Identification of wild grass and cereal pollen

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Annulus diameter and size in pollen of 80 North European Poaceae species were measured. Annulus diameter was considered more reliable for identification of fossil pollen than pollen size because annulus is less modifiable and can be measured on all grains. Surface sculpturing is also useful for identification, and pollen size is useful in cases where preservation is good or moderately good. Pollen of *Glyceria* sp., *Hordeum vulgare* or *Agropyron repens, Secale cereale* and *Avena sativa* were identified in Holocene deposits.

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Due to their uniformity, identification of Poaceae pollen is very difficult and has been considered self-evident only in a few cases *(Secale cereale* and *Zea mays).* Since the publication of Firbas (1937) fossil cereal pollen and wild grass pollen have been distinguished mainly by size criteria; however, this method is not without problems. Other morphological characters mentioned in identification keys are annulus or pore diameter, annulus protrudence and delimitation, and surface sculpturing.

The usefulness of morphological characters for identification of fossil Poaceae pollen

The identification of fossil Poaceae pollen is hampered by the large number of species likely to be represented, by wide overlappings in dimension ranges, and by variability of qualitative characters. Further difficulties arise from size variations due to fossilization and preparation. Bimodality or skewness in size frequency-distribution curves from fossil pollen assemblages may indicate components with different distributions for the dimension measured.

(1) *Pollen size.* Firbas (1937) found that the pollen grains of common cereals are larger than those of the majority of wild grasses occurring in Central Europe,

and showed bimodal size-frequency curves for fossil pollen indicating a mixture of small wild grass pollen and large pollen belonging to cereals or anthropochorous wild grasses. His method has been used i.a. by Troels-Smith (1955) and Beug (1961). Difficulties arise from the fact that fossil Poaceae pollen tend to crumple, and from other modifications of pollen size. The large cereal pollen grains thus crumple more easily than the small wild grass pollen; if only inflated grains are measured in a fossil sample, a size-frequency distribution curve becomes biassed except for cases where preservation is perfect. Troels-Smith (1955) tried to overcome this difficulty by measuring the average diameter rather than the largest diameter in all grains, both inflated and crumpled. Due to the fact that grass pollen grains rarely are spherical, the average diameter of fossil pollen grains must be compared with the same dimension measured in modern grains. The method fails in cases of broken grains (cp. Troels-Smith 1955) or severe crumpling. Accurate measurement is also hampered by variations due to chemical treatment or fossilization conditions, and by swelling if the pollen grains are mounted in glycerol and the slide thickness is smaller than the smallest diameter of the grains (Cushing 1961). Size variations can be eliminated if *Corylus* pollen grains can be measured (Troels-Smith 1955), and swelling of the large cereal pollen grains can be avoided if silicone oil is used as a mounting medium (Andersen 1978b).

(2) *Annulus and pore diameter.* Beug (1961) showed that wild grass and cereal pollen can be distinguished by measurements of annulus width and pore diameter, and Fægri & Iversen (1964) and Leroi-Gourhan (1969) used annulus diameters for the same purpose. Pore diameter and annulus width are difficult to measure, and size-variation curves cannot be produced because a sufficiently small size-class (< 0.5 μm) is unobtainable with a light microscope. Annulus diameters are sufficiently large for measurement with dry-system objectives (size class about 1 μm); they can be measured on all fossil grains and are not modified by pressure from the cover slip.

(3) *Thickness or protrudence and delimitation of annulus.* Beug (1961) and Fægri & Iversen (1964) used these characters as additional criteria for the distinction of pollen of wild grasses and cereals. These characters can only be observed on suitably orientated pollen grains.

(4) *Surface sculpturing.* Grohne (1957) showed that two kinds of sculpturing observable with phase contrast equipment occur in wild grass and cereal pollen, and Beug (1961) distinguished three sculpturing types. Fægri & Iversen (1964) used several terms for description of the surface sculpturing (scabrate, areolate, maculate, verrucate). Electron microscope studies (Rowley 1960, Andersen & Bertelsen 1972, Nilsson et al. 1977) have shown that essentially two types of sculpturing occur: scabrate and verrucate, in the terminology of Iversen & Troels-Smith (1950). The scabrate and verrucate sculpturing can be observed in

phase contrast and can be used for a distinction of certain cereals (Grohne 1957, Beug 1961, Andersen & Bertelsen 1972). Morphological variation and the fact that phase contrast may be difficult to apply to pollen grains that are not well preserved may cause difficulties.

In the present work annulus diameter is considered the most important character for identification of Poaceae pollen, and size and surface sculpturing are considered characters of secondary importance. Measurements of modern pollen and fossil pollen assemblages are shown below.

Material and methods

Modern pollen. Modern pollen from a large number of Poaceae species was prepared and measured under the supervision of Johs. Iversen in connection with the preparation of the pollen key in Fægri & Iversen (1964). Additional material was prepared later. Pollen was collected in nature from flowering specimens and in some cases from herbarium specimens. Each collection usually comprised several individuals. 80 species were examined; in some cases several collections from the same species were prepared.

Dried flowers were mixed with *Corylus avellana* pollen from various sources (see Andersen 1978b), boiled in KOH, sieved, acetolyzed for 1 minute, and transferred to silicone oil via water, ethanol and benzene. Benzene was used as a solvent because it evaporates more quickly than other solvents. Silicone oil was added to the pollen residue transferred to small vials. Surplus benzene was evaporated for one day at room temperature, later in a thermostat cabinet at 50°C. The microscope slides were sealed with cellulose lacquer, later with paraffin (see Andersen 1978b).

Fossil pollen. Fossil Poaceae pollen in sediment and soil samples from Eldrup Forest, Denmark (cp. Andersen 1978a), were measured. The moist or dried samples were boiled in KOH, HF, acetolyzed, and mounted in silicone oil. Benzene was evaporated at 50°C. The pollen grains were measured in unsealed slides.

Measurements. The following parameters (cp. Iversen & Troels-Smith 1950) and statistical expressions were used,

Slide thickness, cp. Andersen (1978b)

M+, largest diameter of a pollen grain

M-, diameter at a right angle to M+

$\frac{M+ \; + M-}{2}$, average diameter, pollen size

M+/M-, pollen index

anl-D, annulus diameter

n, number of grains measured or samples compared

$\bar{x}$, arithmetic mean or average of groups of means s, estimated standard deviation

C, coefficient of variation, numerical value of standard deviation in % of the mean

95% confidence interval of normal distributions

sk, third moment-skewness

v.r., variance ratio

r, coefficient of correlation (least squares)

P, probability of a null-hypothesis. A null-hypothesis is rejected if P is less than 0.05 (marked with an asterisk. Two asterisks indicate rejection at the 0.01 level, three at the 0.001 level).

Poaceae pollen tend to orientate themselves with their largest diameter parallel to the surface of the microscope slide. Only inflated grains were measured in modern samples, inflated and crumpled grains in sediment samples. Inflated *Corylus* grains were measured when seen in polar view (M+ = Lt+). Annulus diameters of Poaceae pollen were measured irrespective of orientation. Size class units were 1.125 and 1.15 μm (M+ and M- of modern grains) and 1.20 μm (M+ and M- of fossil grains and anl-D). 100 modern Poaceae and *Corylus* grains were measured; n for sediment samples varied.

Variation in measured dimensions due to chemical treatment and mounting procedure

Andersen (1978b) showed that *Corylus avellana* pollen measured simultaneously with the Poaceae pollen varied in average size even when drawn from the same source. The size of *Corylus* pollen was influenced by the presence of small remnants of solvent and by the mounting procedures. Variation within a *Corylus* source and size differences between the *Corylus* sources were eliminated if benzene was thoroughly removed and the slides sealed with paraffin.

Fægri & Iversen (1964) showed that size differences among various pollen types mounted in silicone oil and in glycerol are similar to the differences in *Corylus* pollen measured in the same slides. Their table 2 includes four Poaceae species from 26.52 to 39.41 μm in mean size in silicone oil. The increase in glycerol slides is correlated with the increase in *Corylus* pollen size (r = 0.996, P = 0.004**).

Annulus diameters measured on pollen of 37 Poaceae species mounted in silicone oil were compared with annulus diameters of the same species on pollen mounted in glycerol (Beug 1961, *Tabelle* 1, anl-D = *Pore-Durchmesser* + *Annulus Breite* × 2). The annulus diameters in glycerol were slightly larger than those measured in silicone oil ($\bar{x}$ = 1.28, C = 12.20, r = 0.905, P <0.001***). It can be concluded that annulus diameter like pollen size is modified by chemical treatment and mounting procedure.

Standardization of measurements according to *Corylus*

One can assume that modern Poaceae pollen varies in the same way as *Corylus* pollen. As changes in Poaceae and *Corylus* pollen size are correlated, and the size of the *Corylus* pollen collections mixed with the Poaceae pollen is uniform, the size measurements of Poaceae pollen could be standardized by means of the *Corylus* measurements. The standardized *Corylus* pollen size was 24.5 μm, which is close to the size of *Corylus* pollen in noncalcareous sediments (treated with KOH, HF, acetolyzed and mounted in silicone oil, Andersen 1978b). The variation of the individual *Corylus* measurements is small (95% confidence interval = 2% of the mean) and was disregarded.

Pollen grains in silicone oil-slides thinner than their smallest diameter are compressed by the cover slip, and their size may increase slightly due to deformation (up to 6%), whereas the size does not increase further at storage (Andersen 1978b). Large Poaceae pollen in thin slides may thus be slightly too large, whereas the small *Corylus* pollen grains have not increased. Slide thickness was measured in all Poaceae collections in which the smallest pollen diameter was larger than 30 μm. Pollen size may change slightly with storage in silicone oil. Size changes in *Corylus* and Poaceae pollen are correlated; hence measurements carried out a long time after the preparation can be compared with other measurements.

Average mean size and variance between *Glyceria* and *Secale* collections before and after standardization are compared in table 1. The *Glyceria* means were not correlated with the *Corylus* means, and the variation did not decrease significantly after standardization; whereas the *Secale* means were correlated with the *Corylus* means, and variation decreased significantly. Original differences among the *Glyceria* collections thus exceeded differences due to treatment, and the *Secale* collections varied more due to treatment than they did originally. Standardization of pollen size thus may reduce differences caused by treatment.

Annulus measurements of *Glyceria* and *Secale* collections are compared in table 2. The annulus diameters were not correlated with the *Corylus* means, and

Table 1. Average pollen size in *Glyceria fluitans* and *Secale cereale* collections before and after standardization (*Corylus* 24.5 μm). $\bar{x}$ = mean, C = coefficient of variation.

	n	original $\bar{x}$ (μm)	original C (%)	standardized $\bar{x}$ (μm)	standardized C (%)	v.r. (P)	correl. w. *Corylus* $\bar{x}$ (P)	*Corylus* $\bar{x}$ range (μm)
Glyceria	6	35.00	5.43	34.47	4.58	0.350	0.260	22.84-26.21
Secale	8	39.24	7.18	40.10	3.53	0.046*	0.003**	23.22-26.48

Table 2. Average annulus diameter in *Glyceria fluitans* and *Secale cereale* collections before and after standardization (*Corylus* 24.5 μm)

		original		standardized			correl. w.	*Corylus* $\bar{x}$
	n	$\bar{x}$ (μm)	C (%)	$\bar{x}$ (μm)	C (%)	v.r. (P)	*Corylus* $\bar{x}$ (P)	range (μm)
Glyceria	5	9.70	7.28	9.56	9.30	0.33	0.55	23.69-26.12
Secale	9	8.97	7.08	8.90	6.62	0.42	0.25	23.59-26.48

the variation did not change significantly. It can be concluded that original differences among collections exceeded the variation due to treatment, and that standardization of annulus measurements is unnecessary.

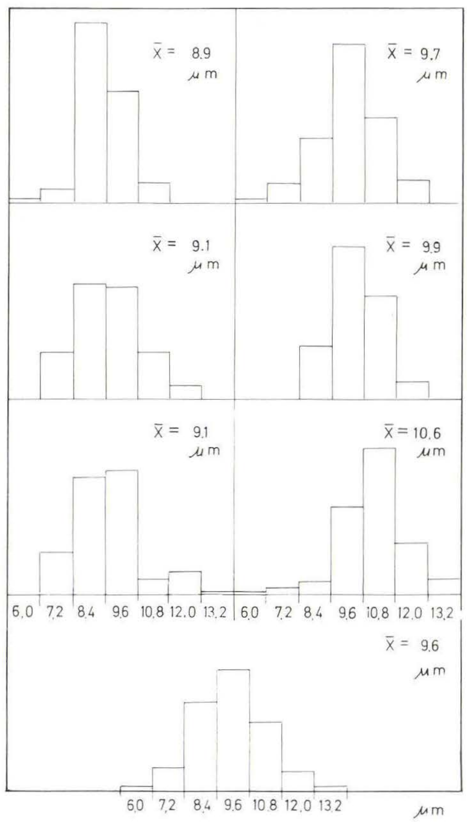

Fig. 1. Glyceria fluitans, annulus diameter. Frequency distribution in 6 collections, and composite population.

Differences among collections. Composite populations

The examples mentioned above show that various collections of a Poaceae species may differ in respect to annulus diameter and pollen size. Each collection represents individuals growing together at one locality. Fossil Poaceae pollen assemblages are likely to derive from an infinite number of individuals in a more or less wide area. The best way to find mean and variance for an infinite population of a species is to measure pollen in surface samples; however, this procedure is impossible for grasses, as the pollen assemblages in surface samples are likely to include many species. Instead, composite populations based on individual collections were calculated for species represented by two or more collections.

The measurements of annulus diameters were performed with the same size class unit. Hence, the number of pollen grains found in identical size classes in the various collections could be added, and size-frequency distribution, mean, and variance of a composite population were calculated (fig. 1). Composite populations were calculated for critical species; it is believed that they express mean size and variation of the species better than the individual collections.

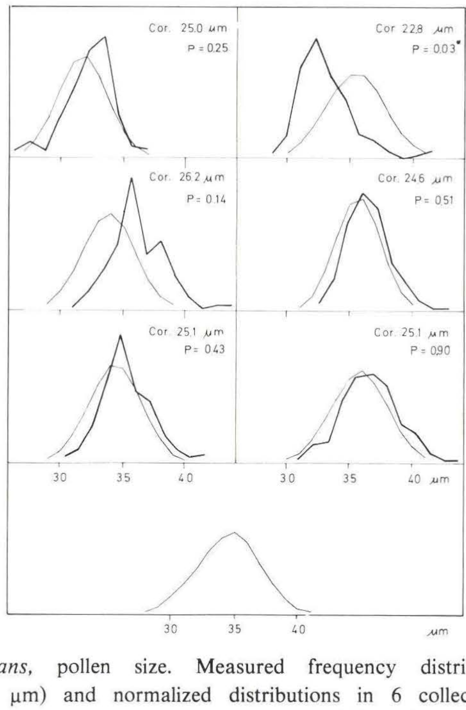

Fig. 2. Glyceria fluitans, pollen size. Measured frequency distributions, standardized (*Corylus* 24.5 µm) and normalized distributions in 6 collections, and composite population. Mean size of *Corylus* pollen and probability of normality (P) for measured distributions are indicated.

Composite populations could not be calculated directly for pollen size because the size class units in individual collections differed. Five out of six size measurements of *Glyceria fluitans* pollen were normally distributed (fig. 2), and it was assumed that the size-frequencies in individual collections generally are normally distributed. A normal distribution based on the standardized mean and variance was calculated for each collection within a species, and the calculated distributions were added to form a composite population as described for the annulus measurements (size class interval 1 μm, fig. 2).

Pollen-morphological characteristics of modern Poaceae species

Data on annulus diameter, standardized pollen size, and pollen index for 80 Poaceae species are shown in table 3 and in fig. 3. Slide thickness is indicated for collections with mean pollen size larger than 30 μm. It was not possible to include all Poaceae species from Northern Europe, and composite populations could only be established in critical cases.

Coefficient of variation (C) reflects homogeneity of individual collections. C for annulus diameter varies from 8.5 to 20.2 and C for pollen size from 3.9 to 9.8. A few collections show a higher C, which might indicate contamination with pollen from another species. *Holcus mollis, Poa compressa, Phleum phleoides* and *Nardus stricta* have high C for annulus diameter (22.5, 21.6, 22.6, 24.7) and *Calamagrostis arundinacea* and *Holcus mollis* high C for pollen size (11.1 and 11.4). The *Holcus mollis* collection may thus contain pollen from another species (with larger pollen), whereas the large variation noticed in only one of the measured dimensions in the other species presumably is accidental.

Slide thickness was considerably smaller than mean pollen size (> 10 μm) in one case *(Secale cereale*, 22 μm); pollen size in this collection was disregarded.

(1) *Annulus diameters.* The species in fig. 3 are arranged according to increasing mean annulus diameter. They were divided into groups and subgroups.

I, mean annulus diameter smaller than 8 μm
- a, no grains with anl-D > 8 μm
- b, 1 - 20% of the grains with anl-D > 8 μm
- c, 20 - 40% of the grains with anl-D > 8 μm

II, mean annulus diameter 8-10 μm, grains with anl-D 8-10 μm predominate.

III, mean annulus diameter larger than 10 μm, grains with anl-D > 10 μm predominate.

Group I comprises only wild grasses, group II wild grasses and cultivated species, and group III cultivated species and one wild grass species.

(2) *Pollen size* (fig. 3). The mean size of pollen grains from cultivated species are larger than 37 μm and only a few wild grasses surpass this limit *(Hordeum*

Table 3. Annulus diameter (anl-D), pollen size (standardized, *Corylus* = 24.5 µm), pollen index and slide thickness (M- > 30 µm) for individual and composite collections of 80 Poaceae species. x̄ = mean, C = coefficient of variation.

	anl-D x̄ (µm)	anl-D C (%)	size x̄ (µm)	size C (%)	index	slide thickn. (µm)
Agropyron caninum L.	6.84	13.7	34.33	9.47	1.07	35
– *junceiforme* A.&D. Löwe	8.89	16.5	39.72	6.92	1.12	32
– *repens* (L.) Beauv.	9.11	14.0	37.33	7.47	1.09	48
– –	8.63	12.3	37.48	8.59	1.11	45
– –	8.68	12.6	38.37	7.63	1.12	45
– – , 3 collections	8.80	13.2	37.72	7.67	1.11	
Agrostis gigantea Roth.	5.72	15.7	22.63	5.62	1.06	
– *spica-venti* L.	6.08	14.0	23.84	5.65	1.06	
– *stolonifera* L.	7.28	12.6	23.57	6.37	1.10	
– *tenuis* Sibth.	6.66	12.8	25.94	7.08	1.05	
Alopecurus geniculatus L.	5.82	20.1	24.91	7.72	1.10	
– *myosuroides* Huds.	6.18	13.8	28.65	9.06	1.14	
– *pratensis* L	6.55	16.0	20.96	6.53	1.08	
Ammophila arenaria (L.) Lk.	8.44	14.9	32.00	7.73	1.13	33
Anthoxanthum odoratum L.	6.66	14.3	29.73	9.81	1.08	
Avena elatior L.	7.51	16.0	31.42	5.46	1.13	33
– *fatua* L.	11.93	10.3	44.24	4.46	1.17	
– *nuda* Höjer	11.60	11.0	40.67	5.26	1.12	34
– *pratensis* L.	7.55	11.5	35.69	8.48	1.14	35
– *sativa* L.	10.91	11.5	38.02	7.11	1.27	50
– –	10.48	16.6	38.99	8.86	1.17	29
– –	11.44	11.8	42.43	5.84	1.26	45
– –	10.07	12.0	44.23	4.74	1.27	38
– – , 4 collections	10.72	13.9	40.92	8.97	1.24	
Baldingera arundinacea (L.) Dum.	7.25	12.4	28.00	7.81	1.09	
Brachypodium pinnatum (L.) Beauv.	6.38	13.0	28.21	4.91	1.09	
– *silvaticum* (Huds.) Beauv.	6.47	15.5	28.32	5.40	1.07	
Briza media L.	5.70	15.3	23.35	7.39	1.08	
Bromus arvensis L.	6.52	13.8	28.05	4.13	1.05	
– *benekeni* (Lge.) Trimen	7.32	11.1	32.33	5.97	1.04	45
– *erectus* Huds.	7.38	11.8	36.54	7.81	1.09	37
– *hordeaceus* L.	7.64	12.3	33.53	4.90	1.04	29
– *racemosus* L.	5.42	16.8	27.32	8.13	1.06	
– *secalinus* L.	7.64	10.6	35.64	5.70	1.06	43
– *sterilis* L.	7.55	10.6	30.14	5.75	1.03	42
– *tectorum* L.	7.48	14.7	30.95	4.88	1.04	50
Calamagrostis arundinacea (L.) Roth.	5.80	15.0	26.47	11.11	1.05	
– *canescens* (Web.) Roth.	5.69	16.5	25.27	6.09	1.07	
– *epigeios* (L.) Roth.	6.34	13.9	30.28	7.45	1.07	
– *villosa* (Chaix.) Mutel.	7.19	14.3	31.34	6.83	1.05	41
Catabrosa aquatica (L.) Beauv.	5.09	15.7	21.77	8.36	1.08	

Corynephorus canescens (L.) Beauv.	4.66	18.0	19.15	7.48	1.07	
Cynosurus cristatus L.	5.26	19.4	26.30	5.56	1.12	
Dactylis glomerata L.	6.40	14.1	29.41	6.87	1.06	
Deschampsia caespitosa (L.) Beauv.	5.83	17.3	23.78	6.92	1.05	
– *flexuosa* (L.) Trin.	5.48	15.5	24.55	6.87	1.07	
Elymus arenarius L.	8.36	14.6	42.57	5.78	1.08	42
– –	8.88	14.1	43.19	5.07	1.09	46
– –	9.40	15.0	45.84	5.57	1.08	41
– – , 3 collections	8.88	15.3	43.86	6.23	1.08	
Eragrostis pooides PB.	5.08	15.9	21.94	9.27	1.04	
Festuca altissima All.	5.84	16.1	23.12	5.80	1.06	
– *arundinacea* Schreb.	6.76	16.4	29.11	6.97	1.10	
– *gigantea* (L.) Vill.	5.62	17.6	31.71	7.70	1.06	37
– *ovina* L.	6.12	15.0	24.03	7.10	1.05	
– *pratensis* Huds.	6.07	17.1	28.89	7.17	1.12	
– *rubra* L.	6.77	13.9	29.56	6.33	1.05	
Glyceria fluitans (L.) R.Br.	8.88	9.6	31.65	6.20	1.07	44
– –	9.70	13.4	33.84	6.09	1.05	34
– –	9.09	13.2	34.44	5.93	1.03	43
– –	9.12	14.1	35.39	6.59	1.05	41
– –	9.94	10.0	35.64	4.87	1.03	30
– –	10.57	11.9	35.86	6.13	1.04	32
– – , 6 collections	9.55	13.6	34.47	7.21	1.05	
– *maxima* (Hartm.) Holmb.	6.73	16.1	28.41	6.53	1.13	
– –	6.56	13.6	29.03	7.84	1.14	
– – , 2 collections	6.64	15.1	28.72	7.22	1.14	
– *plicata* Fr.	9.66	12.4	34.99	7.12	1.03	44
Holcus lanatus L.	4.77	19.1	23.51	4.97	1.07	
– *mollis* L.	5.03	22.5	24.47	11.43	1.04	
Hordeum murinum L.	8.77	16.4	39.10	6.36	1.05	34
– *vulgare* L.	7.99	13.5	36.26	4.77	1.15	
– –	8.63	10.2	37.47	5.34	1.12	42
– –	8.09	11.9	38.14	5.33	1.15	42
– – , 3 collections	8.23	12.3	37.29	5.50	1.14	
Koeleria glauca (Schkuhr.) D.C.	5.16	20.0	23.89	8.81	1.06	
– *gracilis* Pers.	5.05	19.4	25.93	5.20	1.09	
Lolium perenne L.	7.06	15.2	27.84	8.23	1.10	
Melica nutans L.	6.00	18.8	27.86	7.30	1.05	
– *uniflora* Retz.	5.90	19.0	27.84	4.86	1.04	
Milium effusum L.	6.26	18.5	24.71	5.76	1.09	
Molinia coerulea (L.) Moench.	5.93	18.7	24.54	5.11	1.06	
Nardus stricta L.	5.15	24.7	27.30	8.77	1.09	
Phragmites communis L.	5.90	9.0	22.13	6.64	1.04	
– –	5.80	9.9	22.43	3.87	1.09	
– –	5.90	12.9	23.99	5.30	1.07	
– – , 3 collections	5.87	10.7	22.85	6.51	1.07	
Phleum nodosum L.	6.18	18.1	27.86	7.56	1.08	
– *phleoides* (L.) Karst.	5.70	22.6	23.97	6.45	1.08	
– *pratense* L.	5.65	16.8	32.26	5.41	1.08	

Poa annua L.	5.78	18.9	22.78	6.39	1.07	
– *compressa* L.	6.06	21.6	23.79	7.69	1.04	
– *nemoralis* L.	5.89	18.5	26.06	8.40	1.09	
– *pratensis* L.	5.89	20.2	25.74	9.71	1.08	
– *trivialis* L.	5.32	16.4	20.27	5.92	1.06	
Puccinellia distans (L.) Parl.	5.91	18.4	26.95	7.60	1.11	
Secale cereale L.	8.28	10.4	38.17	7.11	1.37	51
– –	8.84	12.0	38.24	5.53	1.41	98
– –	8.69	11.6	39.72	6.37	1.36	39
– –	8.98	9.6	39.97	5.76	1.40	44
– –	8.60	9.3	40.09	5.76	1.41	32
– –	9.71	9.6	41.15	4.84	1.47	40
– –	10.00	16.9	41.49	4.63	1.40	42
– –	8.66	10.1	42.01	5.26	1.39	37
– –	8.65	13.6				22
– – , 9 and 8 collections	8.93	13.2	40.10	6.78	1.40	
Trisetum flavescens (L.) Beauv.	5.58	17.0	24.04	6.35	1.07	
Triticum aestivum L.	11.88	10.8	42.55	5.97	1.13	55
– –	12.22	10.2	45.53	6.34	1.13	47
– –	12.34	8.5	45.88	5.64	1.10	62
– –	10.82	15.4	46.13	4.33	1.13	40
– – , 4 collections	11.81	12.3	45.03	6.33	1.12	
– *dicoccum* Schrank.	13.51	11.5	45.77	5.36	1.10	34
– *compactum* Host.	14.18	12.6	47.19	4.91	1.09	47
– *monococcum* L.	8.26	11.6	36.73	7.17	1.14	39
– –	9.74	12.9	37.22	6.73	1.12	44
– –	9.56	10.9	38.93	7.32	1.13	55
– – , 3 collections	9.19	13.9	37.63	7.34	1.13	
– *polonicum* L.	10.98	11.1	39.57	6.25	1.12	42
– *spelta* L.	12.59	12.2	45.99	4.73	1.11	38

murinum, 65; *Agropyron repens*, 66; *Elymus arenarius*, 67; *Agropyron junceiforme*, 68; and *Avena fatua*, 77; the figures refer to fig. 3).

Pollen size and annulus diameters generally are correlated, with some exceptions. *Festuca gigantea* (14) and *Phleum pratense* (15) have particularly large grains, and *Agrostis stolonifera* (54), *Ammophila arenaria* (64), *Glyceria fluitans* (71) and *G. plicata* (72) have small grains compared with the annulus diameter. The mean sizes of grains with large and small annulus within a species do not differ *(Hordeum vulgare*, table 4).

(3) *Pollen index* varies from 1.03 – 1.15; a higher index occurs in *Avena sativa* (1.24) and *Secale cereale* (1.40, table 3).

(4) *Surface sculpturing*. Pollen grains with scabrate and verrucate sculpturing occur in the wild grasses belonging to group I mentioned above (scabrate, areolate, verrucate or maculate in Fægri & Iversen 1964, Nilsson et al. 1977). The species belonging to group II are scabrate (Andersen and Bertelsen 1972, Nilsson

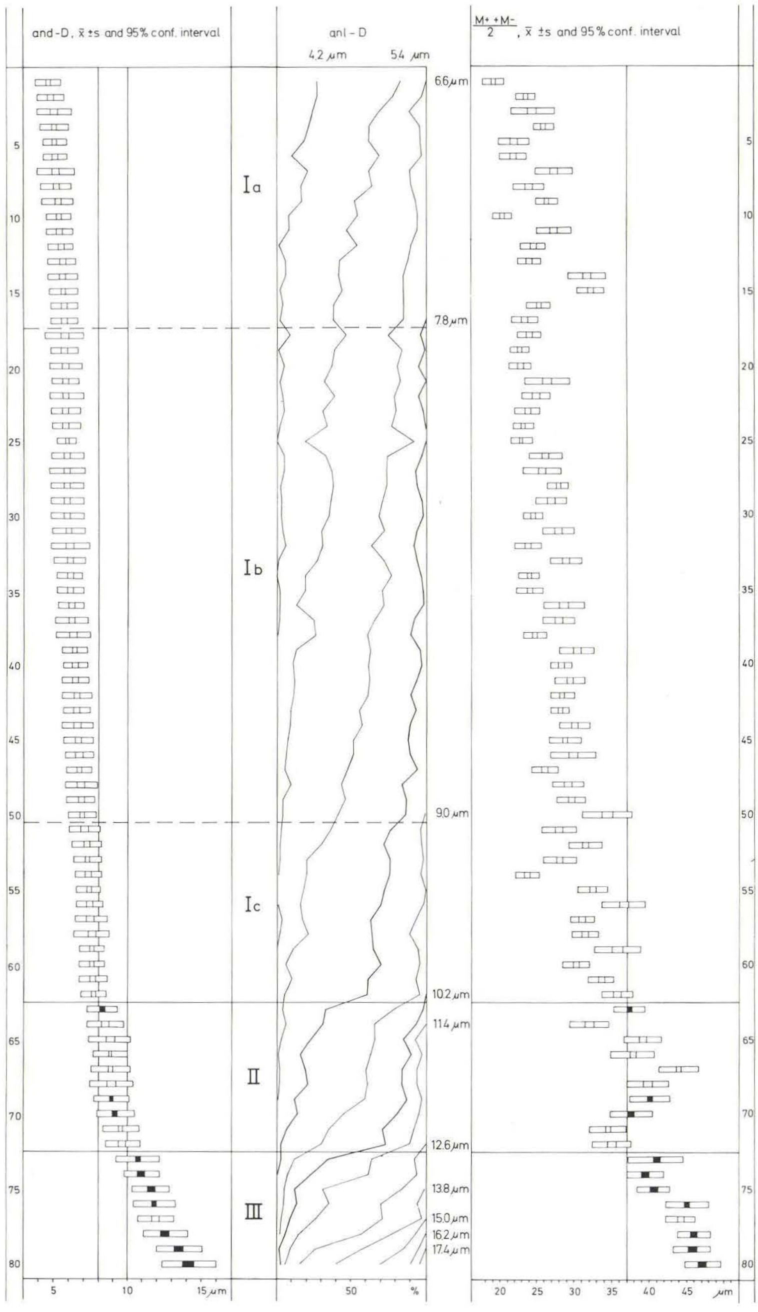
and-D, x̄ ±s and 95% conf. interval
anl - D
4.2 µm
5.4 µm
M+ +M- / 2, x̄ ±s and 95% conf. interval
6.6 µm
7.8 µm
9.0 µm
10.2 µm
11.4 µm
12.6 µm
13.8 µm
15.0 µm
16.2 µm
17.4 µm
Ia
Ib
Ic
II
III
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
5
10
15 µm
50
%
20
25
30
35
40
45
µm

Fig. 3. Poaceae, annulus diameter (anl-D), mean ($\bar{x}$) and frequency distribution (the lines indicate size class limits), and pollen size($\frac{M+ +M-}{2}$ standardized, *Corylus* = 24.5 μm). Numbers of collections are indicated for composite populations (in brackets). Confidence intervals for cultivated species are black.

Ia	1	Corynephorus canescens
	2	Holcus lanatus
	3	– mollis
	4	Koeleria gracilis
	5	Eragrostis pooides
	6	Catabrosa aquatica
	7	Nardus stricta
	8	Koeleria glauca
	9	Cynosurus cristatus
	10	Poa trivialis
	11	Bromus racemosus
	12	Deschampsia flexuosa
	13	Trisetum flavescens
	14	Festuca gigantea
	15	Phleum pratense
	16	Calamagrostis canescens
	17	Briza media
Ib	18	Phleum phleoides
	19	Agrostis gigantea
	20	Poa annua
	21	Calamagrostis arundinacea
	22	Alopecurus geniculatus
	23	Deschampsia caespitosa
	24	Festuca altissima
	25	Phragmites communis (3)
	25	Poa nemoralis
	27	– pratensis
	28	Melica uniflora
	29	Puccinellia distans
	30	Molinia coerulea
	31	Melica nutans
	32	Poa compressa
	33	Festuca pratensis
	34	Agrostis spica-venti
	35	Festuca ovina
	36	Alopecurus myosuroides
	37	Phleum nodosum
	38	Milium effusum
	39	Calamagrostis epigeios
	40	Brachypodium pinnatum
	41	Dactylis glomerata
	42	Brachypodium silvaticum
	43	Bromus arvensis
	44	Alopecurus pratensis
	45	Glyceria maxima
	46	Anthoxanthum odoratum
	47	Agrostis tenuis
	48	Festuca arundinacea
	49	– rubra
	50	Agropyron caninum
	51	Lolium perenne
	52	Calamagrostis villosa
	53	Baldingera arundinacea
	54	Agrostis stolonifera
	55	Bromus benekeni
	56	– erectus
	57	– tectorum
	58	Avena elatior
	59	– pratensis
	60	Bromus sterilis
	61	– hordeaceus
	62	– secalinus
II	63	Hordeum vulgare (3)
	64	Ammophila arenaria
	65	Hordeum murinum
	66	Agropyron repens (3)
	67	Elymus arenarius (3)
	68	Agropyron junceiforme
	69	Secale cereale (9,8)
	70	Triticum monococcum (3)
	71	Glyceria fluitans (6)
	72	– plicata
III	73	Avena sativa (4)
	74	Triticum polonicum
	75	Avena nuda
	76	Triticum aestivum (4)
	77	Avena fatua
	78	Triticum spelta
	79	– dicoccum
	80	– compactum

Table 4. Mean size of pollen grains with annulus diameters smaller and larger than 8 μm in three collections of *Hordeum vulgare*. Significance tests by χ^2 -method (differences in means), and student's t (average difference). $\bar{x}$ = mean, C = coefficient of variation.

	anl-D < 8 μm			anl-D > 8 μm			Diff.
coll.		$\bar{x}$	C		$\bar{x}$	C	means
no.	n	(μm)	(%)	n	(μm)	(%)	(P)
1	39	35.91	4.54	32	36.68	4.84	0.92
2	33	37.35	5.75	67	37.53	5.16	0.89
3	30	37.96	5.59	70	38.22	5.24	0.71
average difference = 0.40 μm, P = 0.17							

et al. 1977, *Hordeum-Typ* in Beug 1961). The sculpturing is seen as isolated dark dots with phase contrast equipment (cp. Grohne 1957, Beug 1961). Verrucate sculpturing occurs in the species in group III (Andersen and Bertelsen 1972, Nilsson et al. 1977). The sculpturing is seen as irregular dark spots in phase contrast (Grohne 1957); however, this sculpturing type may not always be distinguishable from the scabrate sculpturing type. Beug (1961) separated an *Avena-Typ* with *Punktklumpen* from a *Triticum-Typ* with *Punktgruppen* seen in phase contrast. These sculpturing types are difficult to distinguish (illustrations in Beug, 1961).

Identification of Poaceae pollen

Based on annulus diameter, pollen size, pollen index and surface sculpturing, Poaceae pollen can be divided into four main groups.

(1) *Wild grass group*; mean annulus diameters smaller than 8 μm, mean pollen size less than 37 μm, scabrate or verrucate. This group comprises the majority of the wild grass species.

(2) *Hordeum group* (fig. 4); mean annulus diameters 8-10 μm, mean pollen size 32-45 μm, scabrate. This group comprises the following wild grasses and cultivated species (for *Secale cereale*, see below),

Ammophila arenaria	*Glyceria fluitans*
Hordeum murinum	*Glyceria plicata*
Agropyron repens	
Agropyron junceiforme	*Hordeum vulgare*
Elymus arenarius	*Triticum monococcum*

In the measurements of 84 Central European species in Beug (1961, *Tabelle* 1), the following North European wild grasses also belong to this group (for recalculation of annulus measurements see p. 72),

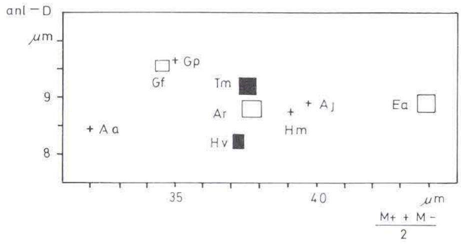

Fig. 4. Hordeum-group, mean pollen size, standardized (*Corylus* 24.5 μm), and annulus diameter. 95 % confidence intervals are indicated for composite populations (cultivated species black). Aa = *Ammophila arenaria,* Gf = *Glyceria fluitans,* Gp = *G. plicata,* Hv = *Hordeum vulgare,* Ar = *Agropyron repens,* Tm = *Triticum monococcum,* Hm = *Hordeum murinum,* Aj = *Agropyron juncoides,* Ea = *Elymus arenarius.*

Bromus inermis (anl-D = 8.8 μm)
Hordeum jubatum (anl-D = 9.6 μm)

(3) *Avena-Triticum group*; mean annulus diameters larger than 10 μm, mean pollen size larger than 40 μm, verrucate. This group comprises one wild grass, *Avena fatua*, and the following cultivated species,

Avena sativa	*Triticum spelta*
Avena nuda	*Triticum dicoccum*
Triticum aestivum	*Triticum compactum*
Triticum polonicum	

Triticum durum in Beug's *Tabelle 1* (1961, anl-D = 11.4 μm) also belongs to this group.

Panicum miliaceum has verrucate pollen grains (Beug 1961, *Avena-Typ*). Mean annulus diameter is 8.0 μm and pollen size seems to be small.

(4) *Secale cereale*; *Secale* pollen grains are scabrate (Andersen & Bertelsen 1972). They are distinguished from species within the *Hordeum*-group by a larger pollen index (1.40, table 3). As noticed by Beug (1961), there is considerable overlapping in ranges of pollen index in *Secale* and other species. *Hordeum vulgare* and *Triticum monococcum* pollen grains have the largest pollen index within the *Hordeum* group (1.14 and 1.13). Annulus diameter in these species is similar to *Secale* (8.23, 9.19 and 8.93 μm). Pollen index is higher than 1.26 in only a few *Hordeum* and *Triticum monococcum* grains (4 and 6%) and smaller than 1.26 in 10% of the *Secale* grains. Pollen grains with pollen index higher than 1.26 are thus likely to belong to *Secale,* whereas 10% of the *Secale* grains (index < 1.26) are likely to become confused with *Hordeum* or *Triticum monococcum*, if their pollen occur together. The oblong *Secale* grains tend to fold along the longer axis and may be identified by shape; measurement of pollen index, however, is not possible in these cases.

Pollen grains of Poaceae can thus be grouped by means of morphological characteristics. Due to the wide overlappings of size ranges, it is necessary to produce frequency distribution curves of fossil Poaceae pollen assemblages, for identifications.

Fossil pollen

Poaceae pollen in Holocene gytta and peat samples from a small wet hollow and two soil profiles i Eldrup Forest, Djursland, Denmark, were examined. A pollen diagram from the hollow was shown in Andersen (1973, cp. 1978a); it comprises the Atlantic, Subboreal and Subatlantic. The pollen samples from the soil profiles were from bleached sand and derive from Medieval time (sections C 19 and E 13 in Andersen 1979).

The Poaceae pollen was examined in the following way:

(1) *Secale* pollen was identified by shape,
(2) annulus diameter was measured,
(3) Pollen grains with annulus larger *than 8* µm were separated into *Hordeum* group and *Avena-Triticum* group,
(4) size was measured in all grains with annulus larger than 8 µm if possible.

Most of the pollen grains in the gyttja and peat samples were moderately crumpled. The pollen grains in the soil samples were strongly crumpled and size was not measured. *Corylus* pollen could not be measured. As the sediments are non-calcareous, it can be assumed that the measurements of fossil and modern pollen can be compared directly (p. 73).

Gyttja and peat samples

Annulus diameter (fig. 5). The frequency curves for grass pollen with small and large annulus (excluding *Secale* and *Avena-Triticum*) show that pollen grains with large annulus are frequent (up to 25%) and constitute about 50% of the Poaceae pollen at the middle levels. The annulus diameter-distributions are bimodal at these levels with modes at the 5.4 – 6.6 and 9.0 – 10.2 µm size classes. Two or more species are thus present in the Poaceae pollen assemblages.

Usinger (1975,1978) has shown that coefficient of variation and skewness index are useful for describing pollen assemblages composed of one or more species with different sizes. The coefficient of variation is low in uniform and high in heterogenous assemblages. Skewness may be calculated as Pearson-skewness or third moment-skewness. Pearson-skewness depends on the difference between the

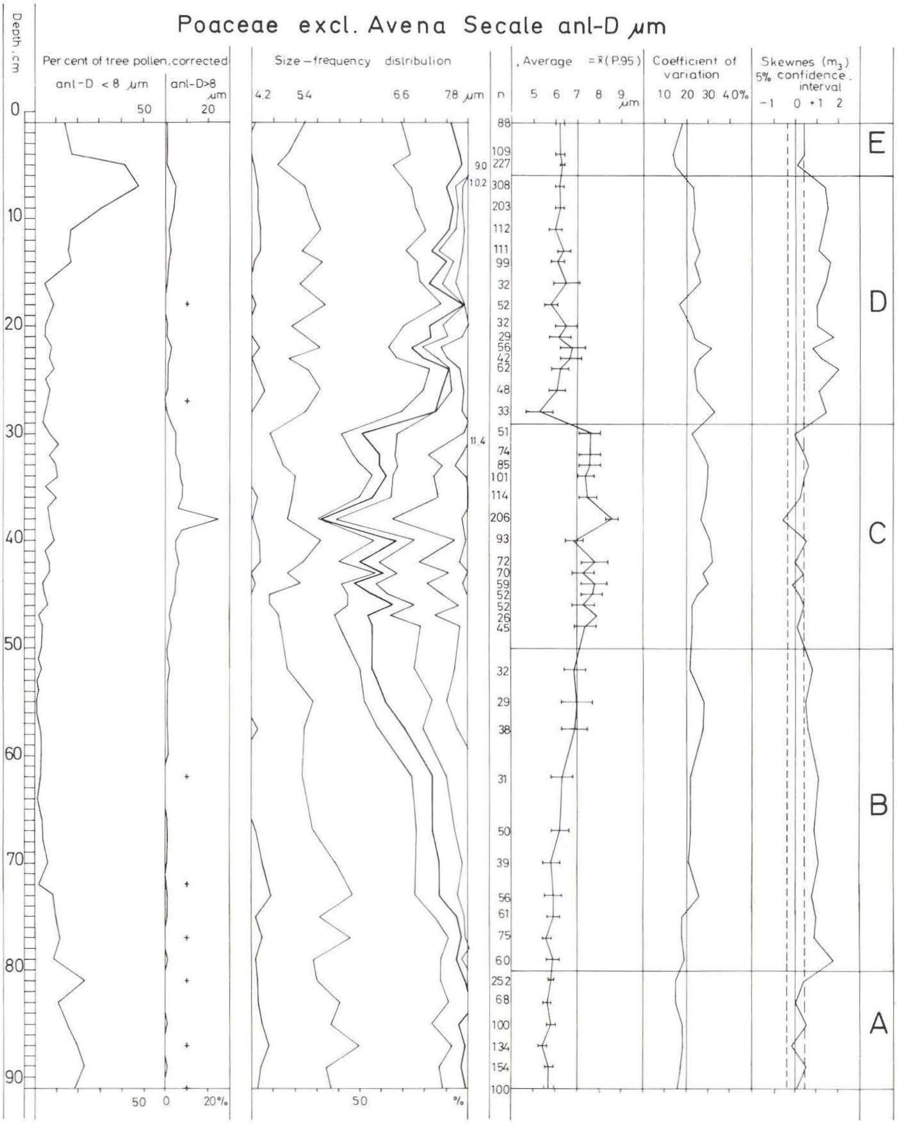

Fig. 5. Poaceae, annulus diameter (anl-D) in Holocene gyttja and peat samples. Frequency (in percent of tree pollen), size-distribution, mean, coefficient of variation and moment-3 skewness.

arithmetic mean and the mode (divided by the standard deviation). Mode could not be calculated accurately in the present distributions because the number of size classes was small. Third moment-skewness was calculated instead. This skewness index is zero in symmetric distributions, positive in distributions skewed to the right-hand side and negative in distributions skewed to the left-hand side. The 0.05 confidence interval for zero skewness varies from ± 0.5 (n = 50) to ± 0.2 (n = 400, Pearson 1931). Confidence interval for n = 100 is shown in fig. 5.

The annulus size-distributions could be grouped in five main levels according to mean, coefficient of variation and skewness index,

A, low means (5-6 µm), low variances (C = 15%), no skewness; unimodal symmetrical distributions; only grains with small annulus,

B, low means (6-7 µm), intermediate variances (C = 20-30%), high skewness (1.0); unimodal positively skewed distributions, grains with small annulus predominate,

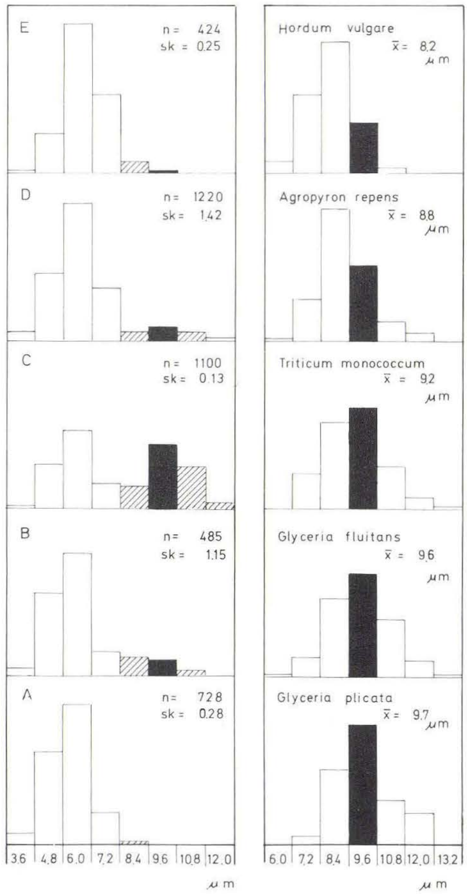

Fig. 6. Poaceae, Holocene samples, annulus diameter. Frequency distributions for levels A-E (see fig. 5) and five modern species. Sk = moment-3 skewness.

C, high means (7-8 μm), high variances (C = 30%), no skewness; bimodal symmetrical distributions, grains with small and large annulus,

D, low means (6 μm), intermediate variances (C = 20-30%), high skewness (1-2); unimodal, positively skewed distributions, grains with small annulus predominate,

E, low means (6 μm), low variances (C = 15%), no skewness; unimodal symmetrical distributions, only grains with small annulus.

The distributions within the levels A-E were summarized into average distributions (fig. 6). The five distributions show a distinctive mode at the 6 μm size class. This mode must be due to one or several wild grass species which have pollen with annulus diameters about 6 μm. These wild grasses were frequent in the lowermost part of the section (fig. 5, 70-90 cm, early Atlantic time) and indicate fair light conditions and abundant local grass populations. They were very rare at 50-70 cm, where strong shade is indicated, and more frequent again above 50 cm. A distinctive wild grass maximum above 10 cm corresponds to a period with grazing (AD 1700-1800, Andersen 1979) and fair light conditions. It is impossible to say which grasses are represented. Species from group Ib in fig. 3 probably contributed a main part of the pollen, and it is not unlikely that *Phragmites* (mean at 5.9 μm) was important.

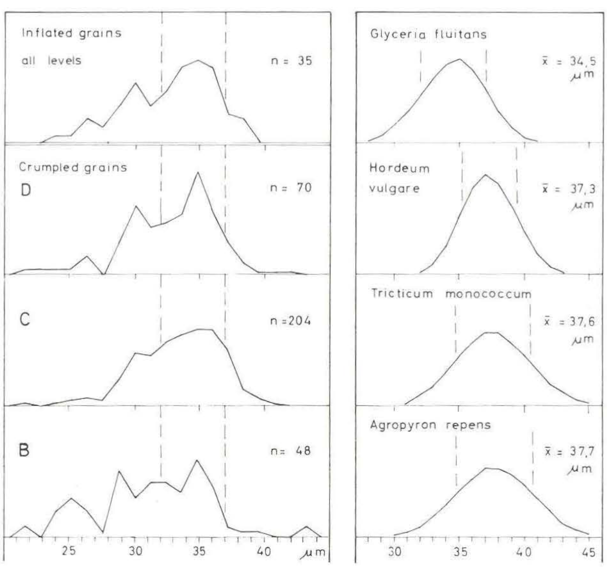

Fig. 7. Poaceae, pollen size. Frequency distributions for grains with annulus diameters larger than 8 μm at the levels B-D ($\bar{x} \pm s$ for *Glyceria fluitans* is indicated) and composite populations of four modern species ($\bar{x} \pm s$ indicated).

The skewed distributions at the levels B and D, and the bimodal distribution from level C indicate the presence of one or more species from the *Hordeum*-group. Pollen grains with annulus diameters 9.6 and 10.8 μm are particularly frequent. Size-frequency distributions in five species, which might have occurred at the site, are shown in fig. 6. *Triticum monococcum* and *Glyceria* resemble the larger mode in the distributions for fossil pollen best; however, it is not possible to say whether *Triticum* or *Glyceria* predominated.

Pollen size. Among the pollen grains with annulus diameter larger than 8 μm, only 35 inflated grains were found (357 measured grains). The size frequency-distribution curve for inflated pollen grains (fig. 7) is negatively skewed with a predominant mode at 35 μm and probably a secondary mode at 30 μm. A similar frequency distribution is repeated in the curves for crumpled grains from levels B, C and D. The average size of the crumpled grains is thus nearly the same as the average size of the inflated grains in this case. The predominant mode is very similar to the mode in the composite population of *Glyceria fluitans* (35 μm), whereas *Hordeum vulgare, Triticum monococcum* and *Agropyron repens* are larger (modes at 37-38 μm). Very few of the fossil pollen grains exceed the maximum size of *Glyceria fluitans* (41 μm); hence, it can be concluded that *Glyceria fluitans* (or *G. plicata*) contributed a major part of the fossil pollen with annulus diameters larger than 8 μm. These species are characteristic of small ponds and apparently occurred abundantly at level C (30-50 cm on fig. 5) at a time when the pond was well illuminated.

The negatively skewed curves in fig. 7 indicate that Poaceae species with pollen grains smaller than 32 μm contributed some of the pollen grains with annulus diameters larger than 8 μm.

The mode at 35 μm is repeated in all the pollen size distributions for individual annulus size classes from levels B – D (fig. 8). Pollen grains with annulus diameters 8.4 μm predominate in *Hordeum vulgare* and *Agropyron repens*; however, no fossil grains with annulus diameters 8.4 μm exceed the size range of *Glyceria* pollen. Hence, no fossil pollen grains of *Hordeum* and *Agropyron* are present. Two fossil grains with annulus diameters 9.6 μm exceed the upper size limit of *Glyceria* pollen (43 and 44 μm). These grains are larger than *Hordeum* and *Triticum monococcum* pollen grains and fall within the size range of *Elymus arenarius* (mean size 43.9 μm). The fossil pollen grains with still larger annulus diameters (10.8 and 12.0 μm) do not exceed the upper size limit of *Glyceria fluitans* pollen. It can thus be shown that hardly any cereals from the *Hordeum*-group occurred.

The distribution curves for grains with annulus diameters 9.6 and 8.4 μm show increasing frequencies of grains smaller than 32 μm, and small pollen grains predominate in the curves from the levels A and E (fig. 8). These pollen grains presumably derive from Poaceae species belonging to group Ic in fig. 3 *(Baldingera arundinacea*?, mean size 28.0 μm).

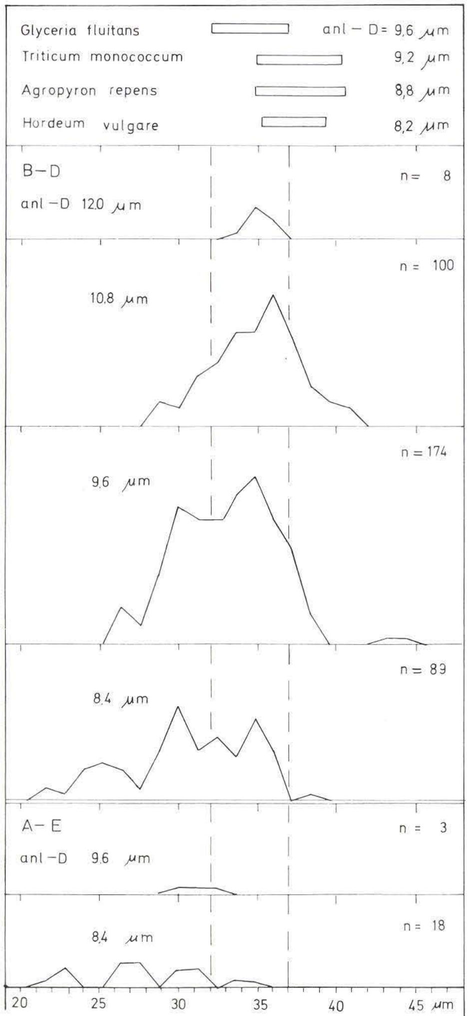

Fig. 8. Poaceae, pollen size. Frequency distributions for grains with various annulus diameters at the levels B-D and A-E, and size ($\bar{x} \pm s$) of four modern species (top).

Several Poaceae species have thus contributed to the fossil Poaceae pollen assemblages measured. The pollen grains with small annulus diameters belong to wild grasses, possibly *Phragmites*. *Glyceria fluitans* (or *G. plicata*) contributed a major part of the pollen grains with large annulus diameters. Other wild grasses and cereals from the *Hordeum* group are unlikely to be represented except for a few grains, which possibly belong to *Elymus arenarius* and were thus transported from populations at the seashore. A more superficial consideration and inaccu-

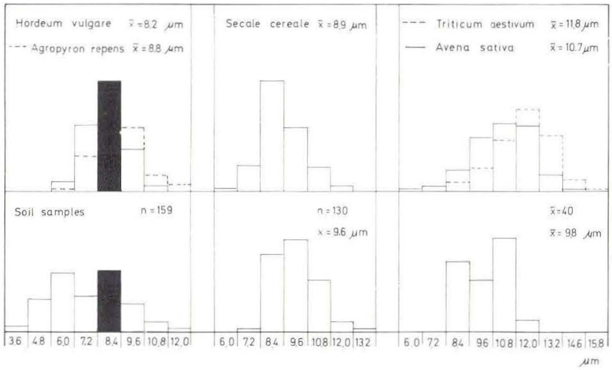

Fig. 9. Poaceae, annulus diameter. Frequency distributions in pollen from soil samples (excluding *Secale* and *Avena – Triticum* group), all *Secale cerale* grains, and all grains referred to the *Avena – Tritucum* group, compared with modern species.

rate measurements might have led to the conclusion that cereals are amply represented.

Soil samples

Annulus diameters of Poaceae pollen from soil samples are shown in fig. 9 *(Secale* and *Avena-Triticum* group ommitted). The frequency distribution curve is bimodal with a mode at 6.0 µm due to wild grasses with small annulus diameters and a mode at 8.4 µm, which coincides with the modes in modern *Hordeum vulgare* and *Agropyron repens* pollen. The samples contain many pollen grains from weeds (i.a. *Centaurea cyanus*), *Secale* and *Fagopyrum* (Andersen 1979) and obviously derive from fields. The *Hordeum* or *Agropyron* pollen grains constitute about 50% of the Poaceae pollen; they could not have been recognized without annulus measurements because pollen size could not be measured.

Secale cereale

Annulus diameters measured on all *Secale* pollen encountered are slightly larger than the mean diameter of modern grains (fig. 9).

Avena – Triticum group

The annulus size-distribution in pollen grains referred to the *Avena – Triticum* group shows a predominant mode at 10.8 µm, and a lower mode at 8.4 µm (fig.

9). The larger mode coincides with *Avena sativa*; no *Triticum* grains thus occur. The smaller mode coincides with *Hordeum*. One suspects that some *Hordeum* grains with intermediate surface sculpturing were erronously refered to the *Avena* - *Triticum* group; hence, only the pollen grains with annulus diameter larger than 8.4 μm were considered *Avena sativa*.

Conclusion

Poaceae species were divided into groups according to pollen characteristics. The wild grass group (1) is distinguished by small annulus diameter and size (the sculpturing is variable); the *Hordeum* - group (2) by intermediate annulus and size, and by scabrate sculpturing; the *Avena* - *Triticum* (3) group by large annulus and size, and by verrucate sculpturing, and *Secale* (4) by oblong shape and scabrate sculpturing. The *Hordeum* - group includes cultivated species and some wild grasses, and the *Avena* - *Triticum* group almost exclusively cultivated species (*Avena sativa* and *Triticum* spp.).

Frequency-distributions for annulus size, and observations of surface sculpturing of Poaceae pollen in Holocene gyttja and peat samples made it possible to detect the presence of a component of wild grasses and a component of species belonging to the *Hordeum* group. Measurements of pollen size indicated that the pollen referred to the *Hordeum* - group derive mainly from *Glyceria (fluitans* or *plicata*). Measurements of annulus diameters in soil samples indicated the presence of wild grass and *Hordum vulgare* or *Agropyron repens* pollen. Pollen grains of *Secale cereale* and *Avena sativa* were also identified.

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Dansk sammendrag

Pollen fra græsfamilien er vanskelige at bestemme fordi de er meget ensartede og fordi der er mange arter. I vegetationshistoriske arbejder er det særlig vigtigt at kunne kende og adskille dyrkede kornarters pollen. Forskelle i pollenstørrelse kan være vanskelige at udnytte, hvis mange af pollenkornene er sammenfoldede og det er bedre at benytte diameter af pore-ringen, som altid kan måles. Overfladeskulptur kan også benyttes.

Diameter af pore-ring og pollenstørrelse er blevet målt på 80 græsarter. Græsarterne kan på dette grundlag deles i 3 grupper, hvoraf den første omfatter vildgræsser, den anden dyrkede arter (byg og enkorn) og enkelte vildgræsser og den tredje dyrkede arter (havre og hvede-arter). Rugpollen adskiller sig fra alle andre ved at være aflange. Eksempler på bestemmelse af fossilt pollen ved hjælp af variationskurver er vist.

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