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Floras of Middle and Upper Pleistocene Age from Brandon, Warwickshire

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FLORAS OF MIDDLE AND UPPER PLEISTOCENE AGE FROM BRANDON, WARWICKSHIRE

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Part I

This flora is interpreted as representing a vegetation of meadow birch woodland influenced by local edaphic conditions of a base rich sandy alluvial environment. It includes important aquatic associations and pioneer associations on sand substrates of different moisture contents. A thermophilous component indicating July mean temperature up to 15 °C is anomalous for this general vegetation type today and suggests that the vegetation was also influenced by the factor of delayed immigration of climax species. It is believed that this is due to the floras existence during an early interstadial of the Saalian, following the refrigeration which brought the Holstein to a close.

Part II

No pollen was obtained, but the plant macrofossils indicate a flora typical of the alluvial environment suggested by the sedimentary context. The vegetation was treeless and was sub-Arctic or even low-Arctic, though the occurrence of *Groenlandia densa* is anomalous. This plant occurs, however, at other mid-Weichselian sites, to which the Brandon flora shows general similarity.

PART I. THE FLORA OF A SILT-FILLED CHANNEL WITHIN THE BAGINTON–LILLINGTON GRAVELS

I. 1. INTRODUCTION

When the silty channel deposits of the Baginton–Lillington Gravels at Brandon (Shotton 1968) were under examination, samples at approximately 5 cm separation were collected for pollen analysis. In addition, whilst the bulk samples were being processed for the separation of insect and other animal remains (Osborne & Shotton 1968), seeds and other plant parts were sorted out and sent to the writer. It is on the basis of this material that this account of the flora of an early phase of Saalian time is written.

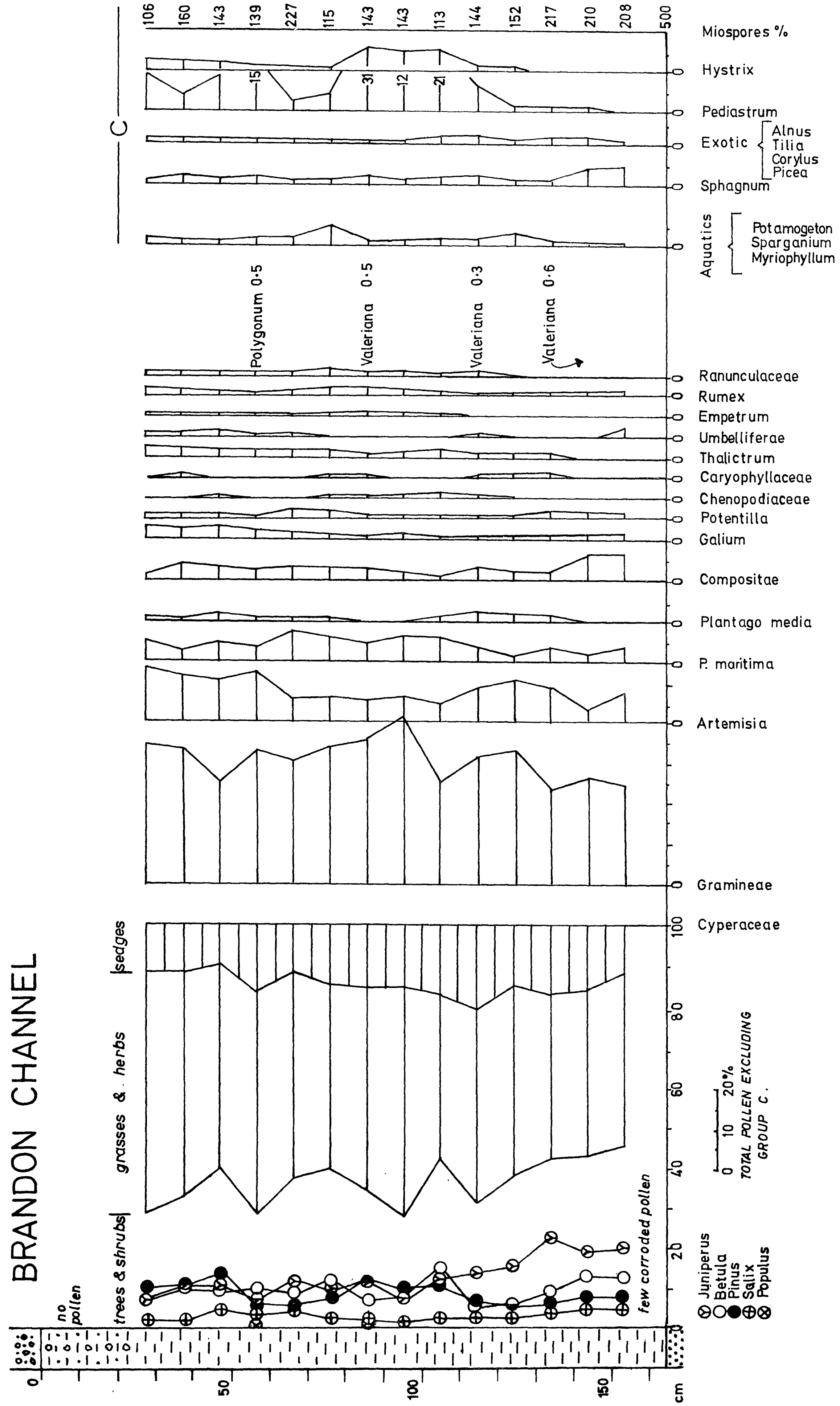
BRANDON CHANNEL
C
Miospores %
106
160
143
139
227
115
143
143
113
144
152
217
210
208
500
Hystrix
15
31
12
21
Pediastrum
Exotic
Alnus
Tilia
Corylus
Picea
Sphagnum
Aquatics
Potamogeton
Sparganium
Myriophyllum
Polygonum 0·5
Valeriana 0·5
Valeriana 0·3
Valeriana 0·6
Ranunculaceae
Rumex
Empetrum
Umbelliferae
Thalictrum
Caryophyllaceae
Chenopodiaceae
Potentilla
Galium
Compositae
Plantago media
P. maritima
Artemisia
Gramineae
Cyperaceae
sedges
grasses & herbs
trees & shrubs
no pollen
few corroded pollen
Juniperus
Betula
Pinus
Salix
Populus
0 10 20%
TOTAL POLLEN EXCLUDING GROUP C.
0
20
40
60
80
100
0
50
100
150
cm

Figure 1

The samples for pollen analysis were prepared by treatment of the sample with potassium hydroxide, hydrofluoric acid and acetolysis mixture, and the residue mounted in silicone oil. The plant macrofossils were separated, together with the other macrofossils, after the washing and sieving of the bulk samples.

A high percentage of the pollen and microspores in the sediments are obviously derived Mesozoic and Palaeozoic miospores, and Quaternary pollen is present in rather low concentrations only. This inhibited the counting of a suitably large number of grains. However, the Quaternary pollen is judged to be mostly primary, the low frequencies of the pollen of thermophilous trees being a good indicator of the small amount of secondary pollen present, both that derived from older Quaternary deposits and that due to long distance wind transport. From each sample, a minimum of 300 potentially primary grains were counted. Though the influence of the secondary pollen on the interpretation of the diagram is slight there is some doubt as to whether some of the rarer types are secondary or not, e.g. *Typha latifolia*.

It is considered unlikely that any of the Quaternary macrofossils identified are derived.

The relative frequency pollen diagram is illustrated as figure 1, and a list of the plants identified as micro- or macrofossils is given in the floral list below.

I. 2. Floral list

The nomenclature is based on Clapham, Tutin & Warburg (1962). The abbreviations are as follows: a, achene; bs, bud scales; fr, fruit; n, nut; o, oogonia; p, pollen; per, perianth segment; s, seed; sp, spore. ( ) indicates that the species is probably derived. The numbers of the macroscopic parts of the plant found are given before the part abbreviation except in the case of a single specimen.

PTERIDOPHYTA	
Polypodiaceae	
Undetermined	sp
GYMNOSPERMAE	
Pinaceae	
(*Picea abies* (L.) Karst)	p
Pinus sylvestris L.	p
Cupressaceae	
Juniperus communis L.	p
ANGIOSPERMAE	
Ranunculaceae	
Caltha palustris L.	
Ranunculus acris L.	
Ranunculus cf. *reptans* L.	

ANGIOSPERMAE (*cont.*)

Ranunculus sceleratus L.	38a
Ranunculus sect. *Batrachium*	56a
Ranunculus sp.	p
Thalictrum minus L.	20a
Thalictrum sp.	p
CRUCIFERAE	
Thlaspi arvense L.	s
Rorippa islandica (Oeder) Borbás	s
VIOLACEAE	
Viola sp.	s
CARYOPHYLLACEAE	
Silene dioica (L.) Clairv.	2s
S. maritima With. or *S. vulgaris* (Moench.) Garcke	5s
Stellaria palustris Retz.	s
Herniaria glabra L.	7s
Scleranthus annuus L.	fr
Undetermined	p
PORTULACACEAE	
Montia fontana L. ssp. *fontana*	s
CHENOPODIACEAE	
Chenopodium rubrum L.	s
Atriplex cf. *patula* L.	33s
Undetermined	p
TILIACEAE	
(*Tilia* sp.)	p
LINACEAE	
Linum perenne agg.	12s
ROSACEAE	
Potentilla palustris (L.) Scop.	2a
P. anserina L.	90a
P. tabernaemontani Aschers or *P. crantzii* (CR.) G. Beck	22a
Potentilla sp.	p
PARNASSIACEAE	
Parnassia palustris L.	2s
ONAGRACEAE	
Epilobium sp.	s
HALORAGACEAE	
Myriophyllum verticillatum L.	4n, p

ANGIOSPERMAE (*cont.*)

Hippuridaceae	
Hippuris vulgaris L.	111fr
Callitrichaceae	
Callitriche cf. *platycarpa* Kütz.	fr. lobes
Umbelliferae	
Bupleurum sp.	p
Apium inundatum (L.) Rchb. f.	2fr
Polygonaceae	
Polygonum aviculare L.	4fr
Polygonum sp.	p
Rumex acetosella L.	31fr
Rumex sect. *Rumex*	fr, per
Rumex sp.	p
Betulaceae	
Betula pubescens Ehrh.	9fr
Betula cf. *pubescens* Ehrh.	125fr, p
Betula cf. *nana* L.	p
(*Alnus glutinosa* (L.) Gaertn.)	p
Corylaceae	
(*Corylus avellana* L.)	p
Fagaceae	
(*Quercus* sp.)	p
Salicaceae	
Populus cf. *tremula* L.	p
Salix sp./spp.	p, bs
Empetraceae	
Empetrum nigrum L.	p
Primulaceae	
Androsace septentrionalis L.	s
Labiatae	
Mentha cf. *arvensis* L.	n
Plantaginaceae	
Plantago media L.	p
P. maritima L.	p
Rubiaceae	
Galium sp.	p
Valerianaceae	
Valeriana officinalis L.	5a, p

ANGIOSPERMAE (*cont.*)

COMPOSITAE	
Achillea ptarmica L.	a
Tripleurospermum maritimum (L.) Koch	2a
Artemisia sp.	p
Leontodon autumnalis L.	a
Sonchus oleraceus L.	a
Crepis sp.	a
Taraxacum officinale agg.	6a
Undetermined	p
POTAMOGETONACEAE	
Potamogeton natans L.	16a
Potamogeton cf. *berchtoldii* Fieb.	4a, leaf tips
P. acutifolius Link	8a, leaf tips
P. filiformis Pers.	5a
Potamogeton sp.	p
ZANNICHELLIACEAE	
Zannichellia palustris L.	3a
SPARGANIACEAE	
Sparganium sp.	fr, p
TYPHACEAE	
Typha latifolia L.	p
CYPERACEAE	
Eleocharis palustris (L.) Roem. & Schult.	308n
Carex spp.	435n
Undetermined	p
GRAMINEAE	
Undetermined	p
CHARACEAE	
Chara sp.	17 o

I. 3. NOTES ON SOME OF THE IDENTIFICATIONS

Herniaria glabra L. The seeds of *H. glabra* can be distinguished from those of the other species which reach northern Europe, *H. hirsuta* L. and *H. ciliolata* Meld. (*H. ciliata* Bab., non Clairv.). Those of *H. ciliolata* are rather similar to but are consistently larger than the *ca.* 1 mm seeds of *H. glabra*. Seeds of *H. hirsuta* are more irregular in shape.

H. glabra also has the widest distribution, reaching southern Sweden and eastern England, where it is a very local plant of dry arable fields and grassland (Clapham, Tutin & Warburg 1962).

Linum perenne L. Since the fossil seeds are identical with those of *L. perenne sensu stricto* it is not felt necessary to refer them to the proposed extinct taxon *L. praecursor* C. M. Reid (see Godwin 1956). Since the identity of *L. anglicum* Mill. (*L. perenne* auct. angl.) is also under review (Ockendon 1965) the identification is made as *L. perenne* agg.

Like *L. anglicum*, *L. perenne* is a plant of grassland on calcareous and sandy soils. It grows today from the Alps to central Russia, with its north and western limits in southern Germany (Hegi 1908–31).

Androsace septentrionalis L. Of the fifteen European species of *Androsace* (Hegi 1908–31) seven are endemic to the Alps and/or Pyrenees and these have provisionally been discounted as possibilities. Seeds of another two species *A. carnea* L. and *A. lactea* L. with central and south-east European distributions have not been examined, but amongst the remaining species *A. septentrionalis* L., *A. chamaejasme* Wulfen emnd. Host., *A. villosa* L., *A. obtusifolia* All., *A. maxima* L. and *A. elongata* L., seeds of *A. septentrionalis* are morphologically distinct on their gross characters. They do show some resemblance however, especially in the fossil state, to immature seeds of *Glaux maritima* L., from which they can be separated by their epidermal cell structure.

One crumpled seed from the Brandon Channel is considered to belong to this species. This is a specially interesting identification because the plant is not native to Britain today, nor has it been previously reported from the Quaternary. However, re-examination of the Primulaceae seeds from the Weichselian site at Upton Warren, also in the English Midlands (kindly lent by Dr I. Strachan), has shown that this plant is present there, represented by five well-preserved seeds.

It is a local plant of sunny, dry, sandy and grassy places, whose distribution extends from the Alps north and west to south-east Norway, south Sweden, north Germany and the Kola Peninsula and eastwards across Asia to North America.

I. 4. INTERPRETATION

(*a*) *Vegetation communities*

Several basic deductions about the vegetation can be made from the factual evidence. The first is that *Betula pubescens* was probably the only tree commonly occurring in the area and that, at least in the immediate vicinity of the site, the woodland was rather open. The role of *Pinus* is uncertain, its pollen frequency being low enough for it to have been derived from some unspecifiable distance away. The other trees—*Alnus*, *Tilia*, *Picea*, etc., with the exception of *Populus*, are regarded as exotic.

Secondly, the rather low pollen frequency of ericaceous plants, even allowing for the normal under-representation of *Empetrum nigrum*—the only one identified—suggests that this group was not common. The field layer of the birch copses/woods was therefore probably dominated by graminaceous rather than ericaceous plants. These associations would show some affinity to the 'meadow birch forests' of north Scandinavia, whilst those in which *Empetrum* was present, i.e. if its occurrence was in the woodlands, might relate to the fresh heath woods (terminology after Hämet-Ahti 1963). This would account for some of the abundant herb and grass pollen, though much of it obviously derives from elsewhere (see below).

The *Juniperus* pollen frequency is notably high. Experience of Arctic and Alpine vegetation has shown that this cannot be derived from *Juniperus communis* ssp. *nana* associations, but must be from relatively tall scrub. Such scrub is a regular minor component of nearly all the Scandinavian birchwood associations.

The status of *Betula nana* is uncertain since its identification is based on only a few pollen measurements, there being too few well-preserved grains for a statistically meaningful result. Its presence, however, would not be inconsistent. It is also a frequent component of the bush/shrub layer of many birchwood associations, as well as occurring in open dwarf shrub heath.

The salices have not been identified beyond the indication that the bud scales probably belong to one or more shrub species. These might also have occurred in the bush layer of the birch woods or as dominants in scrub communities, depending on the species represented and/or the local edaphic conditions.

The specific composition of the herb flora indicates that unshaded competition-free habitats also existed. These plants are particularly those which are typical of arenaceous soils, whose present habitats are principally coastal beaches, dunes, sand or gravel lake or river shores, thin grassland on sand, and in many cases now also occur as weeds of waste places and sandy arable fields. The list below gives those plants which are specifically assignable to such habitats and also a few which though frequent in them also commonly occur elsewhere.

Thalictrum minus
Thlaspi arvense
Silene maritima
Herniaria glabra
Scleranthus annuus
Atriplex cf. *patula*
Linum perenne
Potentilla anserina
Polygonum aviculare
Rumex acetosella
Androsace septentrionalis
Mentha cf. *arvensis*
Plantago maritima
Plantago media
Tripleurospermum maritimum
Artemisia sp.
Leontodon autumnalis
Taraxacum sp.

The associations in which plants of this group grew probably ranged from ones with a low degree of cover with scattered plants in bare sand to herb-rich grass meadows. Whilst the individual associations cannot be elucidated several basic types can be indicated, though these also overlap floristically.

Some of the abundantly represented species often occur in thin dry grassland on sand, i.e. where there is a variable amount of bare soil between the plants, e.g. *Plantago maritima*, *P. media*, *Thalictrum minus* and perhaps *Artemisia*. Whilst it is not known which or how many species are represented by the abundant *Artemisia* pollen one possibility is *A. campestris* which occurs in sandy grassland and has a distribution similar to that of *Herniaria glabra*. Such a community would be the habitat for *Androsace septentrionalis* (Andersson 1950), *H. glabra*, *Linum perenne*, *Potentilla crantzii/tabernaemontani*, etc. Whilst the two *Potentilla* species cannot be separated with confidence the second species would be edaphically and floristically appropriate.

Another community type is that of shores and strandlines, the plants rooted in coarse frequently gravelly sediments, some of them utilizing drift debris as a nutrient source. Although the seashore is a common habitat for most, undisturbed natural river and lake shores are also typical habitats. Again these plants include some which are abundant as fossils. In their maritime habitats five of them are frequent consociates—*Chenopodium rubrum* (and other spp.), *Atriplex patula* (and other spp.), *Silene maritima*, *Tripleurospermum maritima*, *Artemisia* sp. (*A. vulgaris* and the less likely *A. maritima*). It includes associations of both dry (in part the above) and mesic sites. As examples of the latter Clapham *et al.* (1962) mention an association on periodically inundated river banks of *Ranunculus sceleratus*, *Rorippa islandica* and *Chenopodium rubrum*, though these of course also occur elsewhere. Moist sand and gravel is amongst the potential habitats of *Caltha palustris*, *Montia fontana* and *Potentilla anserina*. It is interesting in this connexion that Benum (1958) records *Parnassia palustris* from bare calcareous sand and gravels in north Norway.

Some of these are also tolerant of partial shade and, together with other members of the Brandon flora, are typical plants of the ground layer of meadow *Betula* woods and or wetter *Betula/Salix* woods—*Silene dioica* (*Melandrium rubrum*), *Parnassia palustris*, *Caltha palustris*, *Valeriana officinalis*, *Achillea ptarmica*.

The types of associations on moist bare sandy shores naturally grade into semi-aquatic and aquatic associations. These are the other numerically and specifically rich component of the fossil flora.

Ranunculus sp.
Myriophyllum verticillatum
Hippuris vulgaris
Apium inundatum
Callitriche cf. *platycarpa*
Potamogeton natans
P. cf. *berchtoldii*
P. acutifolius
P. filiformis
Eleocharis palustris
(*Carex* spp.)
Zannichellia palustris
Sparganium sp.
Chara sp.

Eleocharis palustris is characteristically a dominant of associations of shallow water reed swamp on sand and gravel, rooting above and below water level. It may well have mixed with some of the damp-littoral species mentioned above.

Of the abundant deeper water plants *Potamogeton filiformis* can be a dominant in submerged communities and *P. natans* is commonly so in floating leaf communities. In *P. filiformis* associations, e.g. those described by Spence (Burnett 1964) *Chara* is frequently co-dominant and *Zannichellia palustris* often present. *Hippuris vulgaris* again dominates an association of shallow water outside the *Eleocharis* zone.

Hippuris and *P. filiformis* communities are restricted to sand substrates whilst *P. natans* occurs more frequently on organic mud. They do, however, often occur in the same water body. The majority of the species also prefer or are restricted to base-rich water with a pH 7 to 9. *Apium inundatum* also grows on sand substrates, dune slacks being one of its habitats, and whilst it is commonly found in acidic environments it can tolerate higher pH values.

(*b*) *Edaphic conditions*

The diverse ecological evidence mentioned above strongly suggests the prevalence of sandy soils in the vicinity of the site. Although the flora does not include any calcicolous species several are calciphiles—*Linum perenne*, (*Potentilla tabernaemontani*), *Androsace septentrionalis*, *Plantago media*. The general aspect of the vegetation, together with the presence of these species, indicates that these soils had a relatively high base status.

The independent geological evidence supports this interpretation. The lateral interfingering of the fossiliferous organic sediment with sorted sands shows that sedimentation of alluvial sand continued intermittently throughout the period represented by the deposit. Although these sands are highly siliceous the freshness alone of the immature soils would account for a certain base content. There is, in addition, some evidence that calcareous Jurassic or Cretaceous rocks contributed some material to the sediment. Though macroscopic fragments of Mesozoic rocks are rare in these sediments (Shotton 1968), Mesozoic *Classopollis* miospores are fairly frequent. However, the dominance in the secondary microflora of Carboniferous microspores (and the presence of macrospores) is in agreement with the lithological evidence of the coarse sediment fraction which suggests derivation largely from Permo-Carboniferous rocks.

These sands would be well drained where the small-scale relief appropriate to an alluvial environment was suitable, giving xeric conditions on banks, levees, etc., in conditions of low water table; whereas low-lying places would be damp, and/or periodically to permanently flooded.

Because of the little weathered state of the soils, and perhaps also the transport of some calcareous sediment the waters of the area were base-rich, with a pH around 7 to 9.

(*c*) *Climate*

Whilst the certain presence of *Betula pubescens* s.s. gives a minimum figure for the mean July temperature of 12 °C (Iversen 1954) there are several plants whose presence suggests yet warmer conditions. These are plants which today reach only as far north as southern Fennoscandia and which do not reach to high altitudes there or in the Alps (Braun-Blanquet & Rübel 1932–34; Hegi 1908–31; Hultén 1950). They are, however, not all of equal value as thermal indices (Iversen 1954). For example, amongst the apparently 'southern' species which occur, *Myriophyllum verticillatum*, *Potamogeton acutifolius*, (*Potentilla tabernaemontani*?) are ecologically demanding species which may be limited today by edaphic rather than climatic factors.

Whilst heliophilous plants may also be limited by non-climatic factors, *Chenopodium rubrum* for which a wide range of ruderal and natural open habitats exists, might be considered as occupying most of its potential range. This species only occurs south of the 15 °C July isotherm in both Fennoscandia and Britain (Perring & Walters 1962), and in western Britain grows only at low elevations. Two other ruderals have generally similar distributions—*Herniaria glabra* and *Scleranthus annuus*. However, *H. glabra* has a very restricted distribution in Britain whilst *S. annuus* is more widespread there, extending up to the 13 °C July isotherm in the extreme west.

Ranunculus sceleratus also seems to be restricted to areas with mean July temperatures above 14 °C in Fennoscandia and it barely reaches the *Picea* zone in the Alps. In more oceanic Britain it would appear to tolerate colder summers; down to 12 °C in the Orkneys. However, it is absent from Iceland. There is thus an indication that the mean temperature during July at Brandon was as high as 15 °C. However, such conclusions, derived from the application of distributional data to fossil floras, must be regarded as tentative.

The general occurrence of xerophilous communities and of plants of continental distribution such as *Androsace*, *Linum* and to a lesser extent *Herniaria*, might be interpreted as reflecting a greater degree of continentality than now. However, it is more likely that their presence is due only to the edaphic peculiarities of the area. Related to this problem is the occurrence of *Apium inundatum* which has a European–Atlantic distribution (Hultén 1950), in general west of the −2 °C January isotherm (apart from a record in Hegi (1908–31) from central Russia which is not confirmed by Komarov (1934–64)).

I. 5. Discussion and summary

1. With the varied morphology of an alluvial environment and associated variations in edaphic conditions—cut-off pools, sand and gravel point bars and banks, dry levées, wet back-swamps, etc., all the different communities for which there is evidence could occur within a very limited area around the site. It is thus highly likely that the seeds and pollen of plants of all habitats were contributed by the vegetation in the immediate vicinity.

From the evidence a hypothetical though internally consistent picture of the vegetation can be suggested. Birch woods (*Betula pubescens*) of meadow forest type with a rich grass and herb ground flora grew on alluvial mull soils. *Salix* was probably a component of the low tree layer, becoming dominant in the wettest areas. In such birch woods would be an open bush layer of *Juniperus* and perhaps *Betula nana* and *Salix* spp., the last two especially forming zones of scrub fringing river banks and open wet depressions.

The heliophilous communities abundantly represented by fossils would represent the vegetation colonizing the alluvial sediments. Initially, in the relatively xeric habitat of higher bank and bar surfaces, these would be open associations in which annuals and deep rooted perennials would be important. Later, grass would dominate them forming limited areas of ‘thin’ meadow associations. In these, scrub of *Juniperus* and *Salix* would probably become increasingly important. Other plants characteristic of damp/wet bare soils would colonize the more permanently saturated parts of bars, etc., and pool margins. In the pools grew a rich aquatic flora, characteristically including plants of base-rich water and sand substrates.

2. The degree to which the local vegetation at Brandon was representative of the vegetation of a wider area can be assessed by considering the geological context of the site.

The formation to which the fossiliferous facies belongs—the Baginton–Lillington Gravels—is extensive and during the period of alluvial aggradation in which it was being deposited wide plains of sand and gravel must have existed in the system of broad valleys present in the area (Shotton 1953). Brandon lay at the mouth of an eastern tributary valley, there *ca.* 3 km broad, and sedimentation, which at least at Brandon was taking place intermittently throughout the period represented by the organic facies, was probably associated with a system of braided channels across the area.

It is therefore probable that the ecological conditions present at Brandon existed over a wide area and that its vegetation was typical of most of the alluvial plains.

3. Whether or not birch woods can be regarded as the climax vegetation depends upon the evidence of the reputedly thermophilous plants. Whilst the Brandon vegetation floristically has much in common with that of the Fennoscandian sub-Arctic and oceanic sub-Alpine zones where birch forest is the climax vegetation, the presence of this thermophilous element differentiates it, since they indicate July mean temperatures 3 °C or more above the 10 to 12 °C typical of these zones. Accepting their evidence as reliable implies that the absence of other trees, including *Pinus* is due to delayed immigration rather than

to climatic inhibition. This situation has been encountered with late-glacial vegetation, and has been widely discussed, especially for the Weichselian Late Glacial (e.g. Iversen 1954).

4. If the evidence and implications of the thermophilous plants are accepted, i.e. that the vegetation was not in equilibrium with the climate, then it is necessary for at least one colder period to have occurred between the Brandon deposit and the Holstein interglacial which preceded it (Shotton 1953). This would have been responsible for the disappearance of the pine forests and ericaceous heaths which then grew in this part of England (Kelly 1964). Thus the short Brandon interlude, following a period of colder conditions and succeeded by yet colder, represents a minor warm oscillation in the early Saale.

Two successive early Saale interstadials, clearly related in time to the preceding interglacial have been described from Vejlby, Denmark (Andersen 1965) and one interstadial, probably the first from Kilbeg, Ireland (Watts 1959). If allowance is made for the local edaphic influence on the vegetation at Brandon, the regional vegetation can be considered as similar to that of the two Vejlby interstadials. However, no definite correlation can be made and the position of the Brandon interstadial within the early Saale is uncertain.

Part II. The flora of Avon No. 2 terrace at Brandon

II. 1. Introduction

Material was provided from silts and the peat of a small channel at the base of the gravels of No. 2 terrace (Shotton 1968).

Unfortunately no pollen which could be regarded as contemporaneous could be found in the sediments from this site, although Mesozoic miospores were abundant. Presumably this was due to the contemporaneous or post-depositional exposure of the sediments to aerobic conditions. Macrofossils, however, were well preserved, and a list of those identified is given in the floral records below.

II. 2. Floral records

The nomenclature is based on Clapham *et al.* (1962). The abbreviations are as follows: a, achene; bs, bud scales; cal, calyces; cap, capsule; fr, fruit; lf, leaf; n, nut; o, oogonia; s, seed; v, fruit valve. The numbers of each part found are given, except in the case of a single specimen.

Ranunculaceae	
Ranunculus sect. *Batrachium*	a
R. acris L.	a
R. reptans L.	a
Thalictrum alpinum L.	3a
Violaceae	
Viola sp.	5s
Cruciferae	
Draba incana L.	v

Caryophyllaceae	
Silene maritima With./*S. vulgaris* (Moench.) Garcke	14s
Arenaria ciliata agg.	25s
Portulacaceae	
Montia fontana L. ssp. *fontana*	s
Linaceae	
Linum perenne agg.	5s
Rosaceae	
Potentilla anserina L.	s
P. crantzii (CR.) G. Beck/*P. tabernaemontani* Aschers.	s
Saxifragaceae	
Saxifraga tridactylites L.	s
Haloragaceae	
Myriophyllum verticillatum L.	n
Hippuridaceae	
Hippuris vulgaris L.	14fr
Polygonaceae	
Polygonum aviculare L.	fr
P. viviparum L.	fr
Rumex acetosella L.	99fr
Betulaceae	
Betula nana L.	many lf
Salicaceae	
Salix herbacea L.	lf, 2 cap
Salix sp./spp. (non-*herbacea*)	5 cap, bs
Plumbaginaceae	
Armeria maritima (Mill.) Willd.	19 cal
Compositae	
Taraxacum sp.	3a
Potamogetonaceae	
Potamogeton filiformis Pers.	157a
Groenlandia densa (L.) Fourr.	28a
Juncaeae	
Luzula sp.	s

Cyperaceae	
Eleocharis palustris (L.) Roem. & Schult.	37n
Carex sp./spp.	356n
Characeae	
Chara sp.	0

II. 3. Vegetation

Though the macrofossil assemblages can be considered to represent only a fragment of the original flora it is sufficiently characteristic for some deductions to be made about the vegetation.

There is a shrub element represented by *Betula nana*, which in open vegetation is generally associated with ericaceous (incl. *Empetrum*) plants in a low shrub heath. However, this latter group of plants is not represented by fossils, which may or may not indicate their real absence. The *Salix* species are presumably shrub/bush species, occurring either sporadically in a low shrub heath or dominant in wetter areas.

A section of the herb flora can be found associated with such heath communities especially on slightly flushed sites on stream and lake banks or they can be members of grass-dominated meadow associations on mull soils—*Thalictrum alpinum*, *Ranunculus acris*, *Potentilla crantzii*?, *Polygonum viviparum*, *Taraxacum*. *Salix herbacea* whilst being the characteristic dominant of late snow beds, can also be a component of grass-herb dominated associations in snow-protected flushed meadows with or without taller *Salix* scrub.

These vegetation types are not necessarily restricted to open treeless conditions and could be associated with birch (*Betula pubescens* s.l.) woodlands. However, in this case, the absence of the easily dispersed *Betula* fruit probably indicates that tree birch was not present.

Another distinct group of plants is that of bare ground and/or thin xeric grassland on sandy soils—*Arenaria ciliata*, *Armeria maritima*, *Draba incana*, *Linum perenne*, *Polygonum aviculare*, *Rumex acetosella*, *Saxifraga tridactylites*.

The aquatics include plants of deeper water submerged and emerged associations—*Ranunculus* sp., *Myriophyllum verticillatum*, *Potamogeton filiformis*, *Groenlandia densa*; shallower water—*Hippuris vulgaris*; and marginal shallow water and shore associations—*Eleocharis palustris* and carices. *Ranunculus reptans* and *Montia fontana* could also belong to an association with *Eleocharis* on seasonally exposed lake margins. In general the aquatics are plants of base-rich pools with sand substrates.

II. 4. Discussion

1. In the context of the alluvial environment of the site this limited fossil flora could all have been contributed by the vegetation in the immediate vicinity.

2. The general aspect of the vegetation is sub-Arctic, or even low-Arctic if the negative evidence of absence of trees is accepted. However, the presence of *Groenlandia densa* is anomalous since it is a plant of Atlantic distribution whose northern Scandinavian limit is in southernmost Sweden. Nor does it reach high altitudes in the centre of its range, reaching only to 500 m below the tree line in the Alps (Hegi 1908–31). It is abundant at

Brandon and has been recorded from most Weichselian 'Full Glacial' sites (Godwin 1956; Strachan in Coope, Shotton & Strachan 1961; Bell pers. comm.; Kelly unpub.).

3. Floristically the vegetation is similar to other mid-Weichselian sites in the Midlands (Strachan in Coope *et al.* 1961; Kelly unpub.) but they are not sufficiently characteristic to enable their stratigraphical correlation on floristic grounds.

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