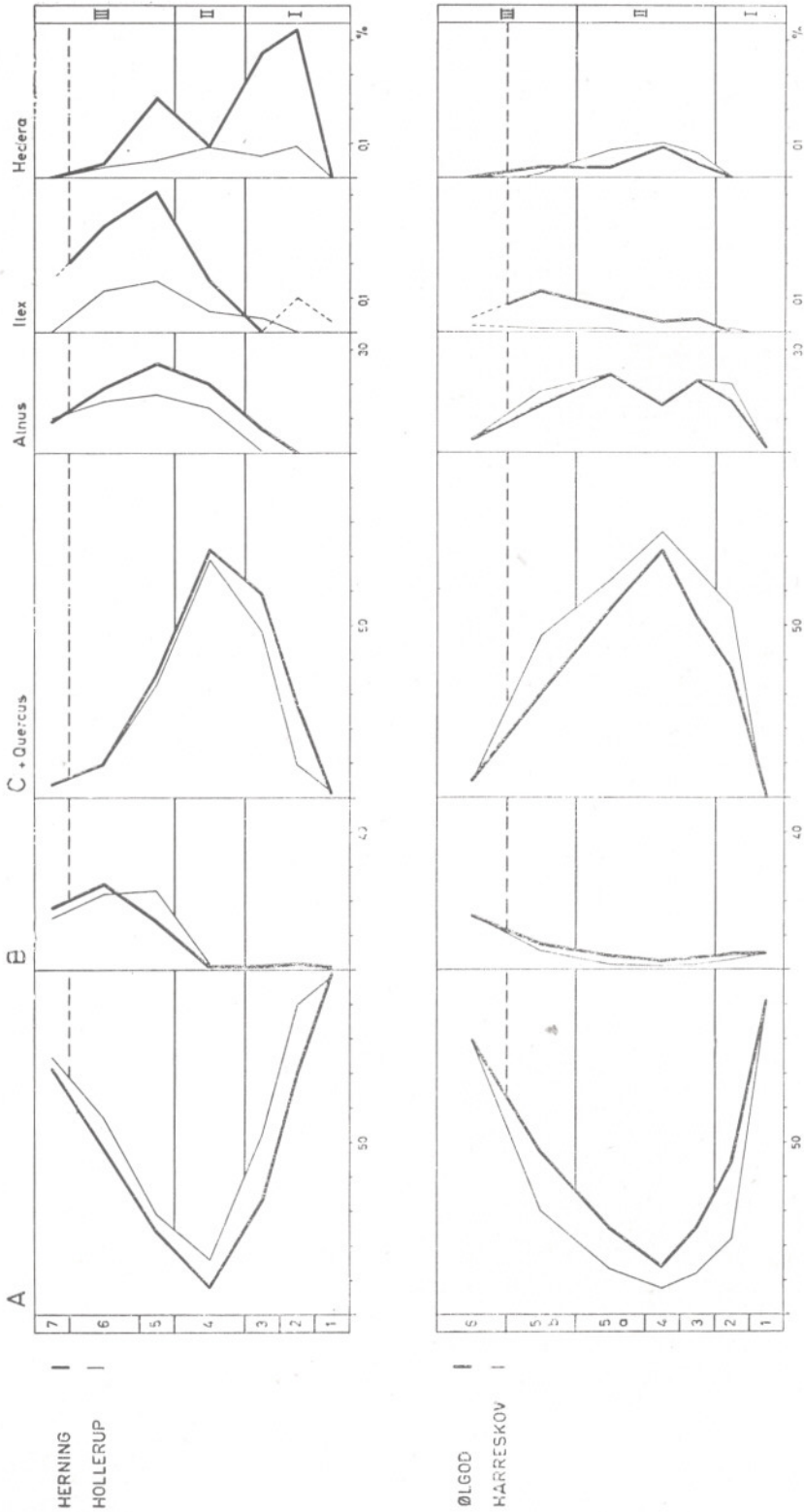
TEXT-FIG. 5 — Average pollen frequencies for plants of various ecological categories (A: lightplants, B: acidophilous plants, C: rich-soil plants), and for *Alnus*, *Ilex* and *Hedera*, from the interglacial sites at Herning and Hollerup (Eemian Interglacial), and at Ølgod and Harreskov (Harreskovian Interglacial), in Denmark. I: protocratic stage, II: mesocratic stage, III: oligocratic (and telocratic) stage.
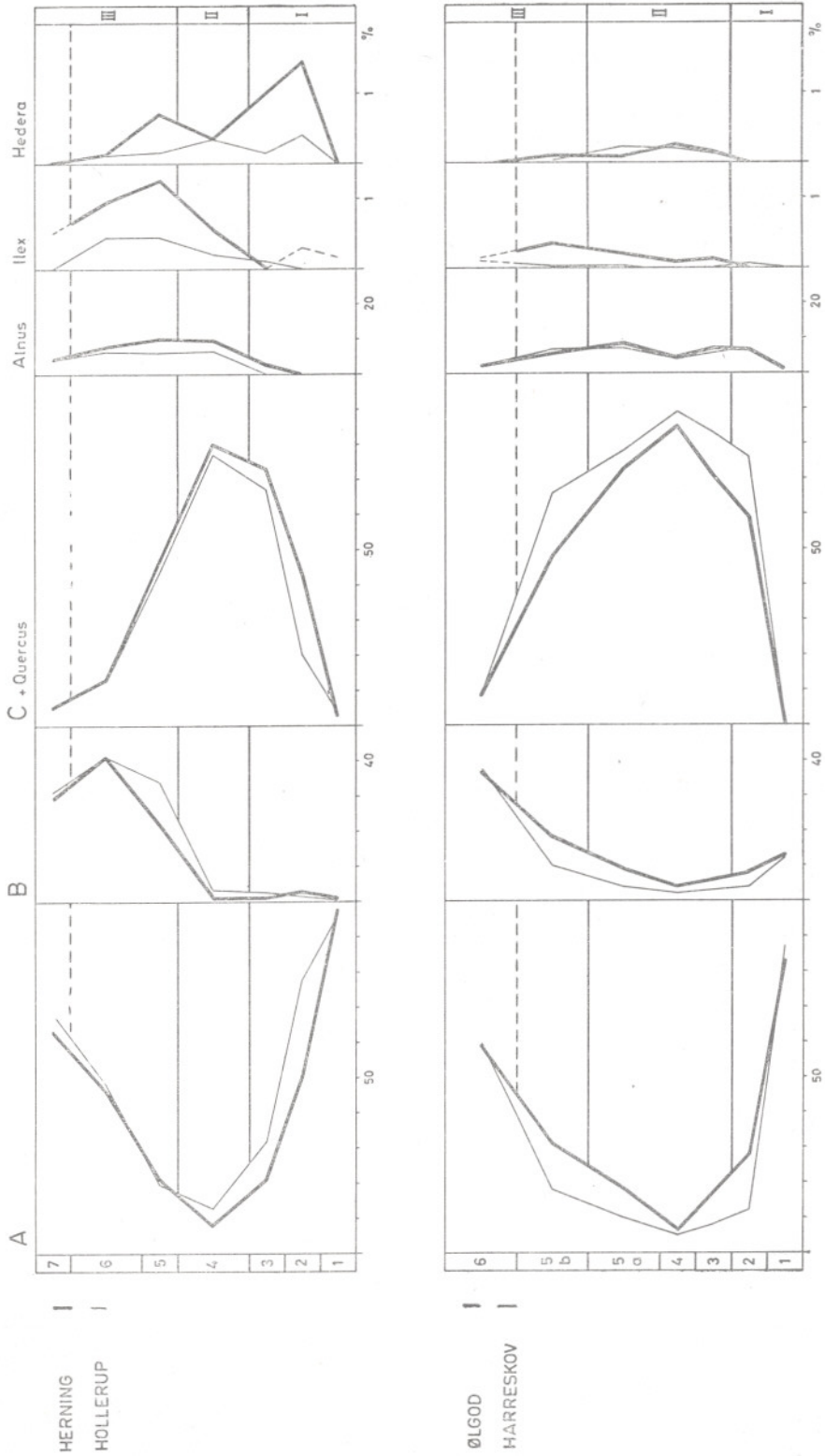
TEXT-FIG. 6 — The same curves as in Fig. 5, but recalculated according to the method of Faegri and Iversen (1964).

The *Alnus* curves in Figs. 5 and 6 are rather unaffected, although this tree rather belongs to the rich-soil group. Such a trend might be expected, as *Alnus* is best equipped to exist on the wettest places, which were least exposed to the effect of soil improverishment.

The curves of *Ilex* and *Hedera* also are interesting. Both plants indicate warm and oceanic climate, but their edaphic requirements differ. *Hedera* climbing into the tree tops is rather independent of shade and diffuses its pollen well, however, it is confined to the better soils. *Ilex*, on the other hand, grows in the forest bottom and cannot flower richly and disperse its pollen in a closed forest, however, it persists on acid mor and develops well in open heath forest. Both plants were rather common in the interglacials, but *Hedera* had its peaks in the earlier parts, whilst *Ilex* reached its maximum frequencies in the later parts, where this plant apparently prospered in the open forests on acid soil.

von Post pointed out the existence of 'revertence' in interglacial and postglacial pollen diagrams (1946). He divided the successions into three stages, and showed that so-called 'terminocratic' elements dominated the early and the late stages, whilst 'mediocratic' elements were confined their middle part. However, von Post's classification was not strictly ecological. *Betula* thus entered the mediocratic group together with *Quercus*, *Ulmus* and *Tilia*, and *Carpinus* and *Fagus* entered the terminocratic group together with *Pinus* and *Picea*. In the present interglacial pollen diagrams, the plants of open forest show typical revertence, and afford a three-fold division of the interglacial succession. Stage I is Iversen's protocratic stage (1958). The forest was unstable, and the dense forest had not yet established itself. The second stage is mesocratic with dense climax forest and brown soil with a mull layer. Stage III I have called oligocratic (ANDERSEN, 1964), because in this stage the soils degenerated independently of climatic change, and open heath forest expanded. The soil degeneration began in the climatic optimum of the interglacials. In the Eemian Interglacial, the mor formation coincided with the immigration and expansion of *Picea* at a time when the soils had matured, whilst *Picea* was present from the beginning of the older interglacial but failed to expand until lime had been removed, and conditions became favourable for the formation of a mor layer. The uppermost parts of the interglacials, with traces of a climatic decline, corresponds to Iversen's telocratic stage (l.c.), initiating the temperature decrease that in the end led to destruction of the forest, and an interruption of the interglacial succession.

I have here mentioned only the coarsest features of the interglacial vegetational successions. Still, the present results suggest that common features exist in interglacial vegetational successions however varied the details of the development may be. It is suggested that forest vegetation in a humid climate may build up to maximum denseness and then retrogress into poorer vegetation types mainly or solely due to its own influence on the substrate.

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