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THE LATE-GLACIAL AND HOLOCENE VEGETATIONAL HISTORY OF
THE ŻUŁAWY REGION, N. POLAND. A BIOSTRATIGRAPHIC STUDY
OF LAKE DRUZNO SEDIMENTS

Późnoglacialna i holocenińska historia rozwoju roślinności Żuław (północna
Polska). Biostratygraficzne badania osadów jeziora Druzno

ABSTRACT. The results of palynological and diatom studies of the deposits of Lake Druzno are presented. Radiocarbon dates and determinations of sedimentary chlorophyll and of water content were carried out in the bottom part of profile (1a). Ten local pollen zones and twelve local diatom zones have been distinguished. The results of these analyses allowed to reconstruct the Late-Glacial and Holocene vegetational history of the Żuławy Region and the history of Lake Druzno from the initial stage dated at $11\,290 \pm 105$ BP. About 7000 BP the beginning of inflow of sea water was observed. Around 6440 ± 50 BP Lake Druzno became a part of the Vistula Lagoon. The process of isolation of the lake from the Vistula Lagoon begun in the period corresponding with zone Dr-9, DrD-11.

INTRODUCTION

A long series of naturalistic and hydrographic studies of Lake Druzno was started as early as the first half of the nineteenth century. Investigation of this lake increased in intensity at the beginning of the twentieth century. Special attention should be given to the palynological study of the sediments from the region of Lake Druzno carried out by Knoblauch (1931). He analyzed only the composition of tree pollen and claimed that the sediments lying above the level of 4 m had been deposited in the Subatlantic period and those below 4.5 m in the Atlantic. A complex limnological study was carried out under the direction of J. S. Mikulski (1955) in 1950—1951. Hydrological studies on the exchange of water between Lake Druzno and the Vistula Lagoon (Z. Mikulski 1964) and the water balance of the lake (Z. Mikulski et al. 1969) were taken up in the sixties.

The present work is a continuation of the studies on the sediments of Lake Druzno initiated in the sixties and carried out by the methods of pollen analysis (Zachowicz 1976) and diatom analysis (Przybyłowska-Lange 1976).

In 1979 a new core (1a) was taken and subjected to close physical and chemical studies and pollen and diatom analyses. Radiocarbon age determinations were also made (in the ^{14}C Laboratory of the Silesian Politechnical University).

The present paper gives the results of studies on the lower part of core 1a, consisting of Late-Glacial and early Holocene sediments. The Holocene part of the profile 1A studied in 1976, is added.

Lake Druzno has been included in Programme IGCP — 158 B as the reference site for the Żuławy area (type region 11, subregion d).

THE PRESENT NATURAL ENVIRONMENT

Characteristics of the study area

a. Geology

Lake Druzno is situated in the Vistula Żuławy (alluvial plains), in the area of the last glaciation (Kondracki 1965). The top of the sub-Quaternary basis of this area is built of Cretaceous formations (Rosa 1963). The Tertiary deposits occur only in small insular patches. In the Pleistocene this region was covered by an ice-sheet several times and its residue is a fairly thick layer of Pleistocene deposits. Grey moraine clay, coming from one of the older glaciations most often forms the bottom of the Quaternary stratum and is overlain by fluvioglacial sands and gravels, several tens of metres thick, and, higher, by two layers of younger morain clay divided by fluvioglacial sediments or clays deposited in ice-dam lakes. The Holocene formations, i. e. gravels, sands, fluvial silts, mud and sand of the lagoon and peats are accumulated here in large amounts. Their thickness often exceeds ten metres.

b. Soils and vegetation

The soils of the alluvial Żuławy region are sandy muds, sands and muds (Witek 1965). South-west of Lake Druzno there are mud-bog soils (soils of meadows and cultivated fields).

River-side forests and alder woods or, more rarely, hornbeam woods grew beside marsh vegetation, in the area of Żuławy before the colonization of the Vistula delta about the thirteenth century (Śröder 1972). Remnants of these forest communities subsist in the fork of the Vistula and Nogat and by the lake shores. At the present time the Żuławy region is woodless and used for farming, field and meadows.

The largest wooded areas subsist on the Elbląg Upland to the east from the Żuławy. They find there favourable conditions owing to the varied ground relief and fertile soils. The beechwoods (*Melico-Fagetum*) prevail here. Communities of mixed pinewood (*Pino-Quercetum*) grow on poorer soils, with the dominance of *Picea abies* on sandy soils and of *Fagus sylvatica* on sandy-clayey soils.

Description of Lake Druzno

Lake Druzno is situated in the central part of the catchment basin of the river Elbląg, surrounded by the Malbork Żuławy, Vistula Lagoon and Elbląg Upland. Now, the region adjacent to the lake is a depression, 1.8 m below sea level. The lake is very shallow, its maximum depth is 3.0 m, averaging 1.2 m. It is classified as a pond-lake (J. S. Mikulski 1955). The lake is 10 km long and 2.2 km wide and its well-developed shore-line is 32.2 km in length. Now the lake is surrounded by embankments, 45 km long, because the neighbouring area is a depression. The bottom of the basin is filled with a 6—8 metre layer of lacustrine gyttja. In the southern and western parts its thickness increases to 10 m or more.

Lake Druzno is characterized by its specific ecological conditions resulting from the physical and chemical properties of its water. The most important of them are the low calcium content and also low quantities of nitrogen, phosphorus, iron and oxygen compounds (Gromadzka 1956), poor transparency of water and its shallowness, slimy bottom and intense processes of decay.

A recent investigation of the vegetation of Lake Druzno (Kluszczyńska et al. 1979) reveals a marked impoverishment of the flora as compared with the results of earlier studies. Such species as *Najas marina*, *Nymphaea candida*, *Nuphar pumilum*, *Elodea canadensis*, *Stratiotes aloides*, *Potamogeton lucens*, *Myriophyllum spicatum* and *Ceratophyllum submersum* still recorded by Schultz (1941) and Mikulski (1955) are not observed any more. *Schoenoplectus lacustris*, *Hottonia palustris*, *Lemna minor*, *L. gibba*, *Utricularia vulgaris* and *Acorus calamus* are disappearing. The vegetation of this lake is characterized by the dominance of few species which generally form monotypic assemblages. These species are *Nuphar luteum* and *Nymphaea alba* in the southern part of the lake and *Nymphoides peltata* in the central and north-western parts. A strip of reed-swamps rims the lake and passes into well-developed emerging communities in the zone of contact with the open water. *Rumex hydrolapathum*, *Cicuta virosa*, *Carex pseudocyperus*, *Typha angustifolia*, *Dryopteris thelypteris*, *Lythrum salicaria*, *Galium palustre* and *G. aparine* are the most common and abundant species here. Patches of alder swamp with *Alnus glutinosa*, *Solanum dulcamara*, *Dryopteris thelypteris*, *Ribes nigrum* and *Frangula alnus* have developed along the southern edge of the lake.

PALAEOECOLOGICAL STUDY

Methods

The core 1a was obtained with a piston corer (Więckowski 1961) from the middle part of the central basin where the water depth reaches 1.4 m. The length of this core was 9.56 m. The core 1A was obtained with the Russian sampler ("Instorf") from the central part of the lake, where the water depth reaches 0.8 m (Fig. 1). Samples for analysis were taken at intervals of 2—10 cm according to lithological changes in the sediment.

The pollen concentration method with *Lycopodium* standardized pellets, described by Stockmarr (1971), was used for pollen analysis only in core 1a. The mineral particles were removed with hot 40% hydrofluoric acid and the organic

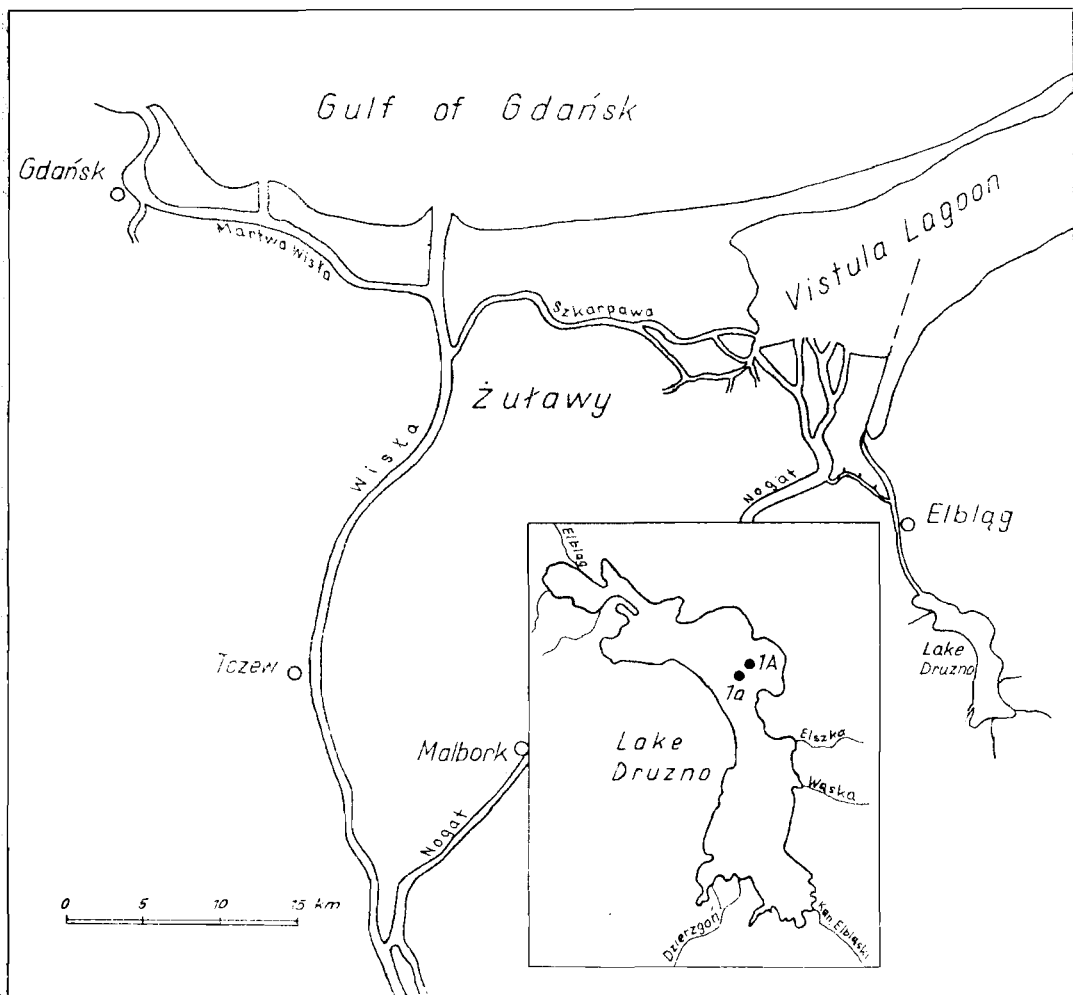


Fig. 1. Lake Druzno. ● — the location of profiles

Table 1

Water content and sedimentary chlorophyll

Depth in m	Water content %	Sedimentary chlorophyll	
		667 nm	749 nm
1	2	3	4
6.20-6.25	177.1		
6.25-6.28	185.0	138.2	13.1
6.28-6.33	201.6	93.2	8.2
6.33-6.39	187.8		
6.39-6.45	230.6	134.5	11.1
6.45-6.50	272.8		
6.50-6.55	339.5	167.3	42.3
6.55-6.60	410.6	111.4	76.3
6.60-6.65	406.3		
6.65-6.70	359.2		
6.70-6.75	337.1	188.0	262.3
6.75-6.80	357.0		
6.80-6.85	359.9		
6.85-6.90	349.3	129.1	239.6
6.90-6.95	331.6		
6.95-7.00	383.1		
7.00-7.05	398.6	185.6	358.2
7.05-7.10	337.9	219.8	568.8
7.10-7.15	349.6	74.1	193.5
7.15-7.20	189.6	29.4	24.6
7.20-7.225	125.2	12.2	3.0
7.225-7.27	100.1	9.2	2.5
7.27-7.29	140.8	22.8	18.2
7.29-7.33	199.8		
7.33-7.36	236.2	21.6	19.4
7.36-7.40	209.7	32.8	26.7
7.40-7.45	346.9	221.0	657.1
7.45-7.49	284.4	348.1	907.5
7.49-7.495	155.9	130.5	210.7
7.495-7.505	162.5		
7.505-7.555	137.9		
7.555-7.595	159.2	80.2	61.0
7.595-7.62	154.3		
7.62-7.66	161.2		
7.66-7.72	149.8	49.7	13.3
7.72-7.77	140.3	60.3	11.7
7.77-7.82	130.6		
7.82-7.87	136.3	77.1	9.4
7.87-7.92	135.1		
7.92-7.97	136.6	51.7	8.9
7.97-8.02	109.7		
8.02-8.06	112.2	77.5	3.9
8.06-8.09	53.5	24.1	3.7
8.09-8.13	110.5	38.0	2.8
8.13-8.18	99.8		

1	2	3	4
8·18-8·195	107·6		
8·195-8·245	108·2	64·2	3·8
8·245-8·275	71·3	29·6	2·8
8·275-8·325	70·7	31·3	4·3
8·325-8·36	59·9	41·1	3·7
8·36-8·40	73·0		
8·40-8·45	45·6	18·2	1·5
8·45-8·49	38·5		
8·49-8·53	37·1	11·1	
8·53-8·57	44·3		
8·57-8·59	44·2		
8·59-8·62	45·8	3·9	
8·62-8·66	33·1		
8·66-8·70	35·7	17·7	1·0
8·70-8·755	53·0	39·7	5·8
8·755-8·805	37·6	43·2	1·0
8·805-8·855	32·7	15·0	5·1
8·855-8·905	34·8	11·2	
8·905-8·955	35·2		
8·955-8·995	30·8	12·1	
8·995-9·04	37·4	5·6	
9·04-9·085	35·3		
9·085-9·13	78·4	19·2	2·9
9·13-9·17	198·3	11·7	1·9
9·17-9·215	188·8		
9·215-9·235	101·2		
9·235-9·27	151·9	9·0	6·2
9·27-9·31	47·1	4·1	1·5
9·31-9·36	21·5		
9·36-9·41	20·9		
9·41-9·46	20·5		
9·46-9·51	20·2		
9·51-9·56	61·5	2·2	

material was subjected to the Erdtman acetolysis (Faegri & Iversen 1975). In pollen analyses about 1000 of tree pollen grains were counted, if possible, and all other pollen and spores found; only in the case of very low frequencies smaller numbers were counted. The results are presented as a percentage pollen diagram and a general pollen concentration curve (Fig. 2).¹

For diatom analysis samples of 1—2 g material were taken. Samples containing calcium carbonate were treated with 10% HCl. The organic matter was oxydized with 30% H₂O₂. The samples with considerable amounts of mineral particles were subjected to flotation (Gleser et al. 1974). In the core 1A about 500 diatom valves were counted from each sample. In the core 1a generally 300 diatom valves were counted; only in the case of very low frequencies smal-

¹ Figs. 2 and 3 under the cover.

ler numbers were counted (depth of 9·27—9·13 m and 8·27—8·18 m). No diatoms were observed in depth of 7·29—7·00 m. The results are presented as a percentage diatom diagram containing the dominants and some characteristic taxons (Fig. 3).

The fresh water diatoms in core 1a were divided according to the pH requirements into: acidophilous, indifferent, alkaliphilous and alkalibiontic ones. The diatoms found in the core 1A were divided according to their salinity tolerance (Kolbe 1927).

The samples designed for chemical analyses were frozen immediately after they had been taken from the core (1a). The water content was removed by lyophilization prior to laboratory examination. The determined loss of mass (calculated in relation to the mass after lyophilization) is given in Table 1. The content of the so-called sedimentary chlorophyll was determined for dried samples. The generally adopted procedure for determining pigments by extraction with an acetone-water mixture (9:1) was completed by transferring the pigment to a small amount (15 cm) of *n*-hexane. In the case of high concentrations of pigments the samples were diluted. Measurements were performed in a "Specord" with UV-VIS spectrometer. The results are presented in Table 1.

Stratigraphy of sediments

The sediment lithology of the cores examined has been described using the simplified system of Troels-Smith (1955).

Lake Druzno, profile 1A

Depth in m	Sediment description
0·00—3·73	olive-green calcareous gyttja Lc 4, Ld +, Dg +, test. moll. +
3·73—4·63	olive-green calcareous gyttja with some detritus gyttja and numerous mollusc shells Lc 4, Ld ++, Dg +, As +, test. moll. +++
4·63—6·49	brown-green calcareous gyttja with some plant detritus and fragments of mollusc shells Lc 4, Dh +, Ld +, part. test. moll. +

Lake Druzno, profile 1a

Depth in m	Sediment description
6·20—6·55	detritus calcareous gyttja. Scanty fauna Ld ² , Lc 2, Ag/As +, test. moll. +
6·55—7·20	compact peat, strongly humified. Pieces of wood and reeds Sh 2, Tl +, Dl 1, Dh 1, Ld ¹ +
7·20—7·27	brown detritus gyttja with admixture of clay Sh 1, Ld 2, As/Ag 1

- 7·27-7·49 brown compact peat, strongly humified, with wood pieces
Sh 2, Dl 1, Dh 1, Dg +, Ld° +
- 7·49-7·82 beige-grey detritus calcareous gyttja, interbedded with brown
detritus gyttja
Dg 1, Ld¹, Lc 2, test. moll. +
- 7·82-7·92 calcareous gyttja with admixture of detritus gyttja. Numerous
faunal remains
Lc 2, Ld¹₂, test. moll. 1
- 7·92-8·06 dark-grey calcareous gyttja with some of detritus gyttja
Lc 3, Ld¹
- 8·06-8·09 grey clay with admixture of detritus gyttja
As/Ag 3, Ld¹
- 8·09-8·27 brown detritus gyttja
Dg 1, Ld¹₃, Ag +
- 8·27-8·66 olive-grey calcareous gyttja with admixture of detritus gyttja.
Not numerous, damaged faunal remains
Lc 3, Ld¹, test. moll. +
- 8·66-8·76 grey clayey calcareous gyttja with plant detritus gyttja
Lc 2, Ld¹, As 1
- 8·76-8·99 grey clayey calcareous gyttja. Not numerous faunal remains,
plant detritus and sand
Lc 2, Ld¹ +, As/Ag 2, Ga +, test. moll. +
- 8·99-9·08 steel-grey stratified clay. Brown coarse-detritus gyttja in in-
terbedded. Fragments of wood, twigs, leaves, faunal remains
and sand
As/Ag 3, Tl¹ +, Dl 1, Dh +, Ld¹, Ga +, test. moll. +
- 9·08-9·13 stratified fine sand and brown coarse-detritus gyttja
Ga 2, Dl +, Dg 1, Ld¹
- 9·13-9·31 dark-brown compact peat with large pieces of wood
Sh 2, Tl²₁, Th +, Dl 1
- 9·31-9·36 dark-brown compact peat with large pieces of wood, sandy
Sh 2, Tl²₁, Th +, Dl 1, Ga +
- 9·36-9·56 beige-grey fine-grained sand
Ga 4

Chemical analyses

a. Water content

The first simplified division of sediments was carried out on the basis of the determination of water content (Table 1). The principle applied consisted in eliminating from a series of results those results which deviated by more than 20% from the mean value for the given series. If such a difference affected at least two successive samples, a new stratum was distinguished.

Otherwise, despite a marked difference, this result was included in the series where it occurred. The purpose of this procedure was to eliminate casual determinations which do not reflect general tendencies prevailing in the given material. Seven horizons in which the nature of samples determines and essential change in their water content have been distinguished in this way (Table 2).

b. Sedimentary chlorophyll

Table 2

Mean water content	
Depth in m	Water content %
6.15-6.50	201.2
6.50-7.15	363.0
7.15-7.29	138.9
7.29-7.49	255.4
7.49-7.97	146.6
7.97-8.25	100.2
8.25-8.40	68.7
8.40-9.09	41
9.09-9.27	160.0
9.27-9.51	26.0
below 9.51	61.5

The term "sedimentary chlorophyll" is used for the degradation products of chlorophyllous pigment, arising from decomposed phytoplankton, phyto-benthos, higher plants and photosynthesizing bacteria.

The group of substances called chlorophylls consists of labile compounds which dissolve readily. Table 1 presents the main identified components of degraded chlorophyllous pigments: pheophytin "a" (max. absorption — 667 nm/and bacteriopheophytin "a"/749 nm). As in the case of the water content, the successive samples with similar content of the sedimentary chlorophyll were grouped in series. Seven different horizons have been distinguished in this way (Table 3).

Table 3

Mean content of sedimentary chlorophyll

Depth in m	Sedimentary chlorophyll		
	667	749	749/667 × 10-2
6.25-7.15	144.1	177.3	123.0
7.15-7.40	21.3	15.7	73.7
7.40-7.59	195.0	459.0	235.4
7.59-8.36	49.5	6.2	12.5
8.36-8.70	12.7	0.6	4.7
8.70-8.81	41.4	3.4	8.2
8.81-9.56	9.0	1.8	20.0

Pollen analysis

The pollen diagrams have been divided into local pollen assemblage zones (Gordon & Birks 1972; Berglund 1979). Five pollen zones and two sub-zones have been distinguished in the profile 1a and five further pollen zones in the profile 1A (Fig. 2).

Zone Dr-1 (*Pinus-Salix* PAZ) is characterized by high values of *Pinus* pollen (to 56%); values of *Salix* pollen reach 8.5% and those of *Cyperaceae* pollen increase towards the upper boundary.

Zone Dr-2 (NAP-*Pinus-Betula* PAZ). Herb pollen (53%) is dominant in this zone, with *Artemisia* (13%), *Gramineae* (16%) and *Cyperaceae* (39%) as main pollen taxa. *Rosaceae*, *Chenopodiaceae* and *Helianthemum* pollen is noted regularly. *Betula* and *Pinus* have pollen values of 30% each. The pollen concentration is low, about 20 000 grains/1 c.c. Two subzones can be distinguished in this zone:

a) The *Empetrum* subzone is characterized by the presence of *Empetrum* and *Ericaceae* undiff., *Populus* pollen occurs at the lower boundary of this subzone.

b) The *Juniperus* subzone is distinguished by the fall of *Empetrum* pollen values and maximum of *Juniperus* pollen (1.9%). *Cyperaceae* pollen values increase.

Zone Dr-3 (*Betula* PAZ). The lower boundary of this zone is placed at the rapid increase in *Betula* pollen, which next dominates throughout the zone, reaching 60–70%. The proportions of *Salix* and *Pinus* pollen fall distinctly and that of NAP fluctuates from 14.9% to 10%. The pollen concentration rises from 30 000 to 70 000 grains/c.c. Single *Ulmus* pollen grains occur throughout and *Quercus*, *Alnus* and *Corylus* pollen appear at the top of zone.

Zone Dr-4 (*Pinus* PAZ). *Pinus* pollen values increase rapidly starting from the lower boundary, and reach 75%. The values of *Betula* pollen show an absolute minimum and there is a constant rise in the values of *Quercus*, *Ulmus*, *Tilia* and *Corylus* pollen. *Alnus* pollen occurs in values reaching 25%. This is a very short zone characterized by a maximum pollen concentration of 570000 pollen grains/1 c.c.

Zone Dr-5 (*Alnus-Ulmus-Corylus* PAZ). A high proportion of *Alnus* pollen (48%) differs it from the zone Dr-4. There is a continuous rise in *Corylus*, *Ulmus* and *Quercus* pollen values. *Betula* has low pollen values; the values of *Pinus* fall continuously and NAP, represented chiefly by *Cyperaceae* pollen, reaches 16%.

Zone Dr-6 (*Quercus-Ulmus* PAZ) is characterized by a constant and consistent increase in the frequency of *Quercus* pollen (above 10%) at the cost of *Ulmus* and *Tilia* percentages. *Alnus* pollen values are constant, about 30%, whereas percentages of *Pinus* fluctuate considerably, from 10 to 37%. *Fraxinus* and *Picea* pollen have continuous low-percentage curves. Single oc-

currences of *Carpinus* and *Fagus* pollen as well as the first man indicators are noted.

Zone Dr-7 (*Quercus-Corylus* PAZ). The lower boundary of this zone is marked out by a decrease in *Ulmus* pollen below the 1% values. The pollen values of *Corylus* are about 10% at the bottom and at the top of zone, reaching 20% in its middle part. *Quercus* pollen values, oscillating between 9 and 14%, predominate among the components of mixed deciduous forest. The values of *Pinus* pollen range from 6 to 35% and those of *Alnus* from 21 to 38%. In the initial part of this zone *Carpinus* reaches higher values. The NAP-values do not exceed 10% throughout this zone.

Zone Dr-8 (*Corylus-Quercus-Carpinus* PAZ). Its lower boundary is placed at the beginning of the continuous pollen curve for *Carpinus*. *Corylus* pollen values show a decrease towards the end of zone. *Alnus* pollen still occurs in values around 30%, *Fagus*, *Fraxinus* and *Ulmus* pollen is present constantly but in small amounts. The values of NAP do not exceed 10%.

Zone Dr-9 (*Carpinus-Quercus* PAZ). Its separation is based on the dominance of *Carpinus* pollen among the components of deciduous forest. The pollen values of *Quercus*, *Tilia*, *Corylus* and *Ulmus* fall towards the end of this zone. At its beginning the rise in *Pinus* pollen values (50%) is accompanied by a decrease in those of *Alnus* (to 15%). This situation is reversed at the top of the zone. NAP percentage show a first rise. Cereals are represented by a continuous but still very low (< 1%) curve.

Zone Dr-10 (*Pinus-Gramineae-NAP* PAZ). The lower boundary of this zone is placed at the fall of *Carpinus*, *Quercus*, *Alnus* and *Betula* pollen values. *Pinus* pollen values rise distinctly to 50%. *Fagus* and *Picea* have continuous curves (> 1%). The NAP curve also shows a rise and reaches values of 60% at the top of the zone. Among NAP, *Gramineae* and *Cerealia* and then also *Artemisia* and *Rumex* are dominant pollen types.

Diatom analysis

Seven diatom zones have been distinguished in core 1a, and five further diatom zones in core 1A (Fig. 3). They are marked with symbol DrD.

Zone DrD-1 (9.36-9.13 m)

The diatoms are represented by a small number of specimens. Hardly 100 valves could be counted from particular samples.

In the lower part of the zone the most abundant are *Fragilaria* species (*F. construens* with var. *venter* and var. *binodis*, *F. brevistriata*), *Gyrosigma attenuatum*, *Amphora ovalis* var. *libyca*, and *Cocconeis placentula*. In the upper part they decrease in number in favour of the rising proportions of terrestrial and aerophilous taxa. The characteristic species are: *Hantzschia amphioxys* with var. *capitata* (up to 20%), *Navicula amphibola*, *N. semen*. *N. mutica*, *Eunotia praerupta*, *E. gracilis*, *Pinnularia borealis*, *P. cf. pulchra*, *P. gracillima*. Other taxa characteristic of this zone are *Pinnularia viridis* var. *commutata*, *Synedra ulna*, *Gomphonema* spp. and *Cymbella* spp.

Zone DrD-2 (9.13–8.96 m)

The change in the composition of the diatom flora is synchronous with the change in the sediment lithology (peat overlain with coarse detritus gyttja). The lower boundary of this zone is marked out by the rise in the number and diversity of diatoms.

The proportions of *Fragilaria pinnata*, *Pinnularia viridis* var. *commutata*, *Diploneis ovalis* with var. *oblongella* and the species of genus *Navicula* increase, *Navicula amphibola* and *N. semen* (arctic diatoms) being the most numerous among them. There occur also many species characteristic of the Late-Glacial sediments, e.g. *Navicula pupula* var. *rectangularis*, *N. abiskoensis*, *N. cuspidata*, *N. dicephala*, *N. mutica*, *Pinnularia* cf. *pulchra*, *P. lagerstedtii*, *P. subcapitata*, *Stauroneis anceps*, *Eunotia praerupta*, *E. lunaris*, *Neidium bisulcatum*, *N. iridis*, *Cymbella aspera*, *C. obtusa*, *Gomphonema constrictum* var. *capitatum* and *Achnanthes linearis*. The species of genera *Epithemia*, *Synedra* and *Cocconeis* show increase of their percentage values towards the top of zone. Planktonic diatoms (*Cyclotella bodanica*, *C. ocellata*, *C. kuetzingiana*, *Stephanodiscus* sp.) appear in very small numbers. The aerophilous diatoms are still present, but their numbers are reduced.

In the lower part of this zone the acidophilous diatoms are still present but they disappear in its upper part while the proportion of alkalibiontic species slightly increase. The alkaliphilous diatoms prevail.

Zone DrD-3 (8.56–8.32 m)

The change in the composition of the diatom flora is connected with the formation of the lake. The change from terrestrial to typical aquatic conditions caused the almost complete disappearance of the aerophilous and terrestrial species.

At the beginning of zone there is a small rise in the proportion of planktonic diatoms (*Melosira italica*, *M. islandica*, *M. granulata*, *Stephanodiscus astrea*, *Stephanodiscus* sp., *Cyclotella bodanica*, *C. ocellata*). There appear some new taxa, absent from the lower part of the core. These are *Rhopalodia* (*R. gibba*, *R. pararella*), *Nitzschia* (especially *N. amphibia*), *Achnanthes* (*A. conspicua*, *A. linearis*, *A. lanceolata*), *Campylodiscus noricus* var. *hibernica* and *Surirella*. The proportion of the *Fragilaria* species (*F. pinnata*, *F. brevistriata* and *F. construens* and var. *venter*, var. *binodia*), *Amphora ovalis* var. *libyca*, var. *pediculus*, *Cymbella* and *Gomphonema* species increase continuously. In the upper part of this zone the fall in the number of *Gyrosigma* coincides with an increase in the specimen percentages of *Navicula* species.

The alkaliphilous diatoms are dominant, and the proportion of the alkalibiontic species (chiefly *Gyrosigma*, *Epithemia* and *Rhopalodia*) rise. In the lower part of this zone the acidophilous diatoms are also present but their composition is changed in comparison with the underlying part. The species of *Eunotia* and *Pinnularia* have been replaced by *Tabellaria flocculosa* and *T. fenestrata*. In the upper part of this zone the acidophilous diatoms disappear almost completely.

Zone DrD-4 (8.32–7.72 m)

The lower boundary of this zone is placed at the rapid decrease of *Gyrosigma* and *Fragilaria pinnata*, *F. construens* and var. *venter*, *F. brevistriata*. *Cocconeis placentula*, *Amphora ovalis* var. *libyca* and var. *pediculus* are dominant in this zone. *Epithemia turgida*, *E. zebra*, and *E. sorex* are observed in smaller numbers. In the lower part of zone the fall in the number of *Gyrosigma* coincides with an increase in the specimen percentages of *Navicula* species mainly *N. oblonga*, *N. schoenfeldii*, *N. radiosa* and *N. gracilloides*, *Stauroneis phoenicenteron*, *Synedra ulna* and var. *biceps*, *S. capitata*, *Cymatopleura solea* and *Fragilaria virescens*. In the upper part of zone *Melosira arenaria* appears (up to 2%).

The alkaliphilous diatoms continue to prevail (up to 84.9%). The percentages of alkalibiontic diatoms decrease towards the upper boundary of zone, while the proportions of indifferent species slightly increase.

Special attention should be given to the fluctuation in the abundance of diatoms observed in this zone. In the lower part of zone (8.27–8.18 m) diatoms occur in small numbers. It is accompanied by the bad state of preservation of frustules and by the appearance of abundant marine diatoms (*Coscinodiscus* sp., *Actinocyclus ehrenbergii*, *Hyalodiscus scoticus*, *Paralia sulcata*, *Diploneis didyma* and *Biddulphia* sp.). In the upper part of zone the diatoms are again abundant.

Zone DrD-5 (7.72–7.45 m)

The distinction of the zone is based on the dominance of *Melosira italica* and var. *valida* (absent from the lower part of profile or present there in very small numbers), and of *Synedra ulna* and var. *biceps* and *S. capitata*. The *Fragilaria* species decrease in number.

The alkaliphilous diatoms predominate. The proportion of indifferent diatoms still increases and in the upper part of zone it reaches 12.8%.

Zone DrD-6 (7.45–6.90 m)

This zone represents a period of changes in the ecological conditions of the lake. In the lower part of this zone the main components of diatom flora are *Fragilaria* (*F. brevistriata*, *F. construens* and var. *venter*), *Amphora ovalis* var. *lybica* and var. *pediculus*. The percentage values of *Gomphonema*, *Cymbella* and *Pinnularia* increase. In the middle part of this zone (7.28–7.10 m) the diatoms disappear nearly entirely. Close examination of the samples obtained from this layer showed only single specimens (Fig. 3). In the upper part of zone the diatoms are again abundant. From here the composition of the diatom assemblages is similar to that in the lower part of zone. The percentage values of alkaliphilous species increase towards the upper boundary, while the proportion of indifferent species falls towards the end of this zone. The acidophilous diatoms are present (up to 1.4%).

Zone DrD-7 (6.90–6.25 m)

This zone is characterized by the presence of halophilous and mesohalobous diatoms, chiefly *Anomoeoneis costata*, *Achnanthes hauckiana*, *Bacillaria para-*

doxa, *Cyclotella meneghiniana*. The oligohalobous indifferent diatoms are decidedly dominant, the vast majority of them being alkaliphilous, littoral species. The most prominent are *Fragillaria construens* with var. *venter*, *F. brevistriata*, *F. pinnata*, *Amphora ovalia* var. *libyca* and var. *pediculus*, *Cocconeis placentula*, and the specimens of *Navicula* and *Nitzschia* (the proportion of this species increases towards the upper boundary).

Zone DrD-8 (6.55–3.54 m)

The oligohalobous indifferent diatoms continue to prevail, but their proportions are markedly lower.

The change of the diatom composition of this zone is marked by the considerable increase in the specimen number of planktonic and meso- and euhalobous species. They reach here the maximum values for the profile. However, their proportions are not the same throughout the whole zone.

The percentages of meso- and euhalobous species vary from 2.8 to 26.9%. The marked increase in their occurrence is noticed three times and the largest one is found in the upper part of zone (3.54–3.36 m). Among the meso- and euhalobous diatoms planktonic species of *Coscinodiscus* (at present *Actinocyclus kuetzingii*) prevail. In smaller numbers are noted: *Achnanthes breviceps* var. *intermedia*, *Actinopterychus serians*, *Caloneis amphisbaena* var. *subsalina*, *Campylodiscus clypeus*, *C. echeneis*, *Cocconeis scutellum*, *Diploneis didyma*, *D. interrupta*, *D. smithii*, *Grammatophora oceanica*, *Navicula digitoradiata*, *N. forcipata*, *Nitzschia scalaris*, *N. commutata*, *Surirella striatula*, *Terpsinoë americana*.

The number of halophilous species varies from 3.9 to 26.9%. Among them the most frequent are: *Anomoeoneis spaerophora*, *Caloneis amphisbaena*, *Cyclotella meneghiniana*, *Nitzschia trybionella* var. *levidensis*, *Surirella ovata* var. *crumena*.

As mentioned above the oligohalobous indifferent diatoms prevail (64.1–89.9%). The most numerous are the planktonic species, chiefly *Stephanodiscus astraea* (up to 38.7%) and *Melosira granulata*. The most numerous littoral species is *Opephora martyi* (up to 24.5%). The *Fragilaria* species, which had been dominant in preceding zones, occur only in small numbers, and towards the end of this zone they almost disappear, except for *Fragilaria inflata*, which appear in this zone for the first time.

Zone DrD-9 (3.54–2.80 m)

The lower boundary of this zone is placed at the rapid decrease of meso- and euhalobous species. The oligohalobous indifferent diatoms are dominant (92.2–99.6%). Among them the planktonic species of *Melosira* are still numerous. The proportion of *Stephanodiscus astraea* falls distinctly.

Zone DrD-10 (2.80–2.25 m)

This zone is characterized by the sudden increase in the percentage of *Navicula scutelloides* (up to 46.2%) and *Opephora martyi* (up to 30.7%). The proportion of planktonic diatoms (*Melosira* species) falls distinctly. The oligohalobous indifferent diatoms still prevail (95.8–97.5%). The meso- and euhalobous species occur only in very small numbers.

Zone DrD-11 (2.25–0.68 m)

The genus *Fragilaria* is dominant in this zone. *F. inflata* with var. *istvanffyi* (up to 23.9%) and towards the upper part of zone *F. construens* with var. *binodis* and var. *venter* are the most numerous species. Other taxa characteristic of this zone are: *Campylodiscus noricus* var. *hibernica*, *Gyrosigma attenuatum*, *Cymbella ehrenbergii* and *Cymatopleura elliptica*.

The main components of diatom flora are littoral species. Planktonic diatoms occur in this zone in small numbers. Towards the end of zone the meso- and euhalobous species almost disappear.

Zone DrD-12 (0.68–0.00 m)

This zone is characterized by the increase in the percentages of *Rhoicosphenia curvata*, *Epithemia turgida*, *E. zebra*, *Cocconeis placentula*, *Amphora ovalis* var. *libyca* and var. *pediculus*, *Stephanodiscus astraea* var. *minutulus*, *Fragilaria pinnata* and *F. construens*. In the upper part of zone there is a rise of *Eunotia*, *Gomphonema* and *Cymbella* species.

The littoral alkaliphilous diatoms prevail. The percentages of alkalibiontic species (chiefly *Gyrosigma* and *Epithemia*) increase in comparison with the preceding zone.

HISTORY OF CHANGES IN THE NATURAL ENVIRONMENT

Vegetational history of the region

Zone Dr-1. It may be inferred from the scanty data obtained that at that time pine forests with an admixture of *Populus* were the dominant plant communities in the study area. *Populus* together with *Betula* and *Salix* may also have formed scrub communities. Waterlogged areas were covered by mires, in which the *Cyperaceae* and *Sphagnum* were the main peat-forming elements. This horizon is dated at $11\,290 \pm 105$ BP.

Zone Dr-2 represents a period when the herb communities predominated over the forest communities which began to withdraw southwards. The xeric grasslands with *Artemisia*, *Caryophyllaceae*, *Chenopodiaceae*, *Helianthemum* and scrubs of *Juniperus* and *Ephedra* expanded. The mires with *Cyperaceae* and *Sphagnum* and shrub communities with *Betula* and *Salix* still occurred in waterlogged habitats. Because of the lack of macrofossils, is difficult to answer the question whether trees occurred in situ in this area, or whether their pollen was transported from long distance. The very low pollen concentration per 1 c.c. suggests that the trees played a minor role. An increase in their frequency becomes visible towards the end of this zone.

Zone Dr-3. The expansion of forest communities, which had begun towards the end of the zone Dr-2, continued into the zone Dr-3. Birchwoods and in the drier places pine-birch woods developed in the study area. Relict steppe-type communities persisted in the driest and exposed places. The small proportion

of herbs indicates that the forest was remarkably closed. Probably, the forest communities with *Betula* developed on the peat-bog itself. The process of encroachment of forest communities upon the bogs is particularly well seen in the following zone.

Zone Dr-4. Pine forests with a small admixture of *Betula* became the dominant forest community in the study area. Some new tree and shrub species — *Ulmus*, *Corylus*, *Alnus* and *Tilia* — appeared in the forests towards the end of zone. The zone is shortened very much and it is impossible to reconstruct the vegetation more fully. The radiocarbon dates obtained for the end of zone Dr-4 /8995±75 BP/ and the beginning of Zone Dr-5 /7050±70 BP/ indicate the break in sedimentation lasting for about 2000 years and preceded by a decrease in the rate of sediment accumulation shown by the highest increase in the pollen concentration (570·000 P/c.c.).

Zone Dr-5 shows the spread of deciduous forests, which covered all fertile soils in the areas neighbouring Lake Druzno. *Tilia*, *Quercus* and *Alnus*, were the main components of forests on the well-drained soils. Carrs woods with *Ulmus*, *Alnus* and *Fraxinus* developed in low lying, waterlogged areas and *Corylus* and *Viburnum* may have occurred in their understorey. The mixed forests on poorer sandy soils were formed of *Quercus*, *Betula*, *Populus* and *Pinus*. These forests gained in importance towards the end of this zone and in the following period (Dr-6).

During the next zone (Dr-7) the plant cover underwent distinct changes. The proportion of *Tilia* and *Ulmus* in the deciduous forests decreased in favour of *Quercus*. This last together with *Pinus*, *Populus* and *Betula* most probably formed the mixed forests on the areas now covered by pine and pine-oak forests. *Alnus* played a more and more important role in the landscape of the Żuławy area and it formed, together with *Fraxinus*, *Quercus* and *Corylus*, riverside forests in habitats periodically flooded, and alder wood in swamp areas with poor drainage. New changes in the landscape were caused by man; traces of his activities appear in the pollen diagram (Fig. 2). It may be supposed that man, to gain ground for his primitive fields, destroyed forests on fertile and dry soils.

Zone Dr-8 shows further changes in the forests of the study area, leading to their degradation. The frequency of *Tilia* and, particularly, *Ulmus* decreased and that of *Quercus*, *Corylus* and *Carpinus* rose in the deciduous forests. The areas occupied by *Pinus* underwent a further reduction. *Alnus* continued expanding; owing to the further rise of the ground water level its favourable habitats increased in area.

Great changes in the natural plant cover are reflected in zone Dr-9, especially in the composition of the deciduous forests. The role of *Tilia*, *Ulmus* and even *Quercus* decreased, they were gradually replaced by *Carpinus* and *Picea*, which became the main components of the forests that later gave origin to the present *Quercus-Carpinetum* community. The role of plants connected with human husbandry (*Cerealia*, synanthropic plants) increased from the

beginning of this period. The communities of open areas rose distinctly in importance. Presumably, all those changes were brought about by several simultaneous factors: the climate — a rise in humidity favoured the degradation of soils; man — who continued to clear the forests on fertile soils to enlarge the cultivated land and pastures; and the changes in the water level of the Vistula Lagoon.

In zone Dr-10 the character of forests and their differentiation resembled those in the previous period. Only the relations between particular components changed: *Carpinus*, *Quercus* and *Alnus* were gradually replaced by *Picea*, *Fagus*, *Pinus* and *Betula*. This tendency in plant succession is also corroborated by some historical data (Witek 1965). Starting from the beginning of this period three basic forest communities developed in the Żuławy and underwent transformations according to the prevailing water conditions. As Ostendorf writes (cited after Witek 1965), they were riverside forests occupying the highest and drained areas, their main components being *Fraxinus*, *Alnus*, *Quercus*, *Populus*, *Ulmus* and more rarely *Carpinus* and *Tilia*; alderwoods, which developed on waterlogged soils, and exuberant willow woods.

The number of open communities increased considerably. In the pollen diagram (Fig. 2) there are distinct indications of the expansion of these types of communities connected with human activity. *Juniperus*, which is a shrub characteristic of loose pine forests or psammophilous communities, arising owing to the secondary encroachment upon the meadows, appeared at that time.

History of the lake

Up till recent time the generally accepted opinion was that Lake Druzno is the remnant of the Vistula Lagoon dating from the period of the Littorina Sea. In the light of new studies it appears that the history of this lake goes back as far as the Late-Glacial. The first deposits of the biogenic accumulation, peats with interbeddings of fine sand, were observed in the initial stage of lake development and were radiocarbon dated at $11\,250 \pm 105$ BP. There are no remains of aquatic plants here, however, diatoms are present though in small numbers. They are as well acidophilous diatoms characteristic of forest bogs as indifferent, alkaliphilous and alkalibiontic ones. Beside the aquatic diatoms, there are also terrestrial species, with *Hantzschia amphioxys* as the most common taxon, found today in the dry habitats. These diatoms represent, most likely, a pioneer stage in the development of the diatoms flora of Lake Druzno.

The next developmental stage of the lake (Dr-2) is marked by the vast diversity of sediments, which reflects the frequently changing hydrological conditions. These changes are also recorded by the local vegetation and by the diatom flora. At the beginning of this stage moss (*Sphagnum*) bogs and sedge-bogs began to develop, replacing forest-bogs; this was followed by the formation of a lake in which aquatic plants developed gradually forming a commu-

nity with *Myriophyllum spicatum*, *M. verticillatum* and *Potamogeton*. The development of the communities with *Myriophyllum* indicates the process of gradual rise of water level and the alkalinity of the substratum. The final stage of zone Dr-2 was characterized by the development of *Typha latifolia* communities. This species, together with the abundant *Cyperaceae* and *Gramineae* may indicate the beginning of overgrowing of the lake margins.

The change in the composition of diatoms at the beginning of zone DrD-2 is marked chiefly by the considerable increase of the proportion of aerophilous and arctic species with *Navicula amphibola* and *N. semen* as the most abundant taxa. In the previously studied profile (IA) from Lake Druzno (Przybyłowska-Lange 1976) a rise in the percentages of these species was found in the sediments referred to the Younger Dryas. In comparison with zone Dr-1 there was no appreciable change in water pH which is evidenced in the presence of acidophilous diatoms. The acidophilous and aerophilous diatoms declined above, whereas the numbers of alkaliphilous and alkalibiontic ones increased (DrD-3) what suggests that the lake water was more alkaline. The lake underwent a gradual eutrophication and the proportion of diatoms typical of eutrophic water bodies increased.

The process of overgrowing of the lake margins continued in the following developmental stage (zone Dr-3). The decline of the *Cyperaceae* and *Gramineae* communities coinciding with the maximum quantities of *Betula* pollen may indicate the encroachment of *Betula* upon the marginal sedge-bogs and their transformation into forest-bogs. Towards the end of the zone Dr-3 *Nymphaea* and *Nuphar* appeared in the lake and *Myriophyllum spicatum* and *M. verticillatum* reappeared indicating the rise of water level. This is also confirmed by an increase in the proportion of planktonic diatoms, chiefly *Melosira italica* (DrD-5), sporadically encountered at the beginning of this stage (DrD-4).

Throughout zone Dr-4 the water pH was still distinctly alkaline, which is evidenced in the similar proportion of alkaliphilous and alkalibiontic diatoms.

Towards the end of the zone Dr-3 (Dr D-5) the diversity and abundance of diatom flora became largely reduced and in the next period diatoms disappeared completely (Dr D-6). The remarkable impoverishment of the diatom flora and of the macrophyte vegetation accompanied by the change of calcareous-detritus gyttja into the peat (8995 ± 70 BP) and again into the detritus gyttja (7050 ± 70 BP) proves the temporary transformation of the lake into a forest-bog and into the lake again (Dr-4, DrD-6). The dates obtained record a gap of about 2000 years in the development of the lake. The lake development began again about 7000 years ago. The initial plant communities were the reedswamps with *Typha latifolia*, *T. angustifolia* and *Sparganium*. Diatoms also reappeared. The most interesting fact is the presence of mesohalobous diatoms in the peat sediment, what indicates the beginning of inflow of sea water, even though in small amounts, as early as then. A similar phenomenon was also noted for the same period in the Vistula Lagoon (Przybyłowska-Lange 1974).

The transformation of the bog into the lake happened about 6440 ± 50 BP. From this time on Lake Druzno became a part of Vistula Lagoon. The proportion of mesohalobous species characteristic of the littoral sea zone increased then. No planktonic species had, as yet, appeared (Dr D-7). The reedswamp vegetation was pushed off towards the lake margins and the area suitable for the development of wet alderwoods were reduced.

At the beginning of the zone Dr-6 (Dr D-8) further essential changes in the hydrological conditions occurred in the lake. The littoral diatoms, dominant in the preceding zone Dr-5 (Dr D-7), were partly replaced by planktonic diatoms and, besides the mesohalobous diatoms, there appeared euhalobous taxa. The changes of aquatic and reedswamp vegetation and of the diatom communities indicate that the inflow of sea water into the lake were cyclical. The mass occurrence of meso- and euhalobous diatoms with the simultaneous reduction of the aquatic and reedswamp vegetation should probably be referred to the time of an intense inflow of sea water. Between the successive influxes of sea water the lake underwent freshening, which led to the disappearance of meso- and euhalobous diatoms and favoured the development of plant macrophyte communities. The freshening of water was accompanied by the periodical lowering of water level, which was shown by a decrease in the proportion of plankton diatoms and the development of reedswamp vegetation. The highest proportion of marine planktonic diatoms along with the marked reduction of aquatic and reedswamp vegetation, noted in zone Dr-7 (Fig. 2) (end of zone Dr D-8, Fig. 3), should presumably be connected with the last inflow of sea water into the lake. It resulted in an increase of area, depth and salinity of the lake.

As early as the beginning of the zone Dr-8 (Dr D-9) some hydrological changes took place in the lake again. The freshwater planktonic diatoms, occurring in abundance, and the scarce aquatic and reedswamp vegetation indicate that the water level of the lake had not undergone any essential changes. However, the diatoms found here are nearly exclusively oligohalobous indifferent taxa, which indicates that the lake has been freshened. That was not associated with the isolation of Lake Druzno from the Vistula Lagoon, as the composition of the diatom flora of these two water bodies was similar at that time (Przybyłowska-Lange 1974).

The water level began to lower markedly from the beginning of zone Dr-9 (Dr D-10) and then the planktonic diatoms disappeared nearly completely. There appeared communities with *Nymphoides peltata*, *Nymphaea* and *Nuphar*. Single pollen grains of *Trapa natans* were noted and the reedswamp communities gained in importance. It should also be emphasized that *Alnus* expanded distinctly in the second half of this period. The process of shallowing and overgrowing of the lake seems to have been marked then. From the middle of this zone (Dr D-11) some differences between the composition of the diatom flora of the investigated lake and of the Vistula Lagoon are observed. These differences suggest that the process of slow isolation of these two water bodies

had already begun; it was completed in the final phase of zone Dr D-11 (end of pollen zone Dr-9). Since that time the lake has been very shallow, the epiphytic diatoms have been dominant in it and the communities of aquatic and reedswamp vegetation have been very abundant. The rich development of calciphilous *Myriophyllum spicatum* and the increase in the proportion of alkaliphilous diatoms indicate the changes of water pH towards alkalinity. The mass occurrence of *Pediastrum* also proves the shallowness of the lake.

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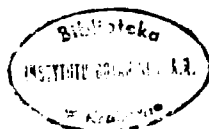
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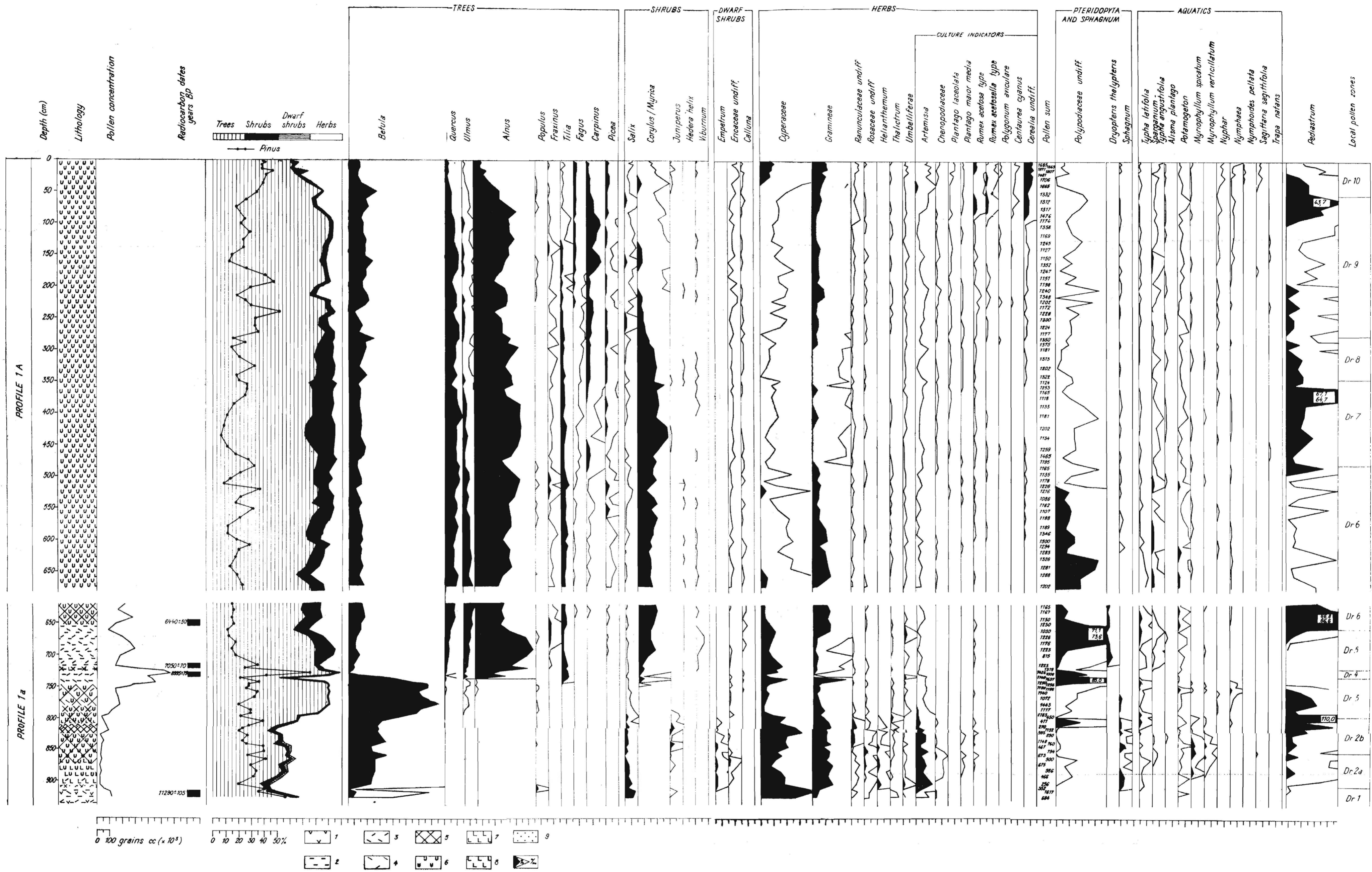


Fig. 2. Combined pollen diagrams of profiles IA and Ia from Lake Druzno. Sediments signatures: 1 — *turfa lignosa* — wood peat (generally), 2 — *substantia humosa* — amorphous humous substance, 3 — *detritus lignosus* and *detritus herbosus* — coarse wood and plant detritus, 4 — *detritus granosus* — wood, plant and animals detritus, 5 — *limus detrituosus* — detritus mud (gyttja), 6 — *limus calcareus* — calcareous gyttja, 7 — *argilla steatodes* — clay, 8 — *argilla granosa* — silt, 9 — *grana arenosa* — fine sand

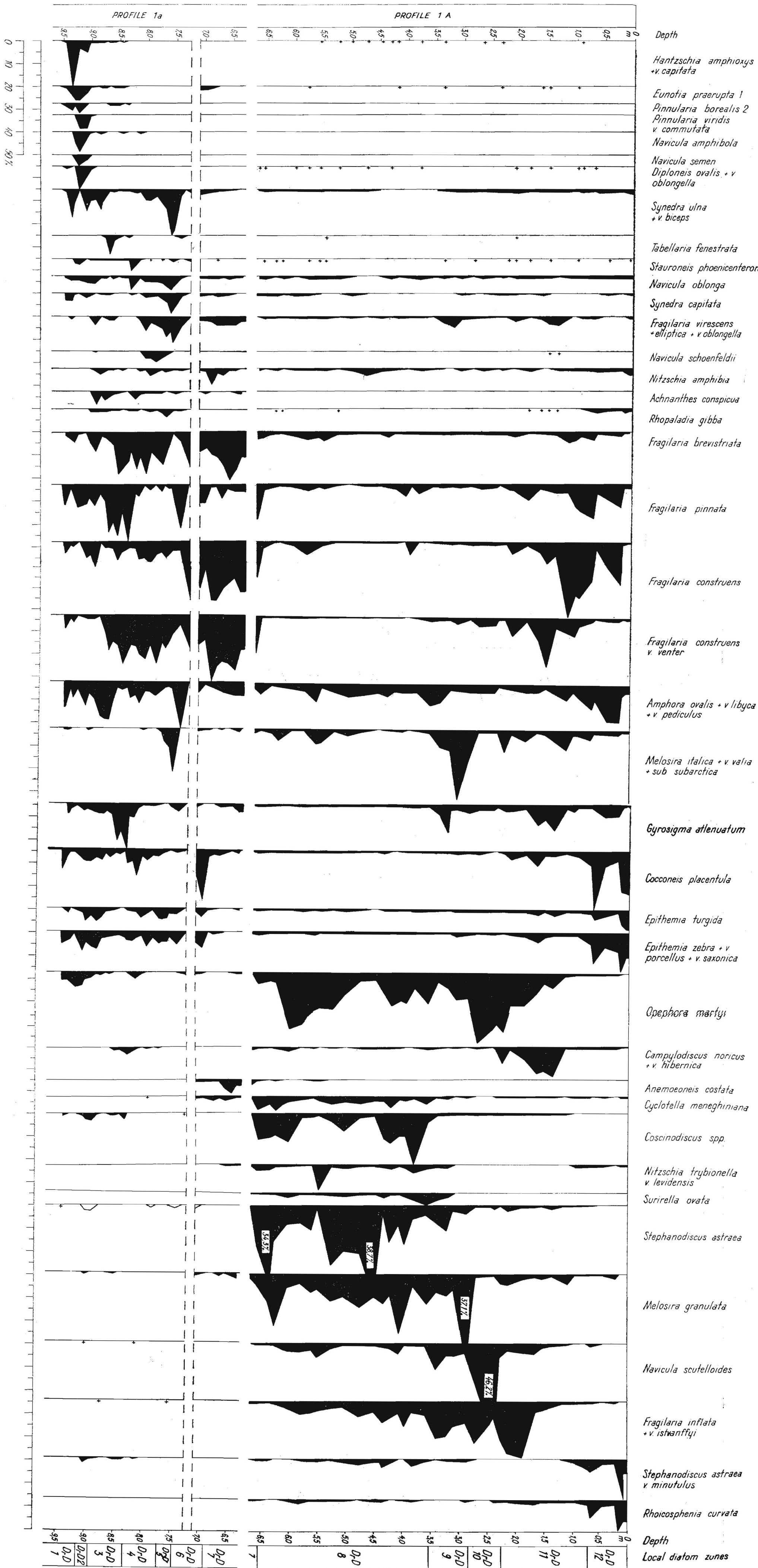


Fig. 3. Combined diatom diagrams of profiles 1a and 1a from Lake Druzno. Diatom taxa not listed in column: 1 — *Eunotia birgibis*, *E. fallax*, *E. pedunculata*, *E. gracilis*, *E. parvirella*; 2 — *Pinnularia cf. pulchra* P. mesolepta, P. subcapitata