The Eemian freshwater deposit at Egernsund, South Jylland, and the Eemian landscape development in Denmark

Svend Th. Andersen

Andersen, Svend Th.: The Eemian freshwater deposit at Egernsund, South Jylland, and the Eemian landscape development in Denmark. *Danm. geol. Unders., Årbog 1974,* pp. 49–70, pls. 11–15, København, 18. september 1975.

The interpretation of the Eemian pollen diagrams from lake deposits is hampered by the insufficient information about the differentiation of the regional vegetation in plant associations. Pollen diagrams from very small hollows or soils record successions of single communities. At Egernsund a succession of *Betula-Pinus-Ulmus, Fraxinus, Corylus, Tilia,* and *Tilia-Carpinus* phases is recorded. *Tilia* forest is lacking further northward in Denmark. A picture of the Eemian vegetational differentiation and landscape development in Denmark is obtained by comparison with other sites.

Lake deposits are to be preferred for a study of general interglacial vegetational conditions by pollen analysis because their pollen content is least affected by local hydroseres. However, two difficulties may hamper an understanding of the true interglacial vegetational conditions, (1) we do not know whether the plants recorded in the pollen mixtures found at the various levels were associated in a uniform vegation or formed a mosaic of various associations and (2) we do not know the true importance of the various vegetational components. It has been pointed out several times that pollen spectra from lake deposits cannot be assumed to reflect the contemporary vegetational composition exactly because of differential pollen dispersal, but this term has been used rather confusingly as it has not always been clear which mechanism was meant. The following may influence pollen dispersal.

(1) Pollen productivity, which varies greatly according to Andersen (1970) and distorts the pollen spectra.

(2) Pollen release into the transporting air streams. This process is quite effective in trees because the flowers are situated in the tree tops, where the wind speeds are high and vertical mixing strong, (Andersen, l.c. and in

print) and less effective in low herbaceous plants, particularly forest herbs and entomophilous herbs with closed flowers.

(3) Transportation efficiency, which in the opinion of Tauber (1965) is highly variable. However, differences in transportation efficiency are probably not as large as estimated by that author. Pollen transported above the vegetation must be a main component of the pollen rain on lakes that are not too small, and pollen may be filtered from those parts of such a cloud which pass the top layer of the vegetation. The filtration efficiencies do not vary greatly at normal wind speeds even when the pollen grains are of different size orders (Andersen, in print), and the pollen representation rates found from lakes and bogs do not differ from those calculated within forests (Andersen 1970).

Pollen diagrams from Eemian lake deposits and regional pollen assemblage zones (p.a.z.) of the Eemian

Pollen diagrams from Eemian lake deposits at Herning and Hollerup in Denmark (Fig. 1) were published in Andersen 1964 and 1966. The following regional p.a.z. can be distinguished (the letters refer to Andersen, l.c.).

E 7 *Pinus*
E 6 *Picea-Pinus-Alnus*
E 5 *Picea-Carpinus-Alnus*
E 4 *Quercus-Corylus-Alnus*
E 3 *Quercus-Fraxinus*
E 2 *Betula-Pinus-Ulmus*
E 1 *Betula*

The zone numbers are indicated on the pollen diagram from Herning, reproduced in Plate 11. The percentages were based on the tree pollen sum including *Corylus* and *Taxus*. At Kollund in southernmost Jylland (Fig. 1) a *Tilia-Corylus-Alnus* p.a.z. occurs between the *Quercus-Corylus-Alnus* and the *Picea-Carpinus-Alnus* p.a.z. (Jessen and Milthers 1928).

The pollen spectra from the Herning pollen diagram were re-calculated with the correction factors found in Andersen 1970, and the new percentages are indicated on the same diagram. The pollen productivity of *Taxus* was considered to be similar to the other high pollen producers as suggested by Beug (in Jung et al. 1972). The *Populus* pollen frequencies were not changed.

The differences between the original and the re-calculated pollen curves

on Plate 11 are not excitingly large. This is mainly due to the fact that most of the trees represented are large pollen producers, and hence a correction does not alter the picture greatly.

One may notice that (1) *Fraxinus* was probably considerably more important within the forest, particularly in the *Quercus-Fraxinus* p.a.z. (E 3), (2) an *Alnus* increase in the *Picea-Carpinus-Alnus* p.a.z. (E 5) is eliminated, and the *Alnus*-frequencies are nearly the same throughout the larger part, and (3) *Picea* becomes somewhat more important.

If differential transportation is important, the trees with large pollen grains would have been more important within the forest. This might be true for *Carpinus* and *Picea* in particular, but it is impossible to estimate such an effect at present. The true vegetational composition cannot have deviated greatly from the one obtained here, unless the filtration efficiencies for *Carpinus* and *Pice*a pollen differed greatly from that of the other tree pollen.

The corrected pollen diagram from Herning may be substantiated by pollen analyses from small hollows such as the one from the Holocene reported in Andersen 1973. Such pollen analyses might also elucidate the problem of how the various trees were associated, because the pollen analyses from sites of that kind are likely to record only the community that grew in the immediate neighbourhood. Very small hollows from the Eemian are of course difficult to locate. However, one was found near Egernsund in southernmost Jylland, and, because of its importance, material was secured in spite of rather difficult sampling conditions. To this may be added that the deposit contains abundant *Tilia*-remains, which lack at most other Eemian sites in Denmark. Single pollen spectra from other similar sites are also mentioned below.

Vegetational development at Egernsund, Flensborg Fjord

Site

The interglacial peat at Egernsund is situated at the bottom of Flensborg Fjord at Egernsund town (Fig. 1). The water depth is 1.40 m, and the distance from the shore is 65 m. The peat extends only 5 × 5 m horizontally. It is located 5 m northwest of a large boulder and on a line extending from the fence between the properties Storegade 42 and 44 of Egernsund town. The peat occupies a hollow, probably a kettle-hole, in boulder clay, which constitutes the sea bottom around the peat.

The peat was discovered during a low water episode in 1935, and was seen again in 1949. The site was re-located by the author and samples down to 20 cm below the surface were secured by swim divers in 1967. In

1970 a float was brought to the location, and a core was extracted with a piston sampler (Merkt and Streif 1970).

Johs. Iversen made a pollen analysis in 1935 and decided that the peat was of Last Interglacial age. He noticed abundant *Tilia* pollen.

The pollen analyses reported below have confirmed that the peat is of Eemian age, and the boulder clay around it is Saalian. Weichselian boulder clay is present in the cliff which borders Flensborg Fjord north of the site and presumably covered the submarine peat before it was removed by wave erosion in the Holocene.

Lithology

The description of the lithology is based on the samples dug out in 1967 and the core from 1970. The peat was situated under a thin layer of living rhizomes of *Zostera marina* and contained channels dug by *Pholas* in its topmost part. The peat layers are extremely hard and compact.

A. 0– 6 cm Brown slightly humified peat with many rootlets. The core contained a piece of wood at 0–5 cm (*Salix* sp.)

B. 6–105 cm Reddish brown peat, which consists mainly of decayed wood (identifiable remains of *Salix* sp. (6–18 cm), cf. *Corylus* sp. (52–70 cm), and cf. *Juniperus* sp. (90 cm)). Slightly stratified. The layering inclined 15° at the top and was horizontal below 46 cm.

C. 105–115 cm Yellowish brown slightly sandy gyttja with much decayed wood, slightly stratified.

D. 115–151 cm Greyish brown argillaceous sand with a few pebbles.

E. 151–155 cm Greyish brown slightly argillaceous sand with pebbles.

The sediment symbols in Plates 13 and 14 are in accordance with Troels-Smith (1955).

Macrofossils

Macrofossils were washed from the 1967-samples and the core. They were kindly identified by Professor G. F. Mitchell, Dublin. The identifications are shown in Table 1.

Professor Mitchell noticed that the *Ilex*-fruitstones were larger than the fruitstones of modern *Ilex aquifolium,* and considers the species identification tentative. Fruitstones of *Ilex aquifolium* have frequently been identified from Eemian deposits in Western Europe; however, the material may need a reconsideration.

52

Andersen: Eemian freshwater deposits

Table 1. Macrofossils identified by G. F. Mitchell. The sample marked "top" is loose debris collected in 1967. The samples at 0–18 cm were dug out in 1967, those at 34–133 cm are from the core.

Depth, cm	from	top	0 / 2	2 / 6	6 / 10	10 / 14	14 / 18	34 / 40	52 / 58	65 / 70	70 / 75	86 / 93	104 / 110	122 / 126	130 / 133
Volume, ml		–	110	200	200	200	200	104	104	87	87	121	104	69	52
Pollen zone		–	5	5	4b	4b	4b	4b	4b	4ab	4a	4a	34a	3	2
Ajuga cf. *reptans* nutlets		.	.	.	.	.	.	1	.	5	.	.	.	.	.
Alisma cf. *plant.-aquat.* embryos		.	.	.	.	.	.	.	.	.	.	.	.	2	.
Carex sp. a trigonous nuts, some with utricles, small		15	.	21	8	105	38	.	.	.	.	2	2	.	.
Carex sp. b biconvex nuts		33	c	200	2	175	23	.	.	.	.	.	.	.	.
Carex sp. c biconvex nuts, small		.	.	.	.	.	.	5	2	.	.	.	.	.	.
Carex sp. d trigonous nuts		.	.	.	.	.	.	.	3	.	1	.	.	.	.
Carpinus betulus fruits		15	.	4	.	.	.	.	.	.	.	.	2	.	.
Corylus avellana nuts		23	.	1	2	.	.	.	.	.	.	8	22	.	.
Cruciferae damaged seed		.	.	.	.	1	.	.	.	.	.	.	.	.	.
Gramineae caryopses		.	.	.	.	.	.	.	.	2	.	.	.	.	1
Ilex cf. *aquifolium* fruit-stones		3	.	1	.	1	13	1	1	.	.	.	.	.	.
Lycopus europaeus nutlets		.	.	.	.	.	.	.	.	1	1	10	.	.	.
Mentha sp. nutlets		.	.	.	.	.	.	.	1	.	.	.	1	.	.
Potamogeton sp. damaged fruitstone		1	.	.	.	.	.	.	.	.	.	.	.	.	.
Quercus sp. acorns and cupules		.	.	.	.	.	.	.	.	1	.	89	.	.	.
Ranunculus sceleratus achenes		.	.	.	.	.	.	5	.	1	1	1	.	.	2
Rubus cf. *idaeus* druplets		9	.	1	3	1	2	.	.	.	.	.	.	.	2
Tilia sp. fruit segments		140	.	15	10	120	116	88	80	127	18	.	.	.	.
Umbelliferae small carpels		.	.	.	.	.	.	.	.	.	.	.	.	.	2
Buds and scales		.	.	.	.	.	.	.	.	9	2	102	16	.	.
Deciduous leaf debris		.	1	2	.	50	c	1	.	.	.	.	.	.	.
Monocot. debris		.	.	2	.	.	.	.	.	.	.	.	.	.	.
Stem nodes		.	.	.	.	1	.	.	.	.	2	2	.	.	.
Cenococcum		1	.	1	75	2	.	.	.	.	.	.	.	.	1
Arthropoda		.	.	1	.	.	.	.	.	.	.	.	.	.	1
Vermes		.	.	.	.	.	.	.	1	.	.	.	.	.	.

53

A few whole fruits of *Tilia cordata* and a few fruits and fruit stems of *Tilia platyphyllo*s (at 34–75 cm) were noticed by the author.

Pollen analysis

Pollen preservation. Two kinds of pollen corrosion occurred, the thinning and the perforation types described by Havinga (1967). Both kinds occurred in the sandy layers (D and E), but they are not easily distinguished in all cases. Specimens indeterminable due to corrosion were rare. The numbers of grains with perforated exines was noted, they include the grains thinned so much that parts of the exine were removed. Percentage frequencies of specimens with perforated exines are shown in Plate 12.

It is difficult to say how corrosion may have influenced the pollen spectra. All taxa were nearly equally attacked in the layers E and D except for *Dryopteris,* the frequencies of which may be somewhat too low there.

The *Corylus* pollen grains were particularly severely attacked in layer C and the lower part of layer B, which contain a *Corylus* pollen maximum. It is not likely that the *Corylus* pollen frequencies are significantly too low there.

Tilia and *Corylus* have equally high frequencies of corroded grains in layer B, and their relative frequencies can hardly have been changed greatly by selective corrosion.

The low frequencies of corroded specimens noticeable in layer A are presumably due to a more acid depositional environment.

The original pollen diagram. A pollen diagram based on the tree pollen sum is shown in Plate 13. Only the most important non-tree pollen curves are shown.

The pollen spectra from the lowermost sandy layers are confusing. The three lowermost pollen spectra appear to be younger than those above them, and the spectrum at 118 cm is older than those above and beneath it. Spectra which appear to be in a correct sequence are connected by curves and the others are indicated by horizontal bars. The curves are similar to those known from early Eemian deposits. The corresponding silhouettes are white in the pollen diagrams. Black silhouettes are shown above the disturbed levels.

The inversions of the original sequence in the sandy layers were definitely not due to the coring operation, but it is not possible to say whether the layers were disturbed in situ or whether older pollen-bearing material was transported into the hollow at various times.

It can be assumed that the total tree pollen deposition varied greatly

because trees with a high or with a low pollen productivity dominated at various times. A curve for the ratio of the tree pollen sum to the sum of the corrected tree pollen values (see below) is shown on the diagram. This curve indicates true variations in the pollen deposition. The figures vary from about 1 to about 4, and changes in the non-tree pollen frequencies calculated as percentages of the tree pollen sum cannot be assumed to show true changes in their pollen deposition.

The tree pollen sums are about 500 in each sample, after correction. The numbers of tree pollen actually counted thus vary from about 500 to about 2000.

Local pollen assemblage zones and age of the deposit. Due to the smallness of the hollow at Egernsund the tree canopy could cover it, and the tree pollen assemblages can be assumed to be of mainly local origin. The sequence is therefore divided into local pollen assemblage zones which are indicated by numbers on the pollen diagram. The local pollen assemblage zones are compared to the Eemian regional pollen assemblage zones in Denmark in Table 2.

An equivalent of the early-Eemian *Betula* regional p.a.z. is missing at Egernsund. The *Betula-Pinus-Ulmus,* the *Quercus-Fraxinus,* and the *Corylus-Quercus* local p.a.z. resemble the Eemian *Betula-Pinus-Ulmus, Quercus-Fraxinus* and *Quercus-Corylus-Alnus* regional p.a.z. in Denmark with the following exceptions.

(1) *Fraxinus* is more frequent in the *Quercus-Fraxinus* local p.a.z. at Egernsund (24 %) than in the corresponding regional p.a.z. (8 %).

Table 2. Eemian regional pollen assemblage zones in Denmark and the corresponding local pollen assenmblage zones at Egernsund.

Regional pollen assemblage zones	Local pollen assemblage zones
Pinus (E 7) *Picea-Pinus-Alnus* (E 6) *Picea-Carpinus-Alnus* (E 5)	(*Tilia-Carpinus* (5))
Quercus-Corylus-Alnus (E 4)	*Tilia* (4b) *Corylus-Quercus* (4a)
Quercus-Fraxinus (E 3)	*Quercus-Fraxinus* (3)
Betula-Pinus-Ulmus (E 2) *Betula* (E 1)	*Betula-Pinus-Ulmus* (2)

(2) *Corylus* is more frequent and *Quercus* less frequent in the local *Corylus-Quercus* p.a.z. than in the *Quercus-Corylus-Alnus* regional p.a.z.

(3) *Alnus* has low frequencies at Egernsund.

The *Tilia* local p.a.z. is equivalent to the *Tilia-Corylus-Alnus* p.a.z. at Kollund, also situated at Flensborg Fjord 13 km southwest of Egernsund (p. 00), but is not recorded further north in Denmark. The *Tilia* pollen frequency at Kollund is 20 % of the tree pollen (including *Corylus*). *Tilia* pollen is very rare at all other Danish Eemian sites including central South Jylland (Agerskov, Andersen unpublished, Fig. 1) and the *Tilia* pollen fre-
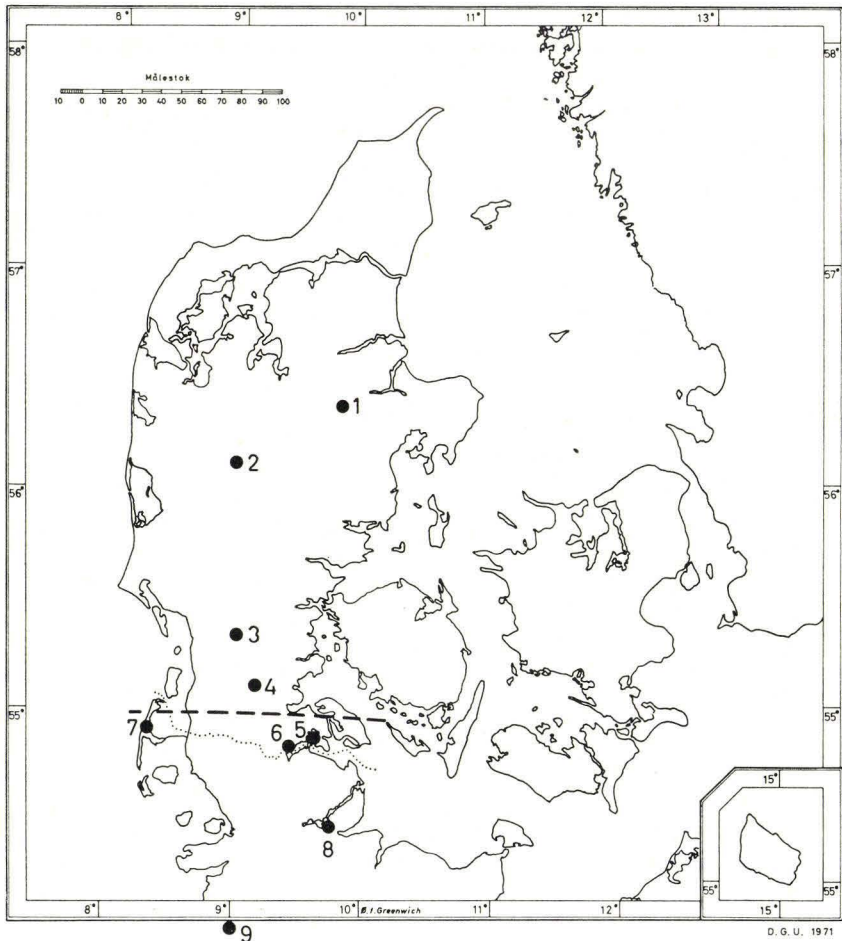
Fig. 1. Map of Denmark showing Eemian sites mentioned in the text. 1. Hollerup. 2. Herning. 3. Hygum Nymark. 4. Agerskov. 5. Egernsund. 6. Kollund. 7. Westerland. 8. Loopstedt. 9. Burg.

quency is less than 10 % in the Eemian pollen diagram from Westerland on Sylt, northwesternmost Germany, published by Averdieck (1967, Fig. 1). *Tilia* pollen is frequent in other Eemian diagrams from northernmost Germany. The one closest to Denmark is Loopstedt near Schleswig (Schütrumpf 1967, Fig. 1) with 19 % *Tilia* pollen (tree pollen, including *Corylus*).

The *Tilia* pollen grains at Egernsund nearly all belong to *T. cordata*. However, at 76 cm, at the transition from the *Corylus* p.a.z. about one fifth of the *Tilia* grains belong to *T. platyphyllos*.

The *Tilia-Carpinus* local p.a.z. at Egernsund is transitional to the *Picea-Carpinus-Alnus* regional p.a.z., which follows after the *Tilia-Corylus-Alnus* p.a.z. at Kollund and the North German sites mentioned above, and equivalents of the Eemian *Picea-Carpinus-Alnus, Picea-Pinus-Alnus* and *Pinus* regional p.a.z. are missing at Egernsund.

The sequence of local pollen assemblage zones at Egernsund are sufficiently similar to the Eemian regional pollen assemblage zones to show that the deposit belongs to a part of the Eemian. It is unknown whether a *Betula* p.a.z. occurs at a lower level, but due to the coarseness of the lowermost deposit it is suggested that the soils were very unstable at that time, and it is possible that the hollow was still filled by dead ice at the time of the *Betula* p.a.z. It is also unknown whether the peat deposition continued throughout the Eemian. Deposits corresponding to the youngest Eemian regional pollen assemblage zones may have been removed by glacial erosion in the Weichselian or by wave action in the Holocene.

The higher *Fraxinus-* and *Corylus*-frequencies in the pollen assemblages at Egernsund and the rareness of *Alnus* and *Picea* compared to the regional Eemian pollen assemblages as noticed above can be explained by the fact that only tree populations restricted to the nearest vicinity of the site are recorded. The presence of a *Tilia* assemblage zone at Egernsund and at Kollund and its absence further to the north show that the northern limit of dense *Tilia* populations occurred somewhat north of these sites in the Eemian (see Fig. 1).

The re-calculated pollen diagram. The pollen assemblages in the interglacial deposit at Egernsund are clearly enough predominantly influenced by tree communities which grew at the site. The low *Alnus* pollen frequencies indicate that no marginal forest developed, and that the site was surrounded immediately by high ground forest.

As the tree canopy could extend over the hollow, vertical tree pollen transport predominated, and pollen transported laterally (extra-local and regional, Janssen 1967) was insignificant in accordance with the experiences from surface samples from forests (Andersen 1970, 1973). The pollen

percentages thus can be transformed to crown area percentages after the method described in Andersen (1.c.). Such a re-calculated pollen diagram is shown in Plate 14.

Corylus formed a canopy and was fully illuminated in the *Quercus-Corylus* p.a.z. and this tree was presumably shaded in the *Tilia* and the *Tilia-Carpinus* p.a.z. Hence, *Corylus* was a large pollen producer in the former and a low pollen producer in the latter zones in accordance with Andersen (1970). The black silhouette on the pollen diagram indicates frequencies divided by 4, and the white silhouette indicates percentages with *Corylus* unchanged and calculated outside the tree pollen total. The black silhouette presumably illustrates the crown coverage of *Corylus* in the *Corylus* zone, and the white silhouette shows its areal participation in the *Tilia* and the *Tilia-Carpinus* p.a.z.

Tree frequencies of less than about 10 % may be due to the presence of pollen of extra-local or regional derivation, and in such cases it is not possible to say whether the tree was present locally with scattered specimens or not. The presence of macrofossils indicate local presence in some instances where the pollen representation is low (*Carpinus* in 3, *Quercus* in 4 a, and *Corylus* in 4 b and 5).

The variations in total tree pollen deposition are eliminated when the tree pollen counts are corrected, and changes in the non-tree percentages based on the sum of corrected tree pollen indicate true changes in deposition. The percentages do not, however, indicate the areal participation of these plants because the pollen frequency depends greatly on the distance from the sampling spot and because their pollen productivity may vary. They can hardly be interpreted in other terms than local presence or absence.

Pollen of anemophilous shrubs and herbs present in low frequencies may have originated from non-local populations because such pollen is produced in large quantities, whereas even low frequencies of entomophilous plants are likely to indicate their presence near the site at the time of deposition.

Plants represented with frequencies less than 0.5 % are indicated by crosses.

Curves for the various shrubs are shown separately in Plate 14. The herbaceous plants are grouped in categories such as "forest", "open ground", "uncertain", "wet ground" and "aquatics" according to their ecological significance. Curves for the various herbaceous plants are shown in Plate 15 together with curves for *Pediastrum* and redeposited Tertiary pollen.

The vegetational succession at Egernsund

The re-calculated pollen diagram is divided into 5 vegetational phases. Their borders are at the same levels as the pollen assemblage zone borders, and the vegetational phases have the same numbers. It should be noticed that whereas the pollen assemblage zones merely signify levels with various characteristic pollen mixtures, the vegetational phases record intervals with various tree communities on the land surface. The shrubs and herbaceous plants occurring near or within the hollow depended on the amount of light which penetrated the tree canopy. Their presence or absence accordingly reflects the denseness of the tree cover around and over the hollow.

(Betula phase). A vegetational phase corresponding to the *Betula* regional p.a.z. is unfortunately not represented. *Betula* forest rich in *Juniperus* and with abundant herbaceous plants initiated the Eemian interglacial succession elsewhere in Denmark.

Betula-Pinus-Ulmus phase (2). *Betula, Pinus* and *Ulmus* constituted 20–40 % each, and *Fraxinus* and *Quercus* were present each with 10–20 % of the crown cover. *Juniperus, Viburnum, Salix* and *Hedera* were present, and herbaceous plants were abundant. Macrofossils of *Ranunculus sceleratus, Rubus* and Umbelliferae are recorded.

Pinus, Betula and *Ulmus* apparently grew in a mixed forest. *Fraxinus* and *Quercus* had immigrated but failed to expand. The tree canopy was open and allowed sufficient light for the growth of the shrubs and the herbaceous plants. *Viburnum, Salix, Hedera, Selaginella*, Gramineae, Umbelliferae, *Dryopteris, Glyceria, Alisma* and *Typha* are likely to have been present just around or in the hollow and there are many scattered records of terrestrial plants. *Artemisia, Selaginella, Saxifraga, Rumex, Ophioglossum* and the Chenopodiaceae are relics from a periglacial vegetation, and *Ulmus, Viburnum, Urtica* and *Humulus* suggest a fertile soil, whereas *Pteridium* indicates acid soil somewhere in the vicinity. The hollow contained a pond with *Callitriche, Ranunculus, Nymphoides, Lemna* and *Pediastrum*.

A slight amount of redeposited Tertiary pollen occurs (Plate 15). The few *Ilex* pollen grains may also have been redeposited, and *Ilex* probably did not immigrate till later as at other Eemian sites in Denmark (Andersen 1969).

Several plants typical of a temperate climate are recorded, and *Hedera* indicates oceanic conditions. Mull or hydro-mull (cp. Lafond 1952) presumably predominated near the site. *Pinus* and *Ulmus* had invaded an open *Betula* forest, but none of these trees attained full population density. It is possible that soil instability due to the melting of buried ice masses still

prevented the establishment of dense forest at that time. The phase is essentially protocratic in Iversen's sense (1958, cp. Andersen 1964, 1969).

Fraxinus phase (3). Fraxinus expanded at the cost of *Betula, Pinus* and *Ulmus,* and constituted up to 70 % of the tree cover, and *Quercus* increased somewhat (20 %). *Populus* is represented, but there were few shrubs and herbaceous plants. The tree cover was apparently dense and the tree-crowns covered the hollow. *Hedera* had sufficient light to climb to the tree tops and flowered abundantly there. *Alisma* macrofossils are recorded.

Fraxinus was more successful than *Quercus* at this site and a damp soil too wet for *Quercus* is suggested. Hydro-mull thus prevailed around the hollow, and the dense *Fraxinus* forest suggests stable soil. The *Fraxinus* phase is transitional to Iversen's mesocratic stage.

Corylus phase (4a). Corylus expanded and attained up to 80 % of the tree cover. *Fraxinus* and *Quercus* decreased, but there is a low *Quercus* peak (20 %) in the middle of the phase. *Corylus* and *Quercus* are also represented by macrofossils. *Betula, Pinus, Ulmus, Fraxinus, Carpinus, Alnus, Taxus* and *Acer* are represented with low frequencies. *Carpinus* fruits are recorded, and *Acer* was probably present locally too, but the other trees mentioned are so scarcely represented that local presence cannot be claimed. There was no *Alnus* forest around the hollow, and the *Corylus* canopy extended over it. Shrubs and herbaceous plants were very scarce. There are a few records of shade tolerant forest herbs such as *Oxalis* and *Sanicula,* and there are macrofossils of *Lycopus, Mentha* and *Ranunculus sceleratus.*

The *Corylus* forest was thus very dense and the light was so scarce that the other trees could not rejuvenate. The *Corylus*-dominance was interrupted by a *Quercus* expansion, but this stage was short and *Quercus* was again suppressed by *Corylus.*

Hydro-mull probably prevailed, and the *Corylus* phase is mesocratic.

Tilia phase (4b). Tilia expanded rapidly and dominated the forest (up to 90 %). The *Tilia* pollen is mostly *Tilia cordata.* As mentioned above *Tilia platyphyllos* pollen is present at the transition from the *Corylus* phase and macrofossils of the species occur. *Tilia cordata* apparently was competitively superior to *T. platyphyllos. Corylus* nuts are recorded, and *Corylus* probably formed an understorey. The pollen productivity of *Corylus* was accordingly low, and the white silhouette on the pollen diagram probably shows its crown coverage truthfully. The curve exhibits three peaks in the *Tilia* phase (20–40 %). The other trees were very scarce.

There is a *Salix* peak; otherwise the shrubs are scarcely represented. There are 2 low *Ilex* peaks, and *Ilex* fruitstones are frequent at a level which cor-

responds to the uppermost peak on the pollen curve. The *Hedera* curve has 2 low peaks, and *Viscum* occurs scatteredly. The upland herbaceous plants were scarce. *Polypodium* is the most frequent one. The curve for wet ground plants shows 2 peaks. The lower peak comprises *Dryopteris, Carex* and *Typha,* and the upper one includes *Carex* and *Osmunda. Carex* fruits are abundant at a level corresponding to the uppermost peak on the pollen curve. Macrofossils of *Rubus, Ajuga, Lycopus, Mentha* and *Ranunculus sceleratus* are also recorded.

There were no aquatic plants, and the high frequencies of *Salix* and the wet ground plants suggest that these plants grew on the peat.

The *Tilia* forest was apparently dense and strongly shading. The variations in the frequencies of *Corylus* and several of the shrubs and herbaceous plants suggest slight variations in the light intensity under the trees. Hydromull or mull probably still prevailed. The appearance of *Osmunda* suggests slightly more acid conditions in the late part of the phase. The *Tilia* phase is essentially mesocratic.

Tilia-Carpinus phase (5). Tilia decreased to 40–50 %, *Carpinus* increased to about 20 % and *Corylus* to 40–50 %. *Carpinus* and *Corylus* definitely occurred in the forest around the site because macrofossils are present. *Betula* and *Fraxinus* also increase (up to about 10 %) and may have occurred near the hollow. *Hedera* increased slightly too, and *Calluna* and *Frangula* are represented. *Thelypteris dryopteris* appeared, and *Dryopteris, Carex, Osmunda, Sphagnum* and *Lysimachia* occurred on the wet ground. *Carex* nuts are abundant.

The tree cover was apparently not very dense. *Betula, Frangula, Calluna, Thelypteris dryopteris, Osmunda* and *Sphagnum* suggest acid conditions. The soil apparently changed into acid mull or mor, and acid water flushed the hollow. Traces of acidification appeared already in the late part of the *Tilia* phase, and the mull apparently degraded into a more acid soil. *Carpinus* tolerates acidity better than *Tilia* and occurs on a wider range of soils than *Tilia* to-day (Ellenberg 1963). Thus the replacement of *Tilia* by *Carpinus* was apparently promoted by soil degradation. A transition to the oligocratic stage (Andersen 1964 and later) is indicated.

Population dynamics at Egernsund

A simplified pollen diagram is shown in Fig. 2, where bars indicate the vertical extension of peaks on the pollen curves suggestive of local presence of the various plants. Particularly high tree frequencies are indicated with black bars, peaks for other plants with white bars.
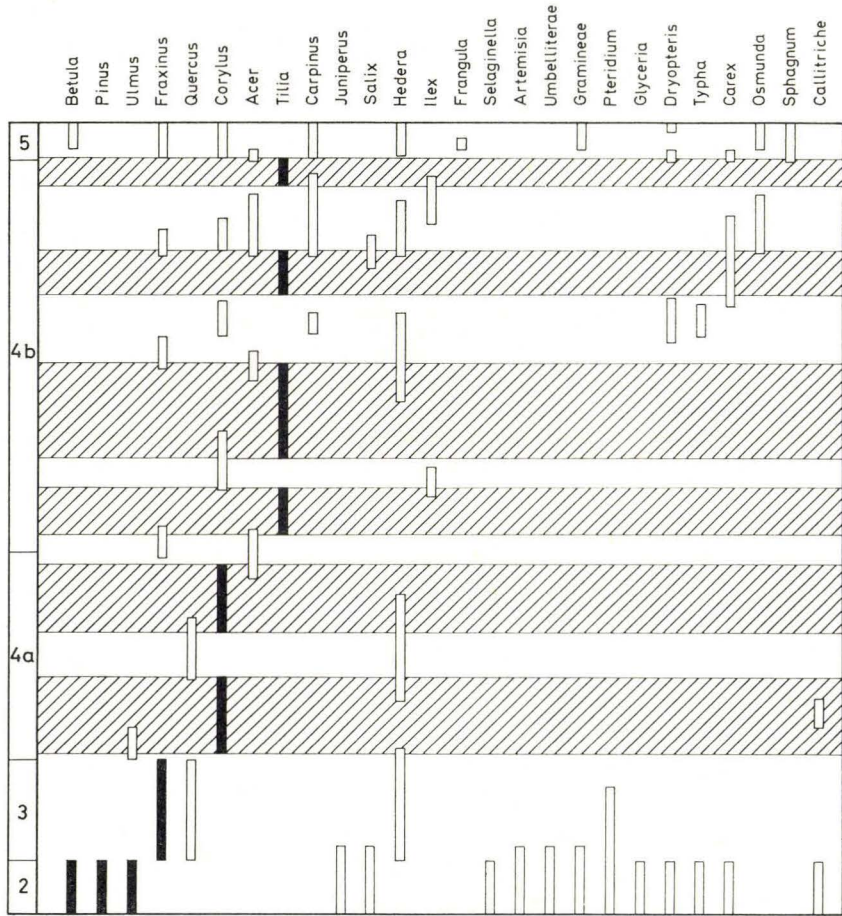
Fig. 2. Diagram showing the vertical extension of pollen and spore maxima. The black bars indicate the dominant plants. Shading indicates stages with a dense tree cover.

Fig. 2 illustrates changes in the density of the tree cover with the non-dominant plants particularly frequent in the stages with a more open tree cover. 6 stages with dense and 7 stages with open tree cover can be distinguished (shaded or white in Fig. 2).

The *Betula-Pinus-Ulmus* phase (2) had many shrubs and herbaceous plants, and the competition pressure was low probably because unstable soil prevented the establishment of a dense tree cover, as mentioned above. The change to the *Fraxinus* phase (3) can be explained as a result of soil stabilization. *Fraxinus* established itself at the cost of *Betula, Pinus* and *Ulmus,* and the illumination under the trees apparently decreased somewhat. Only *Quercus* and *Hedera* were frequent.

62

The *Corylus* phase (4 a) contained 2 stages with dense tree cover and an intermediate somewhat more open stage with low peaks of *Quercus* and *Hedera*.

There was apparently a slightly more open stage again between the *Corylus* and the *Tilia* phases (4 a and 4 b), with low peaks for *Fraxinus* and *Acer*. The *Tilia* phase (4 b) contained 4 dense stages with intermediate more open stages. The following plants had low peaks in the open stages: *Corylus* and *Ilex* (first), *Fraxinus, Corylus, Acer, Carpinus, Hedera, Dryopteris, Typha* (second), *Fraxinus, Corylus, Acer, Carpinus, Salix, Hedera, Ilex, Carex, Osmunda* (third).

The *Tilia-Carpinus* phase (5), was open again with low peaks for *Betula, Fraxinus, Corylus, Acer, Carpinus, Hedera, Frangula,* Gramineae, *Dryopteris, Carex, Osmunda* and *Sphagnum*.

3 tree species dominated the forest in the early *Betula-Pinus-Ulmus* phase, but only one tree species was superior in each of the successive vegetational phases at Egernsund, in turn *Fraxinus, Corylus* and *Tilia*. Each of these tree species was superior to its predecessor and replaced it entirely. Whereas the *Fraxinus* expansion was delayed by soil instability, *Corylus* and *Tilia*, on the other hand, expanded soon after their appearance.

No time factor is known at Egernsund (cp. Watts 1973), however, the steeply rising curves for *Fraxinus, Corylus* and *Tilia* suggest very rapid mass expansions. Hence it is possible that trees of a uniform age predominated in the various forest stages.

If mass expansion resulted in stands of uniform age, as suggested above, the alternation of dense and open stages in the *Corylus* and *Tilia* phases at Egernsund probably reflect alternating generations, each of which reached a mature and then a weakening senescent stage. Mature stands of uniform age are endangered by storm catastrophes even in deciduous forest, as recent events in northern Europe have shown us, and large windthrows may occur in the primeval forests of southeast Europe (Fröhlich 1954). We may have to envisage that cyclic regeneration may be normal in primeval forests at least in limited areas.

Müller (1974) recently estimated the duration of the *Corylus* and the *Tilia*-zones to 2150–2350 years. This figure would allow about 350–400 years for each of the 6 *Tilia* and *Corylus* generations at Egernsund, a maximum age, which is not unlikely.

The Eemian vegetational and landscape development

The Eemian regional pollen diagrams leave us without information as to whether the various species were mixed in a uniform vegetation cover or

Table 3. Pollen assemblage zones and vegetational differentiation in the Eemian in Denmark. The double lines indicate the transitions to strongly acid soil.

Regional pollen assemblage zone	Vegetational differentiation			
	dry	moist	wet	
Pinus	Pinus	Pinus[4]	Calluna[4]	telocra-cratic
Pinus-Picea-Alnus	Pinus	Picea[4]	Alnus[4]	oligo-cratic
Picea-Carpinus-Alnus	Picea	Carpinus[3][4]	Alnus-Fraxinus-Taxus[3]	
Quercus-Corylus-Alnus/Tilia-Corylus-Alnus	Quercus	Corylus/Tilia[1]	Alnus-Fraxinus-Taxus[3]	meso-cratic
Quercus-Corylus-Alnus	Quercus[2]	Corylus[1]	Alnus-Fraxinus-Taxus[3]	
Quercus-Fraxinus	Quercus	Fraxinus[1]	Fraxinus	
Betula-Pinus-Ulmus	Betula, Pinus, Ulmus[1]			proto-cratic
Betula	Betula			

[1] represented at Egernsund
[2] represented at Hygum Nymark (p. 65)
[3] represented at Kollund (p. 65)
[4] represented at Burg (p. 67)

whether a mosaic of various vegetation types occurred. The succession from Egernsund gives a more precise picture, because communities on a single soil type are recorded. When the Egernsund succession is compared with the other information available, a more differentiated picture of the Eemian vegetational development can be obtained. A survey is shown in Table 3.

Betula regional p.a.z.

The *Betula* regional p.a.z. had only one dominant, *Betula,* and it can be assumed that this tree predominated on all soil types.

Betula-Pinus-Ulmus regional p.a.z.

The succession from Egernsund shows that *Betula, Pinus* and *Ulmus* formed a mixed forest community. These trees are also recorded in the regional pollen diagrams and there was apparently no vegetational differentiation.

Quercus-Fraxinus regional p.a.z.

Fraxinus predominated on the moist soil at Egernsund and *Quercus* was probably restricted to the drier sites.

Quercus-Corylus-Alnus regional p.a.z.

Corylus replaced *Fraxinus* on the moist soil at Egernsund, and *Quercus* was of restricted importance. *Quercus* probably tended to prevail on the better drained sites. At Hygum Nymark, near Rødding in central Jylland, a site not yet fully investigated (Fig. 1), the following corrected tree pollen spectrum was recorded.

Quercus	Ulmus	Corylus	Pinus	Betula	Alnus
79 %	3 %	6 %	5 %	7 %	0.4 %

Thelypteris dryopteris is recorded at 9 %, and no other herbaceous plants were represented. The spectrum shows a pure *Quercus* forest on an acid soil, probably acid mull.

Alnus and *Taxus* expanded simultaneously with *Corylus* in the regional pollen diagrams. These trees were not associated with *Quercus* and *Corylus*. A pollen spectrum from Kollund mentioned below suggests that these trees were associated with *Fraxinus* on the wet sites.

Quercus-Corylus-Alnus or Tilia-Corylus-Alnus regional p.a.z.

Quercus presumably still prevailed on the better drained and acid soils. *Tilia* replaced *Corylus* on the moist and fertile sites in southernmost Denmark and northern Germany, and pure *Tilia* forest with some *Corylus* dominated on the moist soil. A sample from the *Tilia-Corylus-Alnus* pollen assemblage recorded at Kollund not far from Egernsund (Fig. 1) by Jessen and Milthers (1928) was re-analyzed, and a re-calculated treepollen spectrum is shown below.

Quercus	Carpinus	Ulmus	Tilia	Corylus	Fraxinus	Taxus	Alnus	Pinus	Betula
4 %	1 %	3 %	28 %	15 %	12 %	15 %	19 %	1 %	1 %

This spectrum has less *Tilia* and more *Fraxinus, Taxus* and *Alnus* than Egernsund. *Fraxinus* and *Taxus* thus apparently were associated with *Alnus* on wet soil. Godwin (1956) mentioned mass occurrences of *Taxus* stumps in East Anglian fen peats from the Holocene, and *Taxus* remains are frequently recorded in Holocene peats in northwestern Germany (Firbas 1949, Averdieck 1971).

The record from Egernsund shows that the moist soils were still favourable in the *Quercus-Tilia-Alnus* regional p.a.z. Traces of acidification occur near the top of the zone.

Tilia platyphyllos was frequent at the beginning of the *Tilia* phase at Egernsund, but this species was soon replaced entirely by *T. cordata*. Fruits of *Tilia platyphyllos* are recorded at 5 sites further north in Jylland, in-

cluding Herning (Fig. 1), and those of *T. cordata* at 4 (Hartz 1909, Jessen and Milthers 1928). *Tilia platyphyllos* was thus present during the *Tilia* expansion stage at Egernsund and colonized far to the north together with *T. cordata*. Little is known about the ability of *Tilia platyphyllos* to compete with *T. cordata* under natural conditions to-day; however, *T. cordata* was superior in competition with *T. platyphyllos* at Egernsund. The lack of a *Tilia* mass expansion further north in Jylland is puzzling. *Tilia* pollen occurs there at very low frequencies just before the transition to the *Picea-Carpinus-Alnus* regional p.a.z. (Plate 11), and it is likely that the oligotrophication which became prominent at that time (Andersen 1964 and later) prevented a *Tilia* mass expansion.

Picea-Carpinus-Alnus regional p.a.z.

Picea and *Carpinus* became dominant in the regional pollen diagrams from Denmark and North Germany, and the *Tilia-Carpinus* vegetational phase at Egernsund is probably transitional to a *Carpinus* phase. A new re-calculated tree pollen spectrum from the *Carpinus-Alnus* pollen assemblage of Jessen and Milthers (1928) at the near-by Kollund site is shown below.

Picea	*Quercus*	*Ulmus*	*Tilia*	*Corylus*	*Carpinus*	*Fraxinus*	*Taxus*	*Alnus*	*Pinus*	*Betula*
4 %	2 %	2 %	5 %	4 %	47 %	6 %	8 %	20 %	1 %	2 %

If compared with the spectrum from Kollund above, it can be seen that *Carpinus* had replaced *Tilia* on the moist ground and that the *Fraxinus-Alnus-Taxus* forest on wet ground was rather unchanged.

Picea was absent at Kollund and Egernsund, and *Picea* thus apparently was restricted to the driest sites, *Carpinus* prevailed on the moist sites, and *Alnus, Fraxinus* and *Taxus* on the wettest ground.

It was earlier assumed (Andersen l.c.) that the general oligotrophication notable in the *Picea-Carpinus-Alnus* regional p.a.z. was promoted by the expansion of *Picea* on the upland soils. The sequence from Egernsund has shown that the low-lying moist soils became acid by a selfinduced process, which promoted the expansion of *Carpinus*. Only the *Alnus-Fraxinus-Taxus* forest on the wet ground was unaffected.

Pinus-Picea-Alnus regional p.a.z.

The *Pinus-Picea-Alnus* regional p.a.z. is known only from lake sites in Denmark. Dücker and Menke (1970) mention an Eemian hydro-mor from

Burg in Dithmarschen (Fig. 1) with an interesting local succession from a *Carpinus-Alnus* phase to a *Picea-Carpinus-Alnus* phase. *Picea* thus replaced *Carpinus* on the moist sites. *Pinus* became increasingly common in the regional pollen diagrams and probably replaced *Picea* on the drier soils. The soils thus became increasingly acid and poor. *Fraxinus* and *Taxus* decreased, but *Alnus* forest was still preserved on the wettest sites flushed by ground-water.

Pinus regional p.a.z.

The *Picea-Carpinus-Alnus* phase in the hydro-mor at Burg mentioned above was replaced by a *Pinus-Calluna* phase. *Picea* and *Alnus* disappeared in the regional pollen diagrams, and *Pinus* and *Calluna* apparently prevailed.

Conclusion

The studies reviewed above allow a more detailed picture of the Eemian vegetational development.

The vegetation in the *Betula* and the *Betula-Pinus-Ulmus* pollen assemblage zones was essentially protocratic in Iversen's sense. The forest was still of a pioneer character, no dense tree cover had developed and open-ground plant communities were frequent. The *Quercus-Fraxinus* pollen assemblage zones had a denser tree cover and initiated the mesocratic stage of the Eemian. The vegetation of the *Quercus-Corylus-Alnus* and the *Quercus-Tilia-Alnus* pollen assemblage zones was essentially mesocratic with a dense tree cover and mull soils; however, the occurrence of *Pteridium* spores in the *Betula-Pinus-Ulmus* and the *Quercus-Fraxinus* pollen assemblage zones (cp. Andersen 1969) and *Thelypteris dryopteris* at Rødding (p. 65) indicate initial acidification of the better drained soils at an early time.

Acidification of the well drained and the moist soils became prominent in the *Picea-Carpinus-Alnus* pollen assemblage zone, and an acidophilous vegetation characteristic of open habitats with *Pinus, Betula, Populus, Ilex, Juniperus, Pteridium* and *Calluna* became increasingly common, emphasizing the transition to the oligocratic stage (Andersen 1964 and later). The wettest habitats with *Alnus-Fraxinus-Taxus* vegetation were less affected. Progressive mor accumulation led to the dominance of *Pinus* and *Picea* in the *Pinus-Picea-Alnus* pollen assemblage zone, and *Fraxinus* and *Taxus* disappeared on the wet habitats, where only *Alnus* remained. *Pinus* and *Calluna* finally became dominant in the *Pinus* pollen assemblage zone, where the disappearance of *Ilex, Pteridium* and *Osmunda* indicates the transition to the telocratic stage (cp. Andersen 1969).

Soil maturation thus profoundly affected the Eemian vegetational development even on fertile soils, and it appears that this process was self-induced and progressed without climatic influence until near the end of the Eemian, where climatic change promoted an expansion of heath vegetation poor in trees (cp. Andersen 1957), the telocratic stage in Iversen's cycle.

Dansk sammendrag

Fortolkningen af pollendiagrammer fra Eem-Interglacialtidens søaflejringer vanskeliggøres dels ved det manglende kendskab til vegetationens reelle sammensætning, dels ved det utilstrækkelige kendskab til dennes uddifferentiering i plantesamfund. Den første mangel kan afhjælpes ved en korrektion af pollendiagrammerne, den anden ved undersøgelse af ganske små mosehuller, hvor kun den omgivende vegetation er repræsenteret. Et sådant lille mosehul i Flensborg Fjord ud for Egernsund er undersøgt. Her findes en succession af birke-fyrre-elmeskov, askeskov, hasselskov, lindeskov og linde-avnbøgeskov. Lindeskov fra Eem-Interglacialtid er i Danmark kun påvist ved Egernsund og ved Kollund, som blev undersøgt af Jessen og Milthers (1928), og nordgrænsen for lindeskov har forløbet i det sydligste Jylland, mens der længere nordpå kun har været spredte lindeforekomster. På grundlag af pollenanalyser fra Egernsund og andre lignende forekomster er det muligt at opnå et billede af skovens sammensætning og jordbundsudviklingen på henholdsvis tør, fugtig og våd bund i Eem-Interglacialtiden (Table 3).

References

Andersen, S. T. 1957: New investigations of interglacial fresh-water deposits in Jutland. – Eiszeitalter Gegenw., 8, pp. 181–186.

Andersen, S. T. 1964: Interglacial plant successions in the light of environmental changes. – Rep. VI. Int. Congr. Quaternary, Warsaw 1961, 2, pp. 359–368.

Andersen, S. T. 1966: Interglacial vegetational succession and lake development in Denmark. – The Palaeobotanist, 15, pp. 117–127.

Andersen, S. T. 1969: Interglacial vegetation and soil development. – Meddr. dansk geol. Foren., 19, pp. 90–102.

Andersen, S. T. 1970: The relative pollen productivity and pollen representation of North European trees, and correction factors for tree pollen spectra determined by surface pollen analyses from forests. – Danm. geol. Unders., II. række, 96, 99 pp.

Andersen, S. T. 1973: The differential pollen productivity of trees and its significance for the interpretation of a pollen diagram from a forested region. – *In:* Quaternary Plant Ecology, edited by Birks, H. J. B. and West, R. G., Blackwell Scient. Publ., Oxford, London, Edinburgh, Melbourne, pp. 109–115.

Andersen, S. T. in print: Wind conditions and pollen deposition in a mixed deciduous forest. I. Wind conditions and pollen dispersal. – Grana, 14.

Averdieck, F.-R. 1967: Botanisch-moorgeologische Untersuchungen am "Tuul" von Westerland (Sylt). – Offa, 24, pp. 84–96.

Averdieck, F.-R. 1971: Zur postglazialen Geschichte der Eibe (*Taxus baccata* L.) in Nordwestdeutschland. – Flora, 160, pp. 28–42.

Dücker, A. & Menke, B. 1970: Eemzeitliche Podsol- und Moorbildung bei Burg (Dithmarschen). – Meyniana, 20, pp. 5–8.

Ellenberg, H. 1963: Vegetation Mitteleuropas mit den Alpen in kausaler, dynamischer und historischer Sicht. – Einführung in die Phytologie. Von H. Walter, Bd. IV, Teil 2. Eugen Ulmer, Stuttgart, 943 pp.

Firbas, F. 1949: Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen. Bd. 1: Allgemeine Waldgeschichte. – Verlag von Gustav Fischer, Jena. 480 pp.

Fröhlich, J. 1954: Urwaldpraxis. 40:jährige Erfahrungen und Lehren. – Neumann Verlag, Radebeul und Berlin. 200 pp.

Godwin, H. 1956: The history of the British flora. A factual basis for phytogeography. – The University Press, Cambridge. 384 pp.

Hartz, N. 1909: Bidrag til Danmarks tertiære og diluviale Flora (English summary). – Danm. geol. Unders. II. række, 20, 202 pp.

Havinga, A. J. 1967: Palynology and pollen preservation. – Rev. Palaeobot. Palynol., 2, pp. 81–98.

Iversen, J. 1958: The bearing of glacial and interglacial epochs on the formation and extinction of plant taxa. – *In:* Hedberg, O. (ed.): Systematics of today. Uppsala Univ. Årsskr. 1958:6, pp. 210–215.

Janssen, C. R. 1967: A comparison between the recent regional pollen rain and the subrecent vegetation in four major vegetation types in Minnesota (U.S.A.). – Rev. Palaeobot. Palynol., 2, pp. 331–342.

Jessen, K. & Milthers, V., 1928: Stratigraphical and paleontological studies of interglacial fresh-water deposits in Jutland and Northwest Germany. – Danm. geol. Unders. II. række, 48, 379 pp.

Jung, W., Beug, H.-J. & Dehm, R. 1972: Das Riss/Würm-Interglazial von Zeifen, Landkreis Laufen a.d. Salzach. – Bayrische Akad. Wiss. Mathem.-naturwiss. Kl. Abh. N. F. H. 151, 131 pp.

Lafond, A. 1952: La conservation de l'humus. – C. R. Ass. Can. de conservation, 1952, pp. 23–40.

Merkt, J. & Streif, H. 1970: Stechrohr-Bohrgeräte für limnische und marine Lockersedimente. Geol. Jb., 88, pp. 137–148.

Müller, H., 1974: Pollenanalytische Untersuchungen und Jahresschichtenzählungen an der eem-zeitlichen Kieselgur von Bispingen/Luhe. – Geol. Jb., A 21, pp. 149–169.

Schütrumpf, R. 1967: Die Profile von Loopstedt und Geesthacht in Schleswig-Holstein.

Ein Beitrag zur vegetationsgeschichtlichen Gliederung des jüngeren Pleistozäns. – *In:* Frühe Menschheit und Umwelt, Teil II, Herausg. Gripp, K., Schütrumpf, R., Schwabedissen, H., Böhlau Verlag, Köln, Graz, pp. 136–167.

Tauber, H. 1965: Differential pollen dispersion and the interpretation of pollen diagrams. With a contribution to the interpretation of the elm fall. – Danm. geol. Unders. II. række, 89, 69 pp.

Troels-Smith, J. 1955: Karakterisering af løse jordarter. Characterization of unconsolidated sediments. – Danm. geol. Unders. IV. rækk (2), 10, 73 pp.

Watts, W. A. 1973: Rates of change and stability in vegetation in the perspective of long periods of time. – *In:* Quaternary Plant Ecology. The 14th Symposium of The British Ecological Society, Cambridge 1972, Blackwell Scientific Publ., Oxford, London, Edinburgh, Melbourne, pp. 195–206.
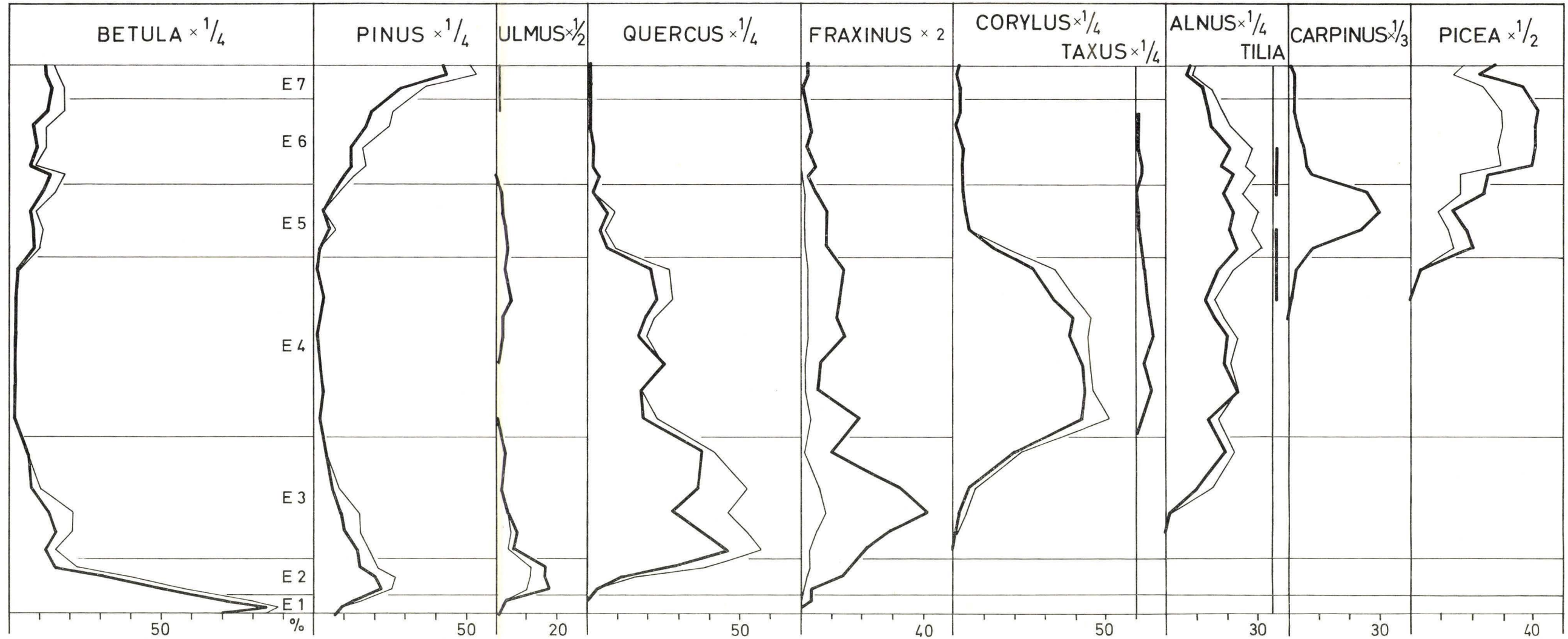
HERNING

Plate 11.

Tree pollen diagram from the Eemian lake deposit at Herning. Thin line, tree pollen
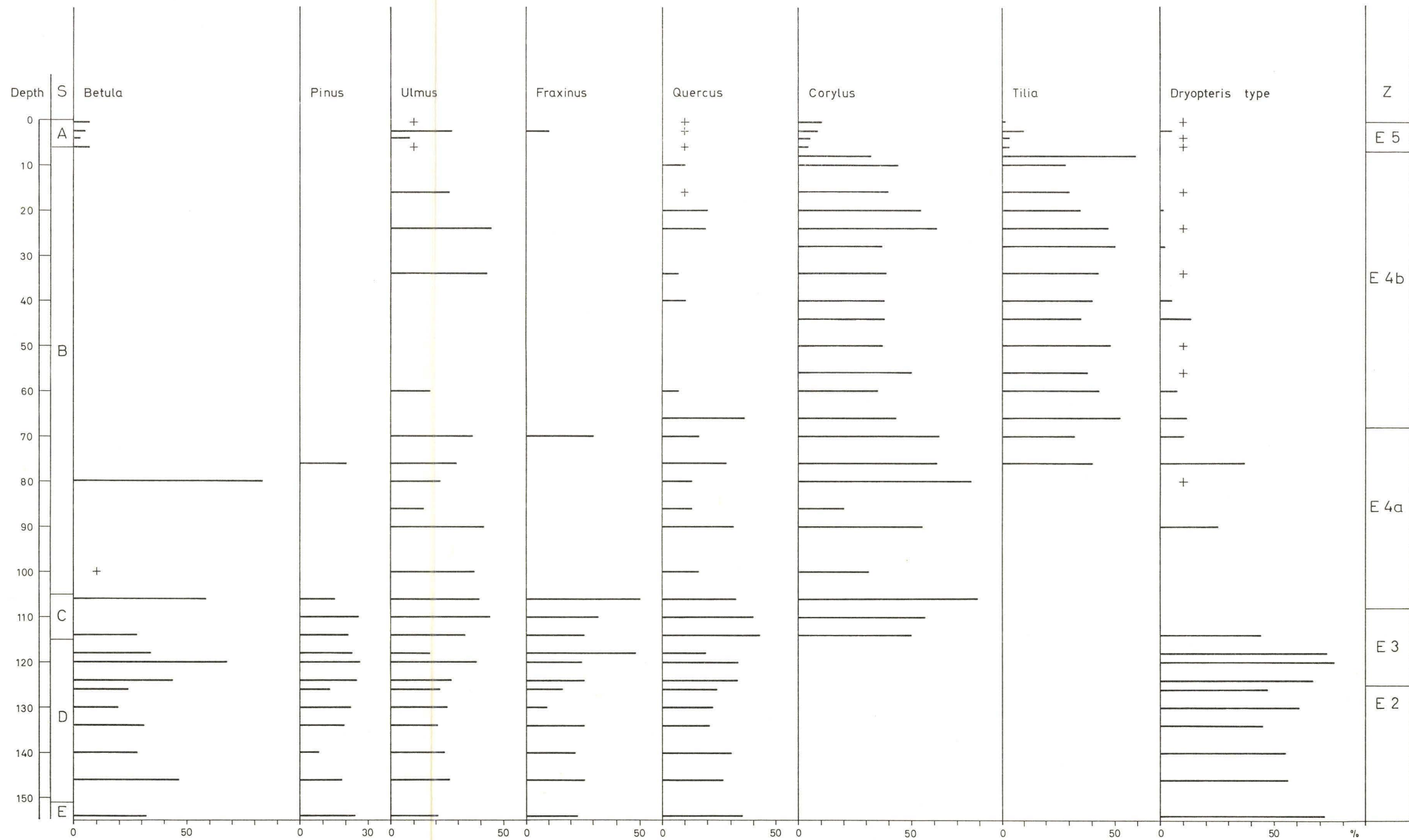frequencies unchanged. Heavy line, tree pollen frequencies, corrected.

Plate 12.

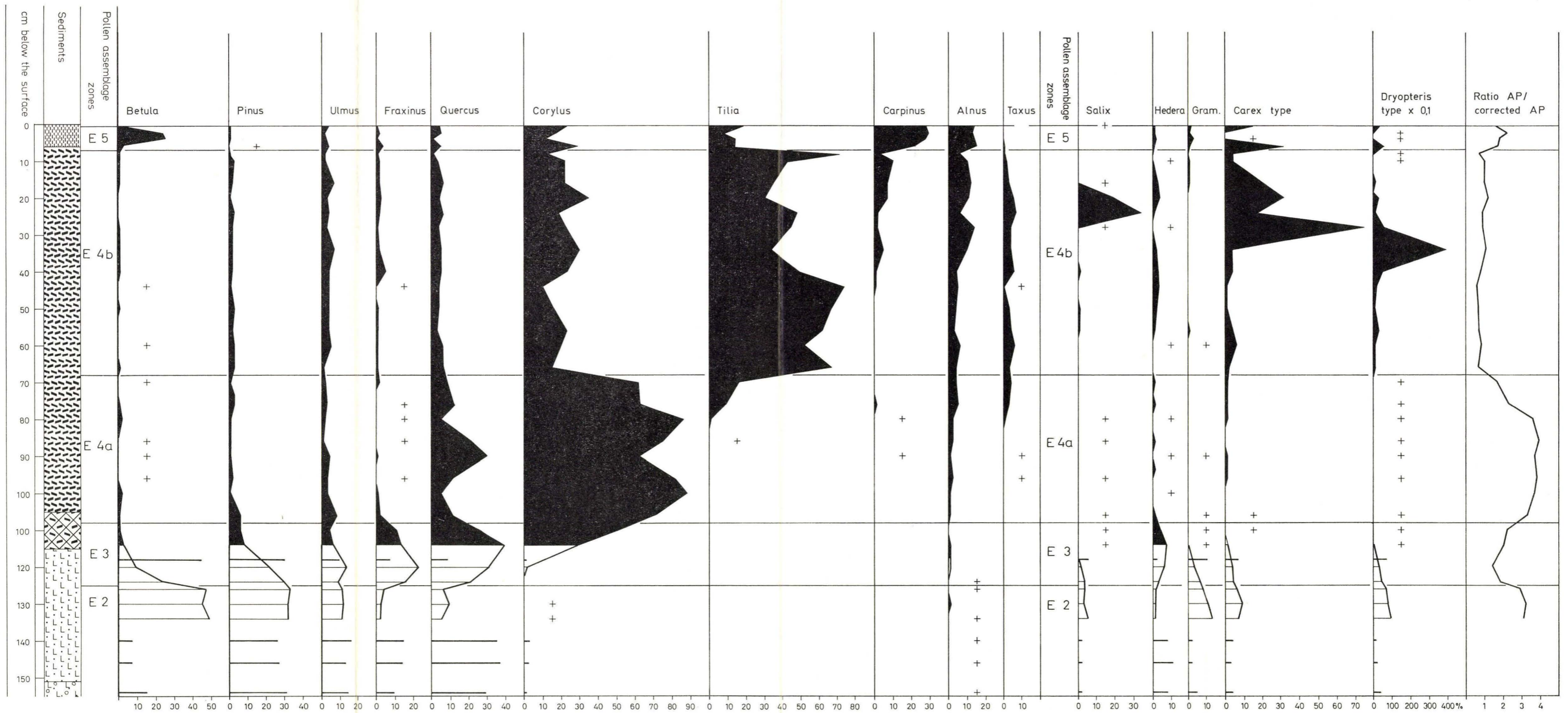Egernsund. Frequencies of corroded grains. – A–E, lithologic units.

Plate 13.

Egernsund. Pollen diagram based on the tree pollen total with tree pollen frequencies unchanged.
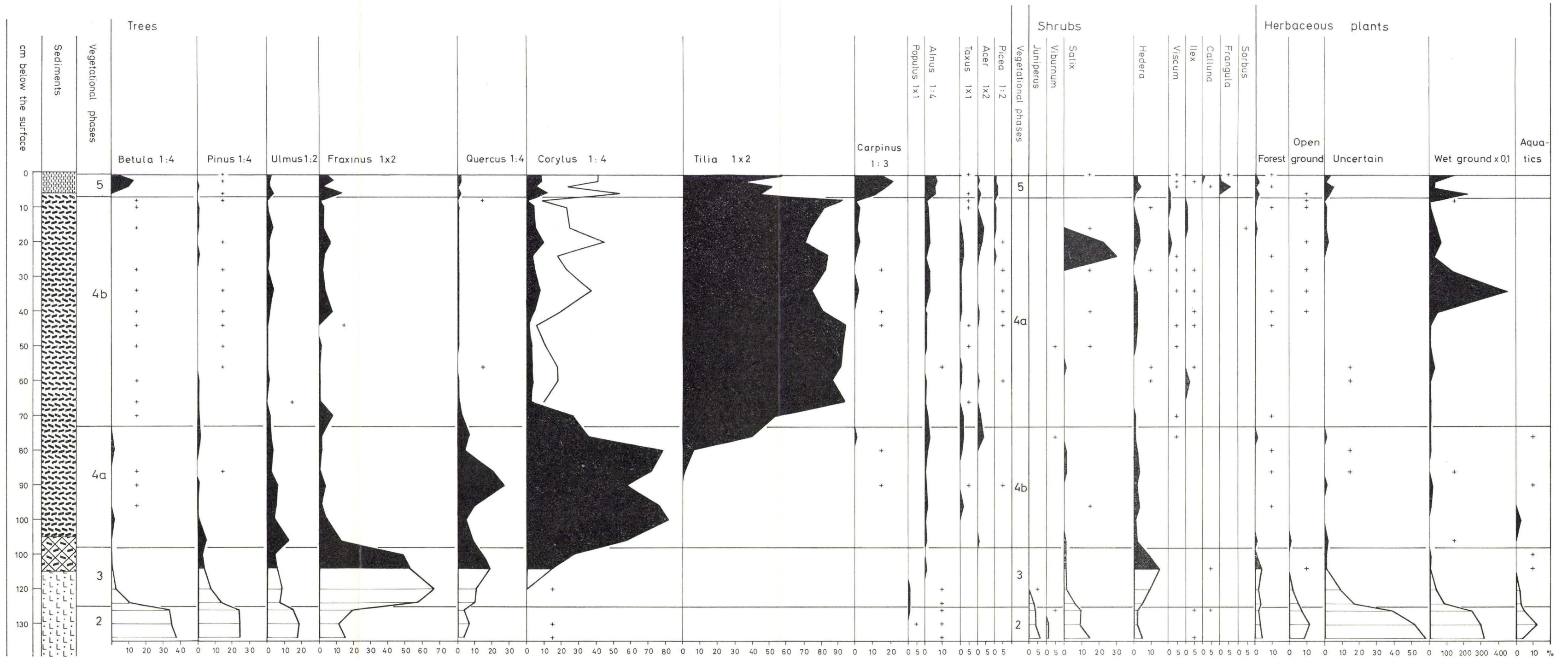
Plate 14.

Egernsund. Pollen diagram based on the corrected tree pollen total with corrected tree
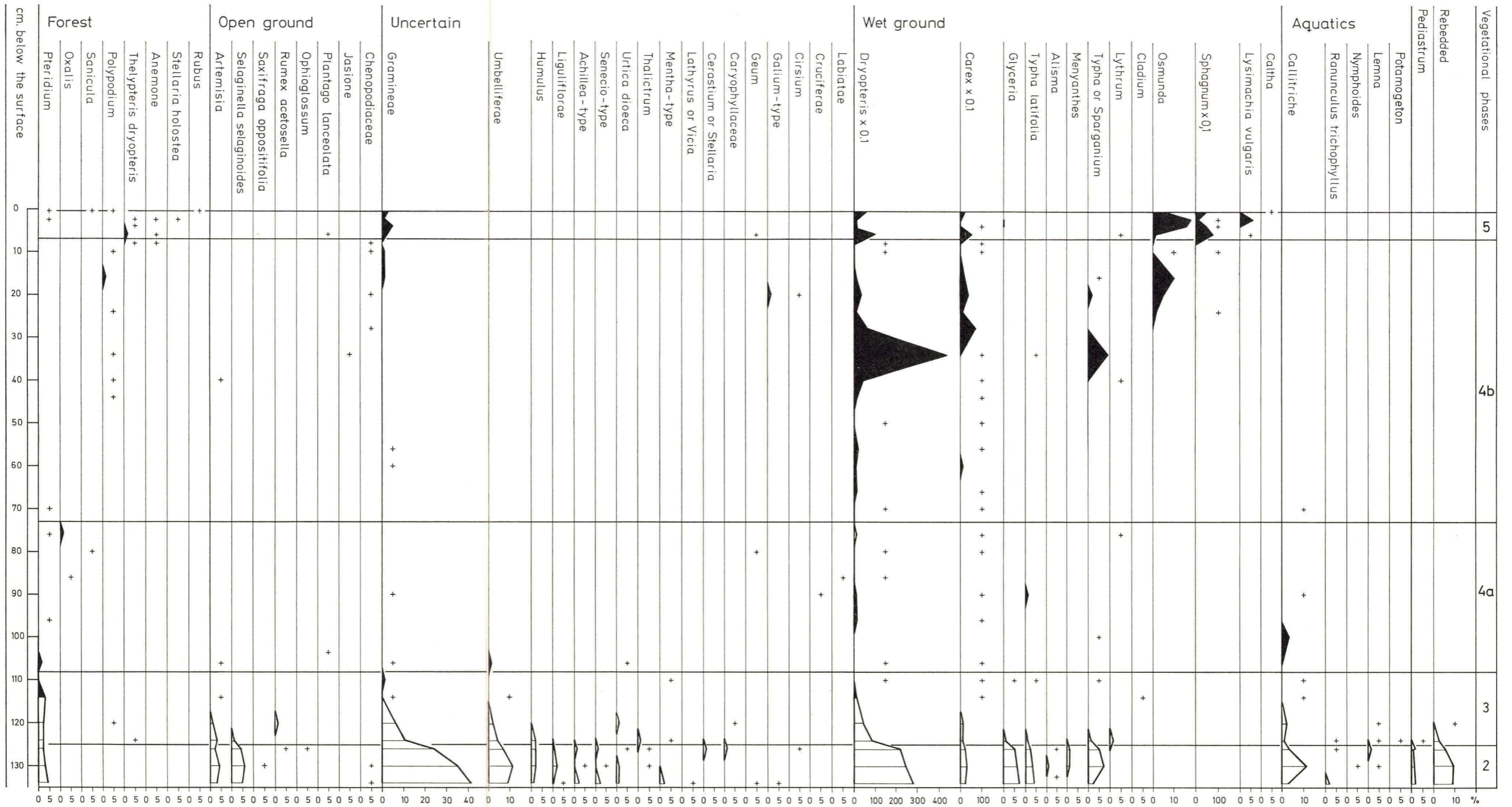pollen frequencies.

Plate 15.

Egernsund. Pollen diagram showing individuel herbaceous plant frequencies based on
the corrected tree pollen total.