LATE PLEISTOCENE DEPOSITS AT WRETTON, NORFOLK

II. DEVENSIAN DEPOSITS

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[Plates 19, 20; pullout figures; pullout table]

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The low terrace at Wretton, Norfolk, is shown to consist of up to 6 m of mainly fluviatile sands and gravels of Devensian age. It contains many organic horizons rich in plant remains, molluscs and bones, and shows well-developed periglacial structures, including involutions and ice-wedge casts. Organic deposits lie in channels beneath, within and above the fluviatile sediments, and also within small depressions, a few metres across, which are interpreted as features formed by the melting of ground-ice mounds. The succession within the terrace is complex, but the detailed sections observed, with petrographical, palaeobotanical and molluscan studies, allow a synthesis of the environmental changes which accompanied terrace formation.

The petrography of the sediments in the depressions indicates that certain of the ground-ice mounds formed in lenses of sandy clay derived from weathered interglacial sediments. The sediments redeposited on the melting of the mounds have a characteristic particle-size distribution. Times of coversand formation within the terrace sequence are identified.

The palaeobotanical study, by analysis of pollen and macroscopic plant remains, reveals a sequence of pollen assemblage biozones. There are three periods with biozones characterized by herb pollen spectra. These are separated by periods with biozones characterized by pollen spectra indicating the presence of woodland. The earlier sequence of the woodland biozones, named the Wretton interstadial, shows birch-pine woodland and heath. The later sequence shows pine-birch-spruce woodland and heath, and is correlated with the Chelford interstadial. A detailed consideration of the flora and vegetation of the herb biozones is given, with a comparison of the pollen spectra with recent pollen spectra from the Arctic. It is concluded that in these biozones vegetation physiognomically akin to grassland prevailed in the region.

Molluscan faunas, found at several horizons, are typical of Early Devensian deposits in other parts of the Fenland drainage basin. The number of species is restricted, but southern forms do survive in small numbers from the Ipswichian interglacial even into the third grassland biozone of the Devensian.

On the basis of the periglacial features and plant and animal remains, it seems that the climate was generally continental, with mean annual temperatures at or below 0 °C, probably as low as −8 °C at times of ice-wedge formation, with mean July temperatures as high as 15 to 20 °C. In the pollen-based interstadials the climate was considerably more oceanic.

The methods of subdivision of the Devensian are considered, and the sequence then correlated with other Early Devensian sites in England and on the Continent. The Wretton and Chelford pollen-interstadials may be of the same age as the Amersfoort and Brørup interstadials respectively of the Netherlands. The associated herb biozones represent periods before, between and after the pollen-interstadials.

The transition from the Ipswichian interglacial to the Devensian in the region of the eastern Fenland margin is considered. Grassland was already present in the late Ipswichian, and the transition to the Devensian was accompanied by a loss of some taxa and a gain of others, with many taxa present in both stages.

The coleopteran and moss assemblages from the deposits are described in appendices. There is an unresolved discrepancy between the environmental evidence of the Coleoptera and the pollen in the later woodland biozone, the Coleoptera indicating a barren sandy landscape.

1. Introduction

In the previous paper on Late Pleistocene deposits at Wretton, Norfolk (Sparks & West 1970), it was shown that the sands and gravels constituting the low terrace of the River Wissey overlay Ipswichian interglacial deposits. Long sections given in that paper (figures 3, 4) show the disposition of the sands and gravels, exposed during 1961–2 during the excavation of the flood relief cut-off channel. In figure 3 of the 1970 paper, at sections WR–WS near Wretton Fen Bridge, silt, with a Devensian mollusc fauna, overlay a weathered marl at about –1 m o.d. At WWa, shown in the same figure, an ice-wedge cast penetrated some 4 m into the sands and gravels of the terrace. The main thickness of the terrace sands and gravels is thus of Devensian age. The present paper describes these terrace sediments, the biogenic deposits associated with them and their contained flora and fauna, and the many structures which they exhibit, principally in the area west of the interglacial exposures, along the length of the flood relief cut-off channel shown in figure 1. The rich vertebrate fauna will be described elsewhere by Dr K. A. Joysey; he reports that bison is abundant, reindeer is common, with mammoth, rhinoceros, bear, wolf, arctic fox, voles and frogs all represented.

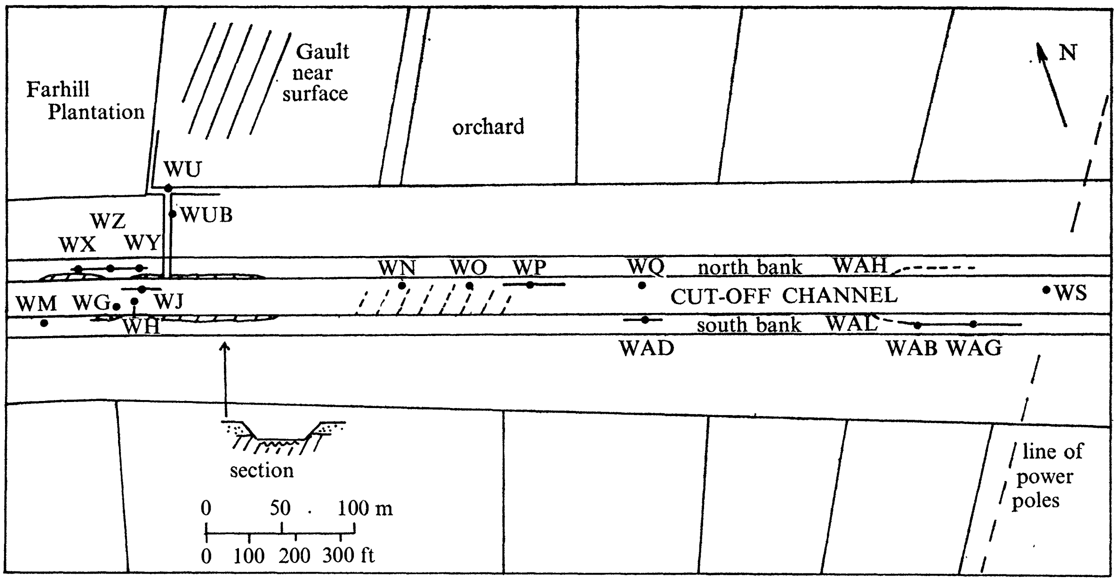


Figure 1. Location of sites along the cut-off channel. The cross-hatching indicates exposures of Gault Clay in channel bank and the broken cross-hatching the approximate extent of the basal muds seen at WH and WO.

2. Stratigraphy

The deposits to be described rest on Gault Clay at depths from 2 to 6 m below the terrace surface, which is at 4 m o.d. Sediments of the top metre in the terrace are of a uniform nature along the length of the cut-off channel from Farhill Plantation east to Wretton Fen Bridge;

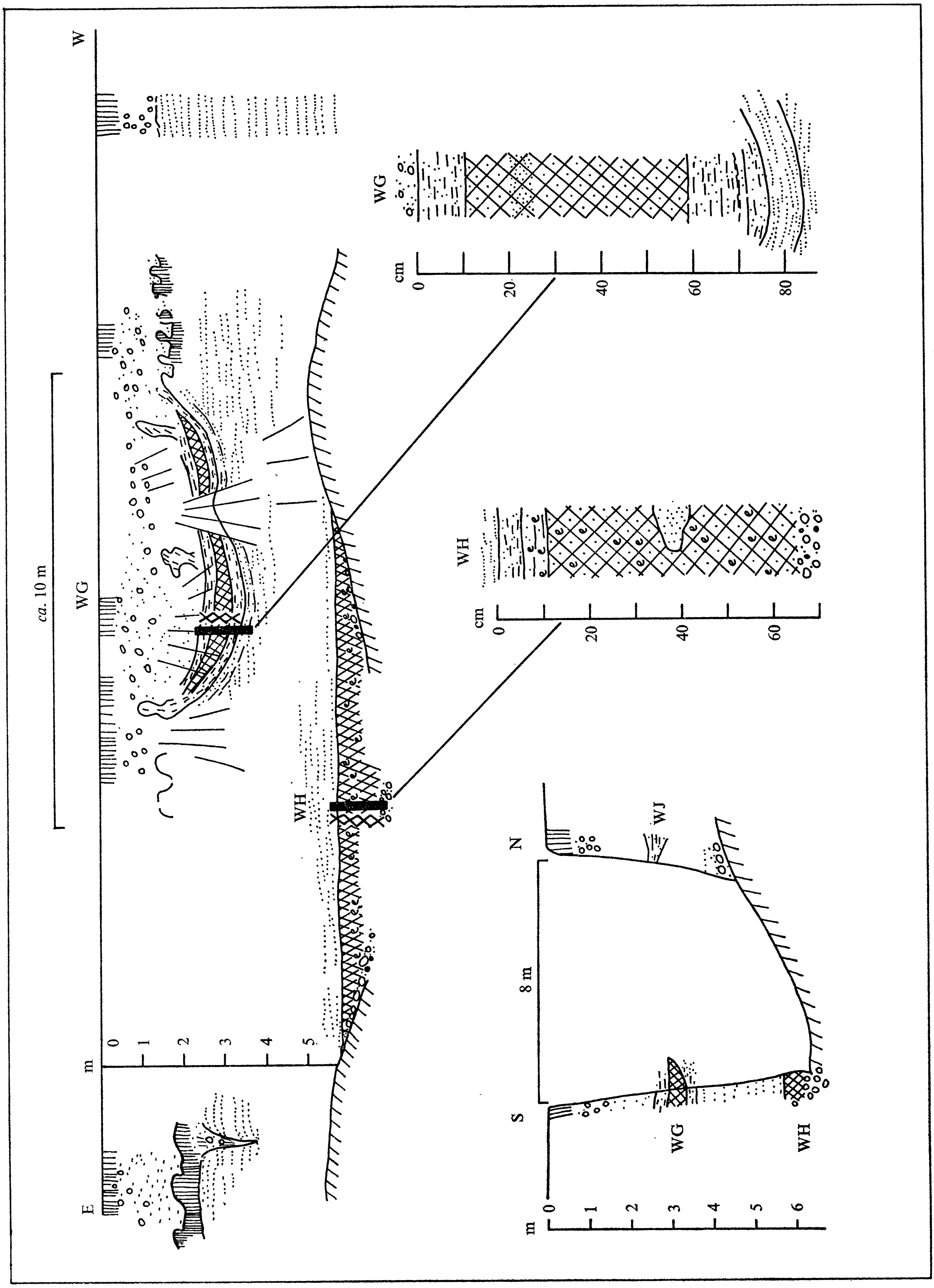


Figure 2. Stratigraphy of sites WG, WH and WJ. Key to sediment symbols in figure 4.

they consist of a reddish sandy gravel or sand contorted in places by frost action, sometimes with a bleached sand above, and at the surface, the humic A horizon of the present soil. Between these uppermost deposits and the Gault lie sands and gravels of the terrace aggradation, quiet-water silts and highly fossiliferous organic deposits.

(*a*) *Description of sites*

The positions of various measured sections are shown in figure 1. The fossiliferous deposits occur in four groups as follows, in order of decreasing age:

(1) Muds below the terrace sediments, resting directly on flint and chalk gravel and Gault Clay (sections WH, WO). The area where these basal muds were exposed is indicated in figure 1.

(2) Muds of the main terrace aggradation, generally undisturbed by much frost action and lying in shallow extensive basins, probably channels (e.g. WAB, WAD, WAG, WAH, WAL).

(3) Muddy silts and sands lying in deeper and narrower basins, associated with much frost disturbance. The basins were shown by excavation to be enclosed hollows (WG, WJ, WX, WY, WZ).

(4) Muds within a metre or two of the terrace surface, much disturbed by frost action, exposed over a wide area and not confined to basins or channels (WU, WUB, WX to WY).

The deposits in groups 1, 2 and 4 are not problematic because their stratigraphic position is straightforward. However, the deposits of group 3 are much more disturbed and the explanation of their formation is less obvious.

Brief descriptions of the detailed sections now follow in the order of the four groups outlined above; the locations of the sites are shown in figure 1. The more complicated sections, in group 3 above, will be described and discussed in more detail in § 2 (*d*). The detailed stratigraphy of the sites analysed for flora and molluscs is given in § 3.

(i) *Basal organic deposits*

WH (*figure* 2). This section showed sandy shelly muds between the main thickness of terrace sands and the gravel immediately above the Gault.

WO (*figure* 4). Here 10 cm of sandy mud occurred between thin sandy gravels, the lower of which rested on Gault. Many bones were found in this region in the basal mud.

(ii) *Organic deposits of the main terrace aggradation*

WAD (*figure* 3). This section showed a channel in the lowest sands of the terrace, about 1 m deep and 15 m wide and filled with sandy mud and moss peat. A wolf skull was found at WAE. Marginal to the channel, quiet-water silts could be traced for several metres; these silts are level with the quiet-water silts of WAL and WAH, which are on opposite sides of the cut-off channel. Contortions in the silt, probably caused by frost action, occur at the base of WAD.

WAH, WAL (*figure* 3). The quiet-water muddy sands and silts of these sections are part of the terrace sequence, probably to be correlated with the silts of WAD. Contortions occur at the base of the silts, as in WAD. To the east both silt horizons rose about 1 m, as shown by the lines in figure 1 at WAL and WAH, and then extended eastwards as far as WS (see figure 1 of this paper and figure 3 of Sparks & West 1970). On the graded north and south sides of the cut-off channel it appeared that the silt ran into the silt layer at + 0.5 m O.D. of section WS (figure 3 of Sparks & West 1970).

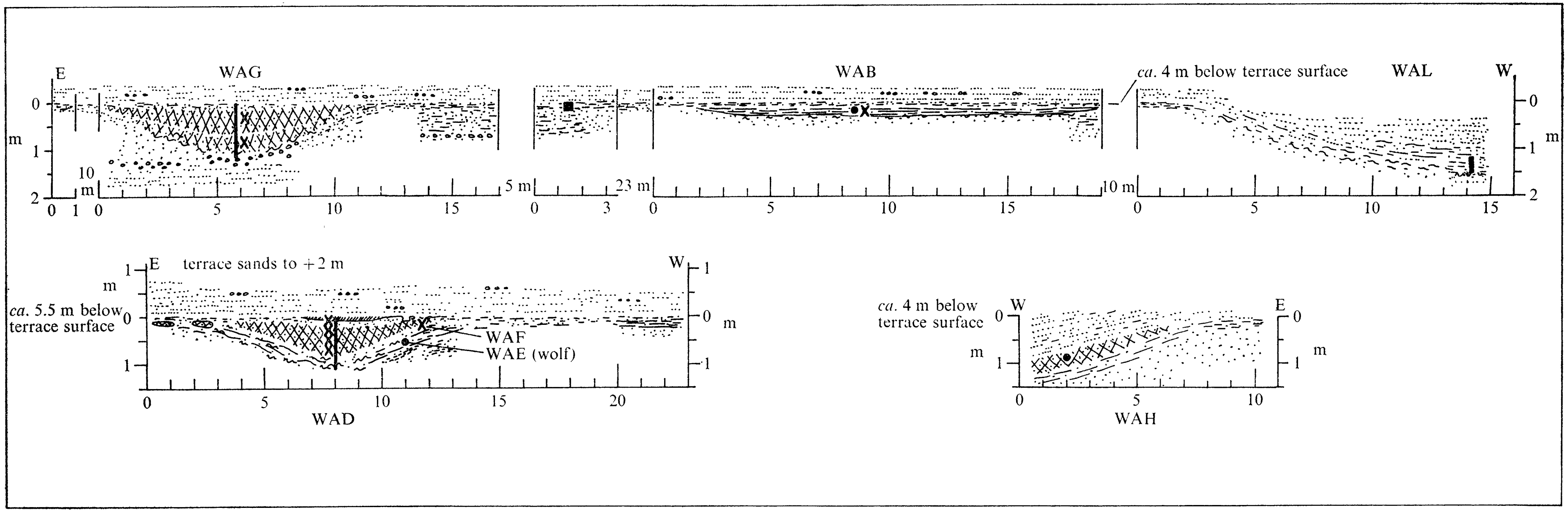


FIGURE 3. Stratigraphy of sites WAB, WAD, WAG, WAH and WAL. Key to sediment symbols in figure 4.

WAB, WAG (*figure* 3). This long section linked up with WAL to the east, and was at a higher level in the terrace than WAD, WAH and WAL. The quiet-water silts extended right along the terrace at some 4 m below terrace surface. WAB was a shallow broad channel filled with muddy silt. The particle-size distribution of the marginal sandy silt of this channel is shown in figure 10. WAG was a channel 10 m wide and 1 m deep filled with sandy mud, and with disturbed bedding at the base, as in some of the previous sections. The organic deposits of these sections are higher in the terrace than those of WAD, WAH, WAL, and are probably younger than them.

WS. This section is described in Sparks & West (1970, figure 3). A grey shelly clay 8 cm thick overlies a weathered horizon at the top of the Ipswichian interglacial deposits. Above it are terrace sands to within a metre of the surface, with a grey silt at 3.5 m depth. The usual reddish gravel overlies the sand in this area near Wretton Fen Bridge.

WN, WP, WQ. It is not certain whether WN, WP and the top of WQ should be in group 2 as a part of the main terrace aggradation, or whether they should be related to group 4 as fillings of channels in the terrace. The flora and mollusc faunas of sediments of group 2 and 4 are similar, so this doubt does not affect the interpretation of the sequence.

WN (*figure* 4). This section showed a very shelly clay lens in bedded sands 50 cm above the Gault. Quiet-water, very shelly silts and muds occur from 2.80 to 1.25 m below the terrace surface, and they are under- and overlain by coarse bedded sands. It is possible that the upper part of this sequence is related to the period of upper mud formation (see section WU below).

WP (*figure* 4). This section was drawn in detail along a central 10 m stretch, along a 1 m stretch 20 m to the east and along a 2 m stretch 10 m to the west. On the terrace sands lie a sequence of quiet-water silts and humic silts at easting 0 to 2 m. At WP 2, to the west, the humic silts are replaced by sandy mud in a shallow basin. A channel was subsequently cut at easting 10 m and migrated west with the deposition of point-bar sands. At easting 3 m migration of the channel ceased and quiet-water silts and muddy silts were deposited in the channel (samples WP 3 to 5) and over the point-bar deposits (samples WP 6 to 8). Coarse bedded sand and unbedded sands, and then gravels were deposited over the muds along the whole section, and the muds then were pierced by an ice-wedge at WP 1, at the east end of the section. It is possible that the channel belongs to the period of upper mud formation (see section WU), and the pre-channel sediments to the main period of terrace aggradation.

WQ (*figure* 4). Above basal gravel (probably resting on Gault), two horizons of grey silty clay occur in the terrace sands. The lower of these may correspond to the grey silt of WAD, at slightly greater depth to the south. Current bedded sands aggrade to 2 m below terrace surface, then there are laminated muddy silts at 2 m, and a series of weakly stratified coarse sand with humic content at 1.6 m and 1 m. The mud at 2 m and the humic horizon at 1.6 m may belong to the main terrace aggradation, being at a similar level to quiet-water deposits at WP and WN. The uppermost humic horizon at 1 m may be correlated with the muddy silt at WP 1 and belong to a much later stage of the terrace aggradation.

(iii) *Organic deposits within basins*

Muddy silts and sands lying within deeper and narrower basins, associated with much frost disturbance. These sections are discussed in more detail later.

WG (*figure* 2). This double basin was first seen in the upper part of the terrace sand as an oblique thin sliver of mud between an upper and lower silt 2 m long and 40 cm deep, when

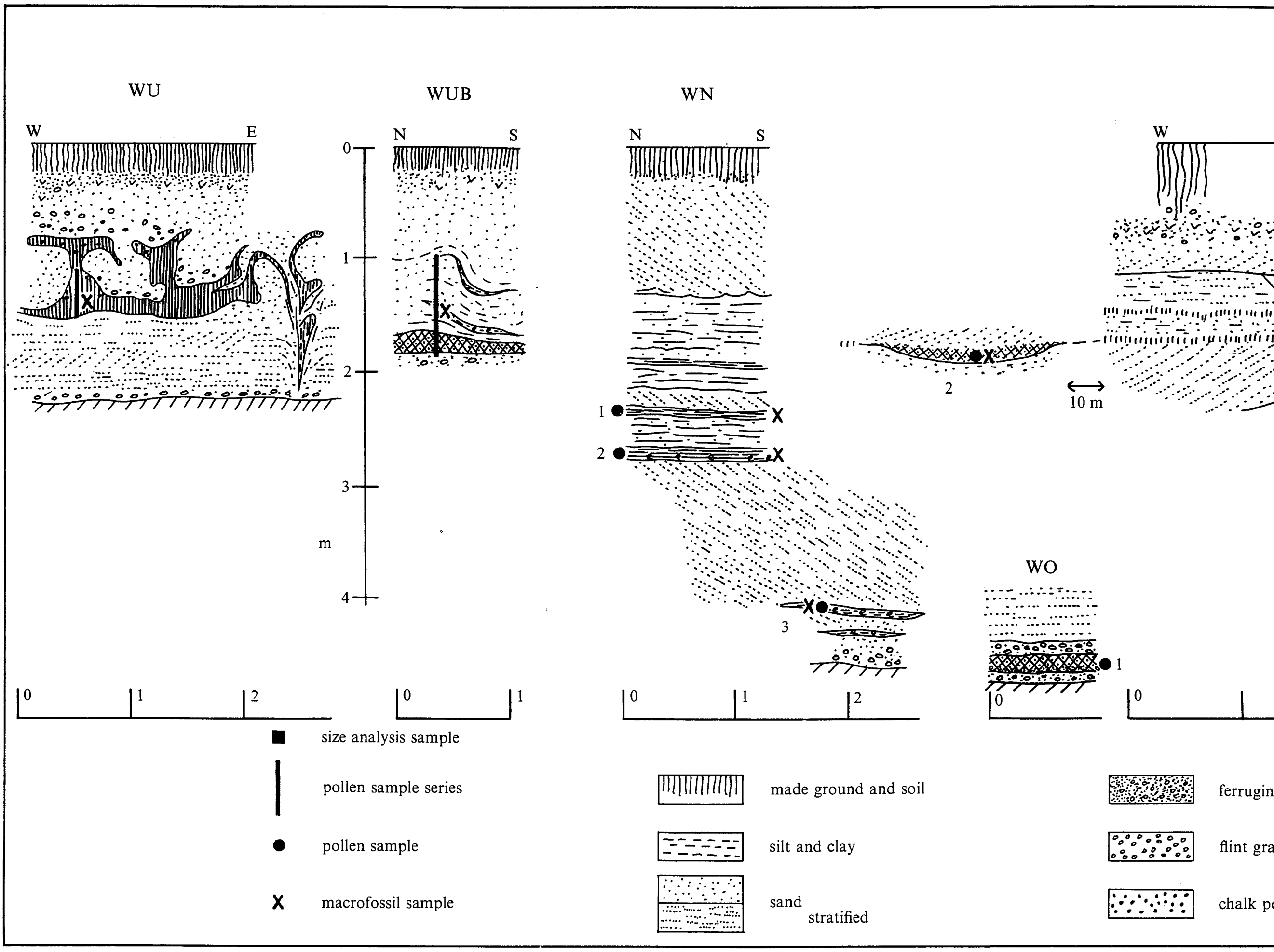
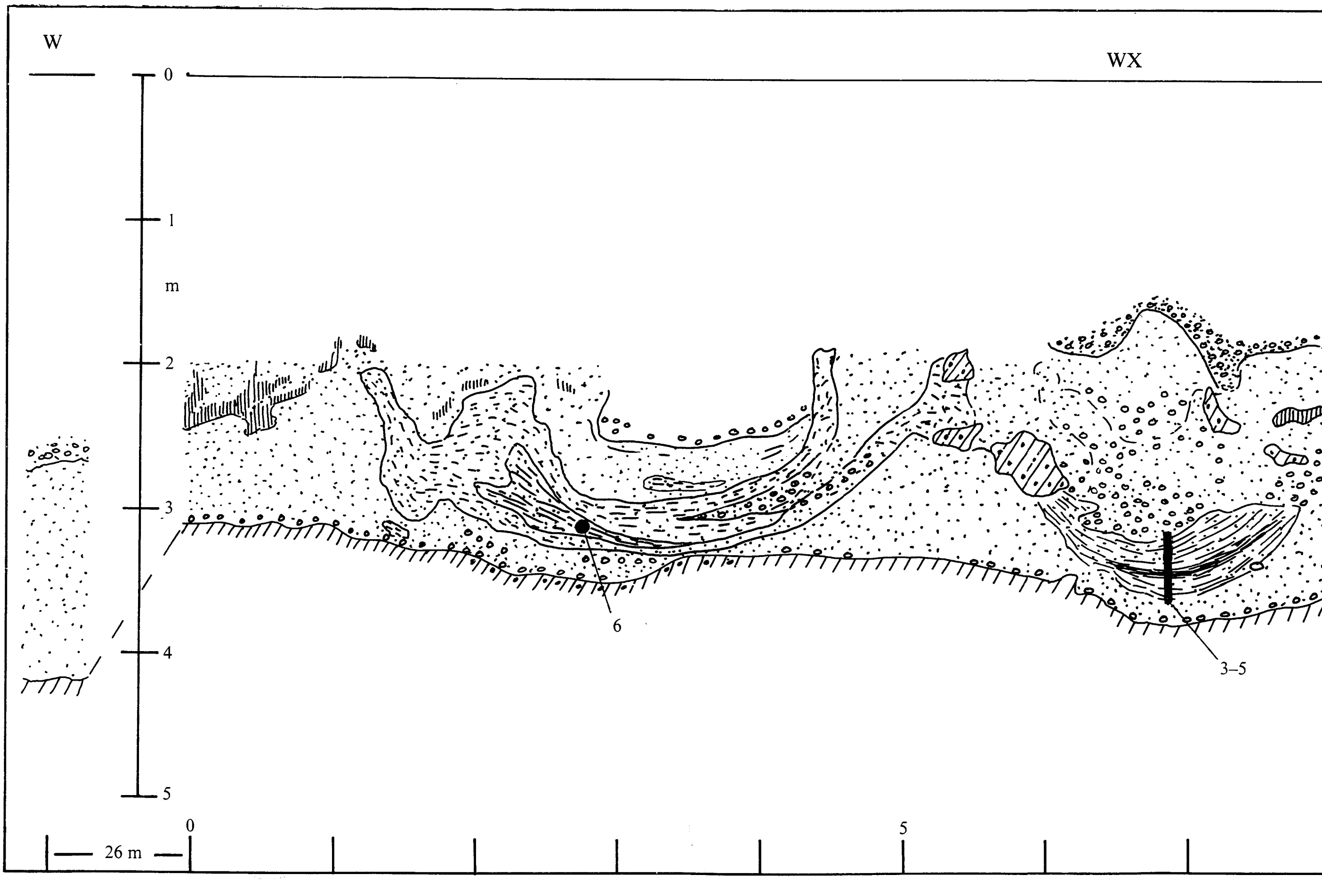
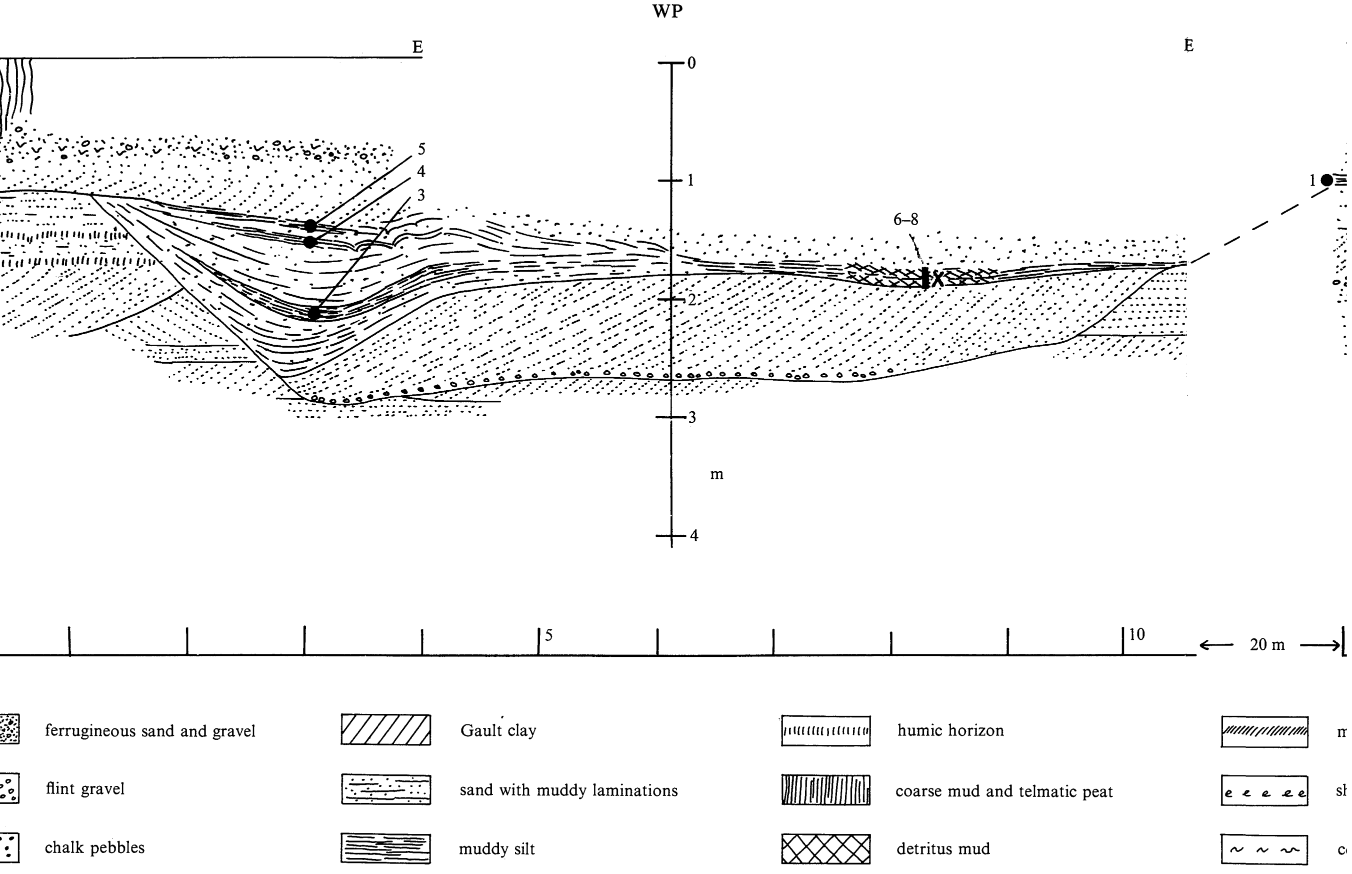
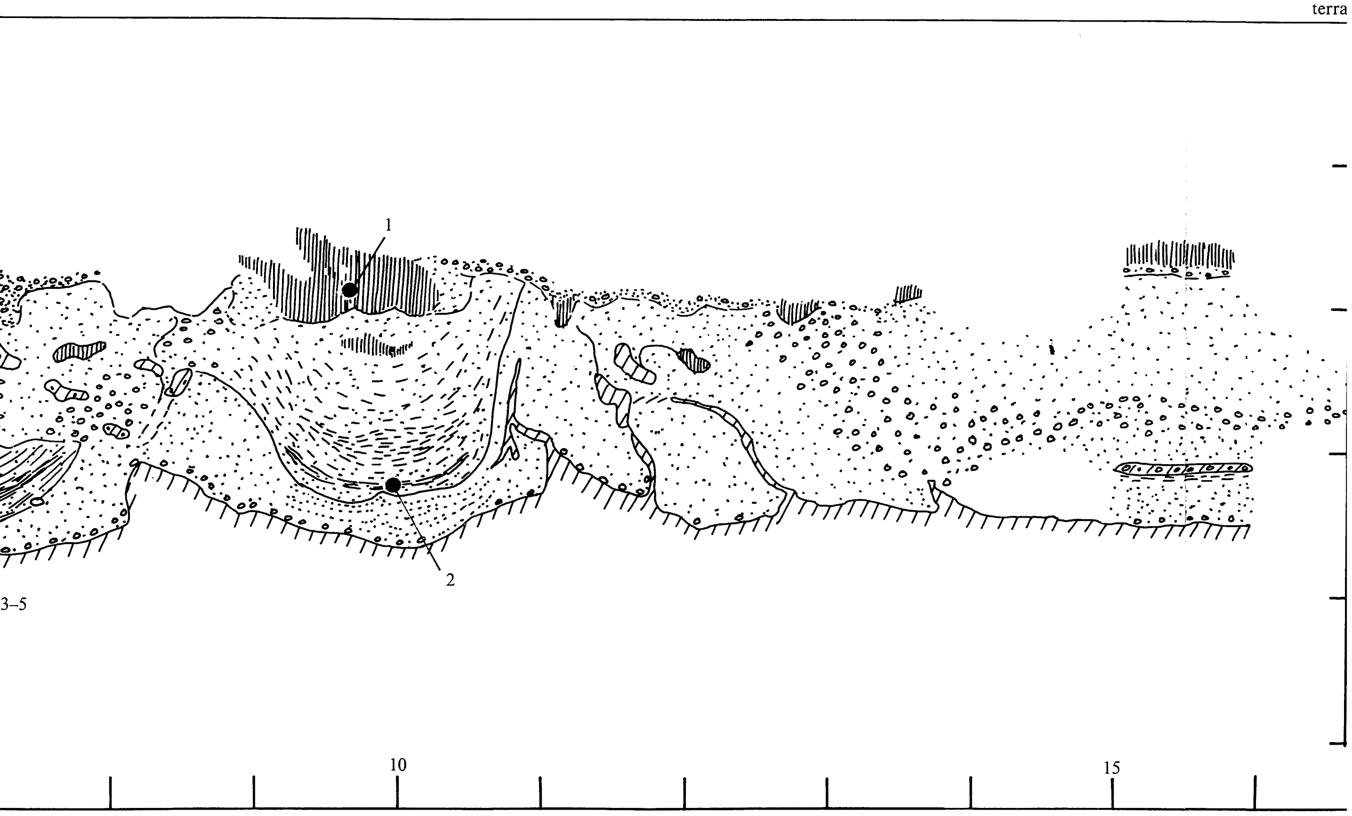


FIGURE 4. Stratigraphy of sites WN, WO, W





, WO, WP, WQ, WU and WUB, and key to sediment symbols used in figures 2-7.



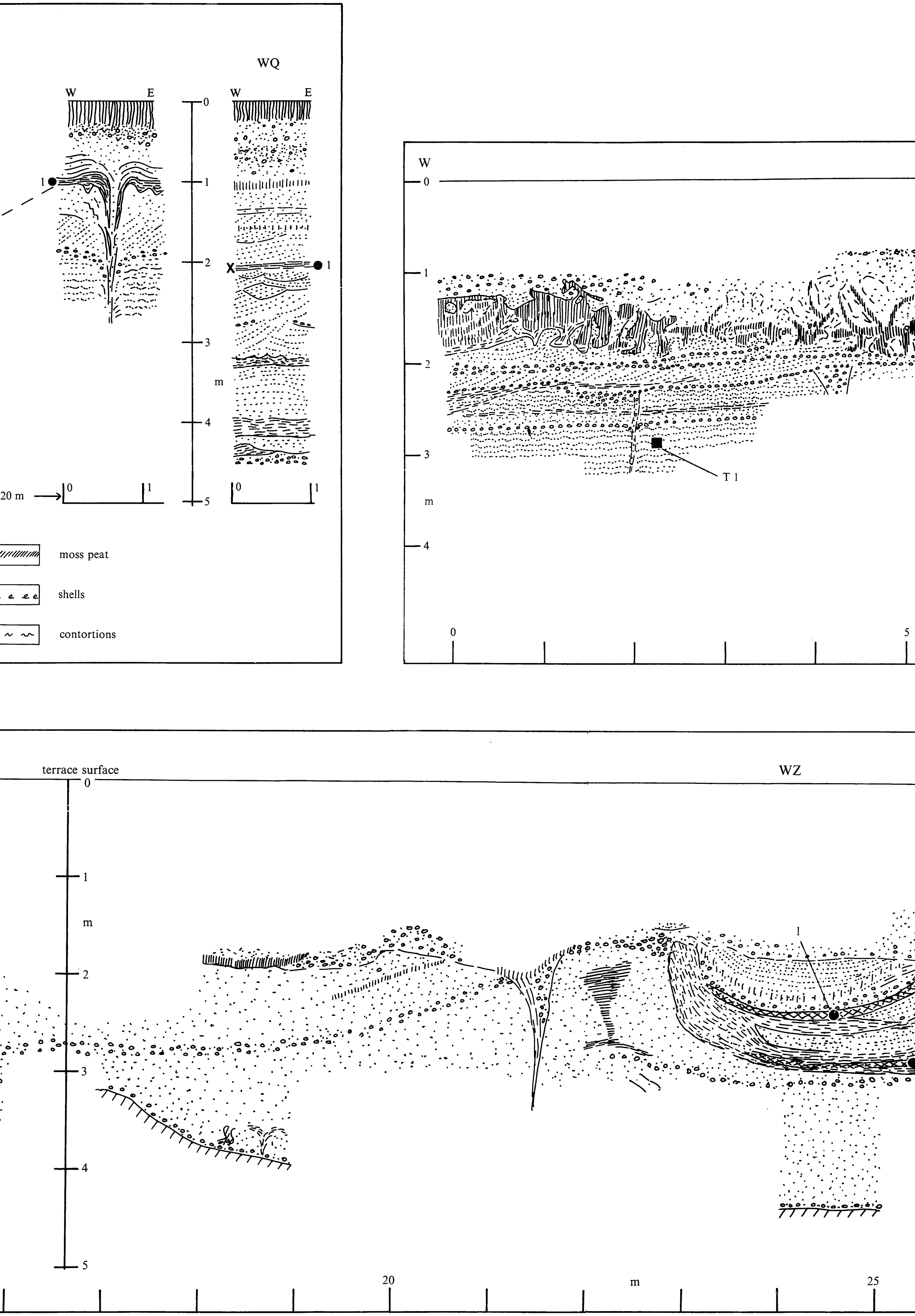


FIGURE 6. Stratigraphy of long section WX, WZ and WY. Key to sediment symbol

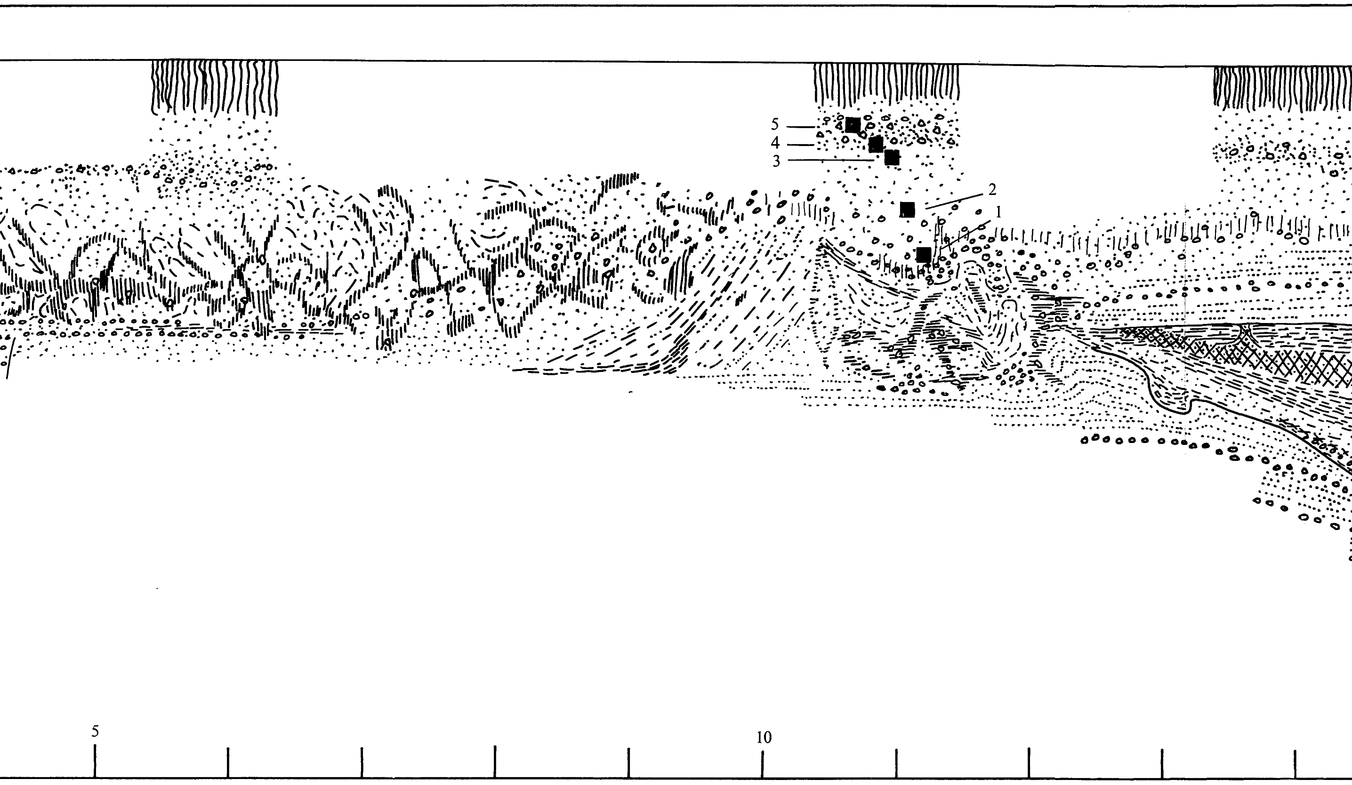
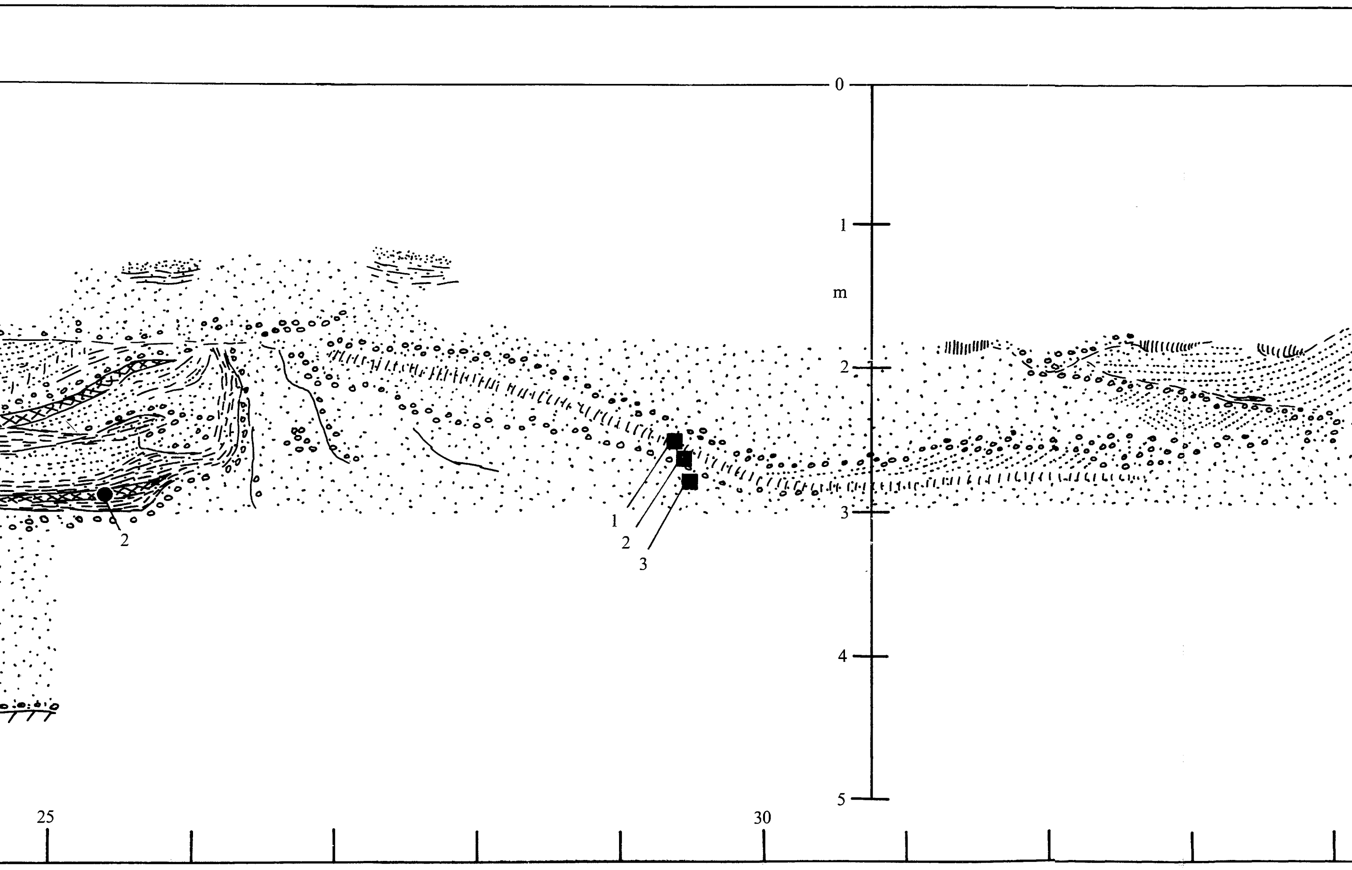
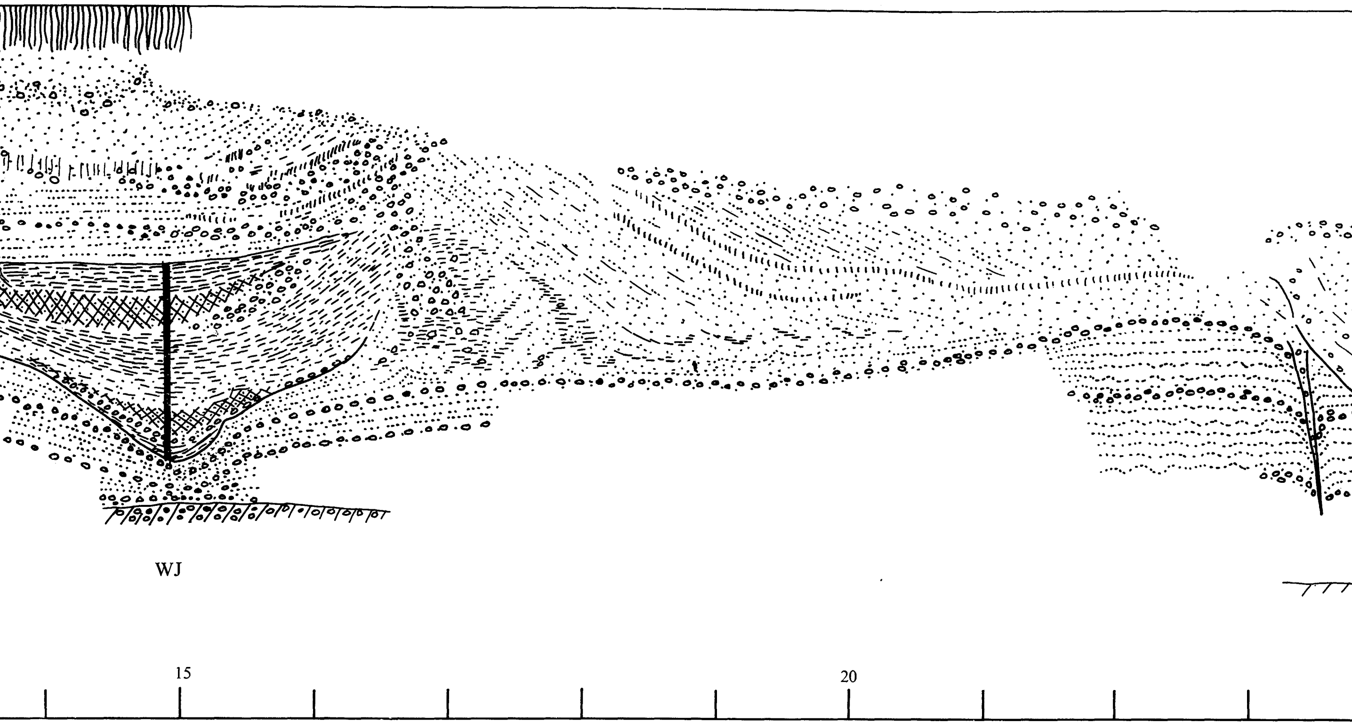


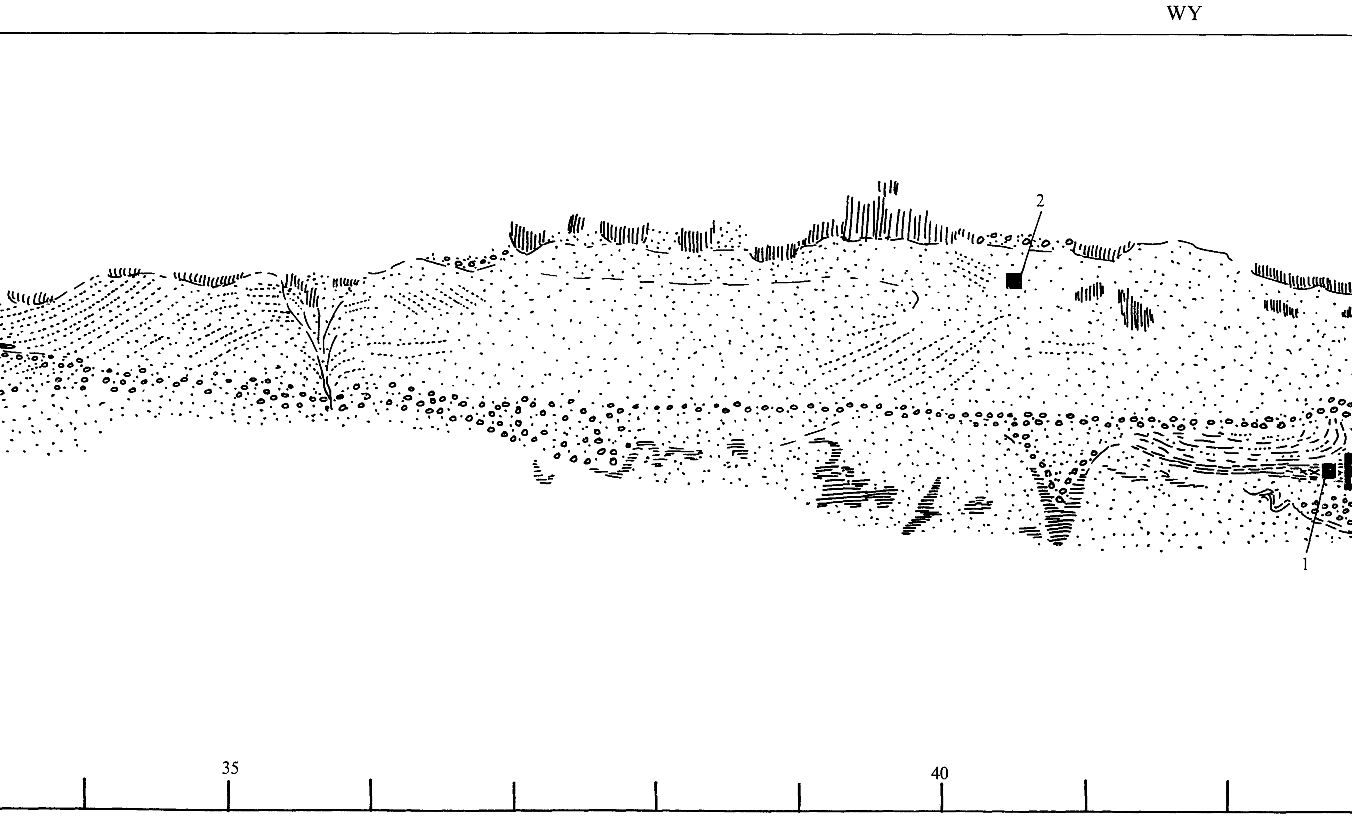
FIGURE 5. Stratigraphy of long section WJ (a few metres north of the sectio

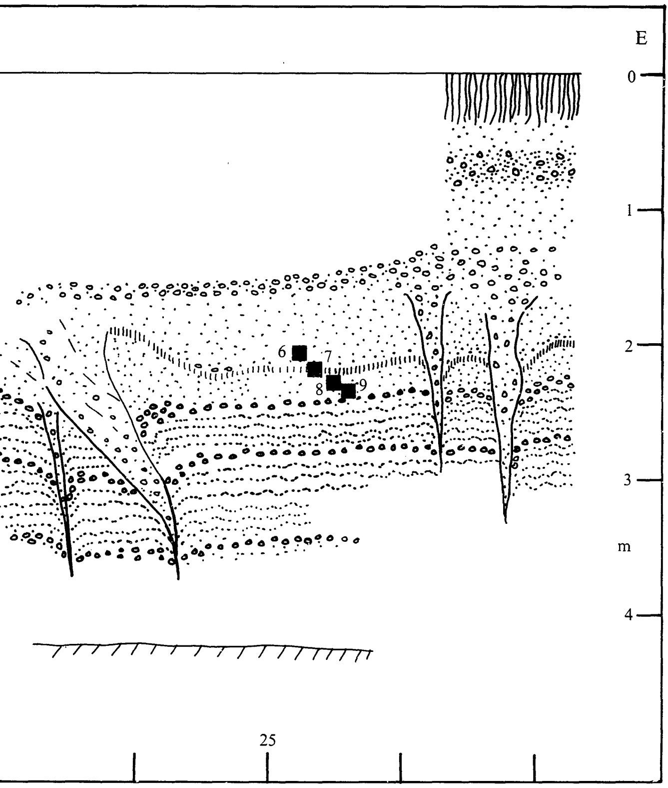


ent symbols in figure 4.



the section given in figure 2). Key to sediment symbols in figure 4.

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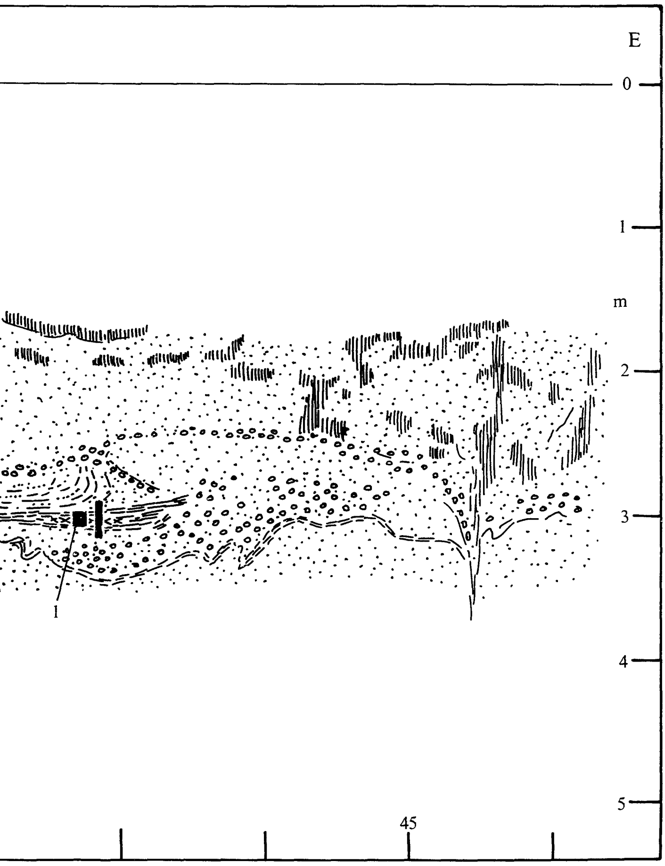
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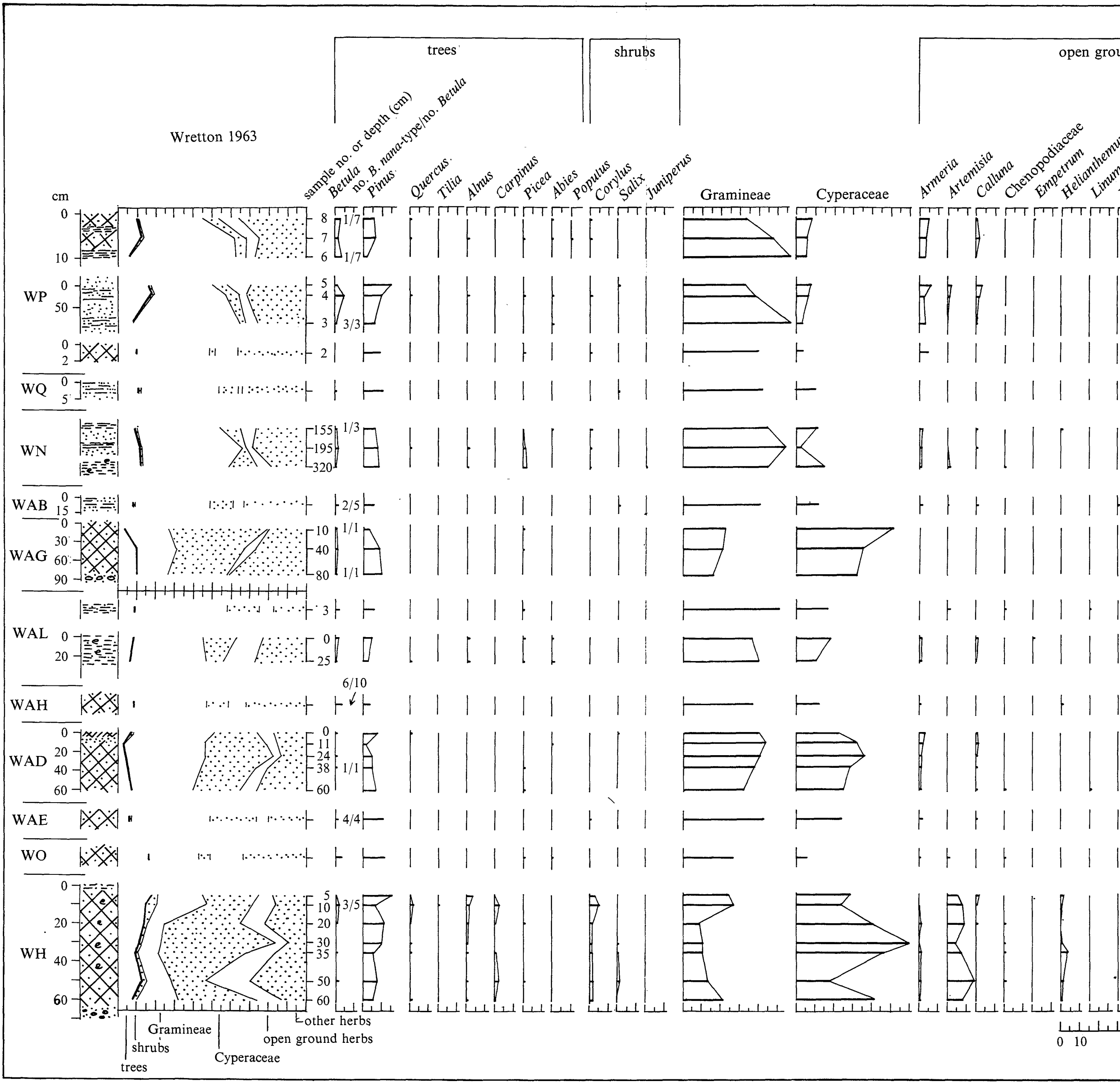
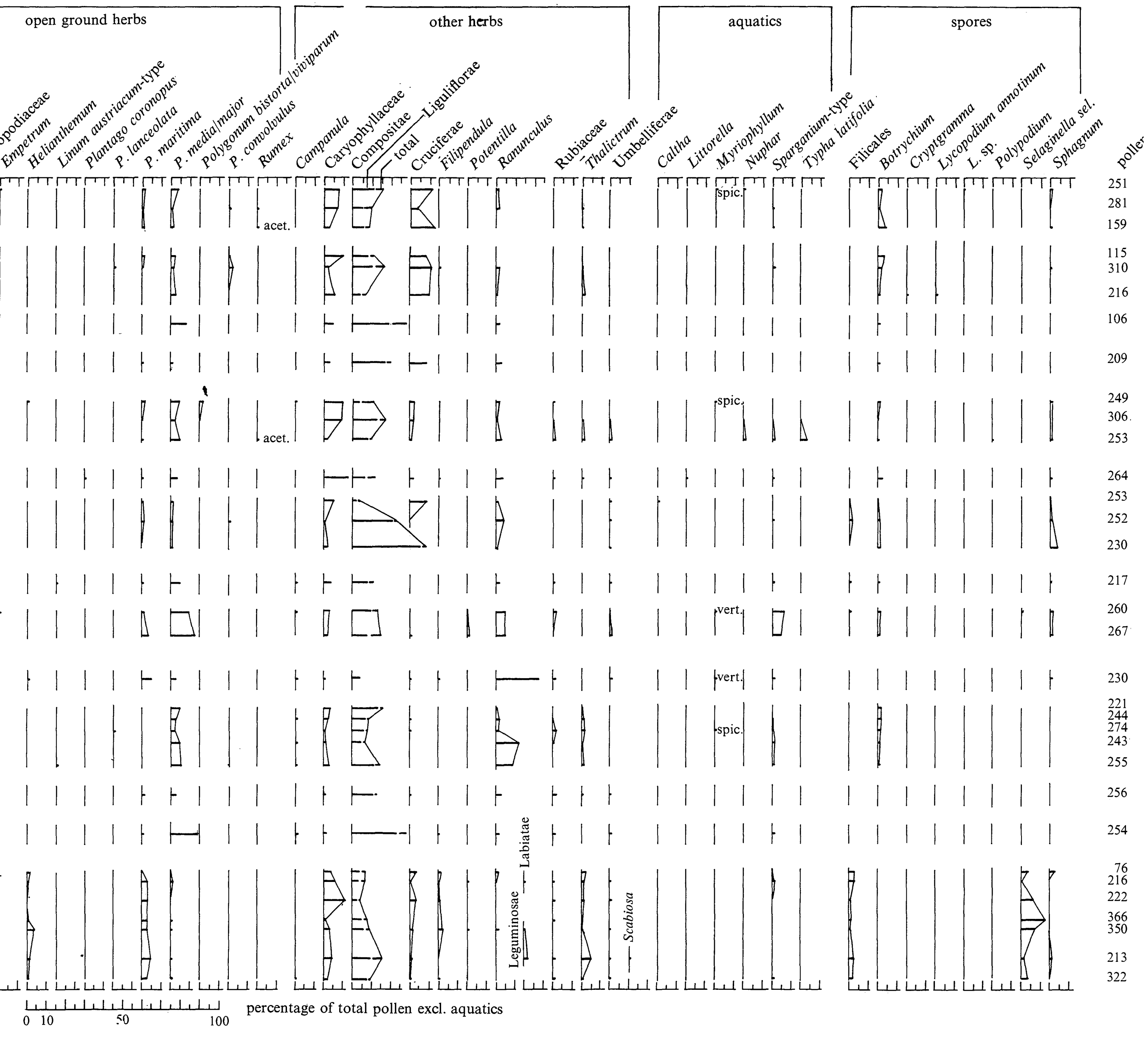
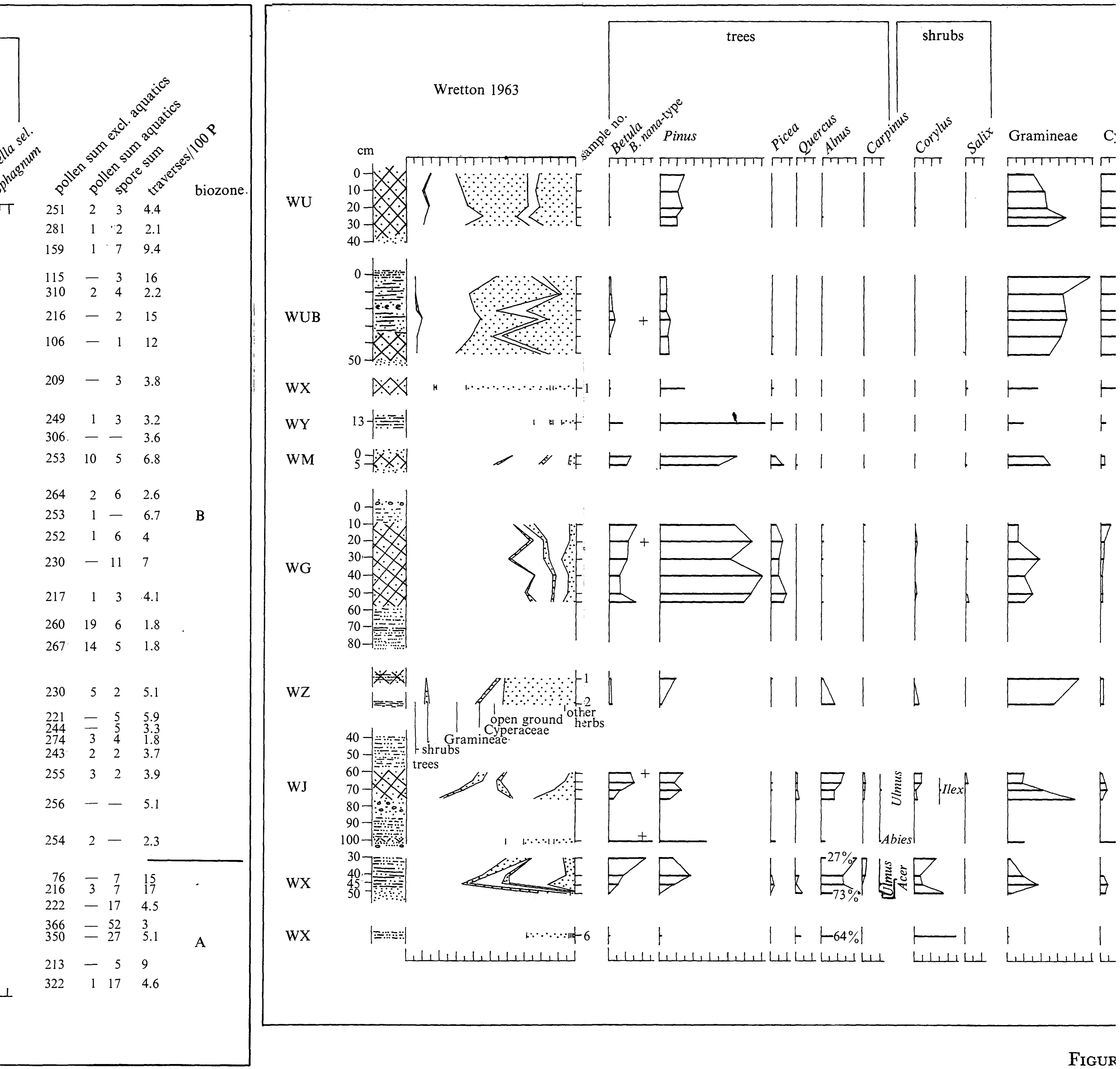


FIGURE 12. Pollen diag



Pollen diagrams from Devensian sediments.



pollen sum excl. aquatics	pollen sum aquatics	spore sum	traverses/100 P	biozone
251	2	3	4.4	
281	1	2	2.1	
159	1	7	9.4	
115	—	3	16	
310	2	4	2.2	
216	—	2	15	
106	—	1	12	
209	—	3	3.8	
249	1	3	3.2	
306	—	—	3.6	
253	10	5	6.8	
264	2	6	2.6	
253	1	—	6.7	B
252	1	6	4	
230	—	11	7	
217	1	3	4.1	
260	19	6	1.8	
267	14	5	1.8	
230	5	2	5.1	
221	—	5	5.9	
244	—	5	3.3	
274	3	4	1.8	
243	2	2	3.7	
255	3	2	3.9	
256	—	—	5.1	
254	2	—	2.3	
76	—	7	15	
216	3	7	17	
222	—	17	4.5	
366	—	52	3	
350	—	27	5.1	A
213	—	5	9	
322	1	17	4.6	

FIGUR

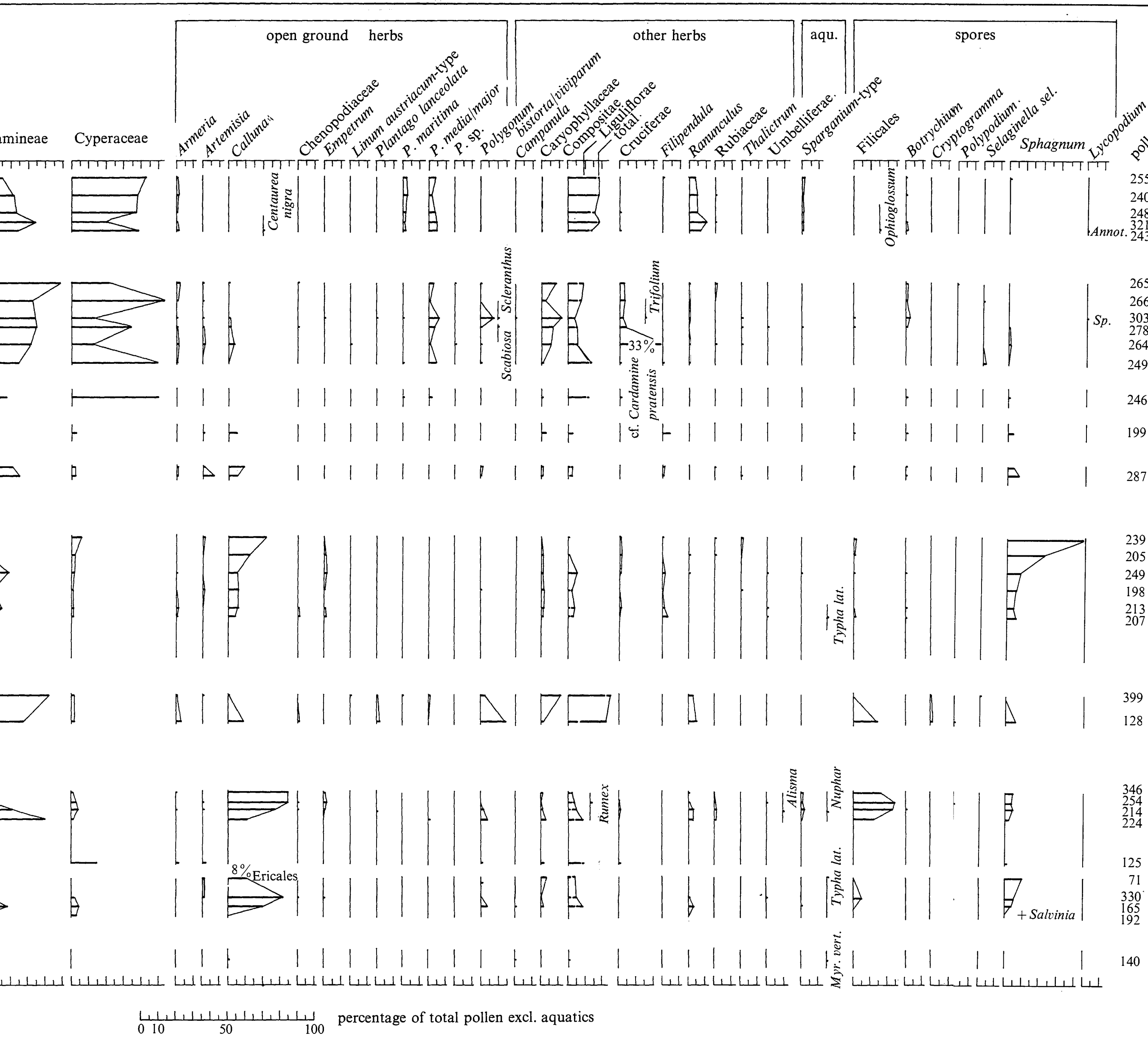
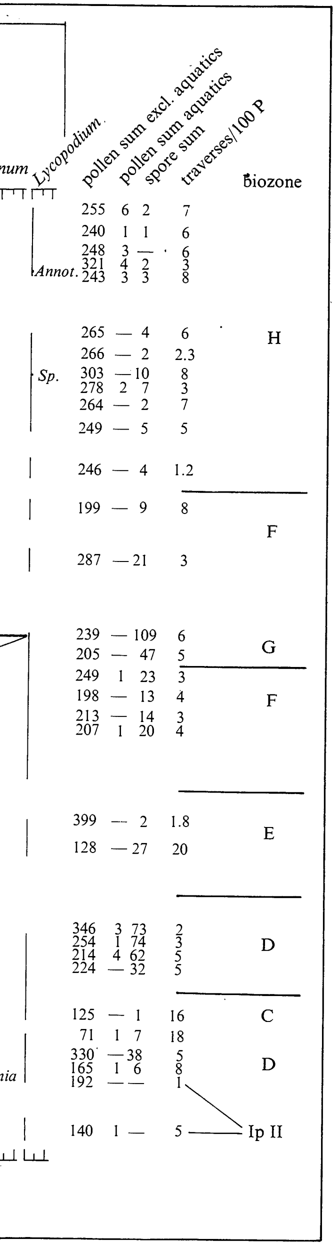


FIGURE 13. Pollen diagrams from Devensian sediments.



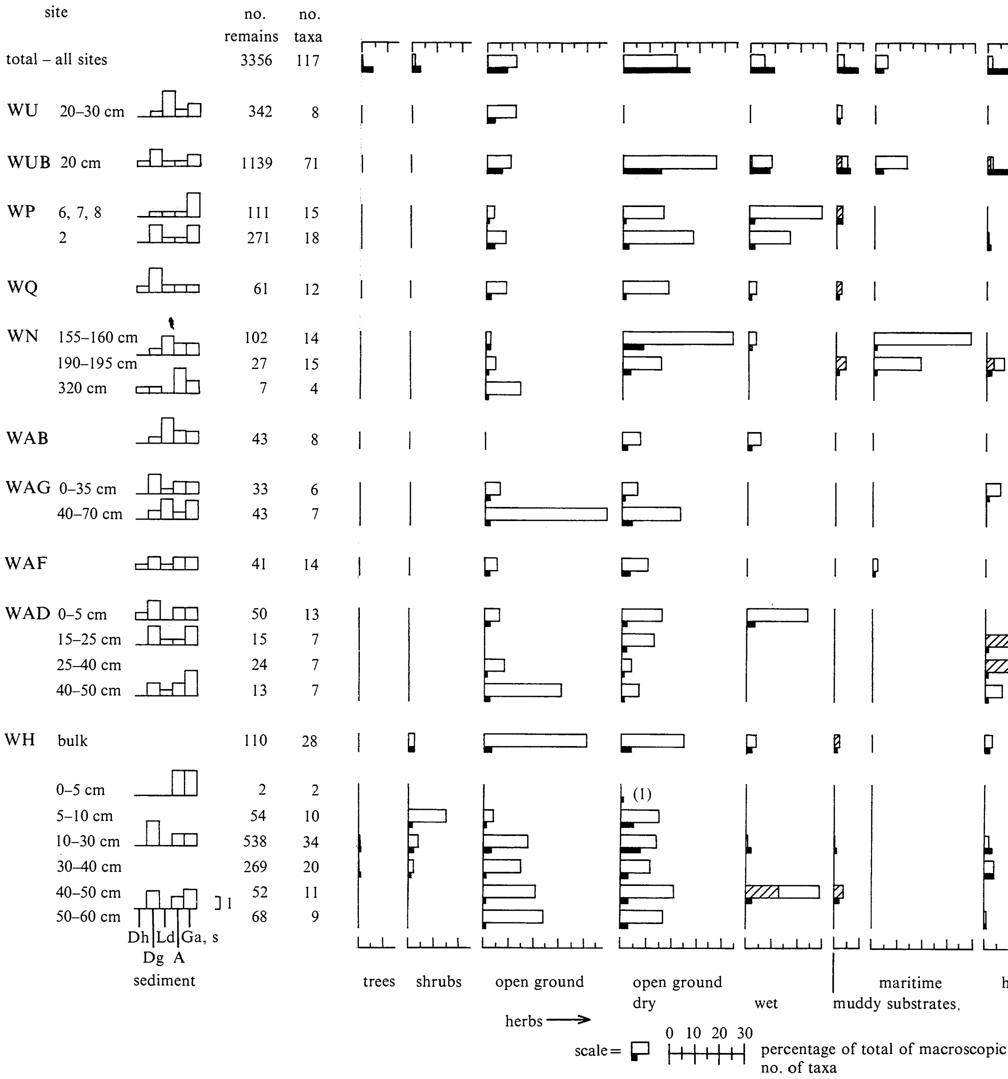
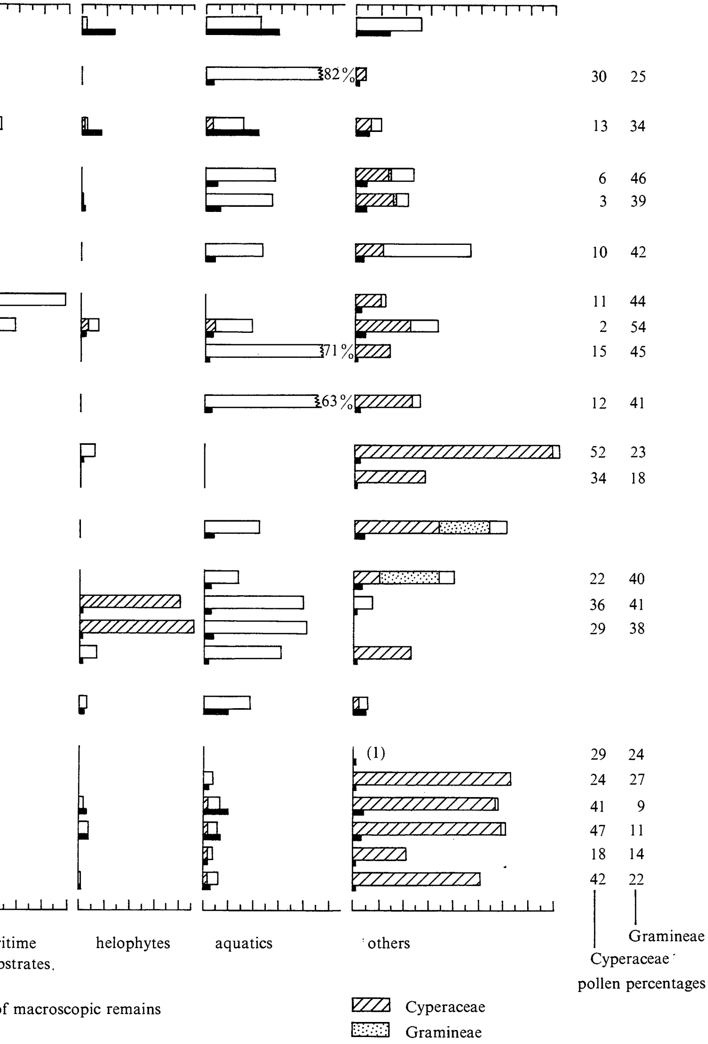


FIGURE 14. Frequency diagram of macroscopic pl



oscopic plant remains.

the central trench of the cut-off channel was dug. A few days later the section shown in figure 2 was seen and within a short time the whole deposit was removed. The silt and mud of the basin filling had disappeared by the time the final south face of the cut-off channel had been excavated, and it is therefore presumed that the deposits were formed in a closed depression. Only the eastern arm of the double basin was examined. The detailed stratigraphy of the basin fill is shown in figure 2. Pollen analyses indicate the filling took place in a woodland interval.

WJ (*figure* 5, *figures* 19–24, *plates* 19, 20). This section showed a basin lying in the terrace sands, with marginal involutions and a raised wall on either side. The basin was enclosed, for it was not visible when the central trench was made, and when the section was later cleaned, the arrangement of the sediments as the filling was dug away clearly indicated a closed hollow. To the east of the east wall unbedded sands occurred, the section being penetrated by casts of ice-wedges. To the west of the west wall fluviatile sands and gravels were overlain by involuted mud. Sand and gravel covered the whole.

WM. This was a small section in the south face of the cut-off channel, showing a 5 cm thick lens of mud about 2 m in length lying about 2 m deep in the terrace sand. On excavation the lens appeared to be saucer-like, lying in a hollow in the sand, bordered clearly by a thin layer of brown sand within the yellow terrace sand, thus resembling the organic horizon in section WY.

WX, *WY*, *WZ* (*figures* 6 *and* 7). This long section of 52 m comprises five depressions: three in a group to the west (WX), a central one (WZ) and an eastern one (WY). All appear to be enclosed hollows; they soon disappeared on excavation, and were not seen in the section when the excavations revealed the WJ section 20 m to the south. The depressions overlie terrace sand, and are overlain by sands and the upper mud and peat seen in the west part of WJ. A similar gravel and sand overlie this peat, as in the section WJ.

(iv) *Organic deposits near the terrace surface*

These muds form a wide spread near the terrace surface, much contorted by frost action (figures 19–24, plates 19, 20).

WU (*figure* 4). The terrace deposits are here very shallow, being only some 2 m thick. The site is near the northern margin of the terrace (see figure 1). A lower bedded sand rests on thin gravel over the Gault. A coarse mud overlies this sand. The mud is heavily contorted by involutions and contains chalk pebbles near its upper surface. An ice-wedge cast penetrates mud and underlying sand. Over the mud lies a sandy gravel with chalk pebbles, then ferruginous sand.

WUB (*figure* 4). The mud horizon of WU is here represented by a more sandy mud at a slightly greater depth than in WU. This site is further from the margin of the pond or channel in which these upper muds were formed. The sandy mud is overlain by shelly mud and thin grey silt layers, both disturbed by involutions, probably attributable to the same period of frost action that contorted the mud at WU.

WG, *WJ*, *WX*, *WZ* (*figures* 2, 5, 6). The same period of mud deposition is represented by the contorted organic deposits towards the top of the terrace in these sections. An eastern limit of the pond or channel is shown at the west wall (easting 10 m) of the basin in WJ (figure 5).

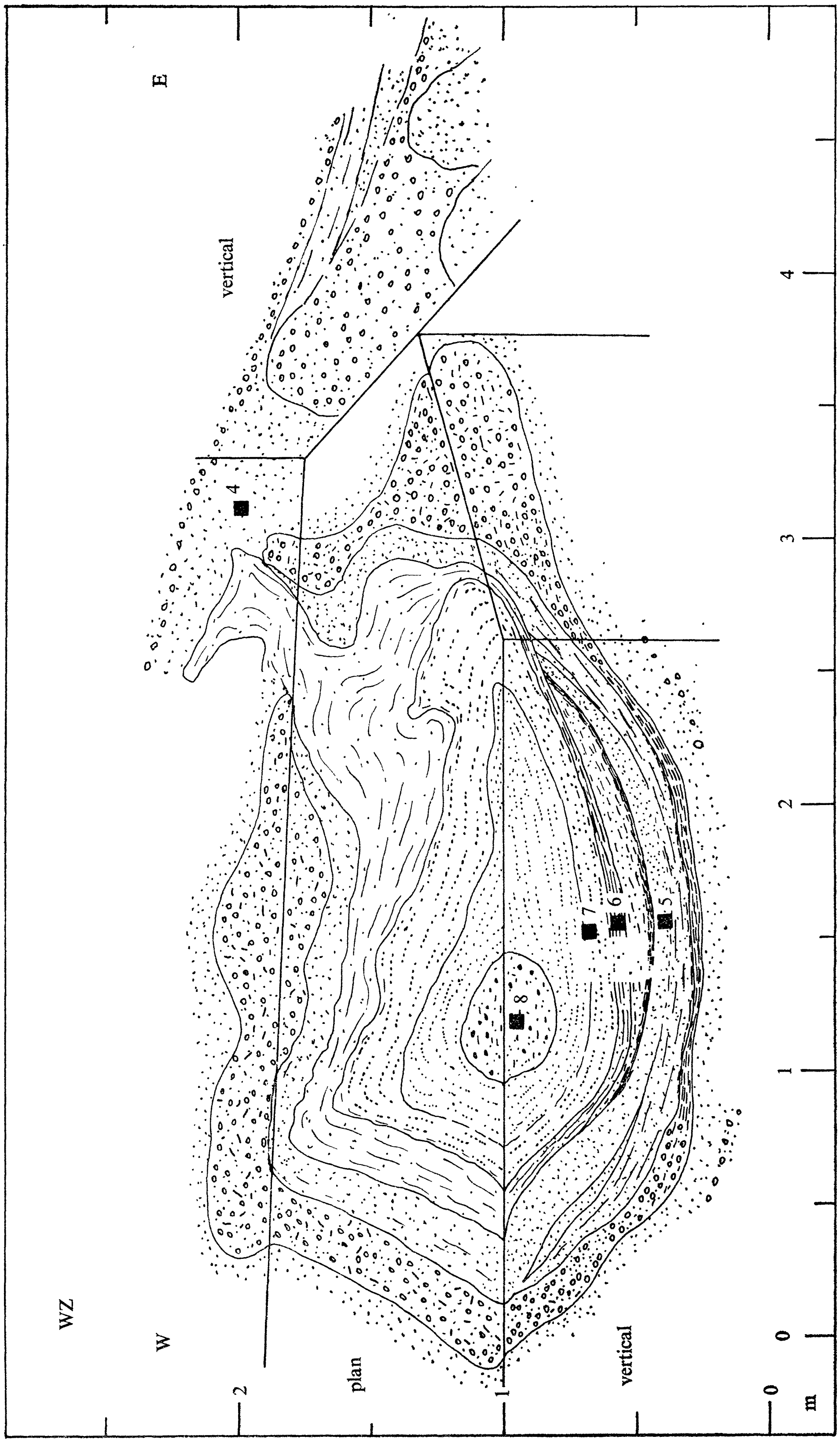


Figure 7. Detailed stratigraphy of site WZ in vertical and plan view. Key to sediment symbols in figure 4.

(*b*) *The sequence of deposits associated with the aggradation of the terrace*

The structure of the terrace sands indicates deposition under low-energy-flow regimes with ripple lamination (figure 5, WJ), trough sets (figure 4, WQ), tabular sets (figure 4, WP) and parallel quiet-water stratification (figure 3, WAB). The aggradation appears to result from deposition on a braided river plain, a former plain of the River Wissey during the Devensian. The organic horizons below the main aggradation (group 1) and those within it (group 2) give evidence of environmental conditions at the beginning of and during the aggradation. Such evidence will be considered later, but it may be mentioned now that the environment is one of periglacial aspect. The sequence of organic horizons related to the aggradation is as follows:

	site	deposition
youngest	WU, WUB	in a large pond or channel near the top of the terrace
	WP	in a meander channel near the top of the terrace
	WN	at three levels in the terrace
	WAB, WAG, WQ, WS	in the middle of the terrace sands
	WAD, WAH, WAL	low in the terrace sands
oldest	WH, WO	in shallow basins or channels in the Gault at the beginning of the aggradation

The oldest of these horizons occurs at a lower level than the interglacial deposits to the east. An episode of downcutting below the interglacial aggradation level must therefore have occurred before their deposition.

(*c*) *Petrography of the deposits*

The samples analysed petrographically were mainly from sections WAB (figure 3), WG (figure 2), WJ (figure 5), WY (figure 6) and WZ (figures 6, 7), but other samples for comparison with these were taken from the terrace sand (T 1, figure 9), the Kimmeridge Clay at Stretham (TL 515743), the Gault Clay at Wretton and at Wissington Factory (TL 663977), the Chalk Marl at Wretton, the Chalky Boulder Clay at Boughton (TF 693025), and the Ipswichian silty clay of section WB at Wretton Fen Bridge. Each was dispersed ultrasonically in 0.05% sodium hexametaphosphate solution and then divided into clay ($< 2\ \mu m$), silt (2–50 μm), fine sand (50 to 250 μm) and coarse sand ($> 250\ \mu m$) by sieving and repeated settling under gravity. The fine sands were subdivided into light and heavy fractions with bromoform (relative density 2.9) and analysed mineralogically with a petrological microscope. The clays were analysed by X-ray diffractometry of lightly compressed powders and oriented aggregates: amounts of clay mica were estimated from the non-exchangeable potassium contents, and the morphology of the clay minerals was studied by electron microscopy. Particle-size distribution was determined in 10 g subsamples by the pipette sampling technique, and the detailed particle size distribution of sand fractions in many samples was determined by dry sieving at $\frac{1}{4}\phi$ intervals ($\phi = -\log_2 d$, where d is the particle size in millimetres). Calcium carbonate and organic carbon were determined by a modification of Shaw's (1959) method.

The fine sand fractions from the Kimmeridge Clay, Gault Clay and Chalk Marl of the Wretton area all contain a restricted suite of minerals, with large amounts of calcite, gypsum, collophane, quartz, limonite, and in the Chalk Marl of glauconite, muscovite and chlorite also;

non-opaque heavy minerals are extremely rare, except for siderite in the Gault Clay. In contrast, the fine sands from all the Pleistocene deposits analysed (except the Ipswichian silty clay) are composed of quartz, alkali felspar and flint, with many types of opaque and non-opaque heavy minerals; muscovite, chlorite, glauconite, gypsum and collophane occur only sporadically and in small quantities. The non-opaque heavy minerals are mainly garnet, amphiboles, epidote, zircon, tourmaline, rutile, anatase, pyroxenes, staurolite, kyanite, andalusite and apatite – an assemblage similar to that of glacial deposits in eastern England. The amounts of sediment in the Devensian deposits at Wretton derived from local Mesozoic rocks are therefore

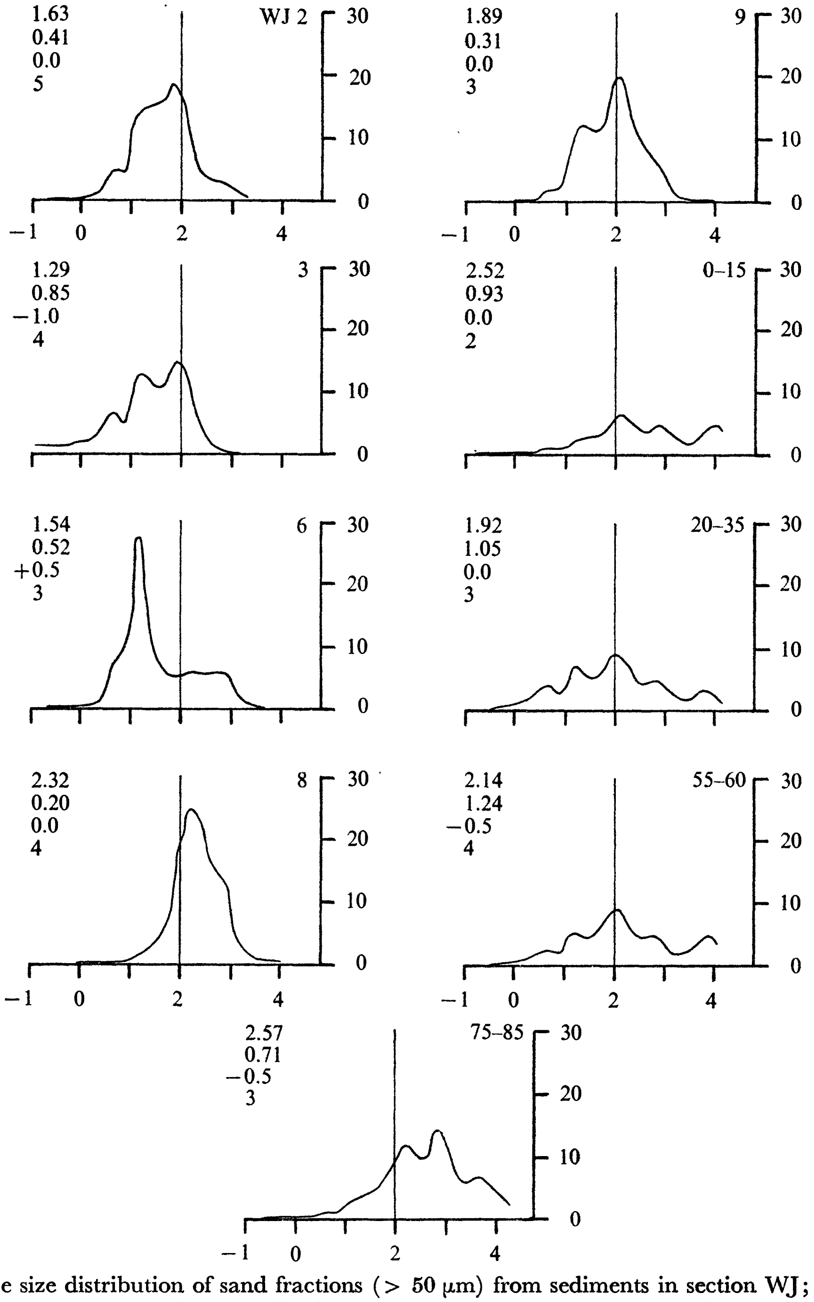


FIGURE 8. Particle size distribution of sand fractions (> 50 μm) from sediments in section WJ; the four figures listed with each curve in this figure and in figures 9 and 10 are the mean particle size and standard deviation (both in ϕ units), the skewness and kurtosis (β_2).

small. The flint was derived ultimately from the Chalk, but most of the sediment must have come either from older glacial deposits or, by outwash, direct from a glacier.

The detailed particle-size distribution of sand fractions from the Devensian deposits reveals a wide range in the degree of sorting of the particles (figures 8 to 10). The river terrace sand (T 1, figure 9) is moderately well sorted, and has a standard deviation of particle size (0.85ϕ) similar to that of many fluviatile sands analysed by Friedman (1961). Several other sands in the Devensian succession (e.g. WJ 3, WZ 7) are similarly sorted (figures 8, 9), and may be fluviatile. However, a few (e.g. WZ 1–4, WY 2, WJ 8) are much better sorted, and have standard

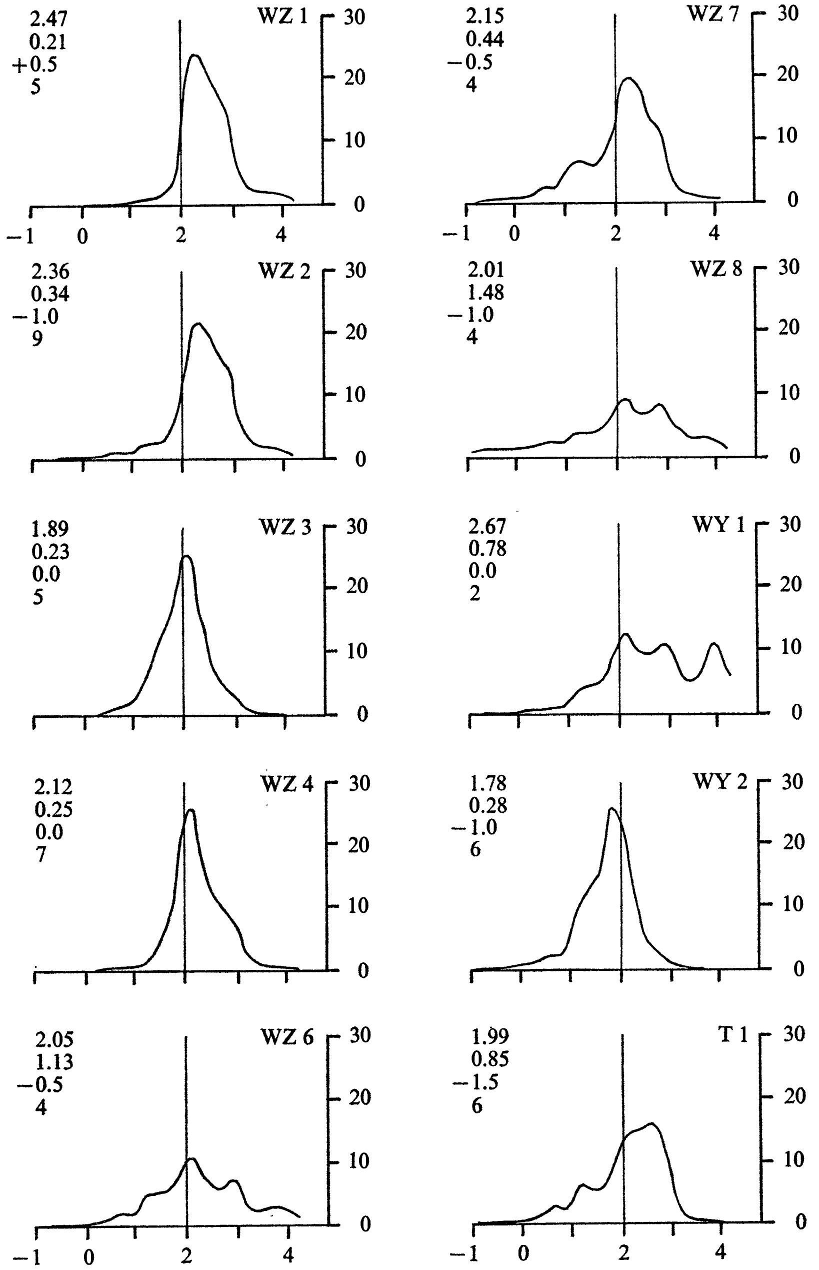


FIGURE 9. Particle-size analyses of sand fractions (> 50 μm) from sediments in sections WY, WZ and terrace sand.

Table 1. Particle-size distribution and organic carbon and calcium carbonate contents of Devensian deposits at Wretton

Amounts of sand, silt and clay in the Kimmeridge Clay, Gault Clay, etc., are expressed on a carbonate free basis.

	figure 5									figure 5 (profile in basin)							figure 2						
	WJ 1	WJ 2	WJ 3	WJ 4	WJ 5	WJ 6	WJ 7	WJ 8	WJ 9	WJ 0–15	WJ 20–35	WJ 35–50	WJ 55–60	WJ 65–75	WJ 75–85	WJ 100	WG 0–10	WG 10–20	WG 20–30	WG 30–40	WG 40–50	WG 50–59	WG 60–73
sand																							
> 250 µm	70.5	73.2	81.2	52.2	65.0	75.1	25.7	19.2	48.5	14.1	31.5	23.1	30.3	15.3	16.5	26.4	18.2	15.3	8.6	10.6	9.9	7.6	18.7
50–250 µm	21.5	23.8	16.9	27.6	32.2	23.1	68.5	79.2	50.1	35.7	38.5	40.1	41.2	50.8	56.5	21.4	36.6	33.4	36.0	30.2	29.7	14.9	47.5
silt																							
20–50 µm	1.0	0.4	0.9	7.5	0.6	0.5	0.3	0.4	0.5	17.8	6.0	7.4	6.7	6.3	4.6	15.0	16.5	15.8	17.0	13.9	19.4	18.9	7.2
5–20 µm	0.5	0.4	0.4	5.8	0.6	0.4	0.4	0.3	0.4	7.9	4.0	5.8	3.8	1.9	1.9	7.1	5.9	9.1	5.3	3.9	8.1	11.1	3.4
2–5 µm	0.6	0.4	0.4	1.1	0.6	0.5	0.8	0.4	0.5	1.3	1.4	1.8	0.7	2.1	3.2	7.3	4.4	2.8	1.6	1.1	4.0	3.1	2.2
clay																							
< 2 µm	4.8	2.4	0.9	5.0	1.0	1.3	5.3	1.8	1.2	16.2	17.0	18.0	13.4	15.2	11.8	16.3	16.6	18.5	20.3	21.7	21.5	26.7	15.5
total	98.9	100.6	100.7	99.2	100.0	100.9	101.0	101.3	101.2	93.0	98.4	96.2	96.1	91.6	94.5	93.5	98.2	94.9	88.8	81.4	92.6	82.3	94.5
organic carbon	0.16	0.04	0.02	0.08	0.02	0.04	0.08	0.03	0.05	0.23	0.47	0.40	0.08	2.73	1.00	3.06	0.23	1.83	1.96	1.98	2.48	3.02	0.26
calcium carbonate	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

	figure 6			figure 7					figure 3	figure 6								
	WZ 1 (S)	WZ 2 (S)	WZ 3 (S)	WZ 4 (S)	WZ 5 (S)	WZ 6 (S)	WZ 7 (S)	WZ 8 (S)	WAB (S)	WY 1	WY 2	figure 5 T 1	Kimmeridge Clay, Stretham	Gault Clay, Wretton	Gault Clay, Wissington	Chalk Marl, Wretton	Chalky boulder clay, Boughton	Ipswichian silty clay, Wretton Fen Bridge
sand																		
> 250 µm	7.5	13.2	58.6	39.1	35.5	35.0	30.7	34.1	11.2	9.4	65.0	37.8	19.4	7.2	3.2	12.1	10.9	1.7
50–250 µm	87.0	83.6	39.9	58.9	50.3	22.5	66.8	43.1	73.9	32.3	33.5	59.6						
silt																		
20–50 µm	0.5	0.8	0.2	0.2	1.7	5.0	0.4	6.4	4.1	19.3	0.1	0.2	35.4	43.4	42.8	66.8	32.8	50.6
5–20 µm	0.2	0.2	0.2	0.5	1.8	3.8	0.2	3.4	1.8	8.8	0.2	0.7						
2–5 µm	0.6	0.2	0.2	0.2	1.3	0.2	0.2	2.4	1.0	3.1	0.1	0.2						
clay																		
< 2 µm	3.3	2.0	1.2	1.3	7.5	9.3	1.2	7.9	4.8	16.4	0.8	1.5	45.2	49.4	54.0	21.1	56.3	47.7
total	99.1	99.6	99.7	99.8	98.1	95.6	99.3	97.3	96.8	89.3	99.3	99.6	.	.	.	.	.	.
organic carbon	0.10	0.06	0.03	0.05	0.18	1.36	0.03	0.98	0.15	0.98	0.03	.	.	.	.	.	.	.
calcium carbonate	.	.	.	.	.	.	.	2.6	.	.	.	0.67	21.3	49.0	35.8	41.7	20.8	24.2

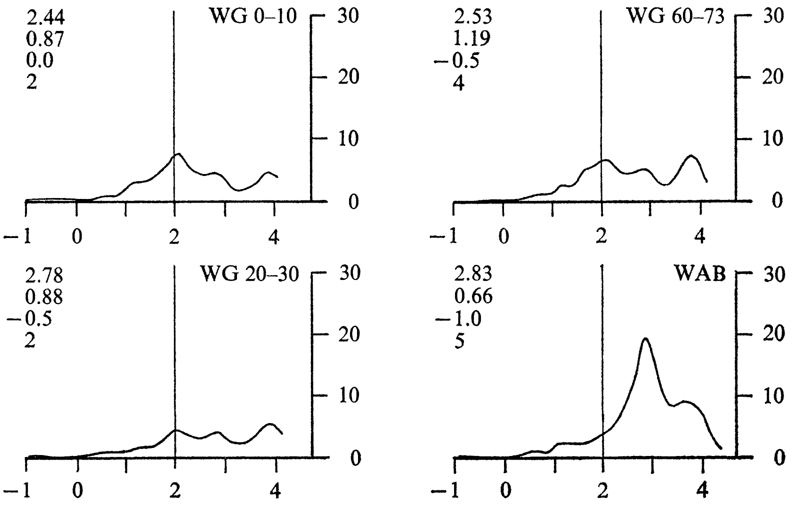


FIGURE 10. Particle size analyses of sand fractions (> 50 μm) from sediments in sections WG and WAB.

TABLE 2. MINERALOGICAL COMPOSITION OF CLAY FRACTIONS (< 2 μm) FROM DEVENSIAN DEPOSITS AT WRETTON

p = present but amount not determined; amounts of expanding minerals, mica and kaolinite recalculated to total 100%

		expanding minerals (%)	mica (%)	kaolinite (%)	quartz	lepidocrocite	chlorite	interstratified mica-chlorite	felspar
WJ 4	figure 5	37	15	48	p	.	.	p	.
WJ 5		60	17	23	p	.	.	p	.
WJ 7		65	20	15	p	p	.	p	.
WJ 0–15	figure 5 (profile in basin)	67	9	24	p	.	p	.	.
WJ 20–35		67	6	27	p	.	p	p	.
WJ 35–50		61	5	34	p	.	p	p	.
WJ 55–60		73	7	20	p	.	.	p	.
WJ 65–75		58	24	18	p	.	p	.	.
WJ 75–85		62	18	20	p	.	p	.	.
WJ 100		52	24	24	p	.	p	.	.
WG 0–10	figure 2	64	11	25	p	.	.	.	.
WG 10–20		66	10	24	p	.	p	.	.
WG 20–30		65	10	25	p	.	p	.	.
WG 30–40		68	13	19	p	.	p	.	.
WG 40–50		70	10	20	p	.	.	.	.
WG 50–59		66	8	26	p	.	p	.	.
WG 60–73		60	10	30	p	.	p	.	.
WZ 1 (S)	figure 6	67	15	18	p	.	.	p	.
WZ 6 (S)	figure 7	65	8	27	p	.	.	p	.
WZ 7 (S)		69	18	13	p	.	.	p	.
WAB (S)	figure 3	69	15	16	p	.	.	p	.
WY 1	figure 6	59	16	25	p	.	.	.	.
WY 2		70	17	13	p	.	.	.	.
T 1	figure 5	55	25	20	p	p	p	p	.
Kimmeridge Clay, Stretham		49	37	14	.	.	.	.	p
Gault Clay, Wretton		53	23	24	.	.	.	p	p
Gault Clay, Wissington		46	24	30	.	p	.	p	p
Chalk Marl, Wretton		43	21	36	.	.	.	.	p
Chalky Boulder Clay, Boughton		50	32	18	p	.	p	p	p
Ipswichian silty clay, Wretton Fen Bridge		48	26	26	p	.	p	p	p

deviations ($< 0.40\phi$) matched only by those of typical beach sands or windblown sands. As it is extremely unlikely that any marine phase is represented in the Devensian succession at Wretton, the well-sorted sands must be windblown coversands. The most poorly sorted sands are those from deposits filling the enclosed basins WG (figure 10), WJ (figure 8), WY and WZ (figure 9).

The clay fractions of all the deposits analysed are composed mainly of expanding minerals (montmorillonite, vermiculite and interstratified mixtures of the two), kaolinite and mica (table 2). The Gault Clay and Chalk Marl both contain lath-shaped expanding minerals, but the montmorillonite in the Kimmeridge Clay and the interstratified montmorillonite–vermiculite in the Chalky Boulder Clay occur in very small, irregular, platy particles. The clay fraction of the Ipswichian silty clay is similar to the Gault Clay, and is probably derived from it, but the origin of the clay in the Devensian deposits is not so clear. Lath-shaped expanding minerals occur in some of the more sandy deposits (e.g. WJ 4 to 6, WY 2, WZ 1, WAB, T 1), suggesting that the small amounts of clay in them are derived from the Gault or Chalk Marl. However, many of the more clay-rich deposits filling the enclosed basins contain very small amounts of clay mica, and their expanding minerals occur as very small and rounded particles. These features suggest strong weathering of the clay before deposition in the basins, and such weathering would have destroyed any resemblance to the Mesozoic clays.

The Devensian sediments are divisible petrographically into two main groups, which correspond to deposits filling the deep enclosed basins (WG, WJ, WY and WZ) and others. The differences between the two groups are expressed in their particle size distribution, sand mineralogy and clay mineralogy. The basin deposits usually contain more clay and silt than the other deposits (table 1), and their sand fractions (50–2000 μm) are less well sorted. Their fine sands contain 8–16 % felspar and little or no pyroxene, whereas the fine sand of the other deposits contains 3–7 % felspar and small but significant amounts of pyroxene. Clay particles in the basin deposits are rounded or irregularly shaped, whereas those in the other deposits are largely subhedral laths and plates; also, the amounts of clay mica in two of the basins (WG and WJ) are much less than in the other deposits. The petrographic uniformity of the basin deposits suggests that they were all derived from the same source or sources. The amount of weathering indicated in their clay fractions is more than could have occurred in a short period of alteration during the Devensian, and should rather be ascribed to a relatively long, warm period, such as the preceding interglacial.

(*d*) *Depositional history*

(i) *The structure and depositional history of section WJ*

This section (figure 5, figures 19–24, plates 19, 20) was drawn to a scale of 4 cm to 1 m. The central feature is a trough with a rim on either side; excavation of this indicated that it was an enclosed basin, because the muddy sediments within it thinned rapidly to the north, and the trough was not seen 5 m to the south during the excavation of the central guiding trench of the cut-off channel. The key to the sequence in this section is in the origin of the basin.

The formation of a steep-sided basin of deposition only a few metres in diameter can most easily be explained as a result of the melting of ice. Wretton is outside the limit of the Devensian ice, the nearest known exposures of the youngest East Anglian till (the Hunstanton Till) being 40 km (25 miles) to the north, so the presence of glacier ice can be excluded. However, ground ice in a periglacial environment is quite likely, especially where permeable terrace deposits rest on an impermeable stratum, such as the Gault Clay. In this situation any segregation or injection ice forming in the waterlogged sediments as a result of hydrostatic pressures accompanying seasonal down-freezing or enveloping permafrost would act as a nucleus for the growth of ground ice (Shumskii 1964). Clear injection-ice forms when there is a large supply of water to the centre of freezing and the rate of freezing is relatively slow. In contrast, segregation ice forms when there is little water but freezing is rapid; fine grained sediments also favour the formation of segregation ice. Further growth of ice around these nuclei, governed by the hydrostatic pressure resulting from down-freezing of the terrace deposits towards the impermeable Gault, would cause the ground to swell and form an ice mound. Subsequent melting of the lenticular mass of ground ice would leave a water-filled hollow, in which sediment derived from various sources might be deposited.

The deposits filling the basin in section WJ differ from the surrounding sandy sediments in containing more clay and silt, and sand that is less-well sorted (figure 8); also the clay is weathered, and the sand contains more felspar but less pyroxene. The extra clay might have been derived by upward injection from a weathered surface of Gault Clay beneath a lens of ground ice, but the lack of Gault-derived sand minerals in the basin sediments indicates that this was at best a minor source of clay. It is more likely that a deposit containing weathered clay existed in the terrace before the ice mound formed; indeed, the presence of a relatively clay-rich horizon was probably responsible for the localization of ground ice at this site. Deposits from all the other basins studied petrographically contain similar amounts of clay (table 1), and can also be distinguished from sediments outside the basins by the same mineralogical features as those shown by the WJ basin deposits. This suggests that the sediment in all the basins had a common origin, even though the basins were seen to be separate and the time of sedimentation in each, as shown by the pollen, was different. The ice mounds therefore formed and melted at different times, but were localized by clayey horizons, possibly the sediment filling a channel or channels near the top of the terrace. The mineralogical features of the basin deposits suggest that the channel sediment was derived largely from soils formed probably on the Chalky Boulder Clay or Gault Clay during a long warm period, such as the preceding (Ipswichian) interglacial. The deposits of such channels have only been preserved, after reworking associated with ice mound formation and melting, where they have been let down into enclosed hollows such as WJ and WG.

Mackay (1963) observed the formation of closed-system pingos in alluvial channels of the Mackenzie delta in Arctic Canada, and the ice mounds at Wretton possibly formed in an analogous situation. If so, the sequence of events at Wretton was as follows. Seasonal down-freezing or permafrost first penetrated rapidly and fairly evenly through the coarser sediments at the terrace surface, but later penetrated more slowly through the clayey channel sediment. The different rates of down-freezing in the channel and the adjacent deposits would then produce a closed system, with hydrostatic pressures developing in and beneath the channel fill. In these conditions ground ice would form and raise an ice mound. However, this is not the only way in which ice mounds could have formed at Wretton. Segregation ice in the buried clayey sediments might have acted as a nucleus for the growth of ground ice, and the hydrostatic pressures might have been supplemented by a supply of water under open system conditions. Even in the present permafrost areas of Siberia it is not always clear if seasonal or other short-lived ice mounds are produced in open systems, closed systems, or partly in both (Shumskii 1964).

The position of the basin in the WJ section indicates that the lens of ground ice started to form at approximately 2.5 m below the present terrace surface, and reached a thickness of at least 2 m. The down-warping of the sands and gravel strings under the centre of the basin was probably caused by ice pressure and compaction as the lens increased in size, but may also have resulted partly from loss of sediment by upward injection. During the growth or decay of the ice lens, disturbance by freeze-thaw action seems to have occurred on either side of the lens. The sands forming the walls on either side were indistinctly layered, with alternate less silty and more silty layers dipping outwards to east and west, which suggests that as the ice mound rose the heaved sediments slid down the slopes of the mound. The seasonal down-freezing or short period of permafrost that resulted in formation of the ice mound was thus associated with a time of low water level. The subsequent melting of the ice lens might have been caused by its exposure to the atmosphere after displacement of the overlying sand, or might simply have resulted from a climatic amelioration.

If the ice mound formed mainly from segregation ice, the basin deposits might be merely the original channel filling reorganized first by the frost heaving, and later by the lowering on subsequent melting. However, the arrangement of sediment units in the basin and the unsorted nature of the deposits (see figure 8) indicate slow melting of the ice core. The basin of sedimentation was evidently slowly enlarged, presumably as melting proceeded, and any original sorting or organization of the channel deposits was lost by reworking and mixing with material eroded from the walls of the basin. This suggests that the ice was mainly clear injection ice. Figure 11 outlines the mode of formation suggested for the basin in section WJ.

There are three organic horizons in the basin (figures 22, 23, plate 20); the uppermost contains no fossils, but the lower two contain pollen and macroscopic plant remains (see page 375). The absence of fossils in the uppermost organic horizon possibly results from a short period of weathering after the pond had been filled with sediment; the arrangement of these upper deposits suggests at least a period of freeze–thaw at this stage. This was followed by erosion of the basin deposits, presumably by the stream that deposited the overlying fluviatile sands and gravels.

The structures and sequences of deposits on either side of the basin are entirely different. To the east, the slope deposits of the ice mound wall run off into unstratified sand, which lies immediately above the stratified sands with strings of gravel (e.g. at easting 25 m). The unstratified sand is divided by a slightly humic, clayey layer into an upper dirtier sand and a lower bleached sand (figure 24, plate 20). The lower sand (WJ 8) is a well-sorted coversand; the upper (WJ 6) is probably also largely coversand, because it contains much well-sorted coarse sand (figure 8), though the standard deviation of its particle size curve is enlarged by the presence of some finer sand. Before and perhaps during the growth of the ice mound, coversand was therefore deposited to the east and terrace aggradation had ceased there.

To the west of the basin the wall is similar to, but steeper than, the eastern wall. However, beyond this there is no evidence of a clear coversand horizon; instead, a series of fluviatile sands with strings of gravel and an overlying contorted mud are present. The silts at the outer base of the west wall of the ice mound run into the fluviatile sands, unlike the relation between the east wall and the coversands. The angle of the west wall seems to have been made steeper by water lapping the west side of the mound.

Within the fluviatile sands and gravels there is an unconformity with truncated ice-wedge casts between a lower group of sands with ripple lamination and an upper series of gravels, sands and silts. This unconformity is probably related to the period in which the basin filled with sediment, and the time of ice-wedge formation was perhaps the same as the period of freeze-thaw of the upper sediments in the basin. The upper series of fluviatile sediments is similar to the deposits resting on the eroded surface of the basin filling, and as both overlie eroded surfaces they are probably contemporaneous. After the period of ice-wedge formation, fluviatile conditions were therefore renewed over and to the west of the infilled basin; the pond sediments were then eroded, the ice-wedges were truncated and filled with gravel, and the

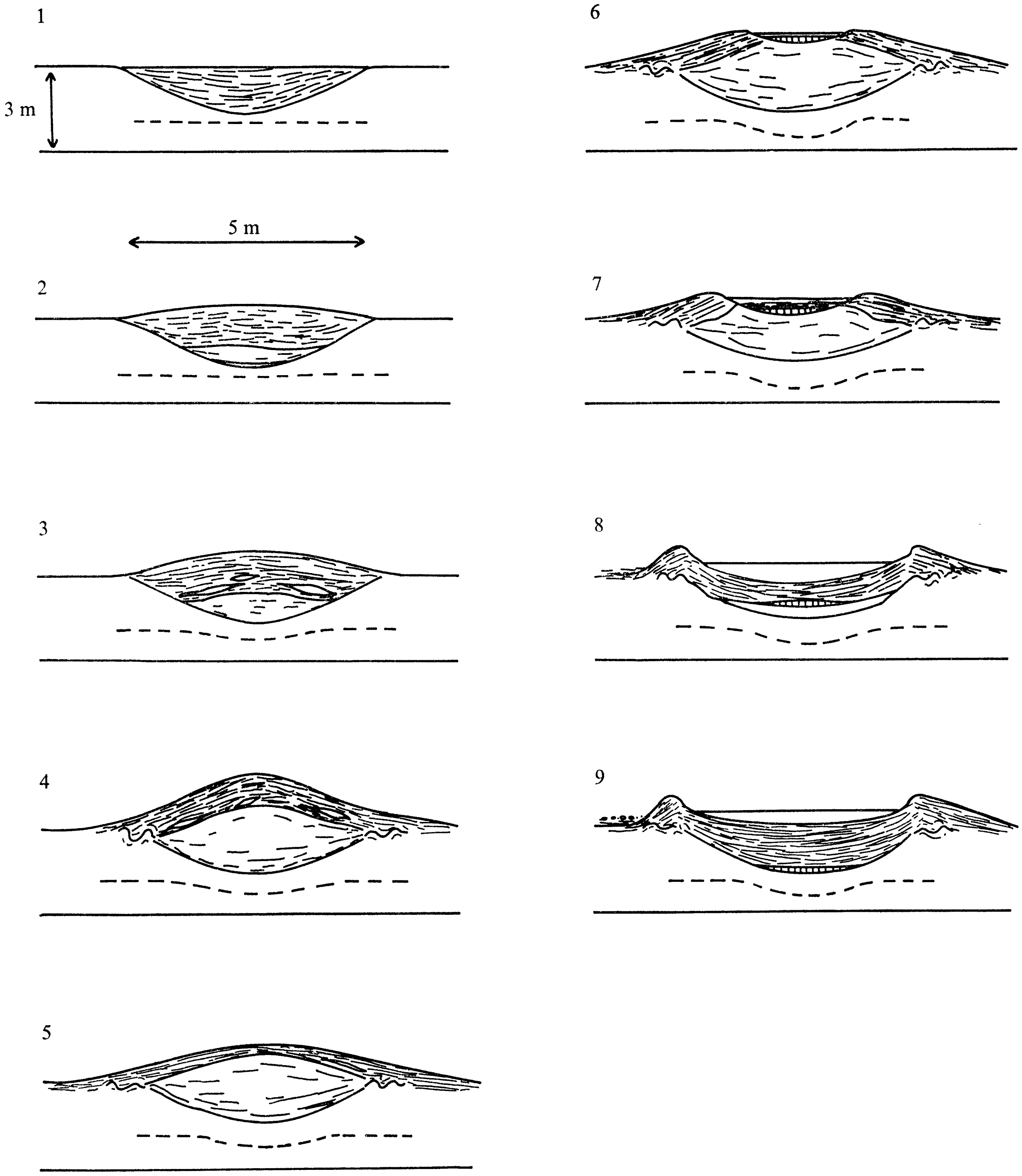


Figure 11. Formation of the WJ basin. 1, channel at terrace surface, filled with fine-grained sediment; 2–5, growth of ground ice and resulting mound; 3, sag of subjacent sediments beneath ice core; 5, movement of overburden down slopes; 6, beginning of thaw; 6–9, melting of ground ice and formation of pond.

upper series of sands and gravels deposited. Eventually a shallow widespread pond formed, in which the overlying mud (of group 4) was deposited.

To the east of the ice mound the coversand is overlain by sandy gravel, which could be traced westwards above the gravels and sands overlying the basin; it then seemed to pass into the upper series of gravels and sands, below the involuted mud, west of the basin. This suggests that the ice-wedge casts east of the basin (figure 5, figure 24, plate 20) are contemporaneous with the casts to the west; the gravels overlap eastwards and fill all the ice-wedge casts.

After deposition of the upper mud a further bed of unstratified sand was deposited, and both this and the upper mud were then strongly affected by freeze–thaw, forming the involutions so well developed in the upper mud. Ferruginous sandy gravel and more sand were then deposited, and the present soil is developed in these. The origin of these youngest sands and gravels is not clear; any stratification they had was lost during the freeze–thaw movements that formed involutions in them. Towards the top the sands are moderately well-sorted (WJ 3, figure 8) and are probably fluviatile, but in their lower parts they are better sorted (e.g. WJ 2, figure 8) and resemble some of the coversands from the Netherlands analysed by Maarleveld (1960). A renewal of fluviatile and aeolian activity thus probably occurred in the final stages of the terrace formation, but any original structure was later lost by frost-working.

Table 3 summarizes the sequence of environmental changes indicated by the stratigraphy of section WJ.

Table 3. Sequence of Devensian events interpreted from sections WJ, WX, WY and WZ†

WX		WZ		WY	WJ	
centre	east					
gravel and sand		gravel and sand		gravel and sand	gravel and sand	
involutions		involutions		involutions and ice-wedges	involutions	
Upper mud		Upper mud		Upper mud	Upper mud	
				coversand		
				fluviatile gravel and sand		
				(WG, WM≡) Filling of basin		
				melts		
				ice lens forms		
	filling of basin					
	melts	fluviatile gravel and sand		fluviatile gravel and sand	fluviatile gravel and sand	
	ice lens forms					
				silt	silt	
		Upper filling of basin			erosion	ice-wedges
		injection			ice-wedges weathering	coversand
Filling of basin		Lower filling of basin	'soil'		Filling of basin	'soil'
				fluviatile gravel		
ice melts		ice melts			ice melts	
ice lens forms		*ice lens forms*	coversand		*ice lens forms*	coversand
					fluviatile gravel and sand	
		terrace aggradation		terrace aggradation		
			Gault Clay			

† Fossiliferous deposits are capitalized.

(ii) *The structure and depositional history of sections WX, WY and WZ*

The long section (figure 6), drawn to a scale of 4 cm to 1 m, represents part of the slightly sloping north face of the cut-off channel. The eastern end of the section is approximately 20 m north of section WJ. Five basins filled with silts and muds occur in this section; the most complete of these (WZ) occurs near the centre of the section.

WZ. This enclosed basin is shown in section in figure 6, and, during its subsequent excavation northwards, in section and plan in figure 7. Its origin is probably similar to the basin in section WJ: an ice mound formed, and the subsequent melting of ice left a pond, in which sands, silts and two fossiliferous organic horizons were deposited. The petrographic distinction between deposits filling the basin and those surrounding it is not as clear in the WZ section as in WJ. The WZ basin deposits contain a little more clay and silt than in the surrounding WZ sediments (table 1), but not as much as the WJ basin deposits. Also, the clay and fine sand fractions of the WZ basin deposits are only just distinguishable mineralogically from those of the surrounding WZ sediments. This suggests that some of the sediment filling the WZ basin was derived from the surrounding deposits, possibly by erosion of the inner walls of the ice mound.

The position of the two horizons in the WZ basin (WZ 1 and 2 at easting 25 m) shows that the shape of the pond changed during the course of its filling. The unconformity below the upper organic horizon (figure 7, horizon 6) suggests that the pond spread laterally at that stage; this probably resulted from the collapse of the eastern wall, which is indicated by the sandy gravel wedge in the east side of the filling (figure 6, easting 26 m). The sides of the basin are much steeper than those of WJ. This steepening occurred partly or even completely after the deposition of beds below the unconformity, and was probably the cause of the collapse of the gravel. It possibly resulted from the injection of sand during a seasonal or perhaps longer period of down-freezing, when strong hydrostatic pressures would develop between the quickly frozen saturated sand and the as yet unfrozen but impermeable muds in the partly filled pond. The main lines of weakness would then occur around the margins of the filling, and upward injection of sand through these would deform the basin.

The structures associated with the walls of the WZ ice mound do not show as much detail as those of the WJ mound. The string of sandy gravel beneath the basin is presumably part of the terrace aggradation, and the ice lens formed above it. The steeply inclined gravel strings immediately to the east might have been injected or deformed by injection, but the sand sequence (at easting 29 m) of WZ 1 (brown humic sand, WZ 2 (reddish sand) and WZ 3 (pale sand) and the associated gravel strings are not steepened so much. These three sands are all very well sorted (figure 9) and are probably wind-blown coversands; the associated gravel strings may be deflation horizons. This aeolian phase was possibly the same as that indicated by the lower coversand to the east of WJ. The brown humic sand and reddish sand indicate a period of soil development after this aeolian phase; over the soil are partly stratified sands with a further gravel string, resulting from the renewal of fluviatile conditions. Yet another bed of gravel overlies these sands, and dips eastwards towards WY; this is covered by a further series of well-sorted coversands (figure 9; WY 2), which are in turn overlain by the upper contorted mud.

The age of the WZ ice mound deposits in relation to the surrounding sediments may be argued as follows. Some of the basin deposits (figure 9; WZ 6 and WZ 8) have very poorly sorted sand fractions, similar to those of the WJ basin sediments, but the stratified sand (WZ 7) overlying the upper organic horizon is moderately well sorted and similar to the terrace sand (T 1, figure 9). This suggests that rising water in the river flooded the pond at this stage, and partly filled it with river sand. This must correspond to a period of fluviatile deposition outside the pond later than the injections of sand that deformed the basin; the most likely period is the one that followed the soil formation indicated by WZ 1 and WZ 2 Table 3 gives the sequence of events inferred from section WZ.

WY. In this part of the section the basal terrace sands are overlain by contorted silt, and then by gravels which extend eastwards to the end of the section. The same gravel overlying contorted silt was also seen at easting 37 m. A basin containing grey clayey sand (WY 1) and brown sandy mud rests on the gravel, and is overlain by sandy gravels which could be traced along the section to WZ. The upper eastern part of the basin filling was contorted before the basin and its surrounding sediments were eroded by the stream that deposited the overlying gravel. This is covered by partly stratified sands, which at WY 2 have the well-sorted nature of coversands. The overlying upper mud is contorted in places, as elsewhere, and is penetrated by two ice-wedge casts at eastings 36 and 45 m.

The gravels overlying the basin truncate the deposits beneath, and thus obliterate any evidence that the basin originated as an ice mound. The basin may be the remnant of a channel cut in the terrace deposits, but this is unlikely because its filling soon thinned out and disappeared as the section was cut back, and because WY 1 is petrographically similar to most of the WJ and WZ basin sediments. An ice mound is therefore the most likely origin of the basin. However, the sand fraction of WY 1 (figure 9) is slightly better sorted than sands from some of the WZ basin sediments (WZ 6 and WZ 8), and may therefore contain some fluviatile sand. Thus fluviatile action may have degraded the walls of the mound and modified the basin fill.

WX. To the west of basin WZ a mass of disturbed and probably injected silt rises vertically. Beyond this are two westward dipping gravel strings, separated by sands containing a humic layer; the upper gravel string is overlain by the upper mud. This sequence is similar to that on the eastern side of basin WZ. The lower gravel string eventually rises sharply at the eastern side of a triple basin structure, which occurs where the Gault Clay comes much nearer to the surface than elsewhere in this part of the cut-off channel. The clear injection features and distortion of the Gault surface probably resulted from the hydrostatic pressures developed by down-freezing of the shallow terrace deposits towards the impermeable Gault.

The central basin is clearly older than the other two, and all three probably originated as ice mounds. A fossiliferous sandy mud at the base of the central hollow is overlain unconformably by sandy gravel containing lumps of clay resembling Gault, which seem to have sludged down from the margins of the basin. The structure to the east has associated masses of similar clay which are inclined towards the basin. These must have been injected during a period of down-freezing after formation of an ice lens. The steeply inclined string of the lower sandy gravel (at easting 14 m) may be the sludged material of the eastern frost mound, probably later steepened by injection between it and the basin. The western basin of the WX section contains a brown muddy sand, the upper parts of which have been disturbed by involution. Inclusions of the upper mud within these involutions shows that this was the same period of involution formation as that which contorted the upper mud elsewhere.

(iii) *The structure and depositional history of section WG*

No detailed description of the WG section (figure 2) was made, because the deposits were entirely and rapidly removed early in the excavation of the cut-off channel. The basin exposed here was totally enclosed (see page 344), and an ice mound is therefore the most likely origin. The deposits of the basin are petrographically similar to those of the WJ basin; the sand fractions are very poorly sorted (figure 10) and contain 10–14 % alkali felspar and little or no pyroxene, and the clays contain only small amounts of mica. The amount of sediment derived from deposits adjacent to the basin is therefore smaller than in the WZ basin. The basin deposits are much more regular than those of WJ or WZ, and their pollen flora indicates the presence of coniferous forest. This suggests that there was a long period of stable sedimentation in the basin after the establishment of more temperate climatic conditions and rapid melting of the mound ice. The less regular filling of basin WZ, and the more rigorous climatic conditions indicated by the pollen sequence of its deposits, points to the slower melting of that ice mound.

The sketch sections and photographs taken before the basin was removed show that the grey silty clays forming the lowest layer in the basin margins were incorporated in the involution affecting the upper mud. This mud was overlain by reddish gravel, which extended over the whole basin.

(iv) *The age relations of the ice mounds and the sequence of terrace aggradation*

Evidence of the relative age of the ice mounds comes from the stratigraphy and pollen analysis of the organic horizons within the basins. The pollen spectra indicate that the WG filling is the same age as the WY filling, and that the WX central basin filling (40–45 cm) is the same age as the 60–75 cm filling of the WJ ice mound. We have to rely on stratigraphical evidence to show more precise age relations, in particular the relation of WX and WZ to WY (and therefore WG) and WJ. The critical relation is that between section WJ and WY. Although the lateral variation of the terrace sediments is considerable, we are here dealing with a small area in which the ice mounds are concentrated (figure 1).

In the west part of WJ, which is immediately south of WY, a silt overlain by gravel occurs at 2.5 m depth. If this is the same silt and overlying gravel that is seen under the basin filling of WY at a depth of 3 m, then the WY ice mound was later than the WJ ice mound. The stratigraphical relation of the WY filling to that of WZ indicates that the latter is the older, for the WZ ice mound heaved at a time of coversand formation older than the gravel strings which traverse the terrace here. The WX east mound is younger than WZ, as shown above, and it is also younger than the central WX mound. The pollen evidence suggests that the filling of the central WX basin is of the same age as the WJ filling. The WZ filling is probably slightly younger than that of WJ and WX centre. The basal pollen spectrum of WZ resembles those of WJ and WX centre, but the upper spectrum is distinctly different. Both WZ and WJ are covered by fluviatile sand and gravel, WZ conformably, WJ unconformably, again indicating a slightly younger age for the melting of WZ. Thus we have a sequence of mound formation, from the oldest to the youngest, as follows: WJ and central WX, WZ, east WX, WG and WY.

Tables 3 and 9 summarize the conclusions drawn about the relative age of the ice mound formation and fillings. Although these conclusions may be considered tentative, it should be remembered that there is no doubt at all that all the ice mound fillings are later than the main terrace aggradation and earlier than the deposition of the upper muds.

3. PALAEOBOTANY: VEGETATIONAL HISTORY

Pollen samples from 19 sites and macrosamples from 12 sites were analysed. Pollen analytical results are presented in the pollen diagrams, figures 12 and 13, in the form of a series of short diagrams, each from one site. The results of analyses of macroscopic plant remains are given in table 5 (numerical analysis of taxa) and figure 14 (analysis of ecological groupings). The nomenclature is that of Dandy (1958), unless other authorities are quoted.

(*a*) *Pollen diagrams and zonation*

The pollen diagrams in figure 12 are from below and in the terrace aggradation (groups 1 and 2 of the sites), except that WP and parts of WN and WQ may belong to group 4. Those in figure 13 are from the basin fillings and the uppermost organic horizons (groups 3 and 4 of the sites). The diagrams have been placed in figure 12 in order of age, the youngest at the top, and similarly, at least as well as can be determined, in figure 13. In table 5, a similar order is maintained, with the youngest sample on the right of the table.

Taking all the Devensian pollen diagrams from Wretton, and assuming their sequence in age as discussed previously to be correct, it is possible to designate a number of pollen assemblage biozones (p.a.b.).† These biozones are shown in table 4; they should be considered as site pollen assemblage biozones. When more is known of Devensian vegetational history, in terms of the spatial distribution or sequence of such biozones in the Early and Middle Devensian, it may emerge that these site biozones have a regional significance. For convenience each pollen assemblage biozone is given a reference letter, shown in table 4. It will be seen from the table that the designation of pollen biozone B is the same as that for pollen biozone H. The stratigraphical evidence for the separation of these two in time is quite clear; this pollen biozone is of a recurrent type.

TABLE 4. POLLEN ASSEMBLAGE BIOZONES OF THE DEVENSIAN AT WRETTON

sites, depths	designation of pollen assemblage biozone	reference letter
WU, WUB WX 1	Gramineae – Cyperaceae – Compositae p.a.b.	H
WG 10–25 cm	*Pinus* – *Betula* – *Picea* – *Calluna* – *Sphagnum* p.a.b.	G
WG 25–55 cm WM, WY	*Pinus* – *Betula* – *Picea* p.a.b.	F
WZ	Gramineae – Compositae p.a.b.	E
WJ 60–75 cm WX 40–50 cm	*Betula* – *Pinus* – *Alnus* – Gramineae – *Calluna* p.a.b.	D
WJ 100 cm	*Betula* – *Pinus* p.a.b.	C
WP, WQ, WN, WAB, WAG, WAL, WAH, WAD, WAE, WO	Gramineae – Cyperaceae – Compositae p.a.b.	B
WH	Gramineae – Cyperaceae – *Artemisia* – *Selaginella* p.a.b.	A

(*b*) *Analysis of macroscopic plant remains*

Figure 14 summarizes certain aspects of the macro analyses given in table 5. Ecological groupings shown in that table are totalled for each level analysed, together with the number of taxa in each group at each level. Remains from WJ and WG are not included in the figure. The sediment content for each level is shown on the left of the figure. On the right of the figure the pollen percentages of Cyperaceae and Gramineae, at or near levels analysed for macro remains, are given in order to show the relation between macro analyses and the greatly changing proportions of these two pollen taxa.

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† The more precise term biozone is used in preference to zone, following the recommendation of Harland *et al.* (1972).

TABLE 5. ANALYSIS OF PLANT MACR

biozone		A												
		WH							WAD				WAF	WA
	type of remains	50–60	40–50	30–40	10–30	5–10	0–5	bulk	40–50	25–40	15–25	0–5		40–70
(1) trees														
Alnus glutinosa (L.) Gaertn.	f	.	.	1	4	.	.	.	.	.	.	.	.	.
c. *Alnus* Mill. sp.	w(+)	.	.	.	.	.	.	.	.	.	.	.	.	.
Coniferae	ch(*), w(+)	.	.	.	.	.	.	.	.	.	.	.	.	.
cf. *Picea* A. Dietr. sp.	ch(*)	.	.	.	.	.	.	.	.	.	.	.	.	.
(2) shrubs														
Betula nana L.	f	.	.	.	1	.	.	.	.	.	.	.	.	.
Salix L. sp.	b	.	.	5	20	8	.	1	.	.	.	.	.	.
Sambucus cf. *racemosa* L.	s	.	.	.	.	.	.	1	.	.	.	.	.	.
(3) open ground														
Cochlearia L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus bufonius L.	s	.	.	.	.	.	.	.	.	.	.	.	1	.
Potentilla anserina L.	a	16	11	41	83	2	.	41	2	2	.	2	.	10
Potentilla L. sp.	a	.	.	.	.	.	.	2	.	.	.	.	.	.
Potentilla L. spp.	a	.	.	.	9	.	.	.	.	.	.	.	.	.
Ranunculus acris L.	a	.	.	.	.	.	.	.	2	.	.	.	.	.
Ranunculus L. subgenus *Ranunculus* section *Ranunculus*	a	.	.	.	2	.	.	.	.	.	.	1	.	.
R. repens L.	a	.	.	.	.	.	.	2	.	.	.	.	1	11
(4) open ground dry and mountain ledges														
Alchemilla L. sp.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
Armeria maritima (Mill.) Willd.	cal	.	.	.	2	.	.	.	1	1	1	7	.	.
Atriplex hastata L. or *patula* L.	s	.	.	.	.	.	.	.	.	.	.	.	.	1
Campanula rotundifolia L.	s	.	.	.	.	.	.	.	.	.	.	.	2	.
Capsella bursa-pastoris (L.) Medic.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Carduus L. sp.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium arvense L.	s	.	.	.	2	1	.	.	.	.	.	.	.	.
C. holosteoides Fr.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Corispermum sp.	a	.	.	.	.	1	.	.	.	.	.	.	.	.
Diplotaxis tenuifolia (L.) D.C.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba L. sp.	cap	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba L. sp.	s	.	.	.	.	.	.	2	.	.	1	.	1	.
Euphorbia cf. *cyparissias* L.	s	.	.	.	.	2	.	.	.	.	.	.	.	.
Herniaria L. sp.	s	.	.	.	1	.	.	.	.	.	.	.	.	.
Leontodon autumnalis L.	a	.	.	.	.	.	.	.	.	.	.	.	.	6
Linum perenne agg.	s	1	2	3	31	.	1	11	.	.	.	.	.	.
Lychnis alpina L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago maritima L.	cap	.	.	.	.	.	.	.	.	.	.	.	.	1
Polygonum aviculare L. s.l.	a	.	.	.	.	.	.	.	.	.	.	1	.	.
Potentilla cf. *argentea* L.	a	.	.	.	2	.	.	.	.	.	.	.	.	.
P. cf. *crantzii* (Crantz) G. Beck	a	10	8	29	24	3	.	13	.	.	.	.	.	.
Rumex acetosella L. s.l.	f	.	.	.	7	.	.	.	.	.	.	.	1	.
Scleranthus L. sp. or spp.	f	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum cf. *officinale* Weber	a	.	.	.	.	.	.	.	.	.	.	.	.	2
Thalictrum alpinum L.	a	1	.	.	.	1	.	.	.	.	.	.	.	.
T. minus L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola L. subgenus *Melanium*	s	.	.	.	.	.	.	1	.	.	.	.	.	.
(5) open ground wet														
cf. *Cardamine pratensis* L.	s	.	.	.	.	.	.	.	.	.	.	6	.	.
Carex section Acutae Christ.	n	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus cf. *conglomeratus* L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis palustris L.	s	.	.	.	2	.	.	2	.	.	.	1	.	.
Polygonum viviparum L.	bu	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus hyperboreus Rottb.	a	.	.	.	.	.	.	.	.	.	.	5	.	.
Stellaria crassifolia Ehrh.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Thalictrum flavum L.	a	.	2	.	.	.	.	2	.	.	.	.	.	.
Valeriana officinalis L.	f	.	.	.	.	.	.	.	.	.	.	.	.	.
Selaginella selaginoides (L.) Link	m	.	.	.	.	.	.	.	.	.	.	.	.	.
(6) muddy substrata, damp/shallow water														
Alisma plantago-aquatica L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
Alisma L. sp.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
Eleocharis multicaulis (Sm.) Sm.	n	.	.	.	.	.	.	.	.	.	.	.	.	.
E. palustris (L.) Roem. & Schult. s.s.	n	.	.	.	.	.	.	2	.	.	.	.	.	.
E. palustris (L.) Roem. & Schult. s.l.	n	.	1	.	.	.	.	.	.	.	.	.	.	.
Eleocharis R. Br. sp.	n	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus flammula L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
Rorippa islandica (Oeder) Borbás	s	.	.	.	.	.	.	.	.	.	.	.	.	.

T MACROSCOPIC REMAINS

B									D				F			F/G	G	H	
WAG		WAB	WN			WQ	WP		WJ				WG					WUB	WU
40–70	0–35	0–15	320	190–195	155–160		2	6, 7, 8	75–85	65–75	35–50	20–35	50–60	40–50	30–40	20–30	10–20	20	20–30
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E. palustris (L.) Roem. & Schult. s.l.	n	.	1	.	.	.	.	.	.	.	.	.	.	.
Eleocharis R. Br. sp.	n	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus flammula L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
Rorippa islandica (Oeder) Borbás	s	.	.	.	.	.	.	.	.	.	.	.	.	.
(7) maritime														
Glaux maritima L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus cf. *balticus* Willd.	s	.	.	.	.	.	.	.	.	.	.	.	1	.
Polygonum oxyspermum s.l.	n	.	.	.	.	.	.	.	.	.	.	.	.	.
(8) fens and reedswamp helophytes														
Berula erecta (Huds.) Coville	f	.	.	.	.	.	.	.	.	.	.	.	.	.
Caltha palustris L.	s	.	.	5	.	.	.	1	1	.	.	.	.	.
Carex cf. *aquatilis* Wahlenb.	n	.	.	.	.	.	.	.	.	11	6	.	.	.
C. rostrata Stokes	n+u	.	.	.	.	.	.	.	.	.	.	.	.	.
C. cf. *rostrata* Stokes	n+u	.	.	.	.	.	.	.	.	.	.	.	.	.
Cicuta virosa L.	f	.	.	.	.	.	.	.	.	.	.	.	.	.
Cladium mariscus (L.) Pohl	n	.	.	.	.	.	.	.	.	.	.	.	.	.
Glyceria cf. *declinata* Bréb.	c	.	.	.	.	.	.	.	.	.	.	.	.	.
Lycopus europaeus L.	n	.	.	1	.	.	.	.	.	.	.	.	.	.
Menyanthes trifoliata L.	s	.	.	2	3	.	.	2	.	.	.	.	.	.
Ranunculus lingua L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
R. sceleratus L.	a	1	.	3	4	.	.	.	.	.	.	.	.	.
Urtica dioica L.	f	.	.	.	2	.	.	.	.	.	.	.	.	.
(9) aquatics														
Callitriche L. sp.	s	.	.	.	.	.	.	.	.	1	.	.	.	.
Ceratophyllum cf. *submersum* L.	f	.	.	.	.	.	.	.	.	.	.	.	.	.
Damasonium alisma Mill.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Groenlandia densa (L.) Fourr.	fst	.	.	1	1	.	.	2	2	2	2	.	.	.
Hippuris vulgaris L.	fst	2	.	5	6	.	.	4	.	1	1	.	3	.
Hydrocharis morsus-ranae L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Myriophyllum spicatum L. or *verticillatum* L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.
Nuphar lutea (L.) Sm.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Oenanthe aquatica (L.) Poir	f	.	.	.	5	1	.	1	.	.	.	.	.	.
Potamogeton alpinus Balb.	fst	1	.	.	1	.	.	2	.	.	.	1	.	.
P. cf. *berchtoldii* Fieb.	fst	.	.	.	.	.	.	.	.	.	.	.	.	.
P. crispus L.	fst	.	.	.	.	.	.	2	.	.	.	.	.	.
P. filiformis Pers.	fst	.	.	1	2	.	.	3	.	.	.	.	.	.
P. natans L.	fst	.	.	.	.	.	.	.	.	.	.	.	.	.
P. obtusifolius Mert. & Koch	fst	.	.	.	.	.	.	1	.	.	.	.	.	.
P. pectinatus L.	fst	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton L. sp.	fst	.	.	1	.	.	.	2	.	.	.	.	.	.
Potamogeton L. sp.	fst	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus subgenus *Batrachium* DC	a	.	.	1	4	.	.	1	2	6	3	5	2	.
Scirpus lacustris L.	n	.	.	5	7	.	.	.	.	.	.	.	.	.
S. cf. *tabernaemontani* (c.c. Gmel.) Palla	n	.	.	.	.	.	.	.	.	.	.	.	.	.
Scirpus L. sp.	n	1	.	1	3	.	.	.	.	.	.	.	.	.
Sparganium erectum L.	fst	.	.	.	.	.	.	3	.	.	.	.	3	.
S. erectum subsp. *neglectum* (Beeby) Schinz & Thell.	fst	.	.	.	1	.	.	.	.	.	.	.	.	.
Sparganium L. sp.	fst	.	.	.	1	.	.	.	.	.	.	.	.	.
Typha L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Zannichellia palustris L.	a	.	.	.	.	.	.	.	.	.	.	1	1	.
Characeae	o	.	.	.	.	1	.	.	.	.	.	.	.	.
Salvinia natans L.	m	.	.	.	.	.	.	.	.	.	.	.	.	.
(10) unclassified														
Cardamine L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	1	.
Carex L. sp.	n	.	.	.	1	.	.	.	3	.	.	5	14	.
Carex L. spp.	n	35	11	160	300	34	1	.	.	.	.	.	.	12
Cruciferae	s	.	.	.	.	.	.	.	.	.	.	3	.	.
Cyperaceae	n	.	.	.	.	.	.	2	.	.	.	.	.	.
Euphorbia L. sp.	s	.	.	2	.	.	.	1	.	.	.	.	.	.
Gramineae	c	.	.	.	.	.	.	.	.	.	.	12	8	.
Juncus L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula DC sp.	s	.	.	.	.	.	.	.	.	.	1	.	.	.
Ranunculus subgenus *Ranunculus* section *Auricomus*	a	.	.	.	1	.	.	2	.	.	.	.	.	.
Stachys L. sp.	n	.	.	.	1	.	.	.	.	.	.	.	.	.
Umbelliferae	f	.	.	2	.	.	.	1	.	.	.	.	.	.
Viola L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	2	.

Key. a, achene; b, bud-scale; bu, bulbil; c, caryopsis; cal, calyx; cap, capsule; ch, charcoal; f, fruit; fst,

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fruit; fst, fruitstone; m, megaspore; n, nut; n+u, nut with utricle; o, oospore; w, wood.

The uppermost level in figure 14 shows ecological grouping of the total macroscopic taxa found. The near absence of remains of trees is expected, but the paucity of remains of shrubs is remarkable. Remains of herbaceous plants are dominant and their variety follows from a wide range of habitats evidently available on or near the terrace surface. The relative frequencies of the ecological groups show considerable changes from level to level. The significance of these changes in relation to sedimentation and vegetational history will be discussed in the site descriptions to follow.

(*c*) *Notes on the identification of plant remains*

Campanula rotundifolia L.

Four fairly well preserved light-brown, compressed oval seeds, 1.0 × 0.6 mm were recovered from WAF, WN 155 to 160 and WUB 20. The surface is smooth and the cells in the middle of the seed, with rounded or pointed ends, are size 55–80 × 15 μm; the cells at the base and apex are broader, shorter and more angular. The thick cell walls, *ca.* 5 μm, are densely but finely pitted. The cell lumina are narrow but distinct. These characters are exactly those of *C. rotundifolia*. The only previous certain identification is made by Bell (1970) from a Middle Devensian site. Bell distinguished the seeds of *C. rotundifolia* from those of similar species on cell size; *C. patula* L. has smaller cells and the non-British species *C. uniflora* larger ones.

Cardamine pratensis L.

In addition to seeds of cf. *C. pratensis*, a number of Cruciferae pollen grains were tentatively referred to this species. They were *ca.* 28 μm diameter, per-reticulate tricolpate grains. In the pollen reference collection the following species showed a similar sized pollen grain of this type: *Biscutella laevigata*, *Cakile maritima*, *Cardamine flexuosa*, *C. pratensis*, *Diplotaxis muralis*, *Sinapis alba* and *S. arvensis*. The fossil grains were most like *C. pratensis* in their reticulum (7 to 9 elements to a mesh), the length of the granules, the thickness of the exine and the sharpness of the furrow boundary. They were therefore referred to cf. *C. pratensis*.

Carex sect. *Acutae* Christ.

Eighteen light-brown biconvex nutlets, without utricles, were recovered; 13 from WH 40 to 50 and 5 from WUB 20. They are 1.1–1.5 × 1.0–1.25 mm, shortly obovate or orbicular with a broad base and short beak. The surface cells are polygonal with raised margins. Particularly well-preserved cells have raised papillae in their centres. Apart from *C. aquatilis*, British species of the section *Acutae* have nutlets broadly similar to these fossils (Nilsson & Hjelmqvist 1967). Since the hybrids within this section are at least partly fertile and have similar faintly nerved utricles (Jermy 1967) it seems unwise to attempt further identification at present.

Carex cf. *aquatilis* Wahlenb.

Twenty-three chestnut-brown biconvex nutlets were found, 17 from WAD and 5 from WUB 20. They are 1.5–1.7 × 1.0–1.1 mm. The surface cells are oblong with raised walls which are sometimes obliquely transverse; they lack papillae and are in longitudinal rows. The nutlets match reference nutlets of *C. aquatilis* but the characteristic lustrous surface is somewhat modified. On account of the similar utricles with ill-defined nerves fossil nutlets with utricles have been confused with those of *C. bigelowii* Torr. However, mature and well-preserved nutlets of *C. aquatilis* are distinguishable from those of other members of the section *Acutae*. The distinction is chiefly on the smooth surface and shape of the cells and lack of papillae. Tentative identification of the nutlets has also been made from the Chelford pollen-interstadial (Simpson & West 1958).

Corispermum sp.

One achene was identified from WH 5 to 10; it is 3.2 × 2.3 mm, strongly compressed, with a narrow marginal wing which is thin and translucent. It exactly matches achenes from Earith, Hunts, identified by Bell (1970) as *Corispermum* sp. Bell considers that the achenes most resemble *C. hyssopifolium* L., *C. intermedium* Schweigger and *C. marshallii* Steven on the basis of the descriptions in Tutin *et al.* (1964), but in the absence of certainly identified reference material the identification remains at the generic level.

Damasonium alisma Mill.

Three black oval seeds were found in WUB 20. One is well preserved, 2.5 × 1.3 mm, and shows the clear U-shape of the embryo with a protruberant rounded black boss on the radicle. The surface pattern is of distinctive irregular transverse ridges, formed by the swollen ends of the longitudinally elongated cells. *Damasonium alisma* has previously been recorded from the Lea Valley (Reid 1949) and recently from a Middle Devensian deposit (Bell 1970).

Euphorbia cf. *cyparissias* L.

Two black seeds were recovered from bulk sample WH, 1 intact, 2.2 × 1.5 mm and half a seed split lengthwise, 2.1 × 1.2 mm. The seeds are oval with rounded bases and sub-obtuse apices and a shallow longitudinal groove; the top is concave on one face and bears the blunt attachment point of the elaiosome. The punctate isodiametric polygonal cells are about 0.02 mm in diameter. Reference seeds of *Euphorbia* spp. of a similar size were heated in dilute NaOH until they became black and the cell patterns were clarified. Seeds of *E. esula* agg. have slightly larger cells up to 0.04 mm diameter; seeds of *E. amygdaloides* L. are usually broader with a more obtuse apex and the base is flattened; the cell pattern, however, is similar. Twelve reference seeds of *E. cyparissias* measured 2.05–2.5 × 1.3–1.65 mm and exactly matched the fossils. *E. cyparissias* has been recorded from Ipswichian deposits (Sparks & West 1959) and the Middle Devensian (Bell 1970).

Glyceria cf. *declinata* Bréb.

One dark-brown flattened caryopsis, 2.15 × 1.0 mm, was identified from WUB 20. The grain is oblong-elliptic with a hilum 1.9 mm long and a bifurcate style base; the cells are polygonal, up to 25 μm diameter. Opaque caryopses with polygonal cells are typical of *Glyceria* species. *G. maxima* (Hartm.) Holmberg and *G. plicata* Fr. have obovate caryopses; *G. fluitans* (L.) R. Br. and *G. declinata* both have oblong elliptic caryopses; but those of *G. fluitans* are generally longer, 2.5 to 3.6 mm. The caryopses of *G. declinata*, 1.5 to 2.3 mm (Borrill 1956), are identical in size, shape and cell pattern to the fossils. *G. declinata* has been tentatively identified from the late Flandrian (Sparks & Lambert 1961).

Herniaria sp.

Five black shiny lenticular seeds of a *Herniaria* were found; 1 from WH 10 to 30, 4 from WUB 20. They range from 0.45 to 0.6 mm diameter and are similar to two of Late Wolstonian age described and illustrated in West, Lambert & Sparks (1964). Seeds of the three species in Britain today do not seem morphologically separable.

Linum

Seeds of *Linum perenne* agg. (Bell 1970) were recorded in section WH and pollen of *Linum austriacum*-type in WAD, WAL, WZ and WUB. Both these taxa are in the *L. perenne* group, where a complex taxonomic situation exists (Ockendon 1971). The pollen grains conform to the morphology of *L. austriacum*-type described by Andersen (1961), with homogenous flat-topped verrucae, polygonal in cross-section.

Lychnis alpina L.

Five black reniform seeds, 0.5–0.7 mm in diameter, were found in WUB 20. Rows of small elongated tuberculate cells radiate from the prominent hilum. Similar fossil seeds of *Lychnis alpina* have been described from a Late Devensian site on the Isle of Man (Dickson, Dickson & Mitchell 1970) and a Middle Devensian site at Earith, Hunts (Bell 1970).

Polygonum oxyspermum s.l.

Numerous trigonous fruits of a *Polygonum* were found in WN 190 to 195, 155 to 160 and WUB 20. The size ranges from 1.7–3.2 × 1.15–1.7 mm; the nuts have two convex faces and one concave face which taper to an acute apex. Some fruits are brown with an undifferentiated granular surface and are obviously immature; mature fossil fruits are black with faint granulae which form narrow ridges down the centre of each face. Their faint granular surface easily separates these fruits from the clearly papillate surface of *P. aviculare* s.l.; the ovoid fruits of *P. maritimum* L. have a less clear granular surface. Fruits of *P. oxyspermum* have similar fruits to the fossils. Although the fossils fall into the size range of ssp. *raii* (Bab.) D. A. Webb & Chater, 2.5–5.5 mm, their shape is more akin to those of ssp. *oxyspermum*, 5 to 6.5 mm (Tutin *et al.* 1964), figured by Styles (1962). This is the first fossil record for the British Quaternary.

Ranunculus section *Auricomus* Spach.

Two well-preserved buff-coloured achenes, 1.3 × 1.1 mm and 1.7 × 1.2 mm were found in WH 10 to 30 and 1 in the bulk sample from WH, size 1.5 × 1.25 mm. The achenes are obovoid, only slightly compressed, and strongly keeled with a ventrally placed style base. The irregular polygonal cells are somewhat rounded, with raised margins. There is no doubt that the achenes are referable to section *Auricomus* though they are smaller than reference achenes of British *R. auricomus* L.; however, they are comparable to some European species within the section.

Ranunculus hyperboreus Rottb.

The yellowish-white to light-brown ovoid achenes were found in seven of the samples; the 48 achenes in WUB 20 range from 1–1.2 × 0.8–1.0 mm. The achenes are characterized by thin walled cells similar to those round the margin of *R. sceleratus* achenes. However, in these fossils the cells cover the central area also. Small bare areas in some fossils reveal the elongate sclerenchyma beneath (Dickson 1970, plate 2*a*). The only difference in appearance between these achenes and recent ones of *R. hyperboreus* lies in the cells which are inflated in the fresh achenes. *R. hyperboreus*, no longer present in the British flora, has been recorded from the 'full-glacial'

(Reid 1949), Middle Devensian (Bell 1970), Late Devensian (Dickson *et al.* 1970) and tentative identifications have been made from a few other sites (Godwin 1956).

Sambucus cf. *racemosa* L.

One dark brown, flattened, ovate seed, with a well-preserved rugose surface, was found in the bulk sample from WH. It is 2.7 × 1.8 mm; reference seeds measure 2.3–3.7 × 1.6–2.3 mm. The seed is exactly similar to recent seeds, but the identification is tentative because seeds of *S. nigra* L. are distinguished from those of *S. racemosa* only by their larger size (our reference seeds are 3.0–4.2 × 1.4–2.0 mm). Seeds of *S. ebulus* L. are more or less orbicular. The excellent state of preservation of the fossil seed points against it having been derived from an older deposit. *S. racemosa* is regarded as an introduced species and has no previous fossil records in Britain. It is a native of Europe and Western Asia.

Scirpus cf. *tabernaemontani* (C.C. Gmel.) Palla

Fifteen well-preserved black biconvex fruits were found in WUB 20. They are 1.8–2.0 × 1.4–1.8 mm and identified as a *Scirpus* species by their obovate shape with one side slightly convex, the other more so. The beak is short and the base short and broad; the cells are polygonal with raised margins and faint papillae are occasionally preserved in the centre of the cells. Species of *Scirpus* in the British flora having similar fruit are as follows. *S. americanus* Pers. has a broadly obovate fruit, rather flattened at the apex and usually with an asymmetrical 'hump'. *S. triquetrus* L. has a similar-shaped fruit to the fossils but the cells are shown by Katz, Katz & Kipiani (1965, fig. 18) to be oblong. Both *S. lacustris* and *S. tabernaemontani* have fruits with similar cells to the fossils, but the fruits of *S. lacustris* usually have a 'bony hump' on one face though it seems from figure 10 in Katz *et al.* (1965) that a broadly convex fruited form does exist. Therefore although the fossils resemble reference fruits of *S. tabernaemontani* in every respect, the possibility of their being *S. lacustris* cannot be excluded, especially since fruits of *S. lacustris* were found in the same sample. The identification is therefore tentative. *S. tabernaemontani* has been recorded fossil from a number of British sites.

Stellaria crassifolia Ehrh.

Sixteen black seeds of a *Stellaria*, 0.8–1.0 mm, were recovered from WUB 20; the concentric, elongated, tubercles are *ca.* 0.025 mm high. Seeds of the most similar British species, *S. graminea* L. have tubercles *ca.* 0.05 mm high. The seeds match those of *S. crassifolia* exactly. Seeds from a Late Devensian site on the Isle of Man (Dickson *et al.* 1970) are larger than the reference seeds and have thus only tentatively been identified. However, certainly identified fossil seeds have been fully described by Bell (1968).

Filicales

The spores referred to under this taxon are monolete spores without perine, and lacking the faint reticulum of *Thelypteris dryopteris*. The taxon is equivalent to the *Thelypteris palustris*-type of Andersen (1961), who reports that similar spores are found in the genera *Asplenium*, *Athyrium*, *Blechnum*, *Cystopteris*, *Dryopteris*, *Phyllitis*, *Polystichum*, *Thelypteris* and *Woodsia*.

(*d*) *Vegetational history: sites of group* 1

(i) *WH* (*figure* 2)

The organic deposit occupies a depression in the Gault, at its deepest 65 cm, and some 12 m wide. The section described, from the deepest part of the depression, is as follows:†

cm	
0–5	grey clayey sand (yellow stratified sand)
5–10	light red muddy sand with shells (Dg 2, A 1, Ga 1)
10–40	red-brown muddy sand with shells
40–65	grey and brown muddy sand (Dg 1½, A 1, Ga 1, Gs ½)
65–70	grey sand with chalk pebbles
	Gault Clay

The organic filling is a shallow-water deposit, probably formed in slowly moving water in a channel, and is sealed by the fluviatile sands of the terrace. Analyses of molluscs, macroscopic plant remains and pollen were made at the point of the described section. An additional bulk sample from the margin of the channel near the top of the organic filling was analysed for molluscs and macroscopic plant remains.

The pollen diagram from WH (figure 12), the sediments of which are below the terrace aggradation, is the oldest of the diagrams indicating predominance of herbaceous vegetation in the Wretton area. The principal n.a.p. (non-arboreal pollen) taxa are Gramineae and Cyperaceae, but also present are the heliophytes *Armeria*, *Artemisia*, *Helianthemum*, *Plantago maritima*, *P. major/media*, and *Selaginella*, as well as taxa of wider ecological amplitude: Caryophyllaceae, Compositae, Cruciferae, *Filipendula*, *Scabiosa*, *Thalictrum*, and Filicales. The abundance of *Artemisia* pollen and *Selaginella* spores distinguishes the pollen diagram from the younger herb biozone diagrams and characterizes the pollen biozone A of the Devensian sequence. The tree and shrub pollen present is principally *Pinus*. Very little *Betula* pollen is present, and there are low frequencies of *Quercus*, *Alnus*, *Carpinus* and *Corylus* pollen. The frequencies of these, and *Pinus*, increases towards the top of the section, as pollen becomes less frequent, indicated by traverses per 100 pollen grains. Pine pollen persists in similar low percentages through all the herb biozones, but the other genera are there more scarcely represented. Their percentages in WH may relate to very scarce presence in the local vegetation, to long-distance transport (perhaps most likely with *Pinus*), delayed deposition from interglacial time, or by reworking from interglacial deposits under fluviatile conditions. The last perhaps is the most likely explanation for the thermophilous genera, because the frequencies rise towards the top of the section, where fluviatile conditions become more evident.

The rise in a.p. (arboreal pollen) percentages at the top of the section may also be related to lower local pollen production as the terrace aggradation started in the area. The distinctness of the pollen biozone A from the later biozones is possibly a result of deposition contiguous to the Gault surface. Most of the younger pollen diagrams come from sediments

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† The sediment descriptions are field descriptions; given in parenthesis are further descriptions, based on the notation of Troels-Smith (1955), after laboratory examination under low-power microscope. The categories of A (As and Ag) and G (Ga, Gs) have not always been subdivided in the descriptions given. In the Troels-Smith system the letters refer to types of component in the sediment (e.g. D, detritus; L, mud; As, clay; Ag, silt; Ga, fine sand) and the numbers refer to the proportion of the component on a 5 point scale (0–4).

formed on the terrace surface and their flora is rather more restricted. A similar difference is seen in the macroscopic plant remains from WH compared with those from younger sediments.

The macroscopic remains from WH were analysed at six levels and a bulk sample was also taken. The results show a rich and varied flora. The predominant ecological categories (figure 14) are open ground herbs, and *Carex*. There is only a low representation of aquatics and heliophytes and of trees and shrubs. The open ground herbs decrease in frequency towards the top, and *Salix* bud-scales increase in frequency towards the top. The sequence reflects an early fluviatile stage with sedge swamp, but poor in aquatics, with a later sedge swamp stage, with *Salix* carr, when remains of open-ground species were not so readily moved into the area of deposition. It is notable that remains of trees and shrubs were restricted to five fruits of *Alnus glutinosa*, one of *Betula nana* and one of *Sambucus* cf. *racemosa*. Twenty-six taxa of non-aquatic herbs were identified. The most frequent were *Potentilla anserina*, *Armeria maritima*, *Linum perenne* and *Potentilla* cf. *crantzii*. There is a small representation of helophytes towards the top of the section, corresponding with the development of marginal sedge swamp; *Menyanthes* and *Ranunculus sceleratus*, and 15 aquatic taxa are present, *Hippuris* and *Scirpus lacustris* being the most common. The wet-ground species *Pedicularis palustris*, *Polygonum viviparum* and *Thalictrum flavum* are also present.

In terms of both the pollen and macros, we then have evidence for aquatic species within the channel on the Gault, for marginal fen and sedge-swamp conditions and for a herb vegetation on the Gault with a rich heliophyte element, already referred to, comprising plants of northern (e.g. *Potentilla* cf. *crantzii*, *Thalictrum alpinum*) and continental (e.g. *Corispermum*) distribution. A number of species are basiphilous (*Cerastium arvense*, *Linum perenne*, *Potentilla* cf. *crantzii*), as might be expected in a soil developed on the calcareous Gault Clay.

The pollen and macro taxa better represented in WH than in the younger herb biozones are, pollen and spores: *Artemisia*, *Chenopodium*, *Helianthemum*, *Plantago maritima*, *Filipendula*, *Thalictrum*, *Selaginella*; macro taxa: *Alnus*, *Salix*, *Betula nana*, *Corispermum*, *Linum perenne*, *Potentilla* cf. *argentea*, *P.* cf. *crantzii*, *Thalictrum alpinum*, *Thalictrum flavum*, *Lycopus europaeus*, *Oenanthe aquatica* and *Ranunculus* section *Auricomus*. This relative richness in certain taxa could result from (*a*) vegetation on the Gault providing a component of the fossil flora, which it had less opportunity to do later as the terrace aggraded over the area, or (*b*) such an early glacial assemblage containing survivors from the preceding interglacial (e.g. *Alnus*, and southern species, e.g. *Lycopus*), or (*c*) climatic regimes different in WH from the later Devensian. There is no clear evidence for the last. It seems likely that the first is most probable, as soil distribution changes must have accompanied the aggradation of the terrace. There is no clear evidence in favour of (*c*), but as will be later demonstrated, the age of WH is Early Devensian, and even though the vegetation has a herbaceous and therefore possibly cold aspect, there is the possibility of survival from the preceding interglacial.

(ii) *WO* (*figure* 4)

This section, just below water level at the time of sampling was as follows:

	grey stratified sand
cm	
0–7	sandy gravel with chalk pebbles
7–17	brown muddy sand (Dg 1, Ld 1, Ag 1½, Ga ½)
17–24	sandy gravel with chalk pebbles
	Gault Clay

Many bones were found here during the excavations and a single pollen sample was taken from the mud adhering to a bovid bone, found in the brown muddy sand. This horizon is at the base of the terrace deposits, but was probably formed at a later stage of the aggradation than WH, since the Gault surface is 130 cm higher than in WH. The pollen spectrum (figure 12) differs from WH in the low frequency of *Artemisia* and absence of *Selaginella*, and it is placed in the Gramineae–Cyperaceae–Compositae pollen assemblage biozone (biozone B), a zone which includes the organic sediments associated with the terrace aggradation (group 2 of the sites). As with these other sites of the terrace aggradation, the spectrum has a low a.p. frequency (16%) mainly *Pinus*. The n.a.p. is principally Gramineae and Compositae, with a similar distribution of herbaceous taxa as at the other sites, apart from a very high frequency of *Plantago media/major* (15%). This high frequency is likely to be directly related to the influence of the animals represented by the bones, and the species concerned is likely to be mostly *P. major*. A similar combination of high *Plantago media/major* frequency and bones is seen in WAL. A further discussion of biozone B is given in the consideration of the group 2 sites.

(*e*) *Vegetational history: sites of group* 2

The sites in this group, their stratigraphy already briefly described on pages 342–344, record periods of organic sedimentation while the terrace was aggrading. They are all placed in the same pollen assemblage biozone (figure 12); that is, the Gramineae–Cyperaceae–Compositae p.a.b. (biozone B). A further consideration of the flora is given in §4. They fall into groups as follows:

WAD, WAE, WAF. A channel filling at 5.5 m below terrace surface.

WAH, WAL. Quiet-water muddy sands and silts, of approximately the same age as WAD, WAE, WAF.

WAB, WAG. Channel fillings at 4 m depth from terrace surface.

WP. A channel filling and associated sediment at 2 m depth in the terrace.

WN, WQ. Sections through the terrace where it is 4 m thick; organic sediments near the base and at 2 and 3 m depth. These sections and WP may belong in part to group (iv).

The sites will now be considered in these groups.

(i) *WAD*, *WAE*, *WAF* (*figure* 3)

These sections are parts of the same 10 m wide channel filling. WAD is at the deepest part of the channel, with detailed stratigraphy as follows:

	pale stratified sand
cm	
0–3	brown laminated mud with moss fragments (Dg 2, Ag 1, Ga 1)
3–10	yellow sand
10–32	brown muddy sand (Dg 1½, Ld ½, Ag ½, Ga 1½)
32–60	brown sand and muddy sand interbedded, contorted in places (at 43 cm: Dg 1, Ld ½, Ag 1, Ga 2)

WAF is from a marginal equivalent of the main horizon of the muddy sand (Dh ½, Dg 1, Ld ½, Ag 1, Ga 1). WAE is from a lateral equivalent of the lower contorted muddy sand (Dh ½, Dg 1½, Ld ½, Ga 1½), and was the place of a find of wolf bones. At WAF, pollen analyses and macroanalyses were made at four levels. A further pollen sample was analysed from WAE and a macrosample from WAF.

The a.p. frequency from WAF and WAE is very low (3 to 9 %) and is mainly *Pinus*, with 1 to 2 % only of *Betula*. The n.a.p. is mainly Gramineae and Cyperaceae. Pollen of *Armeria* and *Plantago media/major* and spores of *Botrychium* are present throughout, high values of Compositae pollen are seen, and higher *Ranunculus* frequencies are present at the base.

The macroscopic remains in these sections are not very abundant. The basal samples are richer in open-ground species (figure 14), the middle samples in helophytes and the upper sample in wet open-ground species. This reflects the incorporation of remains of the terrace surface at the base of the channel (*Potentilla anserina, Ranunculus acris*), with *Caltha palustris, Groenlandia densa* and *Ranunculus–Batrachium*. The higher frequencies of *Ranunculus* pollen at the base are probably related to the presence of these *Ranunculus* species. In the middle samples *Carex* is increasingly represented by macroscopic remains; *C.* cf. *aquatilis, Groenlandia, Hippuris* and *Ranunculus–Batrachium* are present. These levels show correspondingly high frequencies of Cyperaceae pollen. In the uppermost sample the macroscopic flora is much richer. *Armeria maritima*, represented by single specimens in the lower samples, is more abundant, *Polygonum aviculare*, cf. *Cardamine pratensis, Pedicularis palustris, Ranunculus hyperboreus, Ranunculus–Batrachium, Carex* sp. and Gramineae are all present, and were probably in the flora which spread over the channel as it finally filled in. In the marginal macrosample WAF, of the same age as the middle samples of the basin centre, *Juncus bufonius, Ranunculus repens, Campanula rotundifolia, Draba* sp., *Rumex acetosella*, and the halophyte *Juncus* cf. *balticus* must be species of the terrace surface at the time, with *Hippuris vulgaris, Ranunculus–Batrachium, Sparganium erectum* and *Zannichella* originating from the marsh and aquatic flora. *Carex* sp. and Gramineae are also well represented.

The following correlations between pollen and macros appear in these sections, and throw light on the significance of the pollen spectra:

Armeria. Pollen and calyces of *Armeria maritima* occur throughout WAD. *Armeria* must have been a local plant of the terrace surface.

Campanula. Low frequencies of pollen and seeds of *C. rotundifolia* occur. The species must have been growing on the terrace surface.

CRUCIFERAE. Very low frequencies of Cruciferae pollen are present.

Draba sp. and cf. *Cardamine pratensis* are both present macroscopically and must be local.

CYPERACEAE. Relatively high frequencies of Cyperaceae pollen are present throughout WAD, especially in the middle where *Carex* cf. *aquatilis* remains are abundant. These pollen frequencies are evidently related to local species of Cyperaceae.

GRAMINEAE. The higher frequencies of Gramineae in the upper part of the section are associated with abundant caryopses (figure 14). The species of Gramineae must have been prominent in the local flora at the channel edge and probably widespread over the terrace surface.

Sparganium. Low frequencies of *Sparganium*-type pollen are present, and fruitstones of *S. erectum*, which must have been growing at the channel edge.

Ranunculus. The pollen occurs throughout the section. Its highest abundance is at the base where achenes of *R. acris* and *R.–Batrachium* were found. The pollen frequencies at the top, where *R. hyperboreus* achenes were found, are low.

(ii) *WAH, WAL* (*figure* 3)

These sites, on either side of the cut-off channel, are at a similar level to WAD, and lie at the western edge of a 'plateau' of terrace sands which is about 1 m higher (see p. 342 and figure 1).

WAH

	brown stratified sand
cm	
0–22	brown muddy sand (Dg ½, Ld 1, Ag 1, Ga 1½)
22–42	grey muddy silt with a few flints
	brown-grey sand

WAL

	brown stratified sand, with a basal brown laminated silt
0–30	grey silt with shells (Dg ½, Ld 1, Ag 1½, Ga 1)
30–35	brown silt, contorted
	mottled brown and yellow sand

The grey silt contained bones. Four pollen analyses were made from these sections; at 12 cm in WAH, at 0 and 25 cm in WAL, and from sediment attached to a bone in WAL (WAL 3). The pollen spectra are all typical of the biozone B spectra, but show the following variations. In WAH, *Betula* is more abundant (4 %) than usual and *Pinus* less so (4 %); *Ranunculus* shows very high percentages (23 %). In WAL, *Pinus* is again relatively rare (3 to 6 %), as is *Betula* (2 %). There are relatively high frequencies of *Plantago media/major*, *Ranunculus* and *Sparganium*-type. The high frequencies of *Plantago media/major* correspond with bone finds, as at WO.

In both WAH and WAL Cyperaceae frequencies are low and Gramineae high. The siltier facies of sediment at both sites suggests a more fluviatile environment, with a less local source for Cyperaceae, and a strong source for Gramineae pollen either in the terrace 'plateau' to the east or in the region generally.

(iii) *WAB, WAG*

There is a channel filled with organic sediment at WAG, and a broader, shallower channel with a more sandy filling at WAB. The relation between the two is described on page 344 and is seen in figure 3. The stratigraphy of WAB is as follows:

	brown stratified silty sand
cm	
0–15	brown laminated muddy silty sand, with some shells, contorted at the base (Dg ½, Ld 2, Ag 1, Ga 1)
	grey silty sand (A 3, Ga 1)

Particle-size analysis of the silty layer (figure 10) farther to the east (see figure 3) shows a predominance of fine sand with a peak at 3.0ϕ, which contrasts with the less-well-sorted deposits of the basin fillings.

One pollen and one macro sample from the muddy sand were analysed. The pollen spectrum is characteristic of biozone B, but shows a rather high (13 %) percentage of Caryophyllaceae pollen. As with the spectra from the muddy silts of WAH and WAL, the proportion of Cyperaceae to Gramineae is low. The macro remains shows a high proportion of aquatics with few land species (figure 14). The latter are *Diplotaxis tenuifolia* and *Draba* sp. *Ranunculus* *hyperboreus* is present, and the aquatics include *Potamogeton filiformis* (the most abundant species in the sample), *Ranunculus–Batrachium* and *Sparganium erectum*. A few nuts of *Carex* were found. Evidently at WAB there was a broad shallow channel, with an aquatic flora of *Potamogeton filiformis* and *Ranunculus–Batrachium*, with *Sparganium erectum* and *Ranunculus hyperboreus* at the margins.

The stratigraphy of WAG is as follows:

	brown stratified sand
cm	
0–35	brown muddy sand (Dg $1\frac{1}{2}$, Ld $\frac{1}{2}$, Ag 1, Ga 1)
35–80	light brown muddy sand, contorted in places (Dg $\frac{1}{2}$, Ld $1\frac{1}{2}$, Ag $\frac{1}{2}$, Ga $1\frac{1}{2}$)
	flint gravel

It will be noted that the upper half of the filling has more organic detritus and less sand than the lower half. A pollen diagram and two macroanalyses were made from this section. The pollen diagram from WAG differs from the WAB spectrum in the high frequencies of Cyperaceae pollen, lower frequencies of Caryophyllaceae pollen, very high frequency of Compositae Liguliflorae pollen at the 40 cm and 80 cm levels, and high frequencies of Cruciferae pollen at the top.

The macroanalyses (figure 14) show a higher frequency of dry and open ground herbs at the base than at the top, as in WH and WAD. *Potentilla anserina* and *Ranunculus repens* are abundant in the lower half of the channel (more Ga, more Ld). *Atriplex hastata*, *Leontodon autumnalis* and *Taraxacum* cf. *officinale* (related to high Liguliflorae pollen percentages), and *Plantago maritima* also occur with some *Carex* nuts. In the upper sample (less Ga, more Dg), from the top half of the channel filling, *Potentilla anserina* and *Ranunculus repens* are represented by one achene each, *Cerastium holosteoides* and *Cardamine* sp. (related to Cruciferae pollen?) are present and also *Caltha palustris*; there is an increased number of *Carex* nuts, which tallies with increased Cyperaceae pollen percentages. There is an absence of aquatics in this section (cf. WAB). This section shows the infilling of a channel, with a good basal representation of dry land species, and evidence of *Carex* marsh with *Caltha* and *Cardamine* at the top.

Though the matter will be discussed in further detail later, we can now point out that although WAB and WAG are contiguous sites, 52 m apart, their pollen spectra and macro content are very different. The differences point to the local variation of the terrace surface vegetation. A narrow channel occurs at WAG, with a good dry land flora incorporated, perhaps by collapse and reworking of the channel banks, together with the development of a *Carex* marsh. A shallower and broader channel occurs at WAB, with mainly an aquatic flora, and little evidence of vegetation with *Carex*; Cyperaceae pollen frequencies remain low and there is no evidence from plant remains or lithology of the development of a hydrosere.

(iv) *WP* (*figure* 4)

The section is described on page 344. Three sites are concerned: WP 2, a thin lens of muddy sand level with a horizon of humic silt extending several metres; WP 3, 4, 5, a sequence of sands with muddy intercalations in the main channel filling; and WP 6, 7, 8, a more organic horizon, the same age as WP 3, 4, 5, lying on point-bar sands to the east of the channel. At WP 1, farther to the east, the same organic horizon contained only badly corroded pollen and was not studied further.

WP 2. This was a thin organic layer at the same level as an extensive humic horizon in the sand:

yellow sand
cm
0–2 brown muddy sand (Dg 1½, Ld ½, Ag ½, Ga 1½)
yellow sand

One pollen sample and one macrosample were taken from this shallow and several metres wide thickening of the humic layer. The pollen spectrum is included in biozone B. The Cyperaceae pollen percentage is very low, *Plantago media/major* higher than usual and so is the frequency of Compositae pollen. The macroscopic flora is a large one of 18 taxa; comprising both terrestrial and aquatic species (figure 14). The terrestrial species include *Cochlearia* sp., *Potentilla anserina*, *Ranunculus* subg. *Ranunculus* section *Ranunculus*, Draba (73 seeds), *Polygonum aviculare*; the wet-ground species cf. *Cardamine pratensis* and *Ranunculus hyperboreus*, and *R. sceleratus*; and the aquatics *Groenlandia densa*, *Hippuris vulgaris*, *Myriophyllum spicatum/verticillatum*, *Potamogeton*, *Ranunculus–Batrachium* and *Zannichellia palustris*. Numerous *Carex* nuts and a few Gramineae caryopses occur.

In this section there is no relation between abundant pollen taxa and abundant macro taxa. Cyperaceae pollen is low in frequency and *Carex* nuts are frequent. Compositae pollen is abundant, but there are no macros. Cruciferae macros are abundant, but no Cruciferae pollen is present in the pollen count. As already discussed, the sections with low Cyperaceae pollen are characteristic of wide shallow channels with a silty or sandy infilling, and WP 2 conforms to this pattern, in spite of the abundance of *Carex* nuts. The discrepancies between pollen and macros suggest then a different derivation of pollen and macros. A regional pollen rain is preserved in the wide channel (corresponding to the width, at least 12 m, of the humic horizon), with a derivation of terrestrial macros washed in from neighbouring sources.

WP 3, 4, 5. The numbers refer to horizons of pale muddy sand (Dg ½, Ld ½, Ag 1, Ga 2) within the channel fill. Each horizon was a few centimetres thick. One pollen analysis was made from each of three organic levels. They can be considered together with the analyses from WP 6, 7, 8.

WP 6, 7, 8

yellow sand
cm
0–2 brown muddy sand (WP 8)
2–4 pale laminated muddy silt
4–8 brown muddy sand (Dh ½, Dg ½, Ld ½, Ag ½, Ga 2) (WP 7)
8–10 pale laminated muddy silt (WP 6)

Three pollen analyses and one macro analysis were made from this section.

The two series – one in the centre of the channel and one on the point-bar sands – are of similar age, both formed as the channel silted up, after its abandonment as an active channel. WP 6, 7, 8 is more organic and might be thought to contain a record of flora more local than the filling of the channel. There is, however, little evidence for this. The diagrams from both centre and margin are very similar, with high frequencies of Gramineae decreasing upwards, and with notable frequencies of pollen of *Armeria*, Caryophyllaceae, Compositae (mainly Liguliflorae) and Cruciferae. The most obvious differences are the lower frequency of pollen, the presence of *Artemisia* and the higher *Pinus* frequencies in the main channel. All these differences may relate to a mainly fluviatile origin of the pollen, with lower pollen concentration and a better representation of more distant vegetation. The macro analysis (figure 14) of the marginal sample (WP 6, 7, 8) is somewhat similar to the analysis from WP 2, but not so rich. There is a good representation of terrestrial and aquatic species: *Potentilla anserina* and *Draba* sp. are present, and the wet-ground species cf. *Cardamine pratensis* (related to high Cruciferae pollen values), *Ranunculus hyperboreus*, *Eleocharis multicaulis* and *E. palustris*, and the aquatics *Hippuris vulgaris*, *Potamogeton natans*, *Ranunculus-Batrachium*, and *Zannichellia palustris*. *Carex* nuts and a Gramineae caryopsis were also present. At WP 6, 7, 8 there is, then, a good record of the marginal wet-ground flora as well as of aquatic species.

Thus, the low Cyperaceae pollen frequencies are again found with few *Carex* macros in a shallow and wide channel of deposition with mainly inorganic infill, but there is some correlation between macros and pollen (Cruciferae).

(v) *WN, WQ* (*figure* 4)

WQ. In this section of stratified sands and silts the organic horizon at 205 cm was found to be fossiliferous:

cm	
205–210	brown muddy sand (Dh $\frac{1}{2}$, Dg 1, Ld $\frac{1}{2}$, Ag $\frac{1}{2}$, Ga $1\frac{1}{2}$).

A pollen sample and macro sample were analysed from this horizon. The pollen spectrum is a normal one for a shallow channel filling, with low frequencies of Cyperaceae pollen. The macro flora is rather poor but representative of a wide variety of habitats, terrestrial, wet-ground and aquatic taxa. *Potentilla anserina* and *Ranunculus* subg. *Ranunculus* sect. *Ranunculus* and *Draba* sp. are present. The wet-ground taxa *Ranunculus hyperboreus* and *Eleocharis* are present, and the aquatics *Hippuris vulgaris*, *Potamogeton filiformis*, *Ranunculus–Batrachium* and *Sparganium*. *Cardamine* sp. (related to Cruciferae pollen values), *Carex* sp. and *Viola* sp. are also present.

WN. This section of stratified sands contained a basal horizon with organic remains (WN 3) and a higher series of quiet-water sands and silts (WN 1, 2). The lithology of the horizons analysed is as follows (0 cm at 75 cm from terrace surface):

cm	
155, 195	brown muddy silt (Dg $\frac{1}{2}$, Ld $1\frac{1}{2}$, Ag 1, Ga 1)
320	grey shelly silt (Dh $\frac{1}{2}$, Dg $\frac{1}{2}$, Ag 2, Ga 1)

The lower stratified sands contain the streak of shelly silt WN 3. The quiet-water sediments with organic horizons WN 1 and 2 may have been deposited in an abandoned channel, for they resemble the channel filling at WP 3, 4, 5 farther east.

Analyses of pollen and macro remains were made from the three levels. The pollen diagram (figure 12) shows a biozone B type assemblage. Cyperaceae pollen frequencies are again low and Caryophyllaceae are well represented. The macro analyses (figure 14) show a poor flora in the basal sample and richer ones in the upper two. In the basal sample the few remains are mostly aquatic. There is a single achene of *Ranunculus* subg. *Ranunculus*, three fruitstones of *Groenlandia densa*, two achenes of *Ranunculus–Batrachium* and a *Carex* nut. Pollen of aquatics is more abundant in this sample than in the other two (*Nuphar*, *Sparganium*-type, *Typha latifolia*).

The 155–160 cm and 195–200 cm macro samples contain a richer flora, remarkable for a high frequency of maritime species (figure 14). The upper of these levels is far richer than the lower level. Taking these two uppermost levels together, the open-ground species include *Potentilla anserina*, *Ranunculus repens*, *Alchemilla* sp., *Armeria maritima*, *Campanula rotundifolia*, *Capsella bursa-pastoris*, *Cerastium arvense*, *Draba* sp., *Rumex acetosella*. *Ranunculus hyperboreus* occurs in the wet-ground group, together with *Eleocharis palustris*, and *Polygonum oxyspermum* in the maritime group. *Carex rostrata* and *Ranunculus sceleratus* occur in the middle level, and so do the aquatics *Potamogeton* sp., *Ranunculus–Batrachium*, and *Scirpus* cf. *tabernaemontani*, a species with a slight maritime preference. Seeds of *Cardamine* sp. and *Carex* nuts occur in both of the uppermost levels. The fen and aquatic elements rich in the 195–200 cm sample are absent in the 155 to 160 cm sample, which shows the highest percentage of open ground and maritime species in the sites belonging to biozone B. The maritime elements may relate to the salinities caused by permafrost (Bell 1969) although no ice-wedge casts were seen in this section.

(*f*) *Vegetational history: sites of group* 3

(i) *WG* (*figure* 2)

The organic deposit occupies a depression in the terrace sands up to *ca.* 80 cm deep and some 10 m wide. The origin of the depression as a collapsed ice mound is discussed on page 358. The section described, position shown in figure 2, is as follows:

cm	
	stony sand
0–10	grey silty sand
10–59	brown muddy sand (Ld2, A1, Ga1) sandier at 20–25 cm and more muddy (Dg) below 45 cm
59–76	grey silty sand; at 72 cm brown muddy laminae for 0.5 cm
	yellow stratified sand

From this section analyses of the sediment, pollen and macroscopic plant remains were made.

The sediments are poorly sorted (figure 10) and were probably derived from the original deposits in which the ice lens formed (see page 358), with organic matter added from plant growth contemporary with the filling of the depression.

The section is remarkable for its paucity of macroscopic plant remains. Of five levels analysed (table 5), all contained macro remains, but in very low quantities and with few taxa. Only cf. *Alnus* (wood), *Potentilla*, *Ranunculus* subgenus *Batrachium* and *Carex* were found. This paucity contrasts with the rich collections from the organic deposits of the terrace aggradation, and must be related to the poor flora of a closed shallow pool, probably with turbid water, compared with the fossil-collecting ability of the channel-filling processes.

The sediments from 10 to 55 cm were rich in pollen. The more inorganic sediments at 0–10 cm were barren of pollen, and those between 59 and 76 cm contained very few corroded grains, except at 72 cm. At this level, where muddy laminae were present, the corroded pollen was more abundant, and several grains of *Alnus* and one *Carpinus* grain were recorded, but no well-preserved assemblages of the kind found higher in the section were found. The presence of this assemblage of corroded pollen in the lowest sediments of the basin accords with its suggested origin as a melted ice mound, for the assemblage is what was left of a flora associated with the original sediment in which the ice lens formed. At a later stage of the basin filling a contemporary pollen flora became predominant and masked any derived element.

The pollen diagram from 10 to 55 cm is shown in figure 13. It is divisible into two pollen assemblage biozones: F (25–55 cm) *Pinus–Betula–Picea* p.a.b.; and G (10–25 cm), *Pinus–Betula–Picea–Calluna–Sphagnum* p.a.b.

Unlike the flora of the channel fillings of the terrace aggradation, in the WG section tree pollen is predominant, and the presence of a pine–birch–spruce woodland at this time is indicated. Herbaceous taxa are present, but the characteristic taxa of the herb biozones, *Plantago*, Caryophyllaceae and Compositae are much reduced or not recorded (*Plantago*) and we may infer that these taxa are associated with the open vegetation rather than the woodland vegetation of the terrace surface. On the other hand, the pollen of the shade-tolerant and rather thermophilous *Filipendula* (cf. *ulmaria*), possibly a member of local tall herb communities, is characteristic of these pollen biozones, but is found very sparsely in the herb biozones apart from biozone A (section WH), the earliest of such biozones.

The uppermost of the two biozones represents a time of increased significance of *Calluna*, *Empetrum* and *Sphagnum*, with a fall in the frequency of Gramineae pollen, and must reflect the enlargement of a wet heath element in the woodland vegetation with increasing light intensity at ground level.

The pollen spectra of the lower of the two woodland pollen biozones are very similar to the spectra from the organic muds at Chelford, Cheshire, and a further discussion of the vegetational and climatic significance of the assemblage will be found in the paper describing that site (Simpson & West 1958).

A description of the coleopteran fauna of the WG sediments is given by Dr G. R. Coope in Appendix 1. The pollen and beetle evidence for vegetation of this biozone are conflicting, as is discussed therein.

(ii) *WM*, *WY*

WM. At WM, 50 m west of WG, the following section was seen showing a saucer-like lens of mud in the terrace, probably of ice mound origin:

	brown sand
cm	
0–4	brown sandy mud (Dg 2, Ld ½, A 1, Ga ½)
4–7	brown sandy mud (Dg ½, Ld 1½, A 1, Ga ½)
	brown sand

Two pollen samples were analysed from the muds. The spectra (figure 13) are similar to those of WG 25 to 55 cm and are placed in the same pollen biozone F (*Pinus–Betula–Picea* p.a.b.). The only difference is the higher *Artemisia* frequency in WM.

WY. The basin of sediment at WY (figure 6), interpreted as of ice mound origin (p. 358), showed a section as follows:

	brown silt and sand
cm	
0–11	grey silty sand (Ag 3, Ga 1)
11 15	brown muddy sand (Ld 1, Ag 2, Ga 1)
15–30	grey silty sand (Ag 2, Ga 2)
	stony sand

In this sequence pollen was only found in the muddy sand and the pollen spectrum from this horizon is shown in figure 13. It is similar to the spectra from WG 25 to 55 cm and is placed in the same pollen biozone F (*Pinus–Betula–Picea* p.a.b.).

Evidently both WM and WY basins filled during a woodland period similar to that demonstrated in WG. All these sections were at about the same depth in the terrace (3 m), and in the absence of stratigraphical evidence that the sediments are of very different age, it is assumed that the all belong to the same period of woodland dominance.

(iii) *WJ*

The deposits analysed were from the basin described on page 352 and shown in figure 5 and figures 19–24, plates 19, 20. The section from which samples were taken was as follows:

cm	
0–20	grey-blue silty sand
25–45	brown muddy silty sand (Ag 2, Ga 2)
45–59	grey-blue silty sand (Ag 2, Ga 2)
59–76	brown muddy sand (60 cm: Dg $\frac{1}{2}$, Ld 1$\frac{1}{2}$, Ag 1$\frac{1}{2}$, Ga $\frac{1}{2}$) (65 cm: Dg 2, Ld $\frac{1}{2}$, Ag 1, Ga $\frac{1}{2}$) (70, 75 cm: Dg $\frac{1}{2}$, Ld $\frac{1}{2}$, Ag 1, Ga 2)
76–85	brown sand and stones
85–102	grey-blue silty sand and stones, with a muddy horizon at 100 cm (Dg $\frac{1}{2}$, Ld 1$\frac{1}{2}$, Ag $\frac{1}{2}$, Ga 1)
	grey stratified sand and gravel

The thicknesses of the components differ from those in the drawn section in figure 5, because the samples were taken when the face had been cleaned farther back. Analyses were made of the sediment, macroscopic plant remains and pollen.

The sediments within the basin are poorly sorted (figure 8), and are interpreted as largely derived from the original deposits in which an ice mound formed, with the addition of contemporary organic matter at three horizons: 25–45, 59–76 and 100 cm.

More macroscopic plant remains were found (table 5) in the WJ section than in WG, but far less than in the channels of the terrace aggradation. The majority of the remains were in a bad state of preservation. Two higher horizons, 20–35 cm and 35–50 cm, produced only conifer and cf. *Picea* charcoal, while the lowest level analysed (75–85 cm) porduced only conifer wood, two achenes of *Alisma* and two oospores of Characeae. The richest horizon (65–75 cm) produced 2 *Alnus glutinosa* fruits, cf. *Alnus* wood, *Salix* bud-scales, 2 *Selaginella* megaspores, 25 *Alisma* achenes, 5 *Cladium* nuts, 1 *Menyanthes* seed, 1 *Urtica* nutlet, 1 *Ranunculus sceleratus* achene, 3 seeds of *Hydrocharis morsus-ranae*, 3 *Potamogeton* fruitstones, 15 *Typha* seeds, 29 Characeae oospores, 21 *Salvinia* megaspores and 3 Umbelliferae fruits. This assemblage is totally unlike any other of the Devensian assemblages found at Wretton. The problem is to determine which of these remains are contemporary with the basin sedimentation and which might be derived from the original sediment in which the ice mound formed. The bad state of preservation, unusual in macro remains of the Wretton deposits, suggests redeposition. Further discussion is delayed until the pollen analyses have been considered.

Pollen was found in the organic horizon at 100 cm and in the middle organic bed at 60–75 cm (figure 13).

100 cm. This sample near the base of the basin contained 59 % a.p., nearly all *Betula* and *Pinus*, with Gramineae, Cyperaceae and Compositae the predominant n.a.p. The sample is placed in pollen assemblage biozone C (*Betula–Pinus* p.a.b.). The assemblage is different from

any other assemblage at Wretton. It is most like the woodland biozones F and G, but shows little or no pollen of *Picea*, *Calluna* and *Sphagnum*. The vegetation indicated by the spectrum is of open *Betula–Pinus* woodland, with *Armeria*, *Artemisia* and *Polygonum bistorta/viviparum* indicating unshaded and open conditions.

60 to 75 cm. The four pollen spectra from this level are distinct from the analysis at 100 cm. They are included in the pollen assemblage biozone D (*Betula–Pinus–Alnus*–Gramineae-*Calluna* p.a.b.). Disregarding for the moment any possibility of derived pollen contributing to the spectra, the pollen biozone reflects a period of herbaceous vegetation with a scattered representation of *Betula*, *Pinus* and *Alnus*. The high frequencies of Filicales spores characteristic of this biozone may indicate a fern-rich field layer of a type found in the Scandinavian sub-alpine birchwoods. Such communities occur on neutral or slightly acid soils, whereas the heath indicated by the high *Calluna* frequencies suggests the presence of more acid soils.

Two subzones may be distinguished – a lower one at 70–75 cm, with 20–30 % a.p. and high Gramineae frequencies, and an upper one, 60–65 cm, with about 40 % a.p. and higher frequencies of *Betula*, *Pinus*, *Alnus* and *Calluna*. In the lower subzone the vegetation is more open, frequencies of *Betula* and *Pinus* are low, Gramineae frequencies are high, *Calluna* and *Empetrum* are present, as are a number of indicators of unshaded conditions: *Armeria*, *Artemisia*, *Plantago lanceolata* and *Polygonum bistorta/viviparum*. In the upper subzone the frequencies of *Betula*, *Pinus* and *Alnus* rise. The change is most marked with *Betula*. The Gramineae frequencies fall abruptly, as do those of *Polygonum* and Compositae, and *Calluna* frequencies are higher. The change from the lower to the upper subzone reflects an increased importance of trees and heath in the vegetation, but the n.a.p. frequencies remain high and closed woodland is not present. In addition to the taxa mentioned, low frequencies of *Quercus*, *Carpinus* and *Corylus* occur in the zone. The significance of these will be discussed after we have described similar pollen spectra from basin sediments of WX, and WZ.

(iv) *WX* (*figure* 6)

Eastern basin. A sample from brown sand (Ag 2, Ga 2) at the base of this depression yielded no pollen.

Centre basin. A section at the centre of this basin showed the following:

cm	
0–5	grey sand
5–35	brown grey silty sand (Ag 2½, Ga 1½)
35–42	brown muddy sand
42–48	brown muddy silty sand (Ld ½, Ag 2, Ga 1½)
48–53	brown grey sand
	yellow sand

Pollen spectra were obtained at 30, 40, 45 and 50 cm and are shown in figure 13. The two middle samples are similar to the two middle samples of WJ. They show increasing values of *Betula*, *Pinus* and *Calluna*, presence of *Alnus*, low frequencies of *Corylus* and Cyperaceae, and decreasing values of Gramineae and Compositae. There is little doubt that these two WX samples are of the same age as WJ and reflect the same vegetation.

The lowest spectrum at 50 cm is, however, totally different. It shows very low *Betula*, no *Pinus* or *Calluna*, very high frequencies of *Alnus*, higher frequencies of *Quercus* and *Corylus*, and not much variety of n.a.p., with a *Salvinia* massula. It is probable that this spectrum is derived largely, if not entirely, from reworked interglacial deposits which were the basis of the formation of an ice mound as with WJ. It resembles the basal spectrum of WG (72 cm), which likewise contained predominant *Alnus*.

The uppermost sample (30 cm) shows an increase in *Betula*, *Alnus* and *Corylus*, and a decrease in Gramineae, *Calluna*, Compositae and Filicales. Apart from the rise in *Betula*, these changes are the reverse of those which take place between the lowest two samples at 45 and 50 cm. Thus the uppermost and lowermost samples have a certain similarity, apart from the higher *Betula* of the uppermost, and they contrast with the two middle samples. As these two middle samples are more organic than the other two, which are brown sands, it is likely that the differences are related to a predominant contemporary flora in the middle sediments and a predominantly derived flora in the more inorganic sediments above and below.

Western basin. A single sample (WX 6) from brown silty sand from this basin (see figure 6), contained pollen. The spectrum (table 6) is very similar to the lowest spectrum from the centre basin, with very high *Alnus* values, with *Quercus* and *Corylus*. This is an interglacial pollen spectrum and must relate to reworked interglacial sediments, as in the WX centre basin and the base of WG.

TABLE 6. PROPORTIONS OF POLLEN IN AN IPSWICHIAN SPECTRUM (WT) AND TWO DEVENSIAN SPECTRA (BOTH IN WX)

	WT (wood peat)	WX centre 50 cm (brown sand)	WX west (brown sand)
Betula	1	0.5	0.5
Pinus	2	.	1
Quercus	6	5	3
Alnus	61	73	67
Corylus	25	17	26
Gramineae	1	2	0.5
Cyperaceae	1	3	.
other herbs	2	.	2
Filicales	0.5	.	.
Salvinia (massula)	0.5	.	.
a.p. (%)	70	78	71)

percentages of total pollen

(v) *The problem of derived plant remains in the basin sediments*

The separation of contemporary and derived elements in Pleistocene floras presents considerable difficulties. Indeed it is usually impossible to come to firm conclusions on the matter. The problem is usually acute in early-glacial deposits where there is every possibility of movement of interglacial fossils as interglacial sediments are eroded in the glacial climate. But it is essential to try and separate primary and secondary components in order to reconstruct vegetational history in the Early Devensian, about which little is known. The postulated origin of the basins as melted ice mounds, the bad preservation of pollen and macroscopic plant remains in the basin sediments, together with abrupt changes in pollen content associated with sediment changes, all indicate the probability of a secondary element in the analysed floras.

At Wretton there is evidence on this question from a consideration of sediments, of pollen spectra and macroscopic plant remains.

Sediments. There is an alternation of less organic and more organic horizons within the basins (e.g. WG 72 cm, WJ, WX centre). In WG and WX the best preservation is found in the more organic horizons. Following the arguments on pages 373 and 377 about the pollen flora of WG and WX centre, it appears that there were periods of deposition of organic sediment, in which a contemporary pollen flora is represented, alternating with periods of inorganic sedimentation with poorer preservation of pollen. It is concluded that there is a possibility of a secondary element being introduced into the basins with the more inorganic sediment, perhaps at times of colder climate when local organic productivity was not so high.

Pollen. *Alnus*-rich spectra occur at the base of WG, of WX centre and of WX west. Table 6 compares these spectra with that from wood peat in zone Ip II at Wretton, 650 m to the east (sample WT, Sparks & West 1970, p. 10). The similarity between the interglacial spectrum of WT and the WX centre and WX west spectra is clear. At WT, in wood peat, the highest *Alnus* values of the Wretton interglacial are found, associated with high frequencies of *Alnus glutinosa* fruits and cones. In WX centre and WX west, similar spectra are found in brown sand. The occurrence of high *Alnus* interglacial spectra in an inorganic sediment, rather than an organic sediment which might correlate with *Alnus* over-representation, can best be explained by reworking of an interglacial flora into inorganic sediment during the Devensian. Subsequent ice mound formation in the sediments then must have led to a second period of reworking.

The question then arises whether or not the interglacial pollen contributed to the pollen spectra found at higher levels in the basin fillings. In WG this effect was evidently not marked (see page 373). In WJ and WX the problem is more difficult. In WX, if the lowest (interglacial-type) spectrum is taken as an indication of what might later appear in the higher spectra, *Alnus*, *Quercus*, *Corylus* and *Salvinia* are present to be reworked into the upper sediments. The following pollen taxa are well represented in the two middle spectra and absent or with very low values in the interglacial spectra: *Betula*, *Pinus*, Gramineae, *Calluna*, Compositae, *Polygonum bistorta/viviparum*, Filicales and *Sphagnum*. We may therefore conclude that at least these taxa are probably contemporary, and as they indeed give a characteristic stamp to this pollen zone, our deduction as to the contemporary vegetation may be correct. The status of the taxa less well represented, such as *Carpinus*, *Ulmus*, *Acer* and *Ilex*, remains uncertain. It is also uncertain whether *Alnus* in the two middle samples is secondary or primary. As similar frequencies of *Alnus* occur in WJ, where a basal high-*Alnus* level was not found, *Alnus* is more likely to be primary. In the uppermost level of WX centre, there is a recurrence of taxa common in the basal level, except that *Betula* frequencies are higher, and here the sediment becomes more inorganic. It appears that the original sediment with the derived interglacial flora started redepositing, but with *Betula*, which may therefore be a part of the contemporary flora.

Macroscopic remains. Macroscopic plant remains from all the basin deposits were found to be few, except in WJ 65–75 cm. In this sample the organic material contained both fragmentary and flattened pieces of wood (a few up to 0.5 cm long), and mud. The macroscopic remains were also largely fragmentary or eroded, compared with the much better condition of remains from the channel fillings. Thus *Alisma* is represented by embryos, *Alnus glutinosa* by eroded fruits, *Cladium* by large fragments of the woody fruit, *Hydrocharis* by eroded seeds, *Menyanthes* by part of an eroded seed, *Potamogeton* by embryos, *Typha* by embryos, Umbelliferae by eroded fruits, *Selaginella* by flattened megaspores, and *Chara* by flattened oospores. The only well-preserved items were some of the abundant *Salvinia* megaspores and a nut of *Urtica dioica*. This bad state of preservation would be surprising if the plants which gave rise to them were contemporary with the final filling of the basin in Early Devensian times and were growing in or around the pool of water of the melting ground ice lens. It appears much more likely that they were derived in Devensian times into a body of sediment in which the ice lens formed from an earlier deposit rich in macroscopic remains.† The presence of *Hydrocharis* and *Salvinia* suggest that this earlier deposit was interglacial. Both were found in zone Ip II organic deposits to the east (e.g. sections WB and WS of Sparks & West 1970). It has already been noted (p. 353) that the sediment in WJ appears to have been derived from weathered interglacial material.

If the macroscopic remains were derived, then it is perhaps surprising that interglacial pollen types have not also appeared in quantity in WJ. In fact, the situation in WJ is the reverse from WX centre base, where, in the brown sand, there is interglacial pollen but no macros. Perhaps this situation is explicable in terms of sorting of the components of an interglacial deposit during redeposition into the sediments in which ground ice later formed.

In conclusion, we may say that it is not possible to regard any of the macroscopic plant remains of WJ as contemporary, but that there is evidence that elements of the pollen spectra of WJ and WX are contemporary. Inferences regarding the nature of the contemporary vegetation (pp. 375–377) are based on this assumption.

(vi) *WZ* (*figures* 6 *and* 7)

Two pollen samples were taken from this basin in the positions shown in figure 6, near easting 25 m, one from a thin basal brown muddy silt (Ld 1, Ag 2½, Ga ½), the other from the thin upper organic horizon which lies unconformably on the lower basin sediments (figure 7). When first excavated, the latter was a brown muddy sand (Ld 2, Ag 1, Ga 1) which was analysed for pollen. Further excavation (figure 7) showed a less organic marginal facies. The particle-size distribution of this upper organic sediment (WZ 6, table 1, and figure 9) shows the unsorted nature characteristic of the basin fills at other sites.

The two organic horizons contained pollen but no identifiable macroscopic remains. Both pollen spectra are dominated by n.a.p. (88 %) and are included in a Gramineae–Compositae p.a.b. (biozone E), with these two taxa dominating the spectra. Vegetation of a herbaceous type is indicated, with *Armeria*, *Artemisia*, *Calluna*, Chenopodiaceae, *Linum austriacum* type, *Plantago lanceolata*, *P. maritima*, *Polygonum bistorta/viviparum* (to 15 %), and *Cryptogramma* accompanying the high Gramineae frequencies. Carophyllaceae and *Ranunculus*, in addition to Compositae (23 to 25 %), are also well represented.

In spite of the general similarity of the two spectra, they do differ in certain respects. The lower spectrum shows 8 % *Alnus*, 9 % *Calluna*, 14 % Filicales and 6 % *Sphagnum*; all these taxa are much reduced or absent in the upper spectrum, and their loss is balanced by increase in Gramineae and *Pinus*. The presence of *Alnus*, *Calluna*, Filicales and *Sphagnum* in the lower spectrum suggests an affinity of the vegetation with that inferred from the spectra of WJ and WX in pollen biozone D. It is possible that the series from WJ (and WX) through the basal WZ spectrum to the upper WZ spectrum form a transition from a vegetation with few trees to one predominantly herbaceous.

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† At Breda in the Netherlands a rich *Dryas* flora, ^{14}C age 36000 years, in a valley fill contained a large number of Eemian macroscopic fossils (*Carpinus*, *Quercus*, *Corylus*, *Brasenia*) which are thought to have been derived from a local Eemian deposit (W. H. Zagwijn, personal communication, 1965).

The presence of a period of seasonal or long period of freezing between the times of deposition of the two WZ spectra is discussed on page 357. Such a phenomenon is in good accord with the inferred vegetation history during the filling of the WZ basin.

(*g*) *Vegetational history: sites of group* 4

This is the youngest group of organic sediments, occurring within 2 m of the surface and certainly younger than the basin fillings of group (iii). Their situation is described on page 345. The deposits cover a wide area (see sections WG, WJ, WX, WY, WZ of figures 2, 5 and 6) and were evidently formed in a large rather shallow basin which filled with organic mud, subject to later contortion with involutions and penetration by ice wedges. A further consideration of the flora is given in §4.

(i) *WU, WUB*

The contorted organic horizon at WU was a uniform brown sandy mud (Dg ½, Ld 2, Ag ½, Ga 1), apart from chalk pebbles occurring in the upper part. A pollen diagram from a thickness of 35 cm is given in figure 13, and a macro sample was analysed from a central horizon. The upper organic horizon WX (WX 1, see figure 6) showed a similar lithology. A pollen spectrum from this section is shown in figure 13.

The WUB site was *ca.* 15 m south of WU. There is a lower mud equivalent to the mud at WU, with higher levels of muddy and silty sand, very rich in plant remains at 20 cm depth in the measured section, which was as follows (0 cm at 1 m depth in terrace):

	grey silty sand
cm	
0–1	grey clayey sand (Ld ½, As 1, Ag 1½, Ga 1)
1–19	grey muddy silty sand (Dg ½, Ld 1, Ag 1, Ga 1½)
19–21	grey brown muddy sand, very shelly (Dh ½, Dg 1½, Ld ½, As ½, Ga 1)
21–35	grey silty sand with muddy laminations (e.g. 25 cm Dh ½, Dg 1½, Ld ½, As ½, Ga 1)
35–48	brown sandy mud (Dg ½, Ld 2, Ag ½, Ga 1)
	pale stony sand

The deposits above 35 cm represent a different type of filling of the shallow lake, with increased inorganic sediment being brought in. A pollen diagram from this sequence is shown in figure 13. One macro sample, from 20 cm, was analysed.

The pollen spectra from these sites can be grouped into a Gramineae–Cyperaceae–Compositae p.a.b. (biozone H) similar in constitution to biozone B, but younger than the woodland biozones F and G. Taking first the WU site, Cyperaceae pollen frequencies are high throughout and rise in the upper part of the section as the Gramineae frequencies fall. *Plantago maritima* and *P. media/major* frequencies are relatively high, and so are the frequencies of Compositae (mainly Liguliflorae) and *Ranunculus*. *Centaurea nigra* pollen is present. The macro flora is remarkable for a large number of remains with few taxa. The analysis (figure 14) shows high frequencies of aquatic remains. *Potentilla anserina*, *Ranunculus* subs. *Ranunculus* section *Ranunculus* and *Ranunculus repens* (related to high *Ranunculus* pollen frequencies?) are present as terrestrial herbs, and the wet-ground/aquatic species include *Eleocharis palustris*, *Hippuris vulgaris*, *Ranunculus-Batrachium* (very abundant), *Sparganium* sp. (related to *Sparganium*-type pollen). *Carex* nuts are also present. This flora suggests a shallow pool, perhaps drying out from time to time, quite productive of organic mud. The rising frequencies of Cyperaceae pollen compare with a similar situation in WAG, and contrast with the low frequencies on the shallow, wide, less organic channel fillings. There must have been local communities of Cyperaceae, including *Eleocharis*, which contributed relatively more pollen near the top of the section.

The WUB section, with organic deposits of similar age to those of WU, show a generally similar pollen diagram (figure 13) but there are distinct differences, as there are between the macro analyses of the two sites. The WUB macro analysis contains the remarkable total of 71 taxa derived from a much greater variety of habitats than WU (figure 14). This macro analysis comes from the shelly horizon at 20 cm, not the basal sediment, which is similar to that of WU. It appears that the change in type of sedimentation leads to the arrival of a large number of species from a wide variety of habitats.

The WUB pollen diagram (0–48 cm) differs from the WU diagram in the higher frequencies of pollen of *Betula*, Gramineae, *Artemisia*, *Calluna*, *Polygonum bistorta/viviparum*, Caryophyllaceae, Cruciferae, Rubiaceae and *Thalictrum*, more variable frequencies of Cyperaceae pollen, and lower frequencies of pollen of *Pinus*, *Plantago maritima*, Compositae, *Ranunculus* and *Sparganium*. These differences (though the sites are only 15 m apart) and the differences between successive samples probably relate to a more variable flow regime and a deeper water facies of deposition with variable pollen sources under conditions of changing sedimentation. Thus the lower *Pinus* frequencies may be related to higher rates of deposition of local pollen. The basal pollen spectrum (45 cm), in sandy mud, is characteristic for the Gramineae–Cyperaceae–Compositae p.a.b. The 35 cm level is at the top of the muddy sand and shows an abrupt fall of Cyperaceae frequencies and rises in the frequencies of *Artemisia*, *Calluna*, Caryophyllaceae and Cruciferae (cf. *Cardamine pratensis*) pollen. There was evidently a strong pollen source change at the transition from the deposition of the sandy mud to the silty sand, leading to a better representation of plants of mineral soils. At the 25 cm level, in muddy laminations in the silty sand, the variation continues, with *Betula* and Cyperaceae pollen frequencies higher and the Cruciferae values lower. *Scabiosa* pollen occurs in this level. At the 20 cm level, from which the macro sample came, in a thin layer of shelly muddy sand, there are again differences, with low Cyperaceae frequencies and higher frequencies of *Polygonum bistorta/viviparum*. The higher frequencies of terrestrial macro taxa (figure 14) at this level suggest derivation of the sediment from a land surface, with concomitant changes in the pollen spectrum. The 10 cm level is again in a muddy silty sand, showing high Cyperaceae values again, which are in turn reduced and accompany high frequencies of Gramineae pollen at the 0 cm level in grey clayey sand. Again these variations are associated with changes in sediment source.

The WUB macrosample (at 20 cm) gave 71 taxa well distributed about all the herb ecological groups (figure 14). In the open-ground group, *Potentilla anserina* and *Ranunculus repens* are abundant, as in WU. *Cochlearia* sp. and *Juncus bufonius* are also present. In the open-ground dry group, which has no representatives in WU, 15 taxa are represented: *Armeria maritima*, *Atriplex hastata*, *Campanula rotundifolia*, *Capsella bursa-pastoris*, *Carduus* sp., *Cerastium arvense*, *C. holosteoides*, *Diplotaxis tenuifolia*, *Herniaria* sp., *Lychnis alpina*, *Polygonum aviculare*, *Rumex acetosella*, *Scleranthus* sp. (*Scleranthus* pollen also present at this level), *Thalictrum minus* and *Viola* subg. *Melanium*. This is the widest representation of open-ground dry taxa in the Wretton Devensian flora. They are probably derived from communites on the sandy terrace surface as well as on the neighbouring Gault, which rises to the surface 60 m to the north.

Wetter open-ground taxa are also well represented, though absent in WU. They include

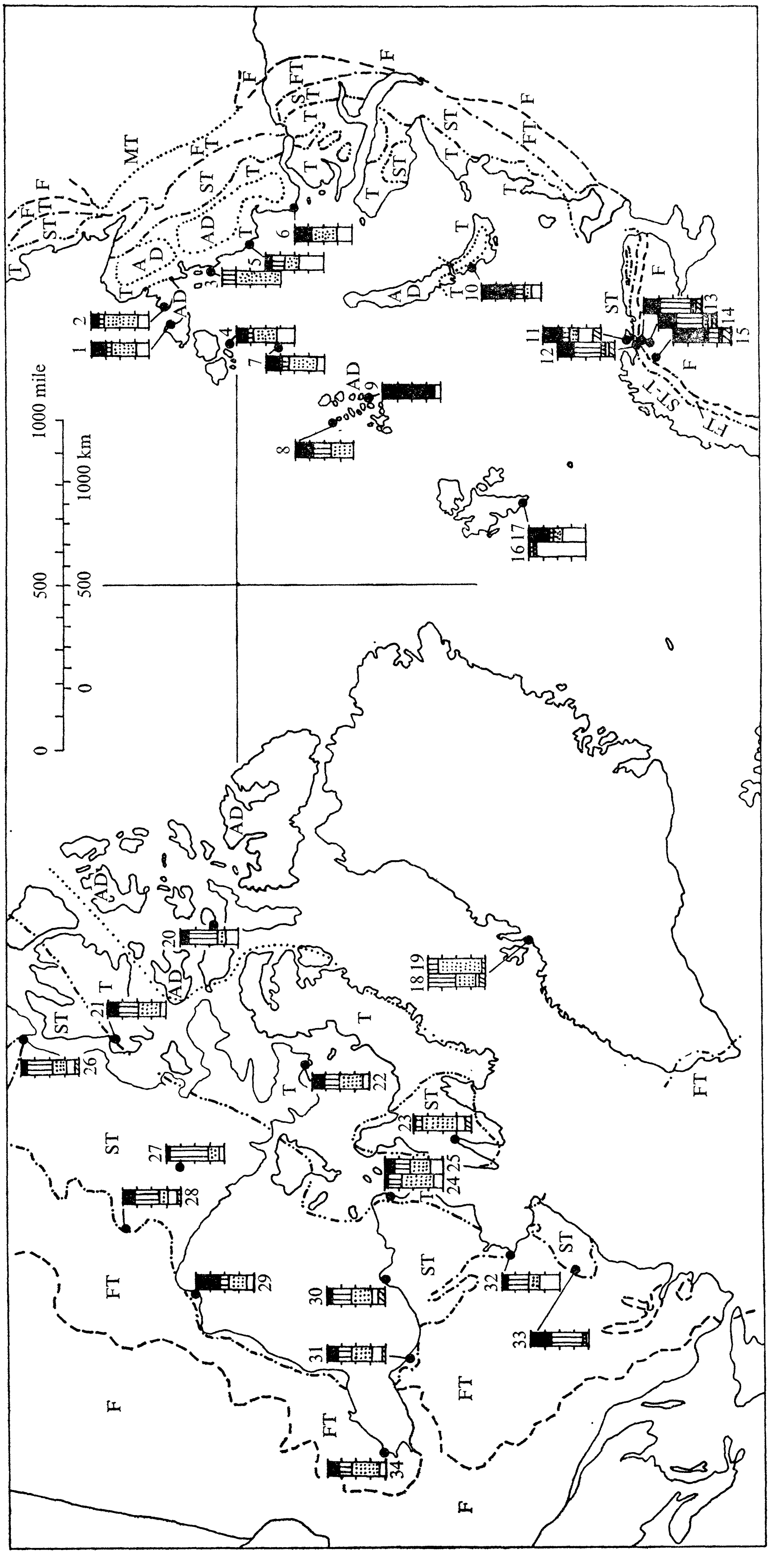


FIGURE 15. For description see facing page.

cf. *Cardamine pratensis*, *Carex* sect. *Acutae*, *Juncus* cf. *conglomeratus*, *Pedicularis palustris*, *Ranunculus hyperboreus*, *Stellaria crassifolia*, *Valeriana officinalis* and *Selaginella selaginoides*. There is again a richer flora of the damp ground/shallow water group than in WU: *Alisma plantago-aquatica*, *Eleocharis palustris*, *Ranunculus flammula* and *Rorippa islandica*. These taxa must derive from the shallow water and damp ground communities around the pool.

The maritime group, absent in WU, is well represented by *Glaux maritima*, *Juncus* cf. *balticus* and *Polygonum oxyspermum*. The WUB horizon is affected by involutions and is penetrated by ice-wedge casts, and it seems reasonable to associate this element with salinities induced by freezing.

The helophyte group, absent in WU, consists of eight taxa: *Berula erecta*, *Carex* cf. *aquatilis*, *C.* cf. *rostrata*, *Cicuta virosa*, *Glyceria* cf. *declinata*, *Ranunculus lingua*, *R. scleratus* and *Urtica dioica*. The aquatic group is also rich, with 22 taxa, compared with the three in WU: *Ceratophyllum* cf. *demersum*, *Damasonium alisma*, *Groenlandia densa*, *Hippuris vulgaris*, *Myriophyllum spicatum/verticillatum*, *Nuphar lutea*, *Potamogeton alpinus*, *P.* cf. *berchtoldii*, *P. crispus*, *P. filiformis*, *P. natans*, *P. obtusifolius*, *P. pectinatus*, *Ranunculus–Batrachium*, *Scirpus lacustris*, *S.* cf. *tabernaemontani*, *Sparganium erectum* and *Zannichellia palustris*. This list represents a very rich aquatic flora which must have been present in the silting-up pool, evidently at a time immediately before a time with evidence for a period of permafrost. The unclassified group includes *Cardamine* sp., *Carex* sp., Cruciferae, *Juncus* and *Luzula*.

A correlation between pollen and macro flora occurs with some taxa, notably *Armeria*, Caryophyllaceae (*Cerastium*, *Lychnis*) and Cruciferae (*Cardamine*, *Diplotaxis*) and *Scleranthus*.

FIGURE 15. Pollen percentages of recent and subrecent samples in the Arctic, related to principal vegetational zones. The scale on each analysis is divided into 25% segments. Taxa are signified as follows: black, *Pinus* + *Picea*; vertical lines, *Betula* + *Salix* + *Alnus*; dotted, Gramineae + Cyperaceae; white, other herbs; diagonal lines, Ericales.

Abbreviations: F, forest; FT, forest-tundra; MT, mountain tundra; ST, shrub tundra; T, tundra; AD, Arctic desert, fell field. These divisions are described in more detail in table 7.

Sources of vegetational zones: Porsild (1958), Böcher *et al.* (1968), Sjörs (1956), Lavrenko & Sochavy (1956). Zones in central and northern Greenland and in Spitsbergen not distinguished.

Sources of samples: 1–10, Kuprianova (1951). 1, grass–moss Arctic desert, Bol'shevik Island, Solnechnaya Bay. 2, grass–moss Arctic desert, Cape Chelynskin. 3, Arctic tundra with moss grass swamp, Pravdy Island. 4, grass moss Arctic desert, Domashnii Island. 5, Arctic tundra with moss–grass swamps, Cape Sterlegova. 6, Arctic tundra with moss–grass swamps, Dikson Island. 7, grass–moss Arctic desert, Vize Island. 8, grass–moss Arctic desert, Rudolfa Island. 9, impoverished dwarf-shrub–moss Arctic desert, Gureka Island. 10, Arctic tundra with moss–grass swamps, Cape Karmakuly, Novaya Zemlya.

11–15, Aario (1940). Average samples I, II, III, IV and VI in table 10. 11, shrub–tundra (I). 12, forest (birch) tundra (II). 13, birch forest (III). 14, birch forest with some pine (IV). 15, pine forest (VI).

16, 17, Srodon (1960). Samples 4 and 8 (north of Hornsund). 16, moss–tundra, low level (41 m a.s.l.) (4). 17, open Arctic desert, high level (500 m a.s.l.) (8).

18, 19, Fredskild (1967). Samples III, 5 and VII, 4 (Semermiut near Jacobshavn). 18, shrub–tundra (III, 5). 19, *Sphagnum-Drepanocladus-Carex* marsh (VII, 4).

20 to 23, 26 to 34, Ritchie & Lichti-Federovich (1967). 20, fell field, Resolute. 21, tundra, Cambridge Bay. 22, tundra, Hall Beach. 23, shrub–tundra, Frobisher. 26, forest–tundra, Coppermine. 27, shrub–tundra, Baker Lake. 28, forest–tundra, Ennadai. 29, forest–tundra, Fort Churchill. 30, shrub–tundra, Port Harrison. 31, forest–tundra, Gt Whale River. 32, forest–tundra, Fort Chimo. 33, forest–tundra, Knob Lake. 34, forest (conifer), Moosonee.

24, 25, Bartley (1967). Samples F and J (Sugluk, Quebec). 24, tundra (J). 25, open tundra, very exposed (F).

4. PALAEOBOTANY: THE FLORA AND VEGETATION OF THE HERB BIOZONES

(*a*) *The relation of the herb spectra to recent pollen spectra from northern treeless areas*

Analyses of recent or subrecent pollen rain are available from Arctic U.S.S.R. (Kuprianova 1951), Spitsbergen (Srodon 1960), northern Finland (Aario 1940), Greenland (Fedskild 1967), northern Canada (Bartley 1967; Lichti-Federovich & Ritchie 1968; Wenner 1947) and Alaska (Livingstone 1955). Some of these analyses have been accompanied by analysis of the vegetation in the areas from which the pollen samples were taken. The results as a whole allow a discussion of certain points important to the interpretation of the herb spectra at Wretton; in particular the characteristics of recent pollen spectra from tundra, the variability of tundra spectra within and between particular types of tundra vegetation, the significance of the a.p./n.a.p. ratio for determining the possible extent of over-representation by pollen introduced by long-distance transport (l.d.t.p.), and the representation of certain taxa by their pollen.

(i) *Subdivisions of tundra and their relation to pollen deposition*

Present tundra vegetation in the north is extremely varied. A number of formations have been distinguished, but the mosaics of vegetation within each of these is very diverse, with drainage, soil, slope, insolation, as well as the usual climatic factors playing an important part. However, it is possible to make broad divisions, mapped in figure 15, as follows (table 7).

The analyses of recent pollen deposition in the Arctic, depicted in part in figure 15, can be related to these major tundra divisions, which are also shown in the figure:

AD. This is characterized by high frequencies of l.d.t.p., associated with low local pollen productivity. Figure 15 shows the importance of the l.d.t.p. element (e.g. nos 8, 9, 10, 17).

TABLE 7. MAJOR DIVISIONS OF TUNDRA

abbreviation on figure 15	North America (Ritchie & Lichti-Federovich 1967, Porsild 1958)	Arctic Scandinavia (Rønning 1960)	North U.S.S.R. (Lavrenko & Sochavy 1956; the numbers refer to their divisions)
AD	fell field, rock desert	regio alpina superior	(1, 2) Arctic deserts (incl. 2 TM, OKM, KM)
T	sedge–moss lichen tundra mature sedge–grass tundra	regio alpina media	(4) Arctic tundras, combined with moss–grass swamps (4) (5) moss and lichen tundras with moss–grass swamps and *Dicranum–Lichenes–Sphagnum* bogs (7) *Carex–Eriophorum* tussock tundras with moss–grass swamps
ST	dwarf shrub–sedge–moss–lichen heath	regio alpina inferior	(6) dwarf shrub–tundra (8) tundra willow scrub, with *Sphagnum* bogs (9) *Betula* Sect. Nanae scrub tundras with *Sphagnum* bogs
FT	sub-Arctic forest tundra	regio subalpina	(10) sub-Arctic forest–tundra with *Picea* (26) sub-Arctic forest–tundra with *Larix* (39) sub-Arctic forest–tundra with *Betula tortuosa*

A reduced number of n.a.p. taxa are recorded, and measurements indicate a low rate of pollen deposition (e.g. 5 per cm^2 per year at Resolute, Cornwallis Island (Ritchie & Lichti-Federovich 1967)).

T. This division is characterized by considerably greater local pollen production (22–65 per cm^2 per year (Ritchie & Lichti-Federovich 1967)), and a reduced frequency of the l.d.t.p. element (e.g. nos 2, 3, 5, 24). Pollen of Gramineae and Cyperaceae is well represented, and a good variety of n.a.p. taxa are seen.

ST. This is characterized by significant percentages of pollen of *Betula* and *Salix* (e.g. nos 27, 33), *Ericales*, Gramineae and Cyperaceae. The spectra from this division may be somewhat similar to those from the forest tundra (FT), but the rate of pollen deposition is lower (52–762 per cm^2 per year (Ritchie & Lichti-Federovich 1967); 220 per 50 g of peat (Aario 1940)) and there is still a significant element of l.d.t.p.

FT. This division is characterized by high frequencies of *Betula* pollen in north Finland (e.g. no. 12) and *Picea*, *Alnus* and *Betula* in northern Canada. Pollen deposition rates are much higher (275–2300 per cm^2 per year (Ritcher & Lichti-Federovich 1967): 1693 per 50 g of peat (Aario 1940)).

From these comments it is possible to conclude that the Wretton herb spectra resemble those from division T above, that which contains sedge–moss tundra and grass tundra. In terms of the dominant pollen types, Gramineae and Cyperaceae, and in the low frequency of l.d.t.p., they resemble spectra described by Livingstone (1955) from surface samples in the coastal tundra at Point Barrow, Alaska, which comprises *Carex*-dominated bog meadows together with more open vegetation on uplifted beach bars and other better drained areas. This comparison cannot yet be confirmed by the determination of the annual pollen deposition rates which characterize different northern plant communities, mentioned above.

(ii) *The extent of over-representation of pollen by long-distance transport*

The a.p./n.a.p. ratios in the tundra areas described in the previous section appear to be governed by three factors: distance of a.p. source, local pollen productivity, and dispersal by prevalent weather systems. These factors are closely interrelated. Thus, on the change from forest to tundra pollen, productivity falls and the l.d.t.p. element becomes proportionately better represented. Within the tundra itself, the proportion of l.d.t.p. rises considerably in the more barren areas. For example, in Spitsbergen (Sroden 1960) samples from lowland well-vegetated areas (no. 16 in figure 15) have a much lower l.d.t.p. proportion than upland barren areas (no. 17), and similarly in northern Quebec there is the same difference between exposed (no. 25) and less-exposed more-vegetated areas (no. 24).

In regard to the importance of regional weather systems in determining the prevalence of l.d.t.p. in northern areas, we may contrast the situation in Greenland, with low-level winds coming off the ice sheet, and reducing the l.d.t.p. of conifers (see sites no. 18, 19 of figure 15), with that in northern Europe and northern Canada where the wind circulation will allow the arrival of conifer pollen from the taiga when the Arctic front lies far north.

In the Wretton herb spectra the n.a.p. percentages are over 80 % of total pollen and *Pinus* pollen exceeds in frequency that of *Betula*. Comparing this situation with that in the Late-Devensian we see much-reduced *Betula* percentages at Wretton, which must be related to the reduced frequency of this genus in the landscape. It does not seem likely that *Pinus* would be present in conditions not favouring *Betula* because the latter (e.g. *B. tortuosa* in Scandinavia) is the tree of the polar tree limit in Western Europe, unless the continentality of climate favoured a coniferous polar tree limit of the type seen east of Scandinavia. We might therefore conclude that the *Pinus* pollen represents long-distance dispersal, and the frequencies seen have a relevance in indicating the low pollen productivity characteristic of tundra compared with forest, but not the lowest of productivities associated with Arctic desert. Easterly winds (see page 409) may have been responsible for the introduction of the *Pinus* pollen that we see in the pollen diagrams.

In the absence of detailed knowledge of Devensian weather systems, a guess cannot be hazarded where the forest limit lay at the time. Polish Weichselian pollen diagrams have similar herb spectra but with rather higher a.p. percentages (especially *Pinus*), so that in all probability we may regard the limit as being hundreds of kilometres away.

(*b*) *The representation of certain taxa at Wretton and in recent pollen spectra*

In this section we take the plant records from the herb biozones and describe and comment on the occurrence of taxa identified by their pollen and macroscopic remains, referring also to the representation of some of the taxa in the studies of northern vegetation and pollen rain already mentioned.

(i) *Tree and shrub pollen taxa at Wretton*

Betula. In the Arctic there is evidence for considerable long-distance transport. Pollen frequencies may show much local variation (e.g. at Semermiut in Greenland, 36 to 1 % (Fredskild 1967)) related to the patchy distribution of the genus with a low regional pollen rain of a few per cent. At Wretton, *Betula* pollen is represented throughout in very low frequencies; a maximum of 5 % (total pollen) was found in WP. A small number of grains were of *B. nana*-type, of smaller diameter and with depressed pores. One fruit of *B. nana* was found in WH, at a horizon where *B. nana*-type pollen was also found. *Betula* must have been scarce throughout the herb periods. *Betula* is a high pollen producer, and evidently shrub vegetation was absent except perhaps in very local habitats.

Pinus. In the Arctic there is evidence for very considerable long-distance transport; e.g. 1700 km in the Soviet Arctic (Kuprianova 1951). At Wretton, the frequency of *Pinus* pollen is variable between 2 and 16 %, and always exceeds the frequencies of *Betula*. The possibility that the *Pinus* pollen originates from a long distance source is discussed above.

Alnus. There is evidence for the same degree of long-distance transport in the Arctic as *Pinus*. *Alnus* is very infrequent in the herb spectra at Wretton, except in WH, where fruits of *A. glutinosa* were recorded and pollen frequencies reach 30 %. It is likely that *A. glutinosa* was present at this time.

Quercus, *Tilia*, *Carpinus*, *Abies*, *Corylus*. At Wretton, these taxa have low pollen frequencies occurring sporadically, except in WH in the basal biozone. It is not possible to say whether the pollen of these taxa in WH is derived from the preceding interglacial or whether it is derived by long-distance transport. The nature of the pollen spectra would suggest that *Quercus*, *Tilia*, *Carpinus* and *Corylus* pollen were secondary or a long-distance element.

Picea. At Wretton, pollen of *Picea* is scattered in occurrence and at very low frequency, compared with the constantly higher frequencies in the woodland biozones F and G. Probably in the herb biozones it has a long-distance origin.

Salix. In the Arctic the representation of *Salix* pollen is very local. There may be a low regional pollen rain; higher frequencies are sometimes found in relation to scrub willow communities. In Spitsbergen, *Salix* percentages are low compared with the frequency of the genus (Srodon 1960). Unlike many other Devensian sites, remains of *Salix* were very scarce at Wretton. Pollen is sporadically represented, in highest frequencies in WH, where *Salix* bud-scales were recorded. It seems likely that there were local willow communities present but not in sufficient quantity to give a consistent pollen rain or the leaf-beds so often found in Devensian floras.

Juniperus. Pollen of *Juniperus* was only found at one site (WN) in very low frequency. The plant must have been rare or absent in the flora of the herb biozones.

(ii) *Herb taxa represented by considerable pollen frequencies at Wretton*

GRAMINEAE. The percentages found in the Arctic are very variable. In northern Quebec the percentages show, with Cyperaceae, the least localization of the taxa studied (Bartley 1967). In Greenland the frequencies show considerable variation, with up to 94 % in pure stands, with a regional representation up to 13 % (Fredskild 1967). In north Finland the percentages in the tundra are very variable. In the Soviet Arctic the pollen was absent in the highest latitudes and most abundant in the tundras of the northern continental coast – that is, in 'moss–grass' Arctic tundras and the southern part of the 'grass–moss' Arctic desert (Kuprianova 1951).

At Wretton the frequencies of Gramineae pollen are generally high, but variable. High frequencies are found at levels where caryopses were recorded and where they were absent. In the discussion of sites it was concluded that this pollen was more likely to be of regional origin. This conforms with the representation of Gramineae pollen in recent Arctic spectra, where though variable, there is a regional representation. A regional vegetation of tundra physiognomy with Gramineae important is perhaps indicated.

CYPERACEAE. In the Arctic, the percentages found are again very variable, perhaps more so than with Gramineae. In northern Quebec the percentages showed, with Gramineae, the least degree of localization, but frequencies varied between 4 and 70 % (Bartley 1967). In Greenland a low (2–0.3 %) regional rain was indicated with local increases from 10 to 73 % associated with sedge communities (Fedskild 1967). In northern Labrador the highest percentages were found in small patches of sedge fen, but samples taken in the extensive and monotonous sedge communities of the tundra often gave low frequencies (Wenner 1947). In the coastal tundra of northern Alaska Cyperaceae frequencies were found to be high (Livingstone 1955). Evidence for the rather local representation of Cyperaceae in northern Canada was brought forward by Lichti-Federovich & Ritchie (1965), who showed that high percentages (up to 25 %) were related to lowland mires. In northern Finland, the percentages were again very variable in the shrub-tundra. In Spitsbergen no Cyperaceae pollen was recorded (Srodon 1960). In the Soviet Arctic few grains of Cyperaceae were recorded, even in the 'grass–moss' Arctic tundras (Kuprianova 1951). It appears that high frequencies of Cyperaceae pollen indicated the local abundance of sedge communities, but that low frequencies do not clearly indicate a local absence or a regional presence of such communities.

At Wretton, Cyperaceae pollen is present at all the sites, but in very variable frequencies. The high pollen frequencies are generally related to a good representation of *Carex* macro remains, including the following taxa: *Carex* section *Acutae*, *C.* cf. *aquatilis* and *C. rostrata*. These must have formed communities in the terrace surface. (Other taxa of Cyperaceae present, but not so abundant as *Carex*, were: *Eleocharis multicaulis*, *E. palustris* s.s. and s.l., *Scirpus lacustris* and

S. cf. *tabernaemontani*). The lower Cyperaceae pollen frequencies are associated with spectra from wide and/or shallow channels with rather inorganic filling, and these spectra may represent a more regional pollen rain, as mentioned in the site descriptions already given. If this is correct, the frequency of *Carex* in the regional vegetation may have been not very high.

Plantago. There are a few isolated records of *P. lanceolata* in all the herb biozones. *P. maritima* is more abundantly represented, especially in WH and WUB, and one capsule was found in WAG. The commonest taxon is, however, *P. media/major.* This reached its highest frequencies in levels containing bones, and it was presumably present in the disturbed ground near water bodies on the terrace surface. It appears that all three *Plantago* taxa recorded were persistent members of the flora. We may note that *P. major* has become established in grassy and disturbed places in W. Greenland and *P. maritima* is widespread in the Arctic.

(iii) *Herb taxa showing considerable variations of pollen frequency at Wretton*

CARYOPHYLLACEAE. Low and variable percentages are generally found in tundra areas. At Wretton this pollen taxon is continuously represented through the herb biozones, but it varies considerably in frequency, as in the Arctic. The highest frequencies are in WH (*Cerastium arvense* and *Herniaria* recorded as macros), WN (*Cerastium arvense* recorded), WP (no macros found), WZ and WUB (*Cerastium arvense*, *C. holosteoides*, *Herniaria*, *Lychnis alpina*, and *Stellaria crassifolia* recorded). All these taxa are insect-pollinated and the pollen frequencies are such as to suggest certainly their very local presence and probably a regional presence as well. In the recent Arctic pollen spectra, there are similar low frequencies of Caryophyllaceae pollen associated with *Cerastium*, *Sagina* and *Stellaria* among other genera, in the Soviet Arctic, Spitsbergen, northern Finland and Greenland.

COMPOSITAE. Compositae pollen is sporadically present in tundra pollen spectra. At Wretton, the Compositae pollen frequencies are considerable throughout the herb biozones. In the pollen diagrams (figures 13, 14) the curve is divided into Liguliflorae and Tubuliflorae, and most of the variation in the frequency of Compositae pollen (4–38 %) is variation in Liguliflorae frequency (except WZ – basal spectrum). The macroscopic remains of Compositae are of *Carduus* sp., *Leontodon autumnalis* and *Taraxacum* cf. *officinale*. The last two were only found in the horizon (WAG 40–70 cm) which showed the highest Compositae Liguliflorae frequencies. An achene of *Carduus* was found in WUB, where the pollen frequencies were lower. *Centaurea nigra* pollen was found in WU. These observations suggest the local representation of Compositae on the terrace surface, but also a wider regional representation.

CRUCIFERAE. In the Arctic spectra Cruciferae pollen is commonly found in very variable frequencies. At Wretton, likewise, this taxon is present throughout the herb biozones sometimes as low frequencies, but sometimes as very considerable frequencies. Many taxa are represented by macro remains: *Cochlearia*, *Capsella bursa-pastoris*, *Diplotaxis tenuifolia*, *Draba*, cf. *Cardamine pratensis*, *Cardamine* and *Rorippa islandica*. There is not a strong correlation between the occurrence of high pollen frequencies and macro remains, except that in WUB both pollen of *Cardamine* (cf.) *pratensis* and seeds of (cf.) *Cardamine pratensis* were recorded. Otherwise macros were present in WH (1 taxon), WAD (2 taxa), WAF (2 taxa), WAB (2 taxa), WQ (1 taxon), WN (4 taxa), WP (3 taxa) and WUB (6 taxa). Evidently these taxa were present in the local communities on the terrace, both in the wetter (*Cardamine pratensis*) and drier (*Diplotaxis*) parts.

Polygonum bistorta/viviparum. At Wretton this taxon occurs sporadically in the herb biozones reaching high frequencies in WZ and WUB. A single bulbil of *P. viviparum*, but no pollen, was found in WH. In recent Arctic pollen spectra *Polygonum viviparum* was found to be very locally represented in Greenland and only in areas where the plant was growing (Fredskild 1967). The sporadic, sometimes high, frequencies of this taxon at Wretton suggest local and discontinuous development of *Polygonum* communities on the terrace surface.

Ranunculus. Continuous low frequencies of *Ranunculus* pollen occur through the herb biozones at Wretton. Taxa represented by macroscopic remains are *R. acris* (1 site), *R. repens* (7 sites), *R.* subgenus *Ranunculus* section *Ranunculus* (7 sites), *R. hyperboreus* (5 sites), *R.* subgenus *Ranunculus Auricomus* (1 site), *R. flammula* (1 site), *R. lingua* (1 site), *R. sceleratus* (4 sites) and *R.–Batrachium* (all sites). The highest frequencies of *Ranunculus* pollen are in WAD, associated with *R. acris*, *R.* subg. *Ranunculus* section *Ranunculus* and *R.–Batrachium*, and in WU associated with the two latter again and *R. repens*. On the other hand, with five taxa in WUB, the pollen frequencies are low. Evidently these taxa were widespread on the terrace surface, contributing a variable pollen rain.

(iv) *Herb taxa showing low pollen frequencies at Wretton*

These taxa are members of the flora of the herb biozones but it is not always possible to assess their importance in the vegetation. The following gives the pollen taxa, notes on associated macros and possible locations of the taxa.

Armeria. Armeria pollen occurs in most of the herb spectra, reaching its highest frequency (6 %) in WP. *Armeria maritima* calyces occur in WH, WAD, WN and WUB. This is the species of the 'full-glacial' flora which has the highest constancy (Bell 1968). It appears to have grown on the terrace surface (p. 381), and may have had a wider distribution in the region.

Artemisia. Artemisia pollen has high frequencies in WH, and scattered low frequencies at other sites. No macroscopic remains were found. The genus is apparently a continuing member of the flora, though it has pollen which is widely dispersed (Fredskild 1967).

Empetrum and Ericaceae. There is an extremely local representation of these taxa in all the Arctic areas studied, except west Greenland where there is a low regional element; *Empetrum* dispersal in this area is reported to be more effective than Ericaceae (Fredskild 1967). At Wretton, in contrast to the high frequencies of *Calluna vulgaris* pollen and low but persistent frequencies of *Empetrum* in the woodland biozones, both these taxa are sparsely represented in the herb biozones. *Calluna* is found at 1 to 3 % at various levels (especially WP and WUB); *Empetrum* is much scarcer. If these taxa were present in the regional vegetation, they must have been rather scarce, in contrast to their importance in the woodland biozones.

CHENOPODIACEAE. *Atriplex hastata* or *patula* seeds were recorded at two sites; member of terrace flora.

Helianthemum. A near-continuous pollen curve in WH; sporadic records later. Possibly *H. canum* in view of abundant leaves, capsules and seeds of this species in the Early Devensian at Sidgwick Avenue, Cambridge (see page 401).

Polygonum convolvulus.

Rumex acetosa/acetosella. R. acetosella nuts were found in WH, WAG, WN, WUB; member of terrace flora.

Rumex sp.

Campanula. C. rotundifolia seeds were found in WAF, WN, WUB; member of terrace flora.

Filipendula. Low frequencies in WH and also in the later of the two woodland biozones; otherwise scattered records.

Potentilla. Very abundant achenes of *P. anserina* were found in all sites except WAF and WAB; member of the terrace flora. *P.* cf. *argentea* and *P.* cf. *crantzii* also present in WH, the latter abundant; possibly the latter is a member of the Gault Clay flora.

Rubiaceae.

Thalictrum. Achenes of *T. alpinum*, *T. flavum* and *T. minus* occur in WH, where the highest pollen frequencies are found, and *T. minus* is in WUB.

Umbelliferae. Fruits of *Oenanthe aquatica*, *Berula erecta* and *Cicuta virosa* were found. These species are members of the local fen and aquatic flora, the first in WH, the last two in WUB.

Sparganium-type. Fruitstones of *Sparganium* sp., *S. erectum* and *S. erectum* subsp. *neglectum* were found, and are local aquatics, as are the following species.

Myriophyllum specatum and *verticillatum.*

Filicales. Scattered records in the herb biozones, but abundant in the woodland biozone D (see page 376).

Botrychium. B. lunaria; possibly this species grew in the regional vegetation.

Selaginella. S. selaginoides; possibly this species was a member of the regional flora on the Gault (see page 366).

Sphagnum. In the high Arctic, *Sphagnum* frequencies are very low, even though *Sphagnum* communities are widespread. Apparently spore production is low or absent. In Spitsbergen, low frequencies of *Sphagnum* are considered to be a result of long distance transport (Srodon 1960). Very low frequencies of *Sphagnum* occur in certain of the herb spectra at Wretton.

(v) *Herb taxa with few records at Wretton*

Centaurea nigra. A record in WU.

Labiatae. Found only in WH. A *Stachys* nut and an *L. europaeus* nut were also found in this site. *Lycopus* was a member of the fen flora in the pre-aggradation channel.

Leguminosae. Very local distribution of this pollen taxon was found in northern Quebec (Bartley 1967). The pollen was only found in the herb spectra of WH.

Linum austriacum-type pollen (see page 363).

Scabiosa. A record in WH and WUB.

Scleranthus. A record in WUB where a *Scleranthus* fruit was found; member of terrace flora.

Trifolium. A record in WUB.

Caltha. A record in WAG at the same level as seeds of *C. palustris*; a member of the fen flora on the terrace.

Littorella. A record in WAB.

Nuphar. A record in WN.

Typha latifolia. A record in WN.

Cryptogramma. Records in WP and WZ. *C. crispa*; a member of terrace flora, since it has a preference for acid soils.

Lycopodium. In west Greenland and Labrador low regional frequencies of *Lycopodium*, especially *L. selago*, occur in the tundra. This taxon was not recorded at Wretton, but the genus was found infrequently in certain of the herb spectra, with records of *L. annotinum* and *L.* sp. in WP.

Ophioglossum. A record in WU.

Polypodium. Records in WN, WZ and WUB.

(vi) *Frequencies of macro taxa*

Twenty-three samples from the herb biozones were analysed for macro remains. The frequency of various taxa in these 23 samples may give an indication of the most characteristic macro taxa of these zones. The number of samples in which the taxa were found is shown in brackets: *Carex* spp. (20), *Potentilla anserina* (18), *Ranunculus* subgenus *Batrachium* (18), *Hippuris vulgaris* (13), *Armeria maritima* (9), *Groenlandia densa* (9), *Draba* sp. (9), *Ranunculus repens* (7), *Ranunculus* subgenus *Ranunculus* section *Ranunculus* (7), *Ranunculus hyperboreus* (7), *Linum perenne* (6), *Potentilla* cf. *crantzii* (6), *Ranunculus sceleratus* (6), *Eleocharis palustris* (6), *Potamogeton filiformis* (6), *Cardamine* spp. (6), *Viola* sp. (6), *Salix* sp. (5), *Potamogeton alpinus* (6), and *Zannichellia palustris* (5).

(vii) *Conclusions*

The combination of pollen spectra, macro remains and geological background allows a reasonable picture of the local flora and vegetation on the terrace surface and a more shadowy picture of the regional flora and vegetation to be obtained. A regional vegetation of tundra physiognomy, probably dominated by grasses, referred to in table 9 as grassland, and with few shrubs, appears to have been present. There was a rich flora of terrestrial, fen and aquatic plants on the terrace surface. The heterogeneity of the distribution of the vegetation and of the processes of sedimentation, such as is seen on modern braided river plains in the Arctic, led to considerable variation in the representation of taxa by their pollen and macro remains, and in some instances it has been possible to relate sedimentary environment to the pollen and macro spectra. Wide shallow channel fills with inorganic sediment appear to give a better representation by the pollen of the regional flora, while deeper narrower fills often give evidence of local vegetation. The representation of terrestrial macro remains is often better at the base of the channel fills than higher up (WH, WAD, WAG), perhaps related to the collapse of channel sides and development of a hydrosere in an abandoned channel. On the other hand in WN terrestrial macros are better represented towards the top of a more inorganic channel-filling, showing a continuation of fluvial sedimentation.

These variations in pollen and macro content contrast with the more uniform and homogenized assemblages seen in lake sediments, and make it possible to isolate certain communities, such as the *Potentilla anserina–Ranunculus repens* community which must have been abundant on the terrace surface near the channels, and the communities of fen and aquatic species already mentioned in relation to particular sites. There is evidence for a relation between vertebrates and *Plantago media/major* pollen frequencies (WO, WAL) which shows the existence of plant communities associated with trampling and disturbance in the terrace surface. The analysis of organic sediments in a fluviatile environment thus allows much more to be said about the origin of the fossils than is the case with lacustrine sediments.

5. NON-MARINE MOLLUSCA (table 8)

Mollusca were found in four of the sections, namely WH (probably the oldest section exposed), which was deposited in the oldest herb biozone, WN which belongs either to the oldest or to the youngest herb biozone, WUB which forms a part of the youngest herb biozone, and WS which cannot be zoned as it contains no pollen. The lack of pollen in WS is very unfortunate,

TABLE 8. ANALYSIS OF MOLLUSCA

SECTION	WS	WS	WS	WUB	WN	WN	WH	WH	WH	WH	WH	WH	WH	WH	
SAMPLE	28 35	20 28	0 20		320	190 195	Bulk	Side	50 60	40 50	30 40	10 30	5 10	0 5	TOTAL
Valvata cristata	2	11		12	55	5		2		2	3	8			100
Valvata piscinalis	1	147		60	132	19				2	16	17	5	1	400
Belgrandia marginata												2			2
Bithynia tentaculata	11	19	2		3			1	1	3	4	8	3		55
Bithynia inflata												1			1
Carychium minimum				4	7			1			2	3	1		18
Carychium tridentatum											3	2			5
Lymnaea truncatula		8		29	112	22			3	3	92	97	43	4	413
Lymnaea palustris	?1	269		26	61	14	2				10				383
Lymnaea stagnalis		6		4	2										12
Lymnaea peregra		3			24	6		1	1	1	4	8	1		49
Aplexa hypnorum					2										2
Planorbarius corneus					2										2
Planorbis planorbis		43	1	11	11	1						2			69
Planorbis (Planorbis) sp	1														1
Planorbis vorticulus									1		2	2	1		6
Planorbis vortex				2	9	2						2		1	16
Planorbis leucostoma	3	953	1	624	112	43		1		1	5	11	1	1	1756
Planorbis laevis					2										2
Planorbis albus					1										1
Planorbis crista		17													17
Planorbis contortus				19	18	2					1	1			41
Segmentina complanata					2		1				1				4
Segmentina nitida				2											2
Ancylus fluviatilis					3	1									4
Catinella arenaria				? 1											1
Succinea putris				1	38	7									46
Succinea pfeifferi		8		95	416	78		18	35	88	492	1537	246	71	3084
Succinea sp.		27													27
Cochlicopa lubrica		1		15	7	2						? 1			26
Columella columella							? 1								1
Vertigo antivertigo				3			1								4
Vertigo parcedentata				1			2								3
Vertigo angustior							1		1		? 1				3
Pupilla muscorum	5	34		3525	821	256		246	97	184	360	120	3	3	5654
Vallonia costata							1								1
Vallonia pulchella		? 4		44	54	5					1	2			110
Vallonia sp.	1			21	12							2	2		38
Hygromia hispida		2		354	380	47									783
Punctum pygmaeum											1	1			2
Euconulus fulvus				1											1
Agriolimax cf. *agrestis*		3			9						5	7			24
Agriolimax cf. *reticulatus*		4			4	1									9
Agriolimax sp.			1					2		2					5
Sphaerium corneum					14	3						2			19
Sphaerium lacustre		2													2
Pisidium amnicum					45							2	1		48
Pisidium casertanum		22		5	27						5				59
P. casertanum var *ponderosa*					14				1						15
Pisidium obtusale		146	? 1		1										148
Pisidium milium					1	2									3
Pisidium subtruncatum					6	1	1								8
Pisidium supinum					21										21
Pisidium henslowanum				1	41	4			2			23	2		73
Pisidium hibernicum					5										5
Pisidium nitidum					26	9						6	7	3	51
TOTAL	25	1729	6	4860	2500	530	10	272	142	286	1008	1867	316	84	13635

as this is the section exposing the Ipswichian–Devensian unconformity, which is only apparent in a complete break in molluscan assemblages and not in any marked lithological difference. It must not be assumed that WS is necessarily very early Devensian as its elevation suggests deposition in an overlapping series, possibly as floodplain deposition if one may judge from the very high proportions of the 'slum' species, *Planorbis leucostoma* and *Pisidium obtusale*.

(*a*) *WH*

This is the only section showing any real sequence of Mollusca, but even here it is limited to a thickness of 60 cm. In general terms there is a curious faunal mixture: associated with southern species, such as *Belgrandia marginata*, which is usually truly interglacial, *Bithynia inflata*, *Planorbis vorticulus* and *Vertigo angustior*, are isolated specimens of cold species such as *Vertigo parcedentata* and *Columella* ? *columella*. The numbers of the latter must be very small as they were only recovered from a bulk sample which was searched for rarities not found in the main sequence: hence the ten specimens listed from this sample only represent a very small fraction of its molluscan content. Quite typical of Devensian deposits are the high proportions of *Succinea pfeifferi* and *Pupilla muscorum*. The form of *S. pfeifferi* is var. *schumacheri* as it often is in deposits of this age both here and abroad. In fact the forms of *P. muscorum* and *S. pfeifferi* are identical with those excellently illustrated by van Regteren Altena (1957) from Velsen in the Netherlands, though this latter deposit is probably more recent (GrN-3007: 38300 ± 900 years) than anything at Wretton.

Ecologically the section is a shallow water or marsh deposit as suggested in figure 16. As the shallow depression in the Gault Clay was filled by aggradation the character of the Mollusca changes from a very high proportion of the xerophile, *Pupilla muscorum*, at the base to a very high proportion of marsh species at the top. The stable small percentage of clean water Mollusca indicates one or several very small streamlets meandering across the area. It is interesting to note that even in the upper part of the deposit at the side (B in figure 16) there is a high percentage of *P. muscorum* as at the base of the main section. Evidently conditions on the adjacent Gault were dry enough and open enough for this xerophilous species throughout.

(*b*) *WN*

It has already been mentioned that this section could be in either an old (B) or the youngest herb biozone. The Mollusca offer no help with this problem as there seem no differences of any magnitude between the faunas of WH and WUB which belong to these two herb biozones respectively. The two fossiliferous horizons of WN separated by 125 cm of sands are extraordinarily similar in their molluscan spectra (figure 17). There is one distinctly southern species, *Planorbarius corneus*, and this may mean a later date than WH, where there are more such species, but such a conclusion is by no means certain.

The two WN horizons represent the deposits of a small stream: the representation of moving-water species is appreciably higher than in WH, but is accompanied by larger numbers of marsh species (e.g. *Planorbis leucostoma* and *Lymnaea truncatula* among the freshwater species and *Succinea pfeifferi* among the land species), thus indicating some streamside marsh development. The high numbers of *Pupilla muscorum*, as in WH, again point to openness and dryness of the areas adjacent to the stream.

The great similarity between the two WN horizons points either to the persistence or repetition of the same environmental conditions or to rapid deposition: in fact, probably to both.

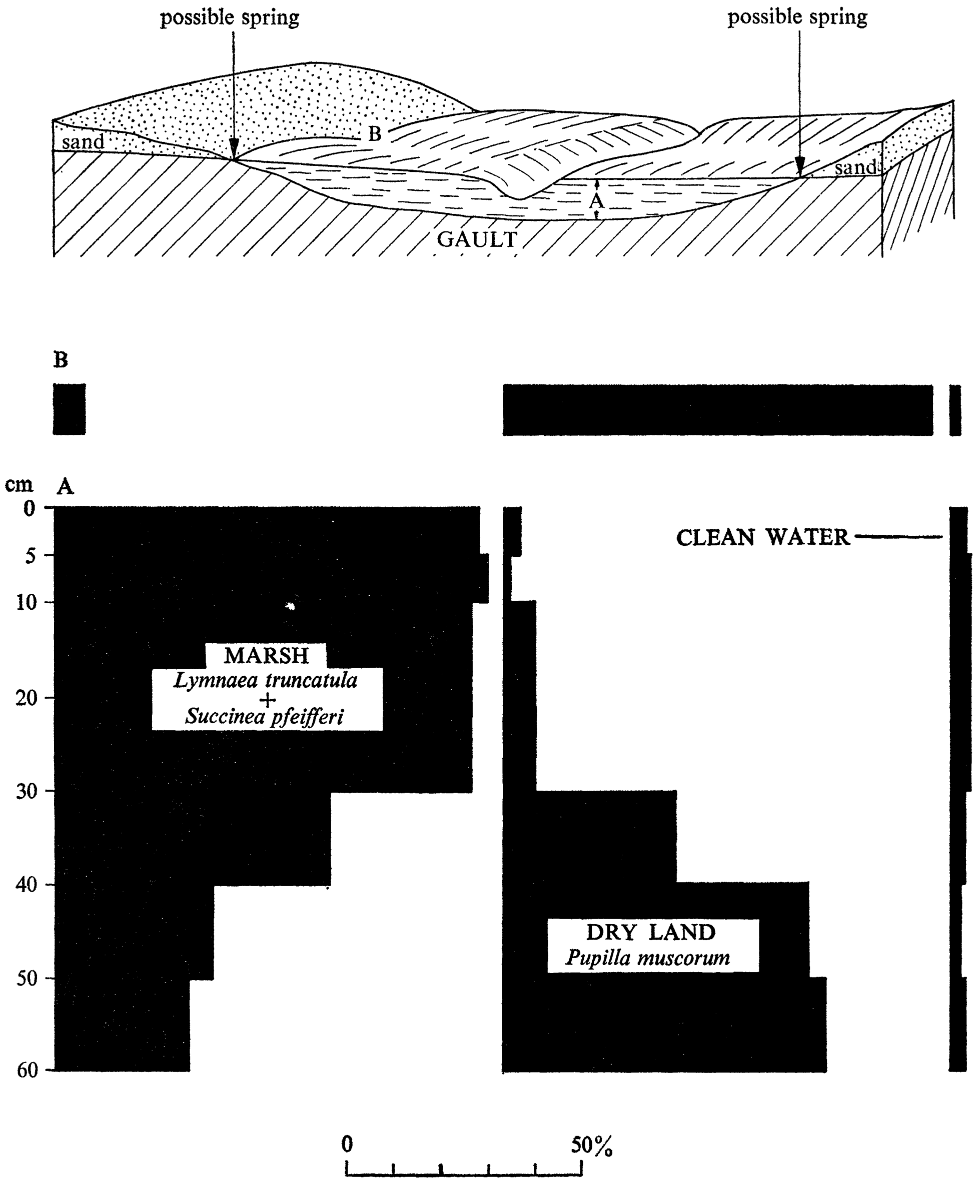


FIGURE 16. Interpretation of section WH in terms of Mollusca.

(*c*) *WUB*

In many ways this fauna is similar to those of WH and WN, perhaps slightly more akin to WN than to WH. Compared with WN the representation of southern species, in this case *Segmentina nitida*, is about the same and again less than in WH, while *Vertigo parcedentata*, a cold species, also appears, but as it was already present early in the Devensian in WH no conclusions of any significance can be drawn.

Compared with WN the representation of open-water species is reduced, while *Pupilla muscorum* rises to about 72 % of the total, so indicating a dominance of open dry environment only matched at the base of WH and from the side of the same deposit at the top. This is all highly consistent with the fact that WUB has the widest representation of open-ground, dry-plant taxa in the whole of the Wretton Devensian deposits.

FIGURE 17. Comparison of Mollusca from faunal horizons of WN.

(*d*) *WS*

The unconformity between the Ipswichian and the Devensian deposits has been illustrated before (Sparks & West 1970, figure 11, in which the notations WS 20 to 28 and WS 35 to 50 need to be transposed in each case to be correct). This deposit shows less dry-land influence than any of those discussed above, the proportion of *Pupilla muscorum* being down to 2 %. Clear, moving-water species, e.g. *Valvata piscinalis* and *Bithynia tentaculata*, are present but overwhelmed by 'slum' species, especially *Planorbis leucostoma* and *Pisidium obtusale*. This suggests a marshy area cut by a small stream or with an open pond removed to a considerable extent from dry-land influences. There are no traces of southern forms, neither are there specifically northern forms, so that, while the restricted fauna suggests adverse conditions, the Mollusca do not enable one to hazard a guess about the place of this deposit in the Devensian sequence.

6. The subdivision of the Devensian and the correlation of the Wretton deposits

(*a*) *The means of subdivision of the Devensian*

The subdivision of the Devensian (or any other cold or glacial stage) may be based on various criteria:

(1) Lithostratigraphy, by the description of a succession of lithological units.

(2) Biostratigraphy, by the description of a succession of biozones, which may be based on plant or animal fossils.

(3) Geomorphology, e.g. by the recognition of terrace sequences.

(4) A stratigraphy of 'environmental' events, e.g. glacial events, periglacial events, which effectively subsumes (1), (2) and (3).

(5) Geochronology, by the application of radiometric dating or varve analysis.

All these criteria are manifestations of the environmental changes, including the passage of time, which took place in the period between the reduction of forest at the end of the Ipswichian interglacial and its re-establishment in the Flandrian; and all need to be considered for the satisfactory definition of substages of the Devensian. However, the state of knowledge does not yet permit such an overall consideration through the length of the Devensian. We have the following situation under the five heads mentioned above:

(1) Lithostratigraphy. Local successions have been recognized, e.g. in the Cheshire Plain (Worsley 1967) Holderness (Catt & Penny 1966), and in the Wolverhampton region (Morgan 1973), but the successions are in their very nature local and correlations between regions are difficult.

(2) Biostratigraphy. Biozones (or assemblages) based on pollen, macroscopic plant remains and beetles have been described and successions of such biozones have been erected. Beetle biozones overlap pollen biozones (Coope, Morgan & Osborne 1971); the response to environmental change with each is naturally different. A July temperature curve (figure 18) has been suggested based on beetle assemblages (Coope *et al.* 1971). In the Netherlands a July temperature curve based on pollen biozones has also been put forward (figure 18).

(3) Terrace sequences, such as that of the Rivers Avon, Severn and Cam, are known from rivers in the glaciated area of England.

(4) Environmental events such as glacial advances and times of permafrost are known from the Devensian. The main glacial advance seems to be in the period 18000 to 15000 B.P. in the Late Devensian (see figure 18). Horizons of permafrost are known in the Early and Middle Devensian.

(5) Radiocarbon dating has been applied to its limits in the late Early Devensian (*ca.* 60000 B.P.).

Subdivision of the Devensian based on radiocarbon dating has been suggested (see page 400), and biozones have been correlated on the basis of such dating. No lithostratigraphical divisions of wide application are yet possible because of the wide regional variation in sequences. We

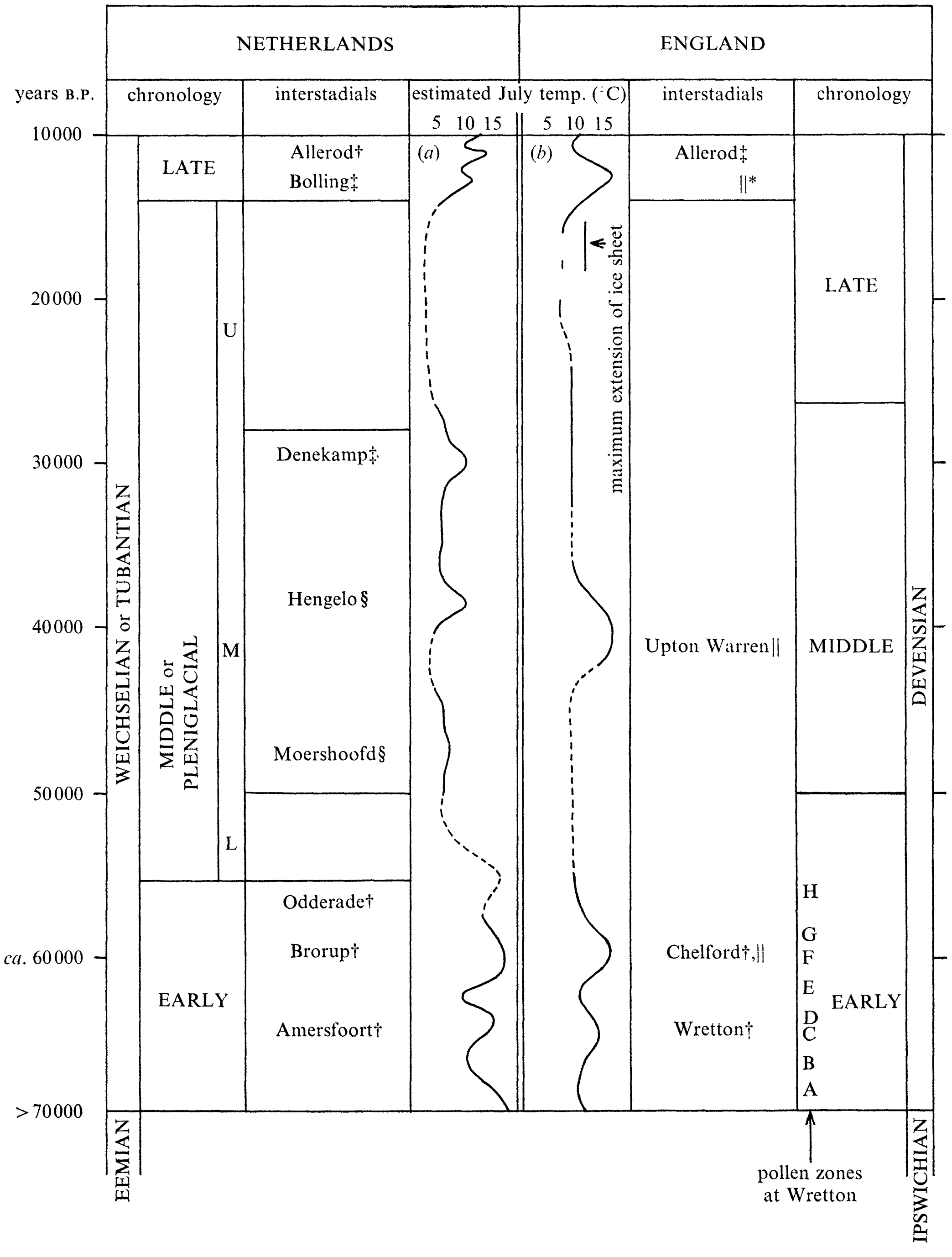


Figure 18. Chronology of the Weichselian in the Netherlands and the Devensian in England, showing the position of interstadials and the basis for their definition. †, pollen-based interstadial, woodland; ‡, pollen-based interstadial, shrub–tundra; §, pollen-based interstadial, tundra; ||, beetle-based interstadial; ||*, beetle-based interstadial of the Late Devensian (Coope *et al.* 1971). *a*, Curve based on palaeobotany; *b*, curve based on beetles back to the Chelford interstadial and below this on palaeobotany.

may note that such a lithostratigraphical division has been possible in the Netherlands (Van der Hammen & Wijmstra 1971), a periglacial area of reduced environmental diversity.

The search for the climatic history of the Devensian has led to the postulation of climatic events based on a particular line of evidence, e.g. interpretation of pollen biozones. Thus the sequence would be divided into stadial or interstadial events depending on the occurrence of herb vegetation or woodland respectively. But the way to a climatic sequence is through both all biological events and all geological events, and a synthesis of climatic history based on all lines of evidence is the aim. The difficulty here is the complexity of climatic change in terms of temperature and precipitation. The study of pollen biozones and beetle assemblages has led to the formulation of 'interstadials' which overlap or do not coincide in time (e.g. the Denekamp interstadial in the Netherlands and tundra beetle faunas in Britain; the Hengelo interstadial (pollen evidence) in the Netherlands and the Upton Warren interstadial (beetle and pollen evidence) in Britain; see figure 18).

The use of the term interstadial based on differing lines of evidence leads to a certain confusion. It would be useful to indicate with the term interstadial the evidence on which climatic amelioration is based; thus we might refer to pollen-based interstadials and beetle-based interstadials. Then when sufficient evidence of climatic history has been adduced formal Interstadials might be defined. There is the additional difficulty of defining what degree of climatic change signifies an interstadial, and what type of climatic change – temperature, rainfall, distribution of temperature, etc. The definition of interstadials shown in figure 18 illustrates the point. It might be better to omit the term interstadial altogether except in the final agreed synthesis, and use merely the biozone descriptions as a basis for stratigraphy. However, the term pollen-based interstadial is used in the following discussion of correlation of the Wretton deposits, as an informal term without a capital, indicating the presence of woodland.

(*b*) *Correlation of the Devensian sequence at Wretton*

(i) *Introduction*

Table 9 summarizes the stratigraphical and palaeobotanical sequences described in §§2 and 3. There is

(*a*) an initial herb period (pollen biozones A and B) preceding and contemporary with the main terrace aggradation of 3–4 m thickness;

(*b*) an a.p. period (pollen biozones C and D), with sediments in ground ice depressions;

(*c*) a middle herb period (pollen biozone E) with sediments in a ground ice depression;

(*d*) a further a.p. period (pollen biozones F and G) with sediments in a ground ice depression; and

(*e*) a final herb period (pollen biozone H) with sediments filling a large shallow pool near the present terrace surface.

The age of this sequence is evidently Devensian, for it forms a unity, with a characteristic flora and fauna, post-dating the Ipswichian interglacial sediments found in the flood relief channel. The Devensian cold stage, and its correlative stage on the continent, the Weichselian, has a complex history, with 'stadial' and 'interstadial' substages within it. We shall first attempt to place the Wretton sequence within the Devensian, then discuss the correlation with the continental Weichselian.

TABLE 9. DEVENSIAN VEGETATIONAL AND STRATIGRAPHICAL SEQUENCES AT WRETTON

pollen biozone (see table 3 for designation)	site	vegetation	substage		stratigraphy (horizontal boundaries uncertain)			
					terrace	periglacial effects	fossiliferous deposits	
H	WU, WUB, WX 1*	grassland	herb substage III		fluviatile deposition fluviatile deposition	involutions, ice wedges cover sand (WY)	muds of group 4 in large pool	
G	WG 10–25 cm	pine–birch–spruce heath	Chelford woodland substage (interstadial)	Early Devensian			basin filling (WG, WY)	group 3
F	WG 25–55 cm, WM, WY	pine–birch–spruce woodland						
E	WZ	grassland	herb substage II		fluviatile deposition	ground ice melts ground ice mounds (WG, WY) ground ice mound (WX east) ice-wedges (WJ)	basin filling (WZ)	
D	WJ 60–75 cm, WX 40–45 cm	birch–pine heath, alder	Wretton woodland substage (interstadial)		soil of WJ, WZ	ground ice melts (WZ) cover sand	basin filling (WJ, WX centre)	
C	WJ 100 cm	birch–pine woodland						
						ground ice melts ground ice mound, covers and (WJ, WX centre)		
B	WAB, WAG, WAH, WAL, WAD, WAE, WO*	grassland	herb substage I		main terrace aggradation	involutions at channel bases (e.g. WAD)	channel deposits of group 2	
A	WH	grassland, shrubs					basal muds of group 1	

* Samples from WN, WP, WQ may be in biozones B or H.

(ii) *Correlation with Devensian deposits in Britain*

In the absence of detailed stratigraphical sequences the Devensian is at present divided on a basis of radiocarbon years, as follows (Shotton & West 1969):

Late Devensian	26000–10000 B.P.
Middle Devensian	50000–26000 B.P.
Early Devensian	preceding 50000 B.P., including Chelford interstadial

The late-glacial part of the Late Devensian covers the period *ca.* 13000 to 10000 B.P. There are very many sequences which contain deposits of this period and as a result the environmental history at this time is well known in most parts of Britain. In the preceding part of the Devensian, however, the reverse is the case. There are not so many deposits known, and their age cannot always be determined closely by their stratigraphical position, so that radiocarbon dating has become the basis for erecting a sequence.

From the palaeobotanical point of view, the 'pre-13000' sites offer fragmentary evidence of vegetational history. Most often the sites are terrace gravel pits, with erratics or channel fillings of organic sediment. Pollen is often badly preserved or absent, while macroscopic remains may be abundant. There are thus few pollen diagrams of any depth from the pre-13000 Devensian in Britain, and it has therefore not been possible to discern more than a bare outline of vegetational history in this period.

At Wretton, however, there is a long sequence of vegetational history comprising both herb and woodland periods. The presence of the *Betula–Pinus–Picea* pollen biozones (F and G) in the middle of the sequence offers the clear possibility of a correlation with one of the few Devensian sites with a pollen diagram – that at Chelford, Cheshire (Simpson & West 1958). This Chelford pollen diagram shows a *Betula–Pinus–Picea* pollen assemblage biozone similar to that from biozone F at Wretton. This is the only such pollen biozone which has so far been found in the Devensian sequence, and it is reasonable therefore to correlate provisionally the Wretton pollen biozones F and G with the Chelford interstadial (which term is based on both pollen and beetle evidence). At Chelford a radiocarbon date has been obtained from tree stumps associated with the organic horizon 60800 ± 1500 years B.P. (GrN-1475).

This correlation means that the sediments of pollen biozones F and G and all horizons older than them are Early Devensian in age. Between the two lower herb periods there is the period with birch–pine woodland (pollen biozones C and D), indicating the presence of pollen-based interstadial conditions. No other site in the British Devensian shows evidence for vegetation of a similar type, and this pollen-based interstadial is named the Wretton interstadial.

The herb pollen spectra from Wretton resemble those from the few other sites investigated pollen-analytically, e.g.:

Colney Heath, Herts.	15360 ± 210 B.P. (Q-385), Godwin (1964)
Upton Warren, Worcs.	41900 ± 800 B.P. (GrO-1245), Coope, Shotton & Strachan (1961)
Earith, Hunts, site 9 and other sections	> 45000 B.P. (Birm-86), Bell (1970)

These sites are all in terraces and their pollen spectra show low a.p. frequencies (*Pinus* usually much better represented than *Betula*), with high frequencies of Gramineae, Cyperaceae and Compositae, and rich in the variety of n.a.p. taxa.

The macroscopic floras from these sites, and from other sites from which macroscopic floras have been obtained, belong to the so-called 'full-glacial' flora, and are generally similar in constitution to the macroscopic flora at Wretton. Examples of these other sites with a good flora are:

Barnwell Station, Cambridge	19500 ± 650 B.P. (Q-590), Bell & Dickson (1971)
Lea Valley, Herts.	28000 ± 150 B.P. (Q-25), Reid (1949)
Great Billing, Northants.	28225 ± 330 B.P. (Birm-75), Morgan (1969)
Brandon, Warwicks.	30766 ± 537 B.P. (Birm-27), Shotton (1968) 520 Kelly (1968) 32270 ± 1029 B.P. (Brim-10), Kelly (1968) 971
Syston, Leics.	37420 ± 1670 B.P. (Birm-78), Bell, Coope, Rice & Riley (1972) 1390
Earith, Hunts, site 7	42140 ± 1890 B.P. (Birm-88), Bell (1970) 1530
Sidgwick Avenue, Cambridge	'early-glacial' Lambert, Pearson & Sparks (1963)

These floras have been considered in detail by Bell (1968, 1969, 1970). This type of flora evidently occurred over a long time range in the Devensian, and it will be of interest to learn more of its differentiation in space and time.

In the Cambridge region two terraces are ascribed to the Ipswichian and Devensian (Sparks & West 1965). The High or Barnwell Terrace contains the Histon Road Ipswichian interglacial deposits. The Intermediate Terrace, some 6 m lower, contains the Sidgwick Avenue site (Lambert *et al.* 1963) with a rich flora and fauna. The Barnwell Station beds (19500 B.P.) contain a cold flora and a cold mollusc fauna and lie in a buried channel beneath the Cam. The Intermediate Terrace is considered to be 'early-glacial'. Unfortunately no pollen was found at Sidgwick Avenue, but the macroflora is similar in constitution and aspect to that at Wretton, with about 52 taxa of the 95 taxa at Sidgwick Avenue being found at Wretton. An interesting identification at Sidgwick Avenue was *Helianthemum canum* (L.) Baumg., based on many leaves, capsules and seeds. *Helianthemum* pollen was most common at Wretton in the earlier tundra period (WH), and it may be that the Sidgwick Avenue sediments and WH, both of which are the early sediments of an aggradation on the Gault, were formed at roughly the same time. This correlation would support the ascription already made of the Sidgwick Avenue flora and fauna, and the Intermediate Terrace, to an 'early-glacial' time.

Certain features of the mollusc faunas of the sites at Earith, Sidgwick Avenue and Wretton support these correlations. It must be said, however, that if there was only the evidence of the Mollusca, no sure correlation would be possible as it is highly likely that the molluscan faunas in the early parts of glacial periods will prove to have a similar restricted aspect and be dominated by local variations of the environment. These three deposits all lie topographically in terraces which have surfaces at about 4 m O.D. on the Fen margins and rise gently upstream. In addition, the aggradation of Devensian deposits directly on the eroded surface of the Gault at Wretton and Sidgwick Avenue is similar. Thus there is a convergence of evidence none of which is convincing on its own.

The Mollusca of these three sections have been listed together by Sparks (1964, table 1) and it is apparent that there is a broad similarity in the species concerned and in the presence in small numbers of southern species. Thus, at Wretton there are *Belgrandia marginata* (which also occurs at both other sites), *Bithynia inflata, Planorbarius corneus, Planorbis vorticulus* and *Segmentina nitida* (which occur at neither of the other sites), *Vertigo angustior* (which occurs at Sidgwick Avenue but not at Earith), while from Earith can be added *Acroloxus lacustris* and *Corbicula fluminalis* and from Sidgwick Avenue *Truncatellina cylindrica* and *Vallonia enniensis.* None of these is common at any site, but there are so many species that a hypothesis of contamination from Ipswichian interglacial deposits can probably be dismissed. Of particular interest is the fact that the *Corbicula* from Earith is a fragile juvenile less than 2 mm in diameter and not a battered adult. Adult shells are well known as derived shells – for example, on the northern shore of the Stour estuary at Stutton in Suffolk, where they are being derived from an Ipswichian brickearth and incorporated in a modern beach deposit. Thus all the sites in comparable topographical situations and with comparable floras have very similar associations of non-marine Mollusca.

(iii) *Correlation with the Weichselian sequence on the Continent*

The best-known sequence of the Weichselian is in the Netherlands. Figure 18 shows the Netherlands divisions, with summaries of the environmental history. It is based on the work of Zagwijn (1961), Zagwijn & Paepe (1968) and van der Hammen & Wijmstra (1971). The Odderade pollen-based interstadial of Averdieck (1967), known from a site in Schleswig-Holstein, is added to the sequence. The Brørup pollen-based interstadial is named after the Danish site described by Andersen (1961), with which a Netherlands pollen-based interstadial can confidently be correlated. Otherwise the names are of Netherlands origin.

In the Early Weichselian (EW) there are three pollen-based interstadials. The Amersfoort interstadial (radiocarbon date: GrN-1397 63500 ± 900 B.P., considered a minimal date; see van der Hammen, Maarleveld, Vogel & Zagwijn 1967) is represented by detailed pollen diagrams (Zagwijn 1961), as is the Brørup interstadial (Zagwijn 1961). The Odderade interstadial with pollen diagrams from Odderade (Averdieck 1967) may be present in the Netherlands (Zagwijn & Paepe 1968). At Odderade, the horizon ascribed to this interstadial lies above a horizon correlated with the Brørup interstadial. All these three Early Weichselian interstadials show high frequencies of a.p., mainly *Betula* and *Pinus* in all three, and *Picea* in the two younger ones. The interstadials are separated by stadials with high frequencies of n.a.p.

There are three pollen-based interstadial periods in the Middle Pleniglacial. These are represented by organic deposits with floras considered to be indicative of climatic amelioration, e.g. a change to shrub tundra from tundra. The Moershoofd interstadial complex (43000–

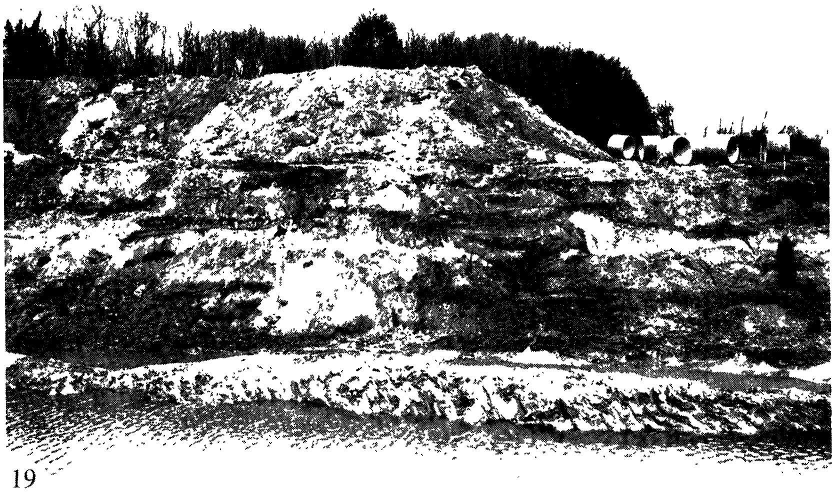
DESCRIPTION OF PLATE 19

FIGURES 19–21. Section WJ (see figure 5).

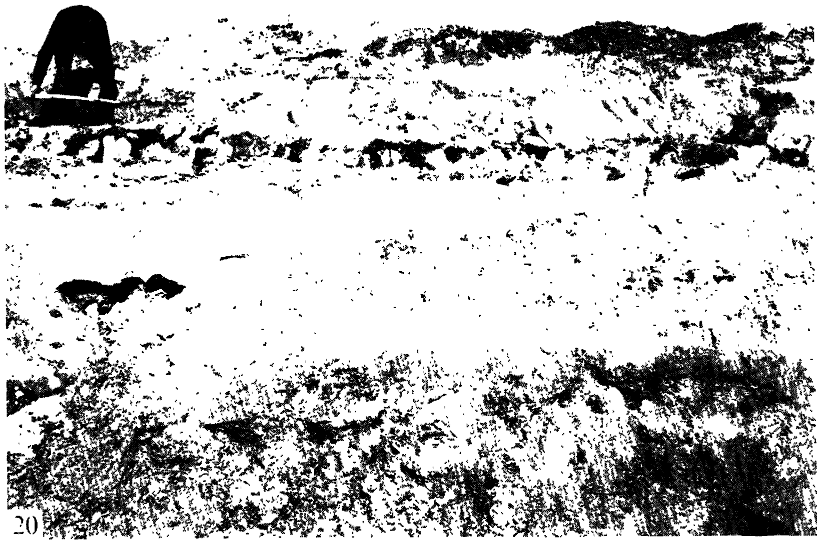
FIGURE 19. The whole length of the section, on the north side of the flood relief channel. The WJ basin and its two marginal ridges are seen to the right of centre. The upper mud of biozone H is seen on the left towards the top of the terrace surface. Professor Chmielewski, on the far right, is standing on the terrace/Gault Clay boundary.

FIGURE 20. Easting 0 m to easting 8 m. The involutions of the upper mud horizon are being exposed by Professor W. Chmielewski.

FIGURE 21. Easting 6 m to easting 12 m. In the centre is the western rim of the basin WJ.



19



20

21

FIGURES 19–21. For description see facing page.


22


23


24

FIGURES 22–24. For description see facing page.

50000 B.P.) shows pollen diagrams with high n.a.p.; the Hengelo interstadial (37000–39000 B.P.) shows increases in the steppe element (*Artemisia*) pollen frequencies, and the Denekamp interstadial (29000–32000 B.P.) increases in *Betula* pollen frequencies. Between these interstadials are sediments with pollen diagrams with high n.a.p., and above them (upper Pleniglacial) are barren inorganic sediments showing evidence of strong periglacial action (stone pavements, ice-wedge casts, etc.).

The Late Weichselian contains the Bølling pollen-based interstadial, showing an increase in *Betula* pollen frequencies, and the Allerød pollen-based interstadial with increases in *Betula* and *Pinus* pollen frequencies.

The correlation of the Wretton pollen biozones F and G with the Chelford interstadial has already been discussed. The Chelford interstadial, with its organic horizon indicating a period of coniferous forest with *Pinus*, *Betula* and *Picea* was correlated (Simpson & West 1958) with the Brørup interstadial (Andersen 1961), an interval with evidence for a similar type of forest. The major difference between the two is the absence of *Picea omorikoides*-type pollen at Chelford. This occurs in organic deposits correlated with the Brørup interstadial at Brørup, Odderade and Amersfoort. The Odderade interstadial at its type site also shows a lack of *P. omorikoides*-type pollen. It is possible that the Chelford and Wretton horizons concerned may be correlated with the Brørup or Odderade interstadials. Radiocarbon dates for the Brørup interstadial are 57700 ± 700 B.P. (GrnN-1729) and 59100 ± 700 B.P. (GrN-1470) and for Chelford 60800 ± 1500 B.P. (GrN-1475). Dates of > 53000 B.P. (GrN-4100) and 58100 ± 650 B.P. (GrN-4671) have been obtained from the Odderade interstadial. Further evidence is needed of the stratigraphical relations and age of the Odderade interstadial before it can be decided satisfactorily whether the Chelford and Wretton horizons are to be correlated with the Odderade or Brørup interstadials. We prefer the latter correlation for the present on the grounds that the Brørup interstadial appears to be more widely represented than the Odderade and therefore Chelford and Wretton are more likely to belong to this interstadial.

If this correlation is correct, it would seem reasonable to correlate the older interstadial at Wretton (pollen biozones C and D)with the Amersfoort interstadial (Zagwijn 1961). There is in fact some palynological evidence to support such a correlation. The tree representation is similar, with *Betula*, *Pinus* and *Alnus* predominant, and little *Picea* present. In certain of the Amersfoort interstadial pollen diagrams Ericales rises in the upper part of the diagrams, as at Wretton. A peak of Gramineae pollen is often present at the beginning of the Amersfoort interstadial (see WJ 75 cm), and Filicales (*Dryopteris thelypteris*-type spores of Zagwijn (1961)) are also shown on the Amersfoort pollen diagrams. Although it is probable that the presence of both these taxa are related to local environmental changes resulting in vegetation and sediment changes, it is interesting to note the similarity with the lower pollen-based interstadial at Wretton.

DESCRIPTION OF PLATE 20

FIGURES 22–24. Section WJ (see figure 5) (*continued*).

FIGURE 22. Easting 9 m to easting 17 m, showing the basin sediments of WJ.

FIGURE 23. Easting 13 m to easting 22 m, showing the eastern rim of the basin WJ.

FIGURE 24. Easting 22 m to easting 27 m, showing ice-wedge casts penetrating coversands and terrace sediments.

These correlations imply that the three herb periods at Wretton are to be correlated with the herb periods seen in the Netherlands before the Amersfoort interstadial (pollen biozone EW 1a Zagwijn 1961) between the Amersfoort and Brørup interstadials (EW II), and after the Brørup interstadial (PW). The pollen spectra for the latter two at Wretton and in the Netherlands are generally similar, with low frequencies of *Betula* and *Pinus*, high frequencies of Gramineae and/or Cyperaceae and a variety of n.a.p. taxa.

On the other hand the pollen diagrams from pollen biozone EW 1a in the Netherlands are entirely different from pollen diagrams of the earliest herb period at Wretton (pollen biozones A and B). The EW 1a diagrams show considerable frequencies of *Betula*, *Pinus* and Ericales. Zagwijn (1961) envisages a subarctic heath landscape, with a rather oceanic climate. In the correlative pollen biozones in Denmark (W 1, W 2a, b of Andersen (1961)), a heath of a similar type is deduced from the pollen diagrams (W 1), followed by a high n.a.p. phase (W 2a, b) more like those at Wretton; a similar heath zone is also seen in the correlative zone FW 1 at Odderade (Averdieck 1967). This heath vegetation is totally different from that indicated by Wretton pollen biozones A and B. At first sight it might seem that, even allowing for local differentiation of floras, it would be unlikely that they could be of the same age. But we note that EW 1a biozone of the Netherlands, the W 1 biozone of Denmark and the FW 1 biozone of Schleswig-Holstein show a close affinity with the final interglacial pollen biozones of their areas, the changes across the interglacial/glacial boundary indicating the opening out of the forest, a fall in *Picea* pollen frequencies and the spread of heath.

A similar effect can be noted if we compare the only site where late Ipswichian interglacial deposits (biozone Ip IV) are known, at Histon Road, Cambridge (Sparks & West 1959) and Wretton pollen biozones A and B. Many pollen taxa and macroscopic taxa are common to both. The pollen diagrams both have *Pinus* as the principle tree pollen type, and their n.a.p. list from both sites is rather similar. The main difference is the greater percentage of a.p., principally *Betula* and *Pinus*, at Histon Road. Of the 46 macrotaxa in biozone Ip IV at Histon Road, 28 are represented in the Wretton macroflora (see §8).

As in the Netherlands, Denmark and Schleswig-Holstein, therefore, the change from the flora of the temperate interglacial to the flora of the succeeding cold period is marked by a diminution of forest cover. The expansion of heath seen on the Continent is absent in our area, though there are low values of *Calluna* pollen and a seed of *Arctostaphylos uva-ursi* in biozone Ip IV at Histon Road.

If the correlations are correct, then, we might conclude that the differences between Wretton pollen biozones A and B and the continental biozones EW 1a, W 1 and FW 1 might indeed be the result of a differentiation of flora between our area and the Netherlands, northwest Germany and Denmark. Such a differentitaion might be related to climatic differences and edaphic differences. For example, the great contrast between the calcareous soils of the eastern margin of Fenland (see also §8) and the sandy soils of the Netherlands and on the drift of northwest Germany and west Jutland. The differentiation appears to have been lost in Denmark in the W 2a, b biozones immediately preceding the first interstadial and in the Netherlands and Schleswig-Holstein at the time of the Amersfoort interstadial and in the subsequent stadial and interstadial floras, as the comparison between the later Wretton pollen zones and the continental pollen zones shows.

7. Evidence of Devensian climates at Wretton

(a) *Geological evidence*

(i) *Involutions*

These occur in two horizons at Wretton. A lower one, with weak disturbance of the sediments, within the terrace sequence, at the base of the channels containing organic deposits (e.g. WAD, WAH, WAL, WAG) and a younger, much better developed series, seen in horizontal section as small polygons near the terrace surface (WU, WUB, WX). Involutions are the result of freeze/thaw cycles on sediments of different grain size and water content, and indicate the presence of an active layer over an impermeable horizon. The impermeability may be due to permafrost, but at Wretton the Gault Clay could have provided it, so that the involutions do not necessarily indicate permafrost. The two horizons then indicate periods of freeze/thaw activity on the terrace surface at two times. It has been estimated by Shotton (1962) that mean annual temperatures must be at least 7 °C lower than present, probably more to give sufficient strength to the freeze/thaw cycle to produce polygonal soils and involutions in Midland England.

(ii) *Ice-wedge casts*

Ice-wedges only develop in permafrost, and, according to Péwé (1966) in Alaska only in permafrost when mean temperatures are at or below −6 °C. In the Arctic ice-wedge polygons are widespread in river flood plains where the climate is continental. They are usually only found in sand when the water content is high (Shumskii 1959), as it must have been at Wretton, with sand resting on impermeable Gault Clay. Moreover, they are usually only found in sand and gravel in the more northern part of their distribution. Thus an estimate of −8 °C or lower would probably be nearer the mark. In northern Eurasia, active ice-wedges are present only in tundra in the western and eastern maritime areas, which have depressed summer temperatures. In the central, more continental area, with warmer summers up to summer mean monthly temperature of 19 °C, taiga is also present in the ice-wedge region.

At Wretton there are two ice-wedge horizons (tables 3 and 9), one in the interval between the two woodland substages and one subsequent to the deposition of the organic muds of group 4 (WU, WUB, WX) (pollen biozone H). The latter is associated with the upper series of involutions discussed above. We may infer that at these two times in the Devensian sequence, mean annual temperatures were at or below −8 °C, at least for some years.

(iii) *Ground ice mounds*

Evidence for the former existence of ground ice mounds is widespread in East Anglia (Sparks, Williams & Bell 1972). The development of ground ice mounds indicates freezing of the sediments in the terrace. The ground ice mounds at Wretton are not of the large, long-lived and perennial pingo types of the Arctic (see Shumskii 1959, Lundqvist 1969). It has been suggested (pp. 353 to 354) that they are either seasonal or small, short-lived perennial mounds, resulting from the formation of segregation and/or injection ice. The development of such mounds as these depends on azonal geomorphological and hydrological factors.

According to Shumskii (1959) seasonal ice injections occur mainly in the southern part of the permafrost region in the U.S.S.R. and almost completely disappear at high latitudes, where the active layer is thin. Perennial injections are most common where there is an outlet for sub-permafrost water and the permafrost is thin (that is, in the peripheral southern area of the permafrost region), also on the freezing of closed systems (pingos) throughout the permafrost region. Mounds associated with segregation ice also have a wide distribution in the permafrost area and in areas of severe winter freezing. In the absence of knowing whether the Wretton mounds are seasonal or perennial and having concluded that both segregation and injection ice may have played a part in them, we cannot make definite conclusions regarding their climatic significance, except that one or few successive winters were cold enough to facilitate formation of ground ice.

The process of formation envisaged, say for WJ (see pages 352 to 356), involved substantial amounts of injection ice. Either, then, there was seasonal freezing down to the Gault or there was permafrost down to the Gault, i.e. a development of thin permafrost. The first of these would require a considerable winter temperature drop, with an active layer of a few metres, implying also warm summers. The development of permafrost would require a climatic regime of the type described above; that is, with much lower mean temperatures.

Shumskii (1959) reported that seasonal injections are very rarely found outside the region of permafrost in the U.S.S.R. He mentions Kakakhstan only as an area where they are well developed. This is a region of very continental climate and low rainfall, with January mean temperatures of about −10 °C and July mean temperatures of 25 °C, a climate of the same type but probably more extreme than that which may have obtained at Wretton in the Devensian. The dry summers of such a climatic regime could have been the cause of the treelessness of the herb biozones. Otherwise seasonal mounds are much more commonly associated with springs in the permafrost region. It cannot therefore be concluded that the Wretton mounds are associated with permafrost.

The time of mound formation cannot be exactly determined. Table 9 shows the relation between the pollen biozones and the suggested times of mound formation, placed in the initial and second herb biozones in the sequence. As regards the melting of the mounds, the fills of three of them (WG, WJ and WX centre) contain woodland pollen assemblages, so that these mounds may have melted out to the accompaniment of woodland development. In WZ, however, the fill contains herb pollen spectra; this mound appears to have melted out under cooler conditions, perhaps after the exposure of the ice core by slumping of the cover.

The geological evidence therefore suggests periods of continental climate, with winter temperatures sufficiently below 0 °C for the formation of the ground ice mounds, and with mean annual temperatures at or below −8 °C at the times of ice-wedge formation.

(*b*) *Palaeobotanical evidence*

(i) *Herb biozones*

We have already compared the Wretton herb pollen spectra with recent spectra from the Arctic tundra (see pages 384 to 391) and mentioned similarities, with the conclusion that the Wretton spectra represent physiognomically a tundra† type of vegetation. Tundra at present occupies a wide range of climates, from those with rather mild winter to much more continental conditions such as those seen in northern U.S.S.R. Forest growth is limited by the low summer temperatures and insufficient length of growing season, so that the northern forest limit is thought to coincide with a line representing a daily mean temperature of 10 °C or more on 60 to 70 days of the year. Wretton lies at a much lower latitude than present Arctic tundra, and

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† The term here is used in a physiognomical sense. It is a Lappish word meaning the vast, nearly level regions of northern Russia and similar areas in Siberia and Alaska.

whatever the seasonal distribution of climate may have been, a longer growing period would be expected than farther north. Under such a situation the exclusion of tree growth might be due to a lack of summer warmth. Coope *et al.* (1971) have suggested on the basis of insect faunas of the cold periods of the Devensian that average July temperatures were as low as 10 °C, and such low temperature might have restricted tree growth. However, lack of tree growth could be caused by low rainfall and dry summers, without the summer temperatures being necessarily low. Such a climatic regime is widespread in the steppe of the U.S.S.R. The low frequencies of Ericales pollen suggests a continental rather than oceanic herb vegetation, and perhaps a conclusion can be drawn from the pollen evidence that the climate was continental, but that July temperatures were either below 10 °C if we favour low temperatures causing treelessness, or as much as 15–20 °C or even higher if we favour aridity as a cause of treelessness.

Either of these alternatives can be reconciled with the geological evidence, even though the times of ice-wedge formation and ground ice formation and of fossil preservation do not coincide.

Further evidence of climate may be obtained from the plant taxa identifications. The climatic interpretation of 'full-glacial' floras has been discussed by Bell (1969, 1970). The following plants, given in present distribution groups, of the Wretton list are of interest in a discussion of climate:

arctic-alpine or arctic:

Betula nana	1 fruit in WH
Lychnis alpina	5 seeds in WUB
Potentilla cf. *crantzii*	abundant in WH
Ranunculus hyperboreus	In WAD, WAB, WN, WQ, WP, and WUB
Thalictrum alpinum	2 achenes in WH

continental:

Artemisia (pollen)	high frequencies in WH; scattered records at other sites
Corispermum	1 seed in WH
Linum perenne	frequent in WH

southern (absent north of the Arctic Circle):

Berula erecta	1 fruit in WUB
Ceratophyllum cf. *submersum*	1 seed in WUB
Damasonium alisma	3 seeds in WUB
Diplotaxis tenuifolia	2 seeds in WAB, 4 in WN and 165 in WUB
Groenlandia densa	in WH, WAD, WN, WP, and WUB
Lycopus europaeus	1 nut in WH
Potamogeton crispus	WH, WUB

It will be seen that there is the mixture of distribution groups normal to Devensian floras. There is evidence for a strong continental element in WH (biozone A), further supporting the evidence for continentality of climate already discussed. In the deposits younger than WH, of the continental taxa named, only *Artemisia* is represented. It is not possible to say whether this is caused by a change in climate or by the fact that later floras are more representative of the terrace flora than the Gault flora. As *Artemisia* is represented in lower frequencies in younger sediments, the latter seems more likely. The continentality of the climate is also indicated by the presence of halphytes, which are characteristic of saline habitats induced by permafrost and drying winds, such as might be associated with the aridity of climate already discussed. The two groups following are those described by Bell (1969):

obligate halophytes:

Glaux maritima	10 seeds in WUB
Juncus cf. *balticus*	WAF and WUB
Polygonum oxyspermum	WN and WUB

facultative halophytes:

Armeria maritima	calyces in WH, WAD, WN, WUB; pollen in all herb spectra except WAG and WQ
Atriplex hastata or *patula*	WAG and WUB
Plantago maritima	1 capsule in WAG; pollen in all herb spectra, except WAD. High continuous values in WH
Potamogeton filiformis	WH, WAB, WQ, WUB
Potentilla anserina	WH, WAD, WAG, WN, WQ, WP, WU, WUB
Ranunculus sceleratus	WH, WN, WP, WUB
Zannichellia palustris	WAD, WAF, WP, WUB

These halophytic species occur through the oldest herb biozone, a few are present in the pollen spectra of the middle herb biozone, and they are again well represented in the youngest herb biozone, which is antecedent to the period of involution formation and ice-wedging.

Thus the flora of the herb biozones at successive horizons is generally similar. The same type of flora is also found at higher levels in the Middle Devensian (Bell 1970). No pollen-interstadials have been identified from this substage. However, on the basis of insect faunas Coope *et al.* (1971) have distinguished the Upton Warren interstadial (figure 18). The beetles indicate average July temperatues of at last 15 °C, an indication favouring the interpretation of lack of woodland in terms of summer aridity.

(ii) *Woodland biozones*

The climate of the Chelford interstadial was discussed by Simpson & West (1958). The palaeobotany indicated a mean annual temperature of 2 to −3 °C, with average January temperatures −10 to −15 °C and average July temperature 16 to 12 °C. Even if these deductions are perhaps too precise, a continentality of climate is suggested, with summers warm and wet enough for boreal forest growth. Evidence from the insect fauna (Coope 1959) pointed to a similar climatic regime. Any climatic inferences about the Wretton pollen-based interstadial have to be based on the few pollen spectra available. Woodland spread is indicated at this time, suggesting higher summer temperature average at above 10 °C in July. The strong rise of *Calluna* in this woodland biozone, and the frequencies of *Alnus*, might perhaps suggest a more oceanic situation than in the later Chelford interstadial. The high frequencies of *Calluna* suggest the disappearance of permafrost in the interstadial. The eastern limit of *Calluna* in north Europe is near the western permafrost limit.

(*c*) *Molluscan evidence*

Throughout the sections right into the youngest herb biozone there seems to have been the survival in small numbers of southern species of Mollusca: at the same time two species generally reckoned to indicate cold deposits, i.e. *Vertigo parcedentata* and *Columella columella* also occur. It should be noted that all the Mollusca are found in the herb biozones in the severer phases of the Devensian alongside evidence of waste mantle structures requiring considerable winter cold. This is difficult to understand as some of the southern species are freshwater, e.g. *Belgrandia marginata*, *Planorbarius corneus* and *Segmentina nitida*, which presumably could not withstand total freezing of the water they lived in. At present the first of these is confined to a restricted area in southern France, while the latter two do not go much farther north than the latitude of Stockholm at the present time in western Europe. But they both range into Russia and Siberia and in such a distribution may lie the key to their presence in the severer phases of the Devensian at Wretton. Perhaps they can resist cold winters provided that the summers are warm – a conclusion compatible with that derived from the plants and insects. In this connexion the high percentages of *Pupilla muscorum* through the herb biozones is probably significant, as this species is a characteristic dominant of European loess faunas.

(*d*) *Conclusions*

Both the geological and palaeobotanical evidence point to the presence of a continental climate with low mean temperatures at times (ice wedges), but not with necessarily very depressed summer temperatures.

The Mollusca also add support to the idea of continentality of climate. In the continental parts of the U.S.S.R. where Mollusca of the same species are found the winter temperatures are usually lower than those suggested for Wretton in the Devensian but the summers are warm. Most of these stations have winter temperatures of – 10 to – 20 °C but summer temperatures of 10 to 21 °C. Even Archangel has a range from a winter at about – 14 °C to a summer temperature of 15 °C, while the cold pole of the earth on northeast Siberia with winter temperatures of around – 50 °C has a summer temperature the same as that at Archangel.

These conclusions correspond with the combination of coldness and aridity emphasized by Ant (1969) in his general comments on Weichselian faunas. If this is accepted it may be necessary to emphasize the role of local hydrological conditions in the formation of the ground ice structures, but this would be in keeping with present trends in thought. It might also be suggested that the marsh and freshwater environments suggested for many of the sections is hardly compatible with aridity, but wherever one approaches the sides of the deposits aridity is evident, from the Mollusca in sections WH and WUB and from the plants in WUB. Further, if an analogy is useful, it might be mentioned that the extensive shallow-water bodies which physiographic and molluscan evidence can show to have existed in pluvial Quaternary phases in the Sahara seem to have been fringed by poorly vegetated areas. Much of the Wissey basin contains 'breckland' sands which might have added considerably to the arid component of the environmental mosaic.

These estimates of a continental climate tally with the conclusions of Coope *et al.* (1971), based on insect faunas of the Devensian, that a stable anticyclone system became established over eastern Britain, allowing an easterly air stream to displace the westerlies.

This system may have weakened during the pollen-based interstadials, allowing more oceanic conditions to prevail, with the consequent spread of woodland.

8. THE DEVELOPMENT OF THE FLORA, VEGETATION AND MOLLUSC FAUNA FROM THE IPSWICHIAN TO THE DEVENSIAN

(*a*) *Flora and vegetation*

Evidence for the history of flora and vegetation around the eastern fenland margin during the period late Ipswichian to early Devensian comes from the sites at Wretton (Sparks & West 1970) and from the Ipswichian interglacial deposits at Histon Road, Cambridge (Sparks & West 1959), 40 km south of Wretton. All the deposits concerned are terrace sediments, of the Rivers Wissey and the Cam, and although the environment conditions of deposition are varied within and between the sites, it is possible from a study of the pollen diagrams and macro lists to reconstruct the gross changes in flora and vegetation which took place at this time. Fossils are available from biozones Ip II and Ip III at Wretton, Ip III and Ip IV at Histon Road and the Devensian biozones at Wretton described in this paper. Although problems of redeposition occur at the top of Ip IV zone at Histon Road, these are not thought to affect the discussion greatly. The Ip biozone II pollen spectra at Wretton indicate the presence of mixed oak forest. In biozone Ip III at Wretton and Histon Road, this was replaced by *Carpinus–Quercus–Pinus* woodland, with increasing frequencies of n.a.p. In zone Ip IV at Histon Road, *Carpinus* and *Quercus* frequencies fall, *Betula* and *Pinus* are the best-represented trees, and n.a.p. reaches high values. The major difference in tree flora from the Early Devensian is the higher *Betula* pollen frequencies of Ip IV, and the better representation of thermophilous trees.

The retreat of the woodland in Ip III and Ip IV is shown by the considerable frequencies of n.a.p. in Ip III at Histon Road and Wretton and by the higher frequencies in Ip IV (48 to 88%) at Histon Road. At this site there is a wide variety of herb taxa, many common to the Early Devensian pollen diagrams at Wretton. Thus in Ip IV we see high frequencies of pollen of Gramineae, *Plantago media/major*, *P. maritima*, Caryophyllaceae, Compositae and Cruciferae. But there are also differences in the n.a.p. at the two sites. For example, at Histon Road in Ip IV *Centaurea scabiosa* (abundant), *Poterium sanguisorba* (abundant), *Butomus* and *Geranium* are present, but absent in the Early Devensian, while *Botrychium* and *Selaginella* are characteristic of the Early Devensian flora but absent in Ip IV.

The change from the Ipswichian to the Devensian shows, then, no great change in the physiognomy of the vegetation but changes in the constitution of the grassland vegetation which was apparently widespread at the time, with the loss of certain (but not all) taxa of a present temperate distribution in western Europe (e.g. *Poterium sanguisorba*, *Butomus*) and the addition of wide-ranging and more northern taxa. The continuity of many of the taxa considered characteristic of the Devensian is seen in table 10, which lists taxa identified on pollen and macro remains common to Ip II, III, IV and the Early Devensian. The habitats of these taxa vary from terrestrial to aquatic.

The changes of climate which led from the thermophilous woodland of Ip III to the herb vegetation of the Early Devensian thus hardly affected certain elements of the flora. The taxa identified are seed or pollen taxa and such identifications unfortunately do not at present allow us to determine whether biotypic variation took a major part in determining the survival of some taxa and not others.

The kind of changes which are seen at Histon Road and Wretton may not be typical of changes at the same time elsewhere in England. Both sites are on the eastern side of the Fenland, near the chalk escarpment and with deposits laid down by rivers draining the escarpment.

They are also both not far distant from the Fenland embayment in which the sea was present in the Ipswichian (Sparks & West 1970). They are also both in what is for England at the present time rather a climatically continental area with low rainfall. It is also known that the Cam Valley in the Ipswichian interglacial boasted a considerable fauna of large mammals (*Hippopotamus* at Barnwell), and that the Wissey Valley in the Early Devensian must have had a considerable fauna, very rich in *Bison*. Under these conditions of soil, climate and fauna, the presence of grassland in the valleys, and probably more regionally, is not surprising, and species

TABLE 10. SOME PLANT TAXA COMMON TO THE IPSWICHIAN ZONES IP II, III, IV AND THE EARLY DEVENSIAN

	Wretton				Histon Road				Wretton	
	Ip II		Ip III		Ip III		Ip IV		E D	
	m	p	m	p	m	p	m	p	m	p
Alisma plantago-aquatica	×	.	×	.	×	.	×	.	×	.
Armeria maritima	.	.	.	×	.	.	.	×	×	×
Artemisia	.	×	.	×	.	×	.	×	.	×
Atriplex hastata/patula	×	.	.	.	.	.	.	.	×	.
Berula erecta	×	.	×	.	.	.	.	.	×	.
Caltha palustris	×	.	×	.	.	.	.	×	×	.
Cerastium holosteoides	×	.	×	.	.	.	.	.	×	.
Eleocharis palustris	×	.	×	.	×	.	×	.	×	.
Euphorbia cyparissias	.	.	.	.	.	.	×	.	× (cf.)	.
Helianthemum	.	.	.	.	.	.	.	×	.	×
Hippuris vulgaris	×	.	.	.	×	.	.	.	×	.
Filipendula	.	×	.	×	.	×	.	×	.	×
Groenlandia densa	×	.	.	.	.	.	×	.	×	.
Linum perenne	.	.	.	.	.	.	×	.	×	.
Lycopus europaeus	×	.	×	.	.	.	×	.	×	.
Myriophyllum verticillatum	.	×	.	×	.	×	.	×	.	×
Nuphar luteum	×	×	.	.	.	.	.	.	×	.
Oenanthe aquatica	×	.	×	.	×	.	×	.	×	.
Plantago lanceolata	.	×	.	.	.	×	.	×	.	×
P. maritima	.	×	.	×	.	×	.	×	.	×
P. media/major	.	×	.	×	.	×	.	×	.	×
Polygonum aviculare	.	.	.	.	×	.	×	.	×	.
P. bistorta/viviparum	.	×	.	×	.	.	.	.	.	×
Potamogeton alpinus	×	.	×	.	.	.	.	.	×	.
P. crispus	×	.	.	.	.	.	.	.	×	.
P. filiformis	× (cf.)	.	.	.	.	.	.	.	×	.
P. natans	×	.	×	.	.	.	.	.	×	.
P. obtusifolius	×	.	.	.	.	.	.	.	×	.
P. pectinatus	×	.	.	.	.	.	×	.	×	.
Potentilla anserina	.	.	.	.	×	.	×	.	×	.
Ranunculus acris	×	.	×	.	× (cf.)	.	× (cf.)	.	×	.
R. lingua	×	.	×	.	× (cf.)	.	× (cf.)	.	×	.
R. repens	×	.	×	.	× (cf.)	.	.	.	×	.
R. sceleratus	×	.	×	.	.	.	×	.	×	.
R.-Batrachium	×	.	×	.	×	.	×	.	×	.
Rorippa islandica	.	.	.	.	×	.	×	.	×	.
Rumex acetosella	.	×	.	.	.	.	.	.	×	.
Scirpus lacustris	×	.	×	.	×	.	×	.	×	.
Sparganium erectum	×	.	×	.	×	.	×	.	×	.
Urtica dioica	×	.	×	.	×	.	×	.	×	.
Valeriana officinalis	×	.	.	.	.	.	.	×	×	.
Zannichellia palustris	×	.	×	.	×	.	×	.	×	.

m, macro; p, pollen.

of grassland, of disturbed habitats and of maritime distribution found at Histon Road and Wretton would have opportunity for survival from the temperate to cold climate.

The comparison between the Wretton and Histon Road floras emphasizes the difficulty of defining a satisfactory stage boundary at the end of the Ipswichian.

(*b*) *Mollusca*

The general distribution of non-marine Mollusca through the Ipswichian interglacial into the succeeding Devensian has been considered before (Sparks 1964). Although the rich full interglacial faunas of zones Ip II and Ip III found in sites such as the Wretton interglacial sections; Bobbitshole; Stutton; Histon Road, Cambridge; Trafalgar Square, London; Ilford and Selsey do not survive into the Devensian sites marginal to the Fens at Wretton, Earith and Sidgwick Avenue, Cambridge, some elements of it do, as has been stressed earlier in this paper. In fact the fauna at Wretton has more affinity with the Ipswichian fauna than with the cold, loess-type faunas with *Piuplla muscorum*, *Vertigo parcedentata* and *Columella columella* found at many Late Devensian sites. This suggests that there must have been an extremely adverse phase, either very dry or very cold or both, during which the Ipswichian fauna was largely eliminated, but that this phase is not represented in the Wretton deposits unless by the uppermost, unfossiliferous, cryoturbated parts of the deposit. This means that the climate extreme of the Devensian is likely to have occurred late in that glacial period.

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REFERENCES

Aario, L. 1940 Waldgrenzen und subrezenten Pollenspektren in Petsamo Lappland. *Suomal Tie deakat Toin.* **54**, 1–120.

Andersen, S. T. 1961 Vegetation and its environment in Denmark in the Early Weichselian glacial (last glacial). *Danm. geol. Unders.* II Raekke, no. 75.

Ant, H. 1969 Zur Würm-glazialen Überdauerung europäischer Landgastropoden in Eisrandnähe. *Malacologia* **9**, 249–50.

Averdieck, F.-R. 1967 Die vegetationseutwicklung des Elm-interglazials und der Frühwürm-interstadiale von Odderade/Schleswig-Holstein. *Fundamenta* **2**, 101–125.

Bartley, D. D. 1967 Pollen analysis of surface samples of vegetation from Arctic Quebec. *Poll. Spor.* **9**, 101–105.

Bell, F. G. 1968 Weichselian glacial floras in Britain. Ph.D. dissertation, University of Cambridge.

Bell, F. G. 1969 The occurrence of southern, steppe, and halophyte elements in Weichselian (Last Glacial) floras from southern Britain. *New Phytol.* **68**, 913–922.

Bell, F. G. 1970 Late Pleistocene floras from Earith, Huntingdonshire. *Phil. Trans. R. Soc. Lond.* B **258**, 347–378.

Bell, F. G., Coope, G. R., Rice, T. J. & Riley, T. H. 1972 Mid-Weichselian fossil-bearing deposits at Syston Leicestershire. *Proc. Geol. Ass. Lond.* (in the Press).

Bell, F. G. & Dickson, C. A. 1971 The Barnwell Station Arctic flora: a reappraisal of some plant identifications. *New Phytol.* **70**, 627–638.

Borrill, M. 1956 A biosystematic study of some *Glyceria* species in Britain. *Watsonia* **3**, 291–298.

Böcher, T. W., Holmen, K. & Jacobsen, K. 1968 *The flora of Greenland.* Copenhagen: P. Haase.

Catt, J. H. & Penny, L. F. 1966 The Pleistocene deposits of Holderness, East Yorkshire. *Proc. Yorks. Geol. Soc.* **35**, 375–420.

Coope, G. R. 1959 A Late Pleistocene insect fauna from Chelford, Cheshire. *Proc. R. Soc. Lond.* B **151**, 70–86.

Coope, G. R., Morgan, A. & Osborne, P. J. 1971 Fossil Coleoptera as indicators of climatic fluctuations during the Last Glaciation in Britain. *Palaeogeog. Palaeoclimatol. Palaeoecol.* **10**, 87–101.

Coope, G. R., Shotton, F. W. & Strachan, I. 1961 A Late Pleistocene fauna and flora from Upton Warren, Worcestershire. *Phil. Trans. R. Soc. Lond.* B **244**, 379–421.

Dandy, J. E. 1958 *List of British vascular plants.* London: British Museum (N.H.) and B.S.B.I.

Dickson, C. A. 1970 The study of plant macrofossils in British Quaternary deposits. In *Studies in the vegetational history of the British Isles* (eds D. Walker & R. G. West). Cambridge University Press.

Dickson, C. A., Dickson, J. H. & Mitchell, G. F. 1970 The Late-Weichselian flora of the Isle of Man. *Phil. Trans. R. Soc. Lond.* B **258**, 31–79.

Fredskild, B. 1967 Palaeobotanical investigations at Sermermiut, Jacobshavn, West Greenland. *Meddr Grønland* **178**, no. 4, 1–54.

Friedman, G. M. 1961 Distinction between dune, beach and river sand from their textual characteristic. *J. sed. Petrol.* **31**, 514–529.

Godwin, H. 1956 *History of the British Flora.* Cambridge University Press.

Godwin, H. 1964 Late-Weichselian conditions in southeastern Britain: organic deposits at Colney Heath, Herts. *Proc. R. Soc. Lond.* B **160**, 258–275.

Harland, W. B. *et al.* 1972 A concise guide to stratigraphical procedure. *Jl geol. Soc.* **128**, 295–305.

Hedberg, H. D. 1972 Summary of an international guide to stratigraphic classification, terminology and usage. *International Subcommission on Stratigraphic Classification*, report no. 7b.

Jermy, A. C. 1967 *Carex* section *Carex*. *Proc. Bot. Soc. Br. Isl.* **6**, 375–379.

Jessen, K. & Milthers, V. 1928 Stratigraphical and palaeontological studies of interglacial freshwater deposits in Jutland and north-west Germany. *Danm. geol. Unders.* II Raekke, no. 48.

Katz, N. J., Katz, S. V. & Kipiani, M. G. 1965 *Atlas and keys of fruits and seeds occurring in the Quaternary deposits of the U.S.S.R.* (In Russian.) Moscow: Nauka.

Kelly, M. R. 1968 Floras of Middle and Upper Pleistocene age from Brandon, Warwickshire. *Phil. Trans. R. Soc. Lond.* B **254**, 387–400.

Kuprianova, L. A. 1951 Issledovaniya pyl'tsy i spor s poverkhnosti pochvy iz vysokoshirotnykh raionov arktiki. *Bot. Zh., Kyyw* **36**, 258–269.

Lambert, C. A., Pearson, R. G. & Sparks, B. W. 1963 A fauna and flora from Late Pleistocene deposits at Sidgwick Avenue, Cambridge. *Proc. Linn. Soc. Lond.* **174**, 13–29.

Lavrenko, E. M. & Sochavy, V. B. 1956 *Descriptio vegetationis U.R.S.S.* Moscow–Leningrad: Editio Academiae Scientarum URSS.

Lichti-Federovich, S. & Ritchie, J. C. 1965 Contemporary pollen spectra in central Canada. II. The forest grassland transition in Manitoba. *Poll. Spor.* **7**, 63–87.

Lichti-Federovich, S. & Ritchie, J. C. 1968 Recent pollen assemblages from the western interior of Canada. *Rev. Palaeobot. Palynol.* **7**, 297–344.

Livingstone, D. A. 1955 Some pollen profiles from arctic Alaska. *Ecology* **36**, 587–600.

Lundqvist, J. 1969 Earth and ice mounds: a terminological discussion. In *The periglacial environment* (ed. T. L. Péwé), pp. 203–215. Montreal: McGill–Queens University Press.

Maarleveld, G. C. 1960 Wind directions and coversands in the Netherlands. *Biol. Peryglacjalny* **8**, 49–58.

Mackay, J. R. 1963 *The Mackenzie delta area, N.W.T.* Memoir 8, Geographical Branch, Mines and Technical Survey, Ottawa.

Morgan, Alan 1973 The Pleistocene geology of the area north and west of Wolverhampton, Staffordshire, England. *Phil. Trans. R. Soc. Lond.* B **265**, 233–297.

Morgan, Anne 1969 A Pleistocene fauna and flora from Great Billing, Northamptonshire, England. *Opusc. Entomol.* **34**, 109–129.

Nilsson, O. & Hjelmquist, H. 1967 Studies on the nutlet structure of south Scandinavian species of *Carex* *Bot. Notiser* **120**, 460–485.

Ockendon, D. J. 1971 Taxonomy of the *Linum perenne* group in Europe. *Watsonia* **8**, 205–235.

Péwé, T. L. 1966 Palaeoclimatic significance of fossil ice wedges. *Biol. Peryglacjalny* **15**, 65–73.

Porsild, A. E. 1958 Geographical distribution of some elements in the flora of Canada. *Geogr. Bull.* **11**, 57–77.

Reid, E. M. 1949 The Late Glacial flora of the Lea Valley. *New Phytol.* **48**, 245–252.

Ritchie, J. C. & Lichti-Federovich, S. 1967 Pollen dispersal phenomena in arctic–subarctic Canada. *Rev. Palaeobot. Palynol.* **3**, 255–266.

Rønning, O. I. 1960 The vegetation and flora north of the Arctic Circle. *Tromsø Museums Skr.* **8**, 50–72.

Shaw, K. 1959 Determination of organic carbon in soil and plant material. *J. Soil. Sci* **10**, 316–326.

Shotton, F. W. 1962 The physical background of Britain in the Pleistocene. *Adv. Sci.* **19**, 1–14.

Shotton, F. W. 1968 The Pleistocene succession around Brandon, Warwickshire. *Phil. Trans. R. Soc. Lond.* B **254**, 401–415.

Shotton, F. W. & West, R. G. 1969 Stratigraphical table of the British Quaternary. *Proc. Geol. Soc. Lond.* **1656**, 155–157.

Shumskii, P. A. 1959 Podzemnye L'dy. In *Usnovy Geokriologij*, Part I (ed. P. F. Shoezov). S.S.S.R.: Akademia Nauk.

Shumskii, P. A. 1964 *Principles of structural glaciology.* New York: Dover Publications.

Simpson, I. M. & West, R. G. 1958 On the stratigraphy and palaeobotany of a late-Pleistocene organic deposit at Chelford, Cheshire. *New Phytol.* **57**, 239–250.

Sjörs, H. 1956 *Nordisk Växtgeografi.* Stockholm: Svenska Bokförlaget.

Sparks, B. W. 1964 The distribution of non-marine Mollusca in the last interglacial in south-east England. *Proc. malac. Soc. Lond.* **36**, 7–25.

Sparks, B. W. & Lambert, C. A. 1961 The post-glacial deposits at Apethorpe, Northamptonshire. *Proc. malac. Soc. Lond.* **34**, 302–315.

Sparks, B. W. & West, R. G. 1959 The palaeoecology of the interglacial deposits at Histon Road, Cambridge. *Eiszertalter Gegenw* **10**, 123–143.

Sparks, B. W. & West, R. G. 1965 The relief and drift deposits. In *The Cambridge region* (ed. J. A. Steers), pp. 18–40. Cambridge: British Association for the Advancement of Science.

Sparks, B. W. & West, R. G. 1970 Late Pleistocene deposits at Wretton, Norfolk. I. Ipswichian interglacial deposits. *Phil. Trans. R. Soc. Lond.* B **258**, 1–30.

Sparks, B. W., Williams, R. B. G. & Bell, F. G. 1972 Presumed ground-ice depressions in East Anglia. *Proc. R. Soc. Lond.* A **327**, 329–343.

Srodon, A. 1960 Pollen spectra from Spitsbergen. *Folia Quaternaria* **3**, 1–17.

Styles, B. T. 1962 The taxonomy of *Polygonum aviculare* and its allies in Britain. *Watsonia* **5**, 177–214.

Troels-Smith, J. 1955 Characterization of unconsolidated sediments. *Danm. geol. Unders.* IV Raekke, **3**, no. 10.

Tutin, J. G. *et al.* 1964 *Flora Europaea*, vol. 1. Cambridge University Press.

van der Hammen, T., Maarleveld, G. C., Vogel, J. C. & Zagwijn, W. H. 1967 Stratigraphy, climatic succession and radiocarbon dating of the last glacial in the Netherlands. *Geologie Mijnb.* **46**, 79–95.

van der Hammen, T. & Wijmstra, T. A. 1971 The upper Quaternary of the Dinkel Valley. *Med. Rijks. geol. Dienst.* **22**, 55–214.

van Regteren Altena, C. O. 1957 The excavation at Velsen, 5. Pleistocene Mollusca. *Verh. ned. geol.-mijnb., Genoot.* **17**, 121–138.

Vogel, J. C. & Zagwijn, W. H. 1967 Groningen Radiocarbon Dates: VI. *Radiocarbon* **9**, 63–106.

Wenner, C.-G. 1947 Pollen diagrams from Labrador. *Geogr. Annlr* **29**, 137–374.

West, R. G., Lambert, C. A. & Sparks, B. W. 1964 Interglacial deposits at Ilford, Essex. *Phil. Trans. R. Soc. Lond.* B **247**, 185–212.

Worsley, P. 1967 Problems in naming the Pleistocene deposits of the northeast Cheshire Plain. *Mercian Geol.* **2**, 51–55.

Zagwijn, W. H. 1961 Vegetation, climate and radiocarbon datings in the Late Pleistocene of the Netherlands. I. Eemian and Early Weichselian. *Meded. geol. Sticht.* **14**, 15–45.

Zagwijn, W. H. & Paepe, R. 1968 Die stratigraphie der Weichselzeitlichen Ablagerungen der Niederlande und Belgiens. *Eiszeitalter u Gegenw.* **19**, 129–146.

Appendix 1. Report on the Coleoptera from Wretton

By G. R. Coope

Most of the remains of fossil Coleoptera discussed here were obtained by Mr B. W. Sparks in the course of the extraction of the Mollusca. They come from only a limited number of the organic sites at Wretton. The fossils are housed in the Quaternary Entomological collections at the Department of Geology, University of Birmingham.

In table 1 the numbers in each column represent the minimum number of individuals in the samples from each horizon. Although the numbers are small there is a marked difference between the assemblages in samples allocated to pollen biozones A, B and H, interpreted from the pollen data as grassland, and pollen biozones F and G which have been interpreted as indicative of woodland. The relative numbers of fossils from the various horizons cannot be taken as a measure of faunal abundance except in the case of site WG where the samples were processed specially for the recovery of insect fossils. The seeming richness of this site is thus merely a reflection of the greater thoroughness with which it was searched for insect fossils.

Environmental implications of the fossil Coleoptera

The fossil assemblages of Coleoptera fall naturally into two groups. The first of these includes the assemblages from pollen biozones A, B and H and is characterized by abundant Curculionidae (weevils) and few representatives of other families of Coleoptera. The second group comprises the assemblages from pollen biozones F and G and is characterized by the relative abundance of Carabidae and Byrrhidae and the rarity of weevils. The environmental implications of these two groups will be discussed separately.

Table 1. Occurrences of fossil species of Coleoptera from selected sites at Wretton

The numbers indicate the minimum number of individuals of each species in the samples from the different horizons. The numbers shown in parentheses under site WG indicate the occurrence of species in the repeat series of samples from this site.

	pollen biozone A					pollen biozone B		pollen biozones F–G					pollen biozone H	
								F			F/G	G		
	WH					WAB	WN	WG					WU	WUB
	50–60	40–50	30–40	10–30	5–10			50–60	40–50	30–40	20–30	10–20		
Carabidae														
Notiophilus aquaticus (L.)	.	.	.	?	.	.	.	1 (1)	1 (2)	1 (0)	.	.	.	.
Elaphrus cupreus Dufts.	.	.	2	.	.	.	.	.	.	.	.	.	.	.
Bembidion dauricum Motch.	.	.	.	.	.	.	.	1 (3)	1 (0)	.	.	.	.	.
Amara alpina (Pk.)	.	.	.	.	.	.	.	1 (1)	0 (1)	.	.	.	.	.
A. quenseli (Sch.)	.	.	.	.	.	.	.	? (1)	.	.	.	.	.	.
Hydrophilidae														
Helophorus aquaticus (L.)	.	.	.	.	.	.	.	0 (1)	0 (2)	.	.	.	.	.
H. jacutus Popp.	.	.	.	.	.	.	.	.	0 (1)	.	.	.	.	.
H. obscurellus Popp.	.	.	.	.	.	.	.	0 (2)	2 (20)	0 (2)	0 (2)	0 (1)	.	.
Cercyon sp.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Silphidae														
Thanatophilus sp.	.	.	.	.	.	.	.	.	0 (1)	.	.	.	.	.
Staphylinidae														
Olophrum fuscum (Grav.)	.	.	.	?	1	?2	.	.	0 (1)	.	.	.	.	.
Arpedium brachypterum (Grav.)	.	.	.	.	.	.	.	0 (1)	.	0 (1)	.	.	.	.
Dryopidae														
Dryops ernesti Des G.	1	1	1	.	.	.	.	.	.	.	.	.	.	.
Byrrhidae														
Simplocaria metallica Sturm	.	.	.	.	.	.	.	.	0 (2)	2 (0)	0 (1)	.	.	.
Morychus aeneus (F.)	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Byrrhus fasciatus (Forst.) or *arietinus* Steff.	.	.	.	.	.	.	.	0 (1)	1 (1)	1 (0)	1 (0)	.	.	.
Syncalypta cyclolepidia Munst.	.	.	.	.	.	.	.	.	0 (1)	.	.	.	.	.
Scarabaeidae														
Aphodius sp.	.	1	1	.	.	.	.	0 (1)	2 (2)	0 (1)	.	0 (1)	.	.
Aegialia sabuleti (Pz.)	1	.	1	.	.	.	.	.	.	.	.	.	.	.
Curculionidae														
Apion sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Otiorrhynchus arcticus (F.)	.	.	1	4	.	1	.	.	.	.	.	.	.	7
O. nodosus (Muell.)	.	.	.	.	.	.	1	.	.	.	.	.	.	.
O. ligneus (Ol.)	.	.	.	.	.	.	.	.	.	.	.	.	.	2
O. politus (Gyll.)	.	1	3	6	.	.	1	.	.	.	.	.	.	.
Sitona lepidus (Gyll.)	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Notaris bimaculatus (F.)	.	1	.	.	.	.	.	1 (1)	1 (2)	.	.	1 (0)	.	.
N. acridulus (L.)	.	.	.	.	.	.	1	.	.	.	.	.	1	.
N. aethiops (F.)	.	1	.	.	.	.	1	.	.	.	.	.	1	1

Group 1 *assemblages.* The abundance of weevils in these assemblages suggests that the local environment at these times was well vegetated. Unfortunately most of the species are polyphagous and thus little can be said about the specific composition of the flora. However, no obligate woodland species are present here in contrast to the faunas of forested interglacial episodes. Taken as a whole the Group 1 assemblages indicate open, rather marshy grassland with a sandy soil. The Coleoptera provide no evidence of truly aquatic habitats at this time.

The Group 1 beetles provide little evidence of the climate at these times. All the species are still living in the British Isles with the single exception of *Otiorrhynchus politus*, the western extremity of whose range extends from the southern parts of the Kola peninsula, across eastern Fennoscandia and into eastern Europe. Three species, *Otiorrhynchus arcticus*, *O. nodosus* and *Notaris aethiops*, are northern species today and suggest that the climate was cool, though from the limited beetle data there is no evidence that we are dealing here with a tundra environment. The relative abundance of phytophagous Coleoptera in these assemblages is in fact contra-indicative of very cold conditions (Anne Morgan 1970). The rather anomalous occurrence of the relatively southern species *O. ligneus* in pollen biozone H is of dubious significance since it has been found in several assemblages of fossil Coleoptera from deposits that can be allocated to the middle of the Last Glaciation, in company with numerous exclusively high northern species. In summary, the climate of pollen biozones A, B and H seems to have been cool but probably not of arctic severity and of moderate continentality, not more extreme than that found in north-eastern Europe at the present day.

Group 2 *assemblages.* The Coleoptera from pollen biozones F and G were of such outstanding interest that it was important to determine to what extent the specimens found in the first samples were an adequate sample of the fauna of the times. An additional series of samples from site WG was therefore washed specifically for insect remains. Each of these samples weighed approximately 0.25 kg, except for level 40 to 50 from which 1 kg was obtained. The beetle species from this second series were essentially the same as those from the original samples. The abundance of *Helophorus obscurellus* in sample WG 40 to 50 of the second series is partly explicable as a result of the largeness of this sample and partly because this species can be easily overlooked by a non-specialist observer. The close resemblance between the fossil assemblages from these two series of samples strongly suggests that the adequate sample of the beetle fauna of the times was, in fact, obtained. Thus the smallness of the list of species from this site seems to be a real indication of the restriction of the beetle fauna during pollen biozones F and G.

The picture which then emerges of the local environment from a study of the beetle data is one of extreme barrenness. The four species of carnivorous ground beetles, the Carabidae, are all animals of open, rather bare country with thin patchy vegetation. *Bembidion dauricum* and *Amara quenseli* are xerophilous, while *Amara alpina* and *Notiophilous aquaticus* are rather mesophilous. *A. quenseli* is characteristic of loose sandy substrates. The hydrophilid species *Helophorus obscurellus*, the most abundant species and the only one to be found in all horizons sampled, is one of the least water-dependent species of this genus and seems to prefer sandy places, where it has been found under stones or withered grass (Angus 1970). *H. aquaticus* and *H. jacutus* are both species of temporary puddles and do not require either deep or permanent water.

There is little evidence from the beetles of the nature of the scant vegetation. The Byrrhid beetles are obligate moss feeders and are here well represented to the almost complete exclusion of all other phytophagous species. Of particular interest is *Syncalypta cyclolepidia*, which is also a species of sandy places. The moss would have provided habitats for the omaliine Staphilinidae, *Olophrum fuscum* and *Arpedium brachypterum*, which live on the arthropod microfauna in moss or vegetable debris. Only one weevil is present in this assemblage and that, *Notaris bimaculatus*, is associated with reeds, particularly *Typha latifolia.*

The beetle fauna thus provides evidence of two habitats: a barren sandy landscape with little vegetation other than moss and a reedy swamp with only transient aquatic habitats. In this context it is interesting to note that there were no remains of chironomid larvae (flies with aquatic larvae, very common in all ponds and lakes) in any of the samples investigated. Since most of the species are unlikely to have actually lived at the site of sedimentation it seems likely that they represent the 'sweepings of the landscape' brought together either by the wind, perhaps in snow drift during the winter, and deposited at the site during the spring thaws, or washed together during times of flood. The environmental consistency of this assemblage suggests that the barren habitats described above were widespread, and not confined to the immediate surroundings.

The climatic implications of this assemblage are unequivocal. Of the 12 species recognized, five are no longer to be found living in Britain and one (*H. jacutus*) occurs today no nearer than eastern Siberia. Two of the species that still survive in Britain only do so in the highlands of Scotland: *Amara alpina* and *A. quenseli.* The former species is now restricted to remnant populations on only the highest mountain tops. The four species of Carabidae are only found together in alpine habitats in the Scandinavian mountains and on the Arctic tundras. *Amara alpina* is of particular interest because it is a common and almost exclusive member of tundra and alpine communities, one population only being known from a locality within the forest limit (Lindroth 1945). Since this is in a mountainous area the beetles have probably been transported from the alpine zones above. *Helophorus obscurellus* is now restricted in Europe to the north coast of the Kanin peninsula and a site near the estuary of the Pechora river. It is found also on the Siberian tundras and the cold montane steppe of central Asia. *Helophorus jacutus* occurs in central eastern Siberia and ranges as far west as the extreme south-eastern end of the Taimyr peninsula. Of the byrrhid beetles *Simplocaria metallica* and *Syncalypta cyclolepidia* are both boreo-montane in Europe; the latter has also been found at Irkutsk.

In summary then, this assemblage of Coleoptera would only be at home in a climatic regime analogous to that in the alpine zones of the northern mountains or on the tundras of the present day. The restriction of this fauna to only the most cold-hardy species suggests that these conditions were in fact extreme. The occurrence of one exclusively east Siberian species, and the fact that most of the rest of the assemblage can find acceptable habitats there, suggests that the climate was in some aspects markedly continental.

Comparison of the environmental data from the pollen and Coleoptera

There need be no conflict between the environmental implications of the pollen and the Coleoptera of pollen biozones A, B and H. Major discrepancy arises only in the interpretation of pollen biozones F and G. An interpretation of woodland for this horizon seems incompatible on local environmental and on climatic grounds with the data provided by the Coleoptera. A reconciliation between the two interpretations based on a distinction between local conditions inferred from the Coleoptera and regional conditions inferred from the pollen is hardly consistent with the evidence. The local absence of both the trees and of the herbaceous vegetation implied by the Coleoptera is given added support by the conspicuous absence of macroscopic plant fossils from this site. Since the Coleoptera appear to have been swept together from far afield before their incorporation in the basin of sedimentation, any plant debris on the land surface would have been collected and deposited with them. The absence of macroscopic plant remains cannot therefore be accounted for by local sedimentary peculiarities. This sparseness of the ground vegetation becomes difficult to explain if the climate at this time is interpreted as being warmer than that during the episodes that preceded and succeeded it. Furthermore the thermal requirements of the species of Coleoptera from pollen biozones F and G imply regional conditions consistent with those of the tundra and not with the boreal forest. To accommodate these differences would require an extreme thermal gradient between the local habitat and those farther afield. Such gradients might be expected in areas of high relief such as parts of Alaska today, but in a district as flat as Norfolk this option is not available. The evidence of the Coleoptera thus provides no justification for a judgement of Solomon in our efforts to reconcile these different interpetations.

In percentage-pollen diagrams, high relative amounts of arboreal pollen compared with non-arboreal pollen can reflect either real abundance of tree pollen or the scarcity of non-arboreal pollen, raising the 'background noise' of long-distance transported tree pollen to significant levels. Conifer and *Betula* pollen are particularly prone to such transport. If the pollen diagram from site WG admits this alternative explanation, then the interpretation of the environment from pollen and beetle data would be in complete accord. The rise in amounts of *Calluna* pollen and *Sphagnum* spores in the upper samples from this site might well reflect a local increase in acidity rendering an already hostile environment almost intolerable for the insect fauna – an interpretation that would explain the marked impoverishment of the fauna from these upper samples.

In summary, the fossil Coleoptera from the various sites at Wretton indicate that in pollen biozones A, B and H a damp grassland with a cool, moderately continental climate characterized the district but that in pollen biozones F and G this was replaced by a relatively barren tundra with a more extreme cold continental climate. The Coleoptera provide no justification for equating this latter episode with the Chelford interstadial (Coope 1959).

REFERENCES

Angus, R. B. 1970 A revision of the beetles of the genus *Helophorus* F. (Coleoptera: Hydrophilidae) subgenera *Orphelophorus* D'Orchymont, *Gephelophorus* Sharp and *Meghelophorus* Kuwert. *Acta zool. Fennica* **129**, 1–62.

Coope, G. R. 1959 A Late Pleistocene insect fauna from Chelford, Cheshire. *Proc. R. Soc. Lond.* B **151**, 70–86.

Lindroth, C. H. 1954 Die fennoscandischen Carabidae. Eine tiergeographische Studie: 1. *Göteborgs K. Vetensk-. o. VitterhSamh. Handl.* B **6**, 1–709.

Morgan, Anne 1970 Weichselian insect faunas of the English Midlands. Ph.D. thesis, University of Birmingham.

APPENDIX 2. MOSS REMAINS FROM WRETTON

BY J. H. DICKSON

The moss remains from the Ipswichian interglacial layers (table 1) give a marked overall impression of shade-tolerance. They constitute assemblages derived partly from the floors of forests and partly from the trunks of trees. Many of the species could have grown in the carr, often *Alnus* carr, indicated by the pollen and macroscopic fossil analyses (Sparks & West 1970). Several species point to base-rich substrata.

TABLE 1. INTERGLACIAL MOSS REMAINS†

	Ip zone II																									Ip zone III										
	WT	WW				WA											WB								WS	WC										
		85–100	55–85	42–55	36–42	110–120	100–110	90–100	80–90	70–80	60–70	50–60	30–40	20–30	10–20	0–10	110–120	100–110	90–100	80–90	70–80	60–70	40–50	30–40	90–100	240–255	215–230	200–215	180–200	165–180	150–165	100–120	80–100	60–80	40–60	0–10
Amblystegium cf. *varium* (Hedw.) Lindb.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Anomodon viticulosus (Hedw.) Hook. & Tayl.	3	.	5	6	2	.	.	.	.	.	.	.	.	.	.	2	.	.	2	1	.	.	.	.	.	.	.	.	1	3	.	1	.	.	.	.
Antitrichia curtipendula (Hedw.) Brid.	.	.	.	.	.	2	1	.	.	.	.	2	.	.	1	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.
Calliergonella cuspidata (Hedw.) Loeske	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.
Ceratodon purpureus (Hedw.) Brid.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cratoneuron filicinum (Hedw.) Spruce	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Eurhynchium striatum (Hedw.) Schimp.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.
E. swartzii (Turn.) Carn.	.	.	1	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	1	1	1	.	1	.	.	.
Homalia trichomanoides (Hedw.) B., S. & G.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1
Homalothecium sericeum (Hedw.) B., S. & G.	6	.	10	6	.	.	4	.	.	.	4	.	.	.	.	.	1	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.
Hypnum cupressiforme Hedw.	1	.	4	.	4	3	2	.	.	1	.	.	2	.	2	.	2	3	6	3	1	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.
Isothecium myurum Brid.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Neckera complanata (Hedw.) Hüben.	3	1	.	4	.	1	1	3	1	.	.	.	1	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spagnum sp. or spp. (spores)	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

† Figures indicate number of leafy stems.

Of the few Ipswichian bryofloras yet known from Britain (Dickson 1973) the Wretton bryoflora represents the most convincing evidence of deciduous forest. Strikingly similar bryofloras have been recovered from last interglacial deposits at Heligoland (Behre 1970) and at Ejstrup in Denmark (Hartz 1909).

The scanty moss remains from the Devensian (table 2) are chiefly noteworthy for the presence of *Antitrichia curtipendula*, *Aulacomnium turgidum* and *Drepanocladus capillifolius*.

TABLE 2. REMAINS OF DEVENSIAN GLACIAL MOSSES†

	Early Devensian									Middle Devensian
pollen biozone	A	B					B or H			H
	WH	WAD		WAF	WAG		WN		WP 2	WUB
	40	bulk	25–40		0–35	40–70	155–160	320		20
Antitrichia curtipendula (Hedw.) Brid.	1 le	.	.	.	.	.	.	.	.	.
Aulacomnium turgidum (Wahlenb.) Schwaegr.	.	.	.	.	.	.	.	.	2	.
Bryum sp. or spp.	.	.	.	.	.	.	.	.	.	.
Calliergon giganteum (Schimp.) Kindb.	.	.	.	.	1	.	.	.	1	.
Campylium cf. *polygamum* (B, S. & G.) J. Lange & C. Jens.	.	4	.	.	.	.	.	.	.	.
C. stellatum (Hedw.) J. Lange & C. Jens.	.	.	.	.	2	.	.	.	.	.
Cratoneuron filicinum (Hedw.) Spruce	.	1	1	.	1	.	.	.	.	.
Drepanocladus capillifolius (Warnst.) Warnst.	.	.	.	.	.	.	.	1	.	.
Encalypta sp.	.	.	.	2	.	.	1 le	.	.	.
Plagiomnium cf. *rugicum* (Laur.) Kop.	.	.	.	12 le	.	.	.	.	.	.
Pohlia cf. *wahlenbergii* (Web. & Mohr) Andr.	.	.	.	5	.	.	.	.	.	.
Polytrichum sect. *Juniperina*	.	.	.	.	.	3	.	.	.	.
Scorpidium scorpioides (Hedw.) Limpr.	.	.	.	.	.	3 le	.	.	.	.
Spagnum sp. or spp. (spores)	+	.	.	.	+	+	+	+	.	+
Tortula sp.	.	.	.	.	.	.	.	.	.	1 le

† Figures indicate number of leafy stems, except where le indicates leaves.

The single leaf of *Antitrichia* is the only British occurrence in the Early of Middle Devensian. One may wonder if it may have been derived from the Ipswichian layers. *Antitrichia* was abundant in western Britain in Late Devensian zones I to III (Dickson 1973).

Aulacomnium turgidum is a common tundra moss. At present in Britain it is known only from the hills of the Scottish Highlands.

Drepanocladus capillifolius, an often submerged moss of eutrophic water, has a continental range in Europe. It no longer occurs in Britain. There are several Devensian records.

REFERENCES

Behre, K.-E. 1970 Die Flora des Helgoländer Süsswasser-'Tocks', eines Eem-Interglazials unter der Nordsee. *Flora* **159**, 133–146.

Dickson, J. H. 1973 *Bryophytes of the Pleistocene. The British record and its chlorlogical and ecological implications.* Cambridge University Press.

Hartz, N. 1909 Bidrag til Danmarks Tertiare og Diluvial Flora. *Danm. geol. Unders.* **20**, 1–292.

Sparks, B. W. & West, R. G. 1970 Late Pleistocene deposits at Wretton, Norfolk. I. Ipswichian interglacial deposits. *Phil. Trans. R. Soc. Lond.* B **258**, 1–30.

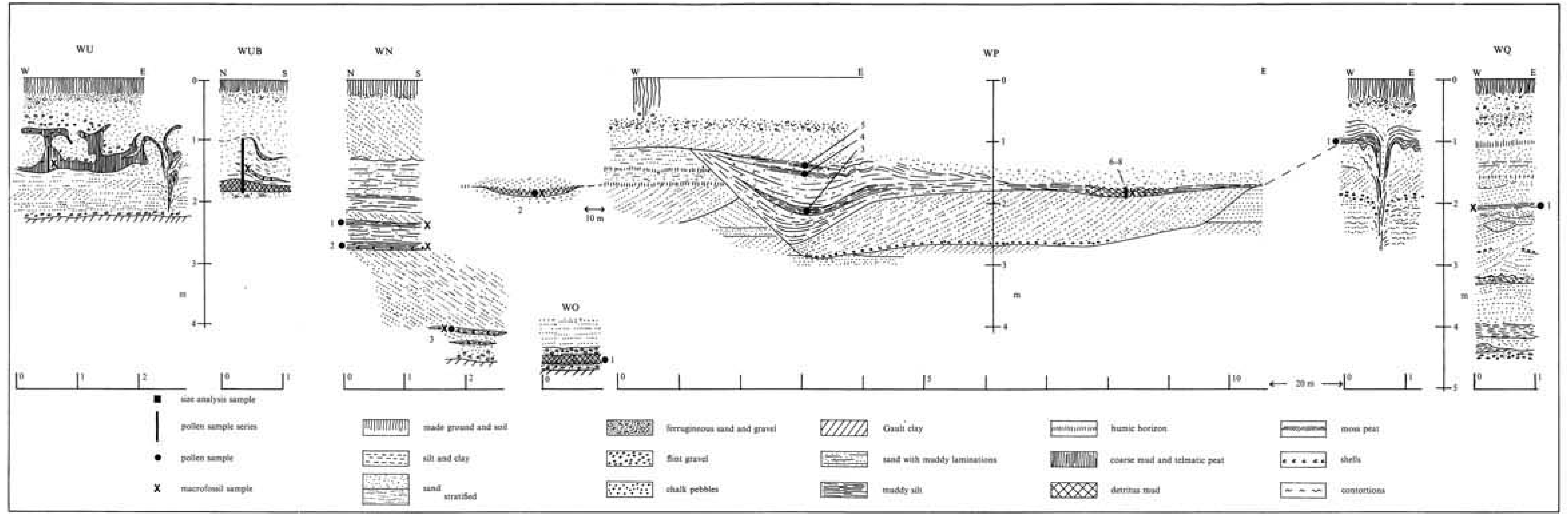


FIGURE 4. Stratigraphy of sites WN, WO, WP, WQ, WU and WUB, and key to sediment symbols used in figures 2-7.

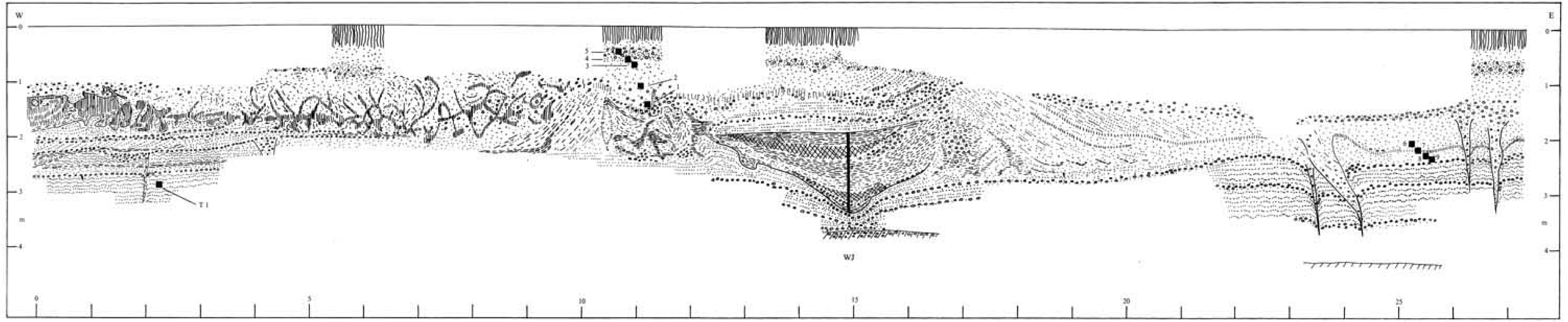


FIGURE 5. Stratigraphy of long section WJ (a few metres north of the section given in figure 2). Key to sediment symbols in figure 4.

FIGURE 6. Stratigraphy of long section WX, WZ and WY. Key to sediment symbols in figure 4.

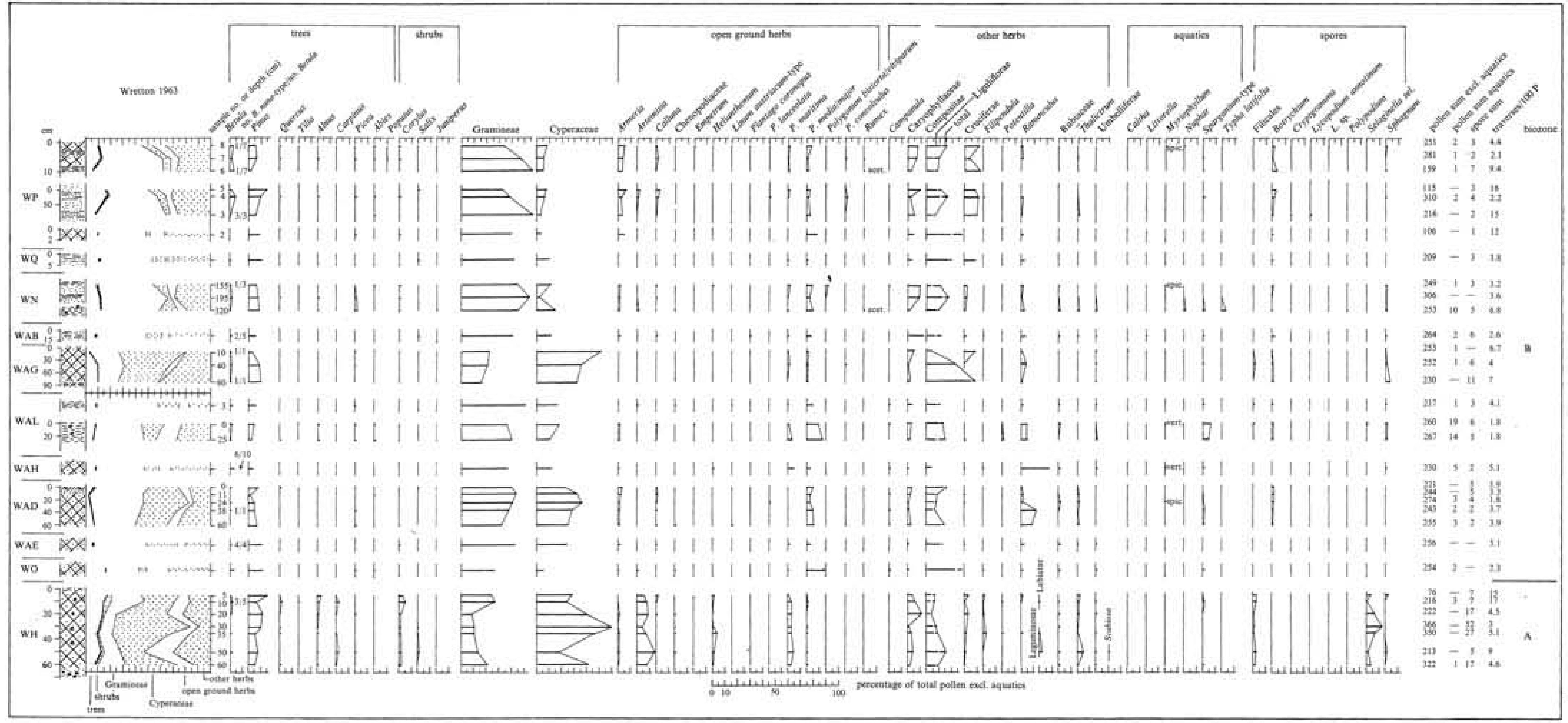


Figure 12. Pollen diagrams from Devensian sediments.

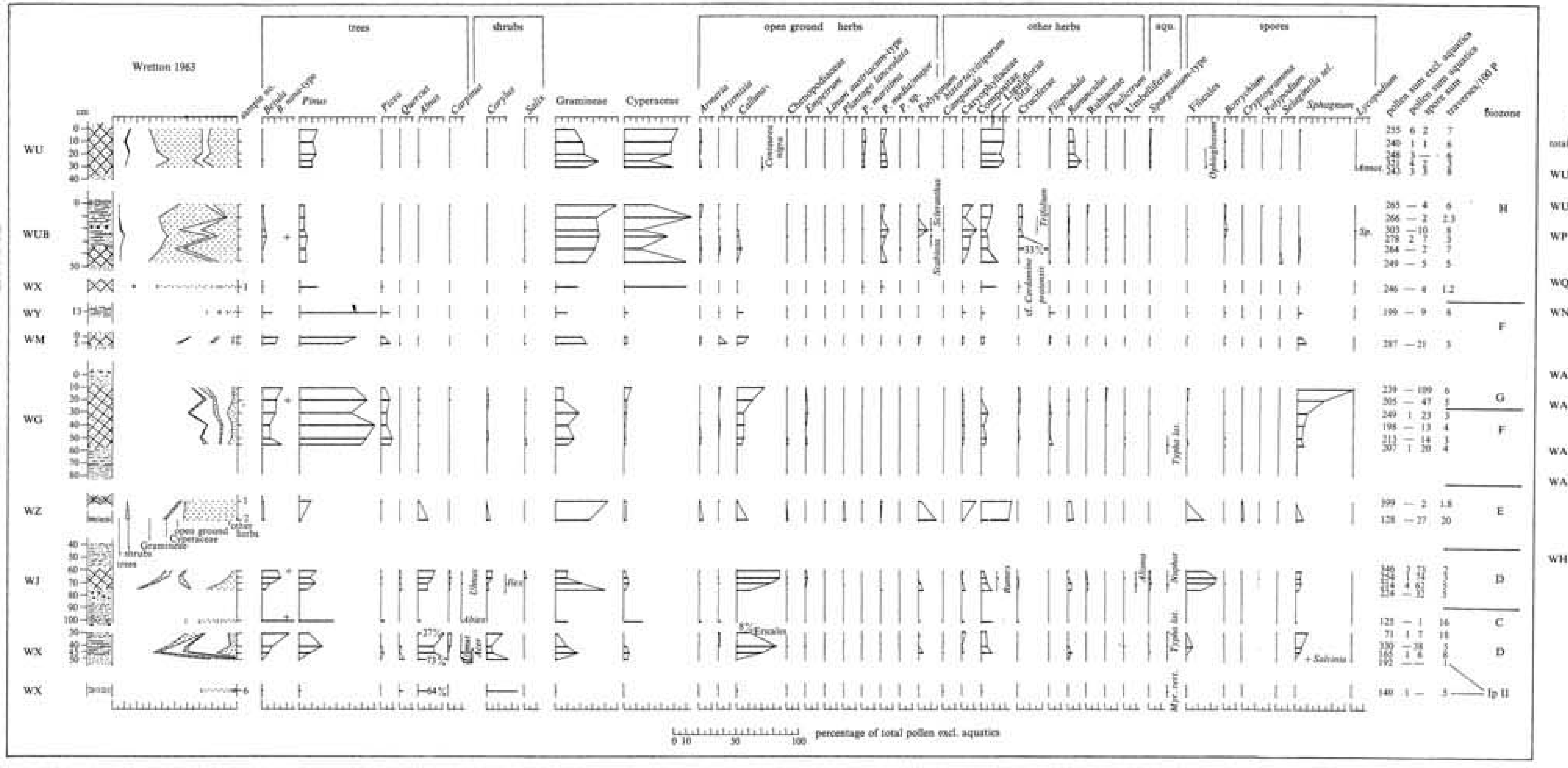


Figure 13. Pollen diagrams from Devensian sediments.

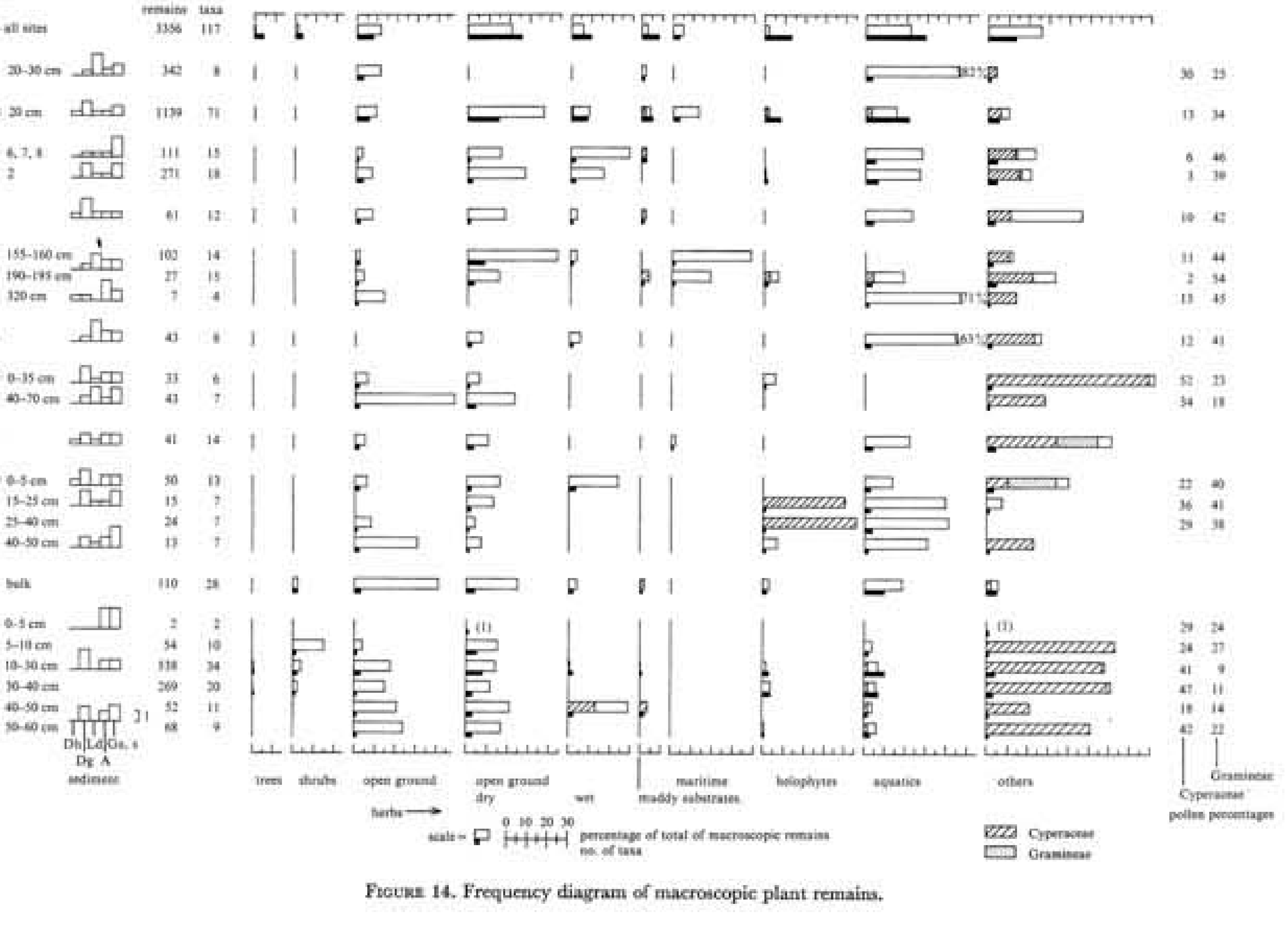
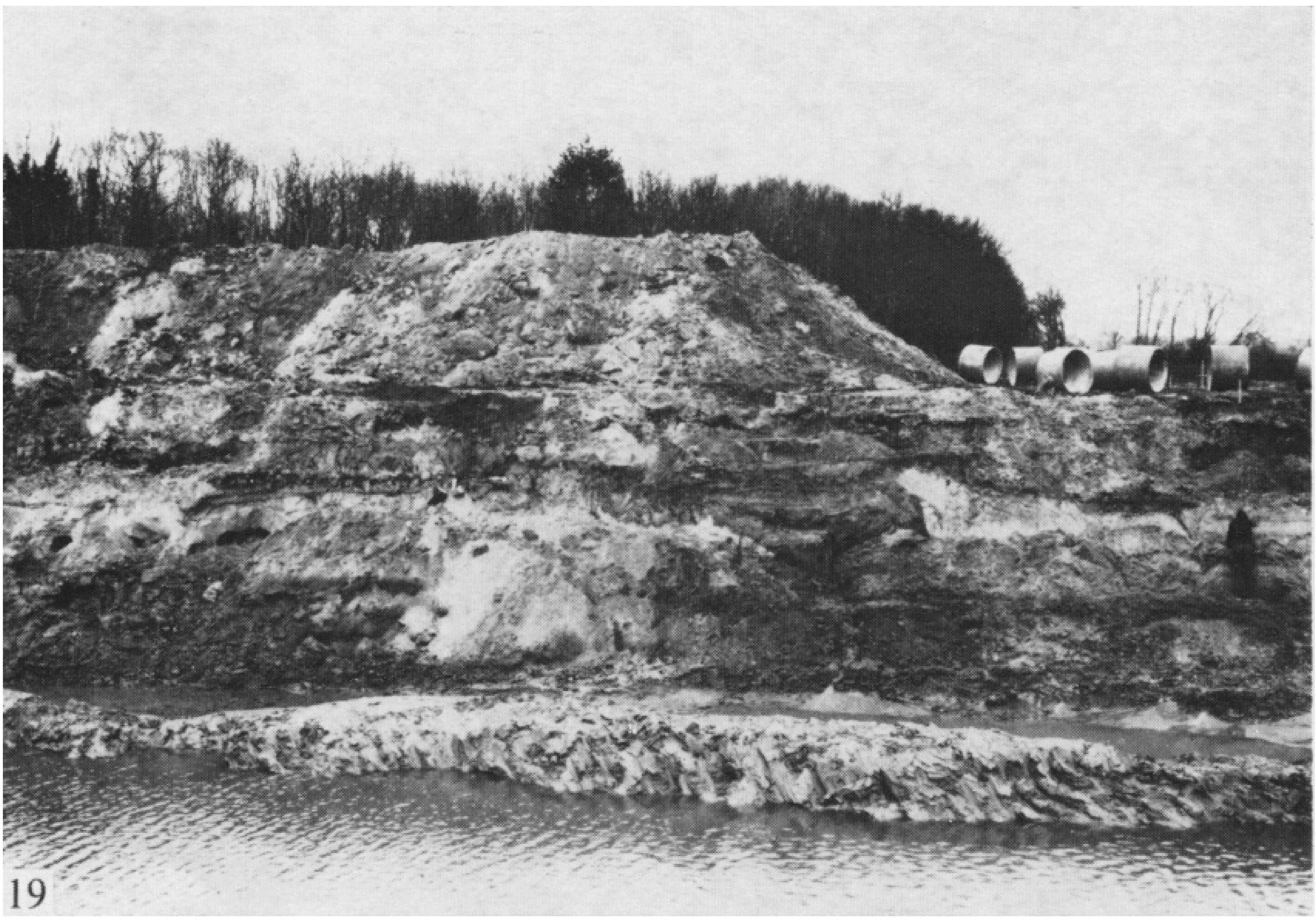


Figure 14. Frequency diagram of macroscopic plant remains.

Table 5. Analysis of plant macroscopic remains

biozone					A												B							D				F		F/G	G	H	
					WH					WAD			WAF	WAG		WAB		WN		WQ	WP			WJ					WG			WHH	WHI
	type of remains	50–60	40–50	30–40	10–30	5–10	0–5	bulk	40–50	25–40	15–25	0–5		40–70	0–35	0–15	820	190–195	150–160		2	6, 7, 8	75–85	65–75	35–50	20–35	50–60	40–50	30–40	20–30	10–20	20	20–30
(1) trees																																	
Alnus glutinosa (L.) Gaertn.	f	.	.	1	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
cf. *Abies* Mill. sp.	w(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.
Coniferae	ch(*), w(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	*	*	.	.	.	.	.	.	.
cf. *Picea* A. Dietr. sp.	ch(*)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*	.	.	.	.	.	.	.	.
(2) shrubs																																	
Betula nana L.	f	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix L. sp.	b	.	.	3	20	6	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.
Sambucus cf. *racemosa* L.	s	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
(3) open ground																																	
Cochlearia L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	2	.
Juncus bufonius L.	s	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.
Potentilla anserina L.	a	16	11	41	33	2	.	44	2	2	.	2	.	10	1	.	.	1	1	2	14	3	.	.	.	.	.	.	.	.	.	41	5
Potentilla L. sp.	a	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	5	.
Potentilla L. spp.	a	.	.	.	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus acris L.	a	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus L. subgenus *Ranunculus* section *Ranunculus*	a	.	.	.	2	.	.	.	.	.	.	1	.	.	.	.	1	.	.	3	6	.	.	.	.	.	.	.	.	.	.	2	14
R. repens L.	a	.	.	.	.	.	.	3	.	.	.	.	1	11	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	60	21
(4) open ground dry and mountain ledges																																	
Alchemilla L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Armeria maritima (Mill.) Willd.	cal	.	.	.	3	.	.	.	1	1	1	7	.	.	.	.	.	1	4	.	.	.	.	.	.	.	.	.	.	.	.	26	.
Atriplex hastata L. or *patula* L.	s	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Campanula rotundifolia L.	–	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Capsella bursa-pastoris (L.) Medic.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	28	.
Carduus L. sp.	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Cerastium arvense L.	s	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.
C. holosteoides Fr.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.
Corispermum sp.	a	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxyria digyna (L.) Hill	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	165	.
Draba L. sp.	cap	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba L. sp.	s	.	.	.	.	.	.	2	.	.	1	.	1	.	.	1	.	.	17	11	78	18	.	.	.	.	.	.	.	.	.	.	.
Euphorbia cf. *cyparissias* L.	s	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Herniaria L. sp.	s	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.
Leontodon autumnalis L.	a	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linum perenne agg.	s	6	2	8	81	.	1	51	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lychnis alpina L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.
Plantago maritima L.	cap	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum aviculare L. s.l.	s	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	706	.
Potentilla cf. *argentea* L.	a	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. cf. *crantzii* (Crantz) G. Beck	a	10	5	20	24	3	.	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex acetosella L. s.l.	[illegible]	.	.	.	7	.	.	.	.	.	.	.	1	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	37	.
Scleranthus L. sp. or spp.	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
Taraxacum cf. *officinale* Weber	a	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thalictrum alpinum L.	a	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
T. minus L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Viola L. subgenus *Melanium*	s	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.
(5) open ground wet																																	
cf. *Cardamine pratensis* L.	s	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	20	28	.	.	.	.	.	.	.	.	.	1	.
Carex section *Acutae* Christ.	n	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.
Juncus cf. *conglomeratus* L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Pedicularis palustris L.	s	.	.	.	2	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.
Polygonum viviparum L.	bu	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus hyperboreus Rottb.	a	.	.	.	.	.	.	.	.	.	.	5	.	.	.	2	.	.	8	2	23	4	.	.	.	.	.	.	.	.	.	48	.
Stellaria crassifolia Ehrh.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18	.
Thalictrum flavum L.	a	.	2	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Valeriana officinalis L.	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Selaginella selaginoides (L.) Link	m	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	21	.
(6) muddy substrata, damp/shallow water																																	
Alisma plantago-aquatica L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Alisma L. sp.	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	25	.	.	.	.	.	.	.	.	.
Eleocharis multicaulis (Sm.) Sm.	n	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
E. palustris (L.) Roem. & Schult. s.s.	n	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	26	.
E. palustris (L.) Roem. & Schult. s.l.	n	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eleocharis R. Br. sp.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	3	.
Ranunculus flammula L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
Rorippa islandica (Oeder) Borbás	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23	.
(7) maritime																																	
Glaux maritima L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.
Juncus cf. *balticus* Willd.	s	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
Polygonum oxyspermum s.l.	n	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	40	.	.	.	.	.	.	.	.	.	.	.	.	137	.
(8) fen and reedswamp helophytes																																	
Berula erecta (Huds.) Coville	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Caltha palustris L.	s	.	.	6	.	.	.	1	1	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex cf. *aquatilis* Wahlenb.	n	.	.	.	.	.	.	.	.	11	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.
C. rostrata Stokes	n+u	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
C. cf. *rostrata* Stokes	n+u	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.
Cicuta virosa L.	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
Cladium mariscus (L.) Pohl	n	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.
Glyceria cf. *declinata* Bréb.	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Lycopus europaeus L.	c	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Menyanthes trifoliata L.	s	.	.	2	3	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Ranunculus lingua L.	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
R. sceleratus L.	a	1	.	3	4	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	9	.
Urtica dioica L.	f	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	6	.
(9) aquatics																																	
Callitriche L. sp.	s	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ceratophyllum cf. *submersum* L.	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Damasonium alisma Mill.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.
Groenlandia densa (L.) Fourr.	fst	.	.	1	1	.	.	2	2	2	2	.	.	.	.	.	8	.	.	.	2	.	.	.	.	.	.	.	.	.	.	6	.
Hippuris vulgaris L.	fst	2	.	5	6	.	.	4	.	1	1	.	3	.	.	.	.	.	.	1	4	4	.	.	.	.	.	.	.	.	.	24	1
Hydrocharis morsus-ranae L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
Myriophyllum spicatum L. or *verticillatum* L.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	2	.
Nuphar lutea (L.) Sm.	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
Oenanthe aquatica (L.) Poir.	f	.	.	.	5	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton alpinus Balb.	fst	1	.	.	1	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
P. cf. *berchtoldii* Fieb.	fst	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
P. crispus L.	fst	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	.
P. filiformis Pers.	fst	.	.	1	2	.	.	3	.	.	.	.	.	.	.	25	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	17	.
P. natans L.	fst	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.
P. obtusifolius Mert. & Koch	fst	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
P. pectinatus L.	fst	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Potamogeton L. sp.	fst	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton L. sp.	fst	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	3	.	.	.	.	.	.	.	8	.
Ranunculus subgenus *Batrachium* DC	a	.	.	1	4	.	.	1	2	6	3	5	2	.	.	1	7	3	.	11	49	20	.	.	.	.	2	8	.	.	.	23	280
Scirpus lacustris L.	n	.	.	5	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.
S. cf. *tabernaemontani* (C.C. Gmel.) Palla	n	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	15	.
Scirpus L. sp.	n	1	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sparganium erectum L.	fst	.	.	.	.	.	.	3	.	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.
S. erectum subsp. *neglectum* (Beeby) Schinz & Thell.	fst	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sparganium L. sp.	fst	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	3	1
Typha L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	.	.	.	.	.	.	.	1	.
Zannichellia palustris L.	s	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	12	3	.	.	.	.	.	.	.	.	.	26	.
Characeae	o	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	29	.	.	.	.	.	.	.	.	.
Salvinia natans L.	m	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21	.	.	.	.	.	.	.	.	.
(10) unclassified																																	
Cardamine L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	1	2	9	.	.	.	.	.	.	.	.	.	.	.	6	.
Carex L. s.a.	c	.	.	.	1	.	.	.	8	.	.	5	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	1	.	.
Carex L. spp.	n	35	11	160	100	31	1	.	.	.	.	.	.	13	26	10	1	9	10	7	41	10	.	.	.	.	.	.	.	.	.	68	14
Cruciferae	s	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	1	.	.	4	.	.	.	.	.	.	.	.	.	.	5	.
Cyperaceae	n	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
Euphrasia L. sp.	s	.	.	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gramineae	c	.	.	.	.	.	.	.	.	.	.	12	8	.	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	.
Juncus L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.
Luzula DC sp.	s	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	.
Ranunculus subgenus *Ranunculus* section *Auricomus*	a	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stachys L. sp.	n	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Umbelliferae	f	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.
Viola L. sp.	s	.	.	.	.	.	.	.	.	.	.	.	3	.	.	1	.	.	.	12	8	10	.	.	.	.	.	.	.	.	.	.	.

Key: a, achene; b, bud-scale; bu, bulbil; c, caryopsis; cal, calyx; cap, capsule; ch, charcoal; f, fruit; fst, fruitstone; m, megaspore; n, nut; n+u, nut with utricle; o, oospore; w, wood.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Figures 19–21. For description see facing page.


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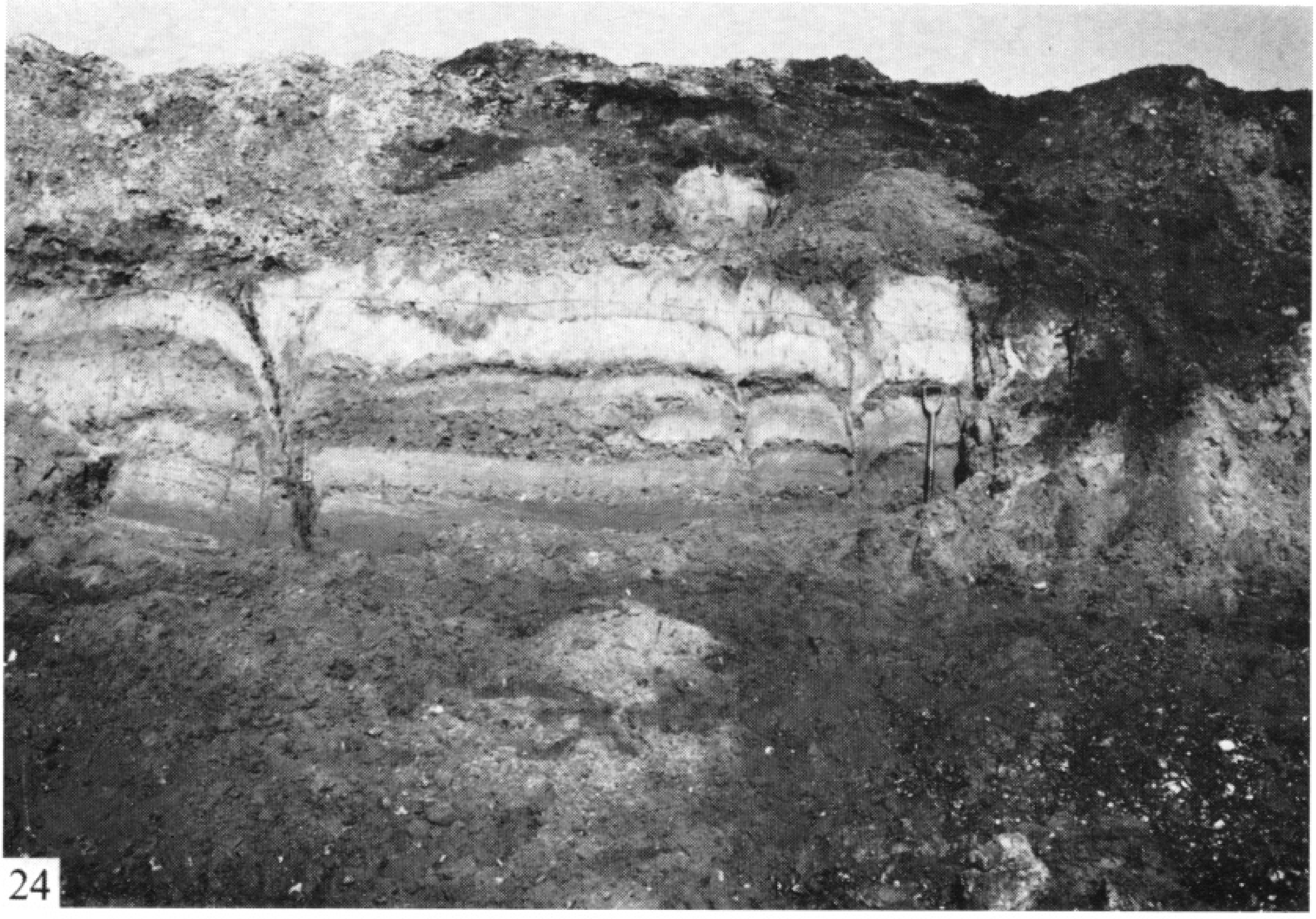
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FIGURES 22–24. For description see facing page.