PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Coastal Interglacial Deposits of the English Channel

R. G. West, B. W. Sparks and A. T. Sutcliffe

Phil. Trans. R. Soc. Lond. B 1960 **243**, 95-133
doi: 10.1098/rstb.1960.0006

COASTAL INTERGLACIAL DEPOSITS OF THE ENGLISH CHANNEL

By R. G. WEST
Subdepartment of Quaternary Research, University of Cambridge

and B. W. SPARKS
Department of Geography, University of Cambridge

With an Appendix on the Mammalia
By A. T. SUTCLIFFE
British Museum (Natural History)

(*Communicated by H. Godwin, F.R.S.—Received* 8 *January* 1960—
Revised 23 *February* 1960)

[Plate 16]

CONTENTS

Fossiliferous Late-Pleistocene deposits on the foreshore of the English Channel at Selsey (Sussex), Stone (Hampshire), and near Arromanches (Calvados), have been investigated. At each site analyses of pollen, macroscopic plant remains and Mollusca have been made and from these vegetational, faunal, environmental and climatic conditions have been reconstructed.

At Selsey, it is shown that the deposits, which lie in a channel cut in Eocene rocks, are of Ipswichian (Eemian or Last) Interglacial age. Pollen analysis of the sediments of the channel filling show they were formed during zones *b*, *c*, *d*, *e* and *f* of this interglacial, which show the succession from open parkland vegetation to birch-, to pine-, to oak-dominated forests. Analysis of the macroscopic plant remains and of the molluscs suggests a rapid climatic amelioration at the beginning of the interglacial, so that by the beginning of zone *f* there are indications of summer warmth exceeding that of the present day in the area. In the upper part of the channel filling, estuarine deposits overlie freshwater deposits. It is shown that the marine transgression causing the change was taking place in zone *f* and was probably responsible later for the raised beach deposits which overlie the channel deposits and which form the cliffs at Selsey Bill.

At Stone pollen analysis shows that brackish water deposits, below present high tide level, were formed in zone *f* of the Ipswichian Interglacial. At that time *Quercus*, *Pinus* and *Acer* were the chief trees forming the forest in the region. The macroscopic plant remains and the Mollusca indicate that the deposit was formed under saltmarsh conditions. As at Selsey, the raised beach gravel found overlying the interglacial deposit is related to the same marine transgression that produced the brackish water conditions.

Near Arromanches, at St Côme de Fresné and Asnelles-Belle-Plage, two deposits showing a change from marine to freshwater sediments were investigated. The analysis of pollen and the Mollusca showed the prevalence of pine forest and its replacement by open steppe-like conditions as the marine regression occurred. After the regression, limon covered the freshwater deposits. The fossiliferous deposits are tentatively correlated with zone *i* of the Eemian Interglacial.

The relative land- and sea-level changes indicated by all the deposits are considered. It is concluded that in the English Channel, during the Ipswichian (Eemian) Interglacial, sea level rose above its present height in zone *f* and fell below it during zone *i*. The Selsey–Brighton raised beach and the Normannien II raised beach are correlated with the same marine transgression. It is pointed out that if the Selsey–Brighton raised beach is to be correlated with the Monastirian II level of 7–8 m, then this level should be correlated with the Ipswichian (Eemian) Interglacial.

1. Introduction

Three fossiliferous Late Pleistocene deposits found on the foreshore of the coasts of the English Channel are described in this paper. Two were certainly formed during interglacial times and are situated at Selsey, Sussex, and at Stone, Hampshire. The third

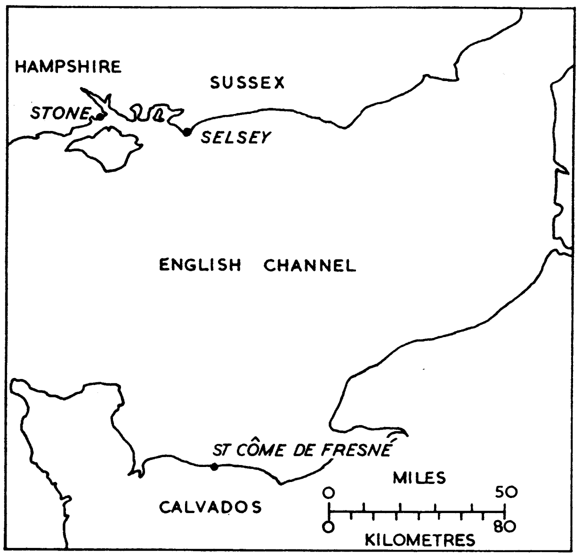


Figure 1. The location of the sites described.

deposit, probably interglacial, is on the foreshore at St Côme de Fresné and Asnelles-Belle-Plage near Arromanches (Calvados), on the north coast of Normandy. The positions of these deposits are shown in figure 1.

Each of these three deposits shows both estuarine and freshwater facies and also contains abundant remains of plants and animals. As a result it has been possible to relate the vegetational and faunal successions to relative changes of land- and sea-level, and all these to climatic changes.

2. Interglacial deposits at Selsey, Sussex

(a) *Stratigraphy*

The interglacial deposits at Selsey are situated on the foreshore between the Lifeboat House and the holiday camp on Selsey Bill, as illustrated in figure 2. They are only accessible for a short time at low tides, when they are seen to lie in a channel trending

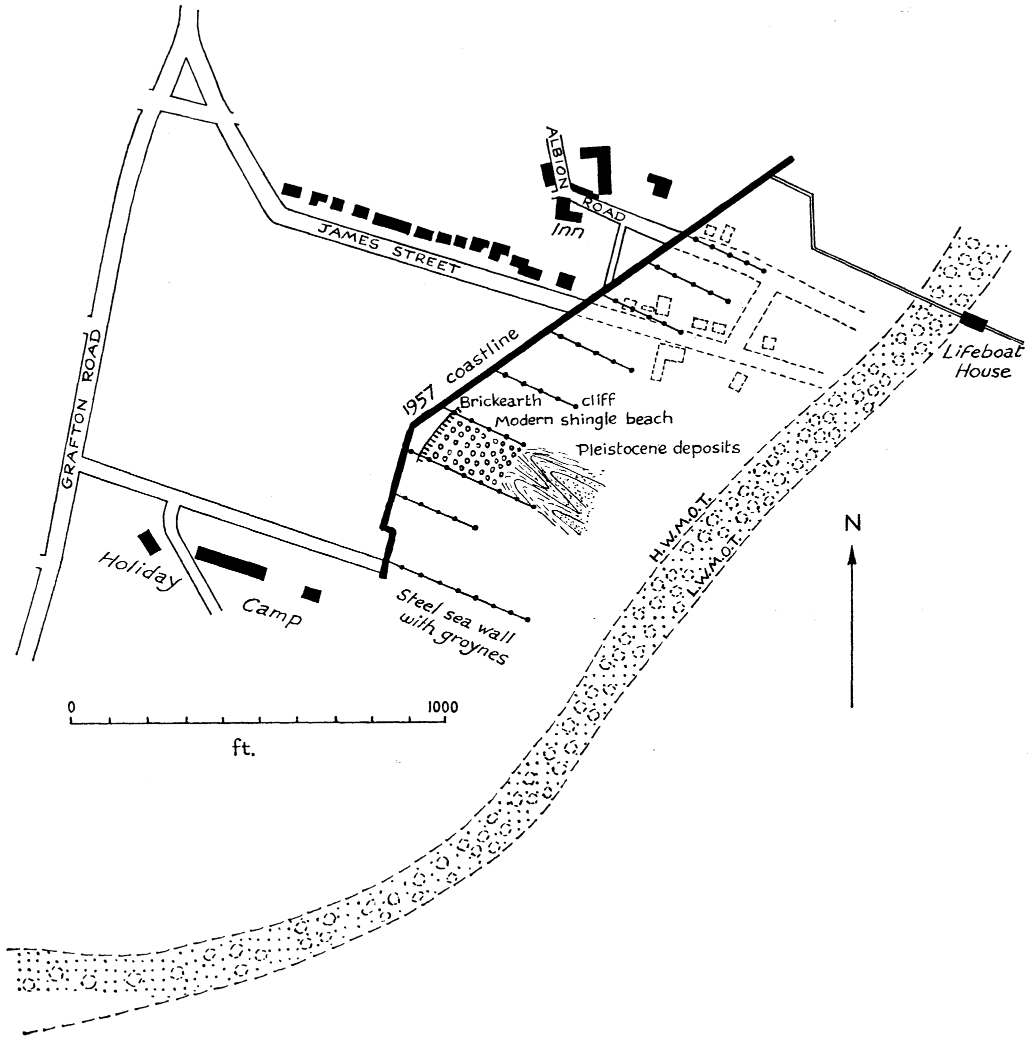


FIGURE 2. Map of the coast at Selsey, showing the position of the interglacial deposits and the amount of recent coastal recession. The map shows the 1957 coastline plotted on the 1932 revision of the 6 in. O.S. map.

north-west to south-east and cut in the Bracklesham Beds. Figure 3 is a sketch of the appearance of the deposits from seawards. Figure 4 is a section compiled from an inspection of the surface outcrops, from small excavations and from a boring near the centre of the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

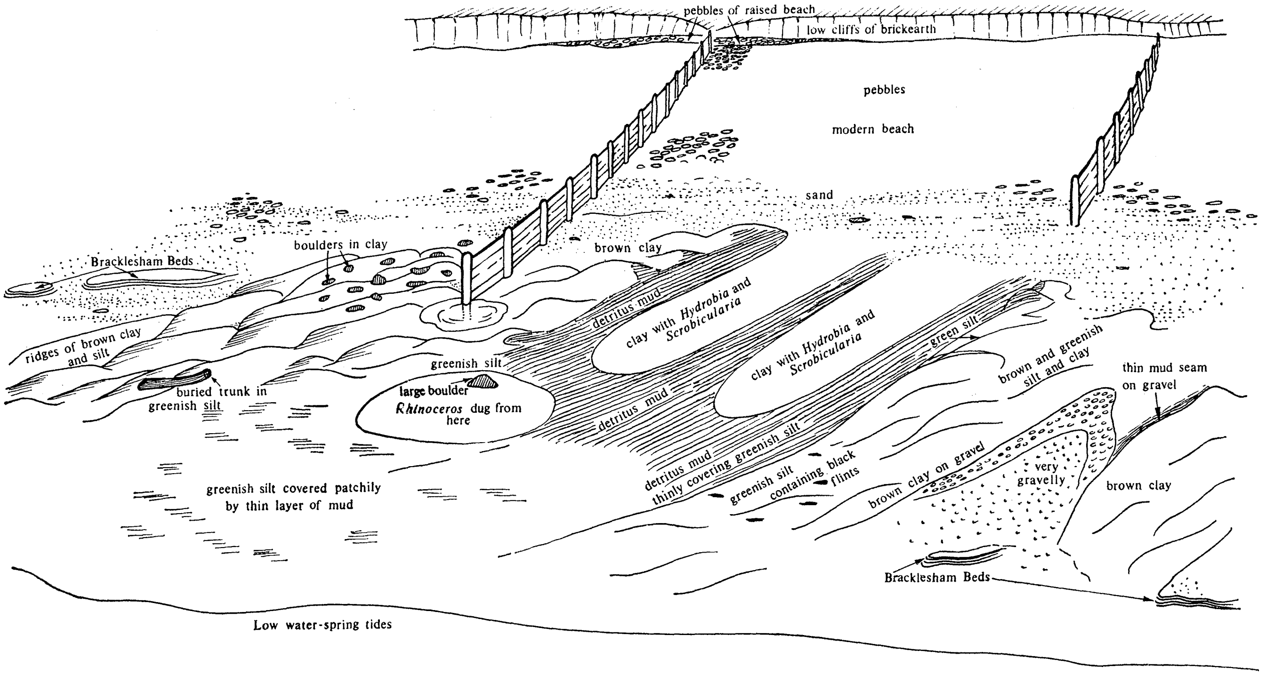


FIGURE 3. Sketch of the Selsey interglacial channel from seawards.

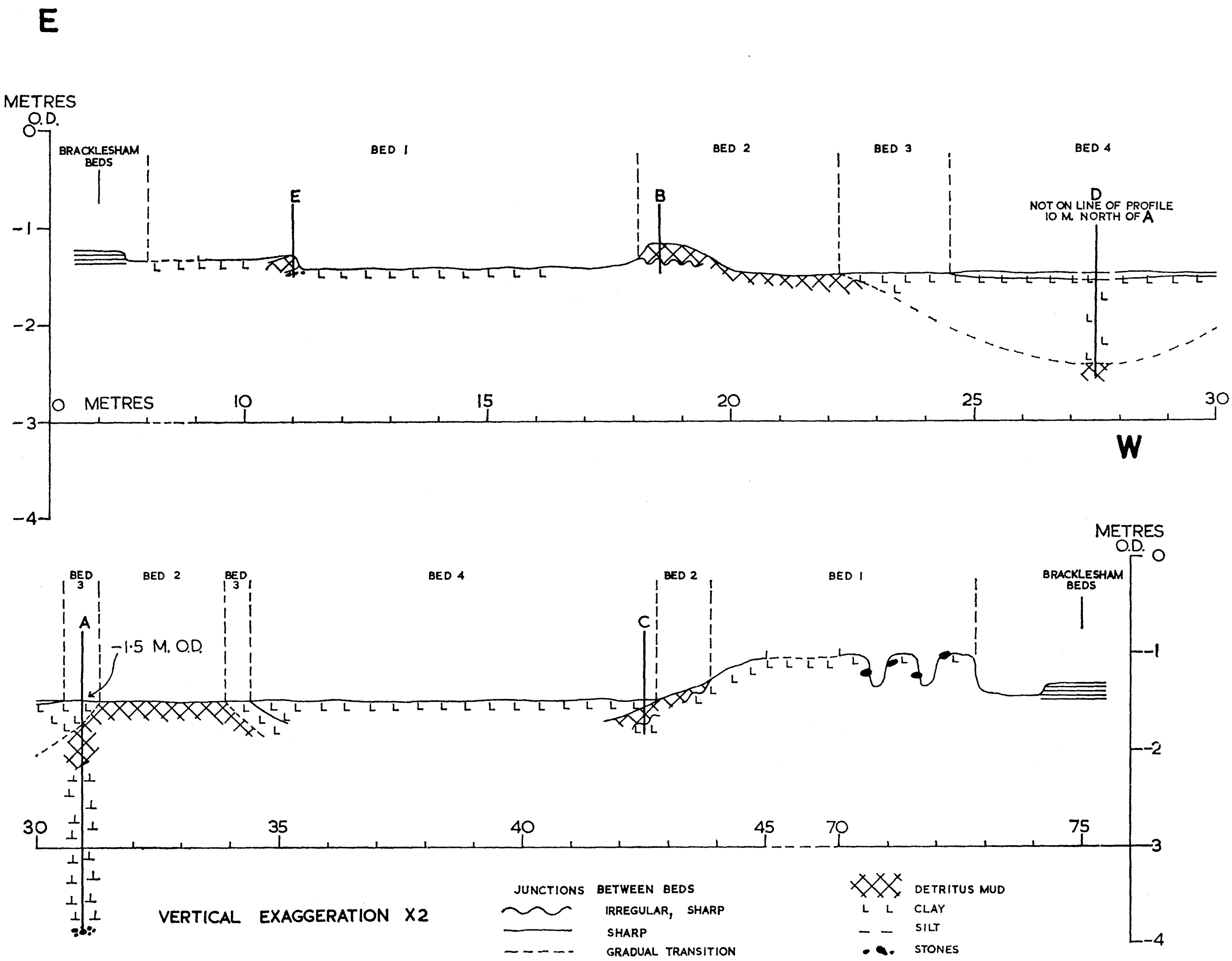


FIGURE 4. East-west section across the interglacial channel at Selsey.

channel. The top of this boring was at $-1\cdot5$ m O.D. Other levels shown in the section were estimated; the distances were paced.

Four series of sediments can be distinguished in the channel filling; they are, starting at the top:

Bed 4. A brown-grey silty clay with *Scrobicularia* and *Hydrobia*, sharply separated from bed 3.

Bed 3. A grey silty clay with abundant *Hydrobia*; a high content of organic mud at the base where there is a gradual transition from bed 2.

Bed 2. A dark brown coarse detritus mud with fragments of wood, some of them large. Shelly except at the base. Conformable through a rapid transition with bed 1 in the centre of the channel, but clearly unconformable on bed 1 at the edges of the channel.

Bed 1. A variable green or brown silt or clay, with varying proportions of organic mud, with bands of pebbles, frequently black flints. On the west side of the channel this bed contains erratic boulders, including hard sandstone, liver-coloured quartzite, whitish weathered granite and pink quartz porphyry.

The distribution of these sediments is shown in the section, figure 4. A large part of the channel is filled with the variable bed 1. The colour variation from green to brown may be due to weathering. The plant remains indicate that this is a freshwater deposit. It is notable in containing erratic boulders of igneous rocks. On the transition to bed 2 the largely inorganic sediments of bed 1 are replaced by the organic freshwater coarse detritus mud. At the margins of the channel an unconformity is clearly shown between beds 1 and 2. This suggests that a fluctuating water level at the time of the transition resulted in the disturbance of the surface of bed 1 at the margins of the channel, and as the water level rose during the deposition of bed 2, an early sign of the marine transgression to follow, detritus mud of bed 2 overlapped the surface of bed 1. From its contained fossils it is clear that the deposition of the clay of bed 3 was the result of an imminent marine transgression. Bed 4, an estuarine brown-grey clay, shows a sharp junction with bed 3; it is probably a weathered product of bed 3.

On the seaward side the channel deposits disappear beneath the sea; at the landward end they disappear beneath the modern beach deposits. As seen in the sketch, figure 3, there is a small cliff about 1 m high exposed above the shingle beach. In this, brickearth can be seen overlying the rounded pebbles of the Late Pleistocene raised beach. These two deposits also form the low cliffs on the south-west side of Selsey Bill, where a characteristic section, opposite Thorney Coastguard Station, showed:

0–30 cm Made ground.
30–130 cm Brickearth.
130–500 cm Shingle with partings of sand (raised beach), disturbed by frost action at the top.

Although the actual contact between the channel deposits and those found in the cliff is obscured by the shingle of the modern beach, there is little doubt that the raised beach shingle postdates the channel deposits. As shown in figure 2 there has been spectacular marine erosion in the last twenty-five years, from the high-water mark of the 1932 revision of the 6 in. map to the present steel sea-wall which is just behind or coincident with the low cliff. Although there may be errors of a few yards in our map, which is based on a pace and compass survey, the conclusion cannot be escaped that in the last twenty-five years the raised beach shingle and brickearth has been stripped back to reveal the interglacial channel deposits below. This agrees entirely with the stratigraphy reported by Palmer & Cooke for this and the Stone deposit (1923, figure 34A and p. 257).

The upper part of the raised beach shingle is disturbed by cryoturbation, which has mixed the pebbles with the brickearth above. Both the brickearth and the cryoturbation are indications of cold climatic conditions subsequent to the formation of the raised beach.

The succession we have described resembles a section of the cliff and foreshore at Selsey Bill given by Reid (1892). He described a hard greenish clay, perhaps equivalent to our bed 1, overlying Bracklesham Beds and overlain by a black estuarine mud, an equivalent stage to our bed 3. This estuarine mud disappeared under the modern shingle and in the cliffs above were seen the raised beach shingle covered by stony loam (brickearth). One significant difference is seen between Reid's and our sections. Reid stated that the basal greenish clay contained a fauna including the southern marine Mollusca characteristic of the so-called 'Selsey mud-deposit', e.g. *Chiton siculus* and *Rissoa cimex*. He considered that this deposit was marine and that the fossils clearly showed 'the influence of warmer seas than those which now wash our shores' (Reid 1892, p. 356). As we describe later, the plant remains from our bed 1 indicate freshwater deposition under conditions probably colder than the present day. We can only conclude that it is not clear what the relation is between our succession and the 'Selsey mud-deposit'.

The deposits at West Wittering seven miles north-west of Selsey described by Reid (1892) are also comparable to those we examined at Selsey. At West Wittering Reid described channel deposits in Eocene clay. On a basal gravel was a laminated peaty clay, the lower part freshwater, the upper part estuarine. The raised beach shingle was observed by Reid to extend over the channel.

Thus the deposits at Selsey described here and those at West Wittering appear to be part of a widespread series of freshwater and estuarine deposits antedating the raised beach, and lying in channels cut in the Eocene rocks of the Selsey Plain. It is shown later that the deposits at Stone, Hampshire, twenty-five miles to the west, belong to the same system of interglacial deposition.

(*b*) *Palaeobotany*

(i) *Introduction*

Samples for palaeobotanical analysis were taken from the pit and borehole at site A and the pit dug at site D. At site A, an excavation was made to a depth of 56 cm. From 56 to 134 cm cores 8 cm in diameter were taken and from these were taken pollen samples and samples for macroscopic analysis. From 134 to 200 cm a single-spiral auger was used, and the samples came from sediments caught in the auger.

(ii) *Pollen diagrams and correlation*

Series of pollen samples were taken from excavations at site A (see figure 4) in beds 1 to 3 and at site D in beds 3 and 4. The results are shown in the pollen diagrams, figures 5 and 6. The few isolated analyses given in table 1 were made from samples from the marginal deposits of the channel in order to confirm the stratigraphy.

Zonation of pollen diagrams. The tree pollen (*AP*) diagram resembles the diagram from the interglacial deposits at Bobbitshole, Ipswich (West 1957), of Ipswichian Interglacial age, and the many diagrams from the Eemian (Last) Interglacial, the continental correlative of the Ipswichian, described by Jessen & Milthers (1928) and van der Vlerk & Florschütz (1950). The tree pollen diagram is unlike those from the two known interglacial periods in England older than the Ipswichian Interglacial, the Hoxnian (West 1956) and Cromerian (Woldstedt 1950) Interglacials. We are able to apply the scheme of

Table 1. Pollen analyses of samples from the marginal parts of the Channel

	site B	site C		site E
	base of mud (bed 2)	brown clay (bed 4)	base of mud (bed 2)	top of brown-black silty mud (bed 1)
	zone *e*	zone *f*	zone *e*	zone *b*
Betula	14	11	5	1
Pinus	39	18	28	2
Ulmus	...	5	2	...
Quercus	47	65	65	...
Alnus	...	1	...	...
total tree pollen grains counted	150	150	150	3
Corylus	...	117	1	...
Salix	11	1	3	1
Hedera	1	3	1	...
Gramineae	39	3	6	35
Cyperaceae	25	1	5	37
Chenopodiaceae	1	1	1	...
Compositae	6	1	...	...
Filipendula	1	1	1	...
Helianthemum	1	...	...	...
Ranunculus	1	1	1	...
Rubiaceae	1	...	1	...
Sium-type	1	1	...	...
Thalictrum	...	...	...	1
Umbelliferae	1	1	...	...
Menyanthes	...	...	1	...
Myriophyllum spicatum	...	2	...	...
M. verticillatum	...	...	...	2
Sparganium-type	24	7	7	2
Typha latifolia	5	...	1	...
Filicales	158	41	55	1
	percentages of total tree pollen			numbers of pollen grains counted

zonation for this interglacial first proposed by Jessen & Milthers (1928). Zones *b*, *c*, *d*, *e* and *f* can be distinguished in the diagrams. The characteristics of these zones and their demarcation are as follows:

Zone *f*. Site D: 0 to 80 cm; Site A: 0 to 50 cm. Zone of *Quercus* (dominant), *Pinus* and *Corylus*. The base of the zone is where *Corylus* begins to rise to high values.

Zone *e*. Site A: 50 to 60 cm. Zone of *Pinus* (dominant), *Quercus* and *Betula*. The base of the zone is where the *Quercus* curve starts to rise.

Zone *d*. Site A: 60 to 66 cm. Zone of *Pinus* (dominant) and *Betula*. The base of the zone is where *Pinus* starts to rise and *Betula* starts to decline.

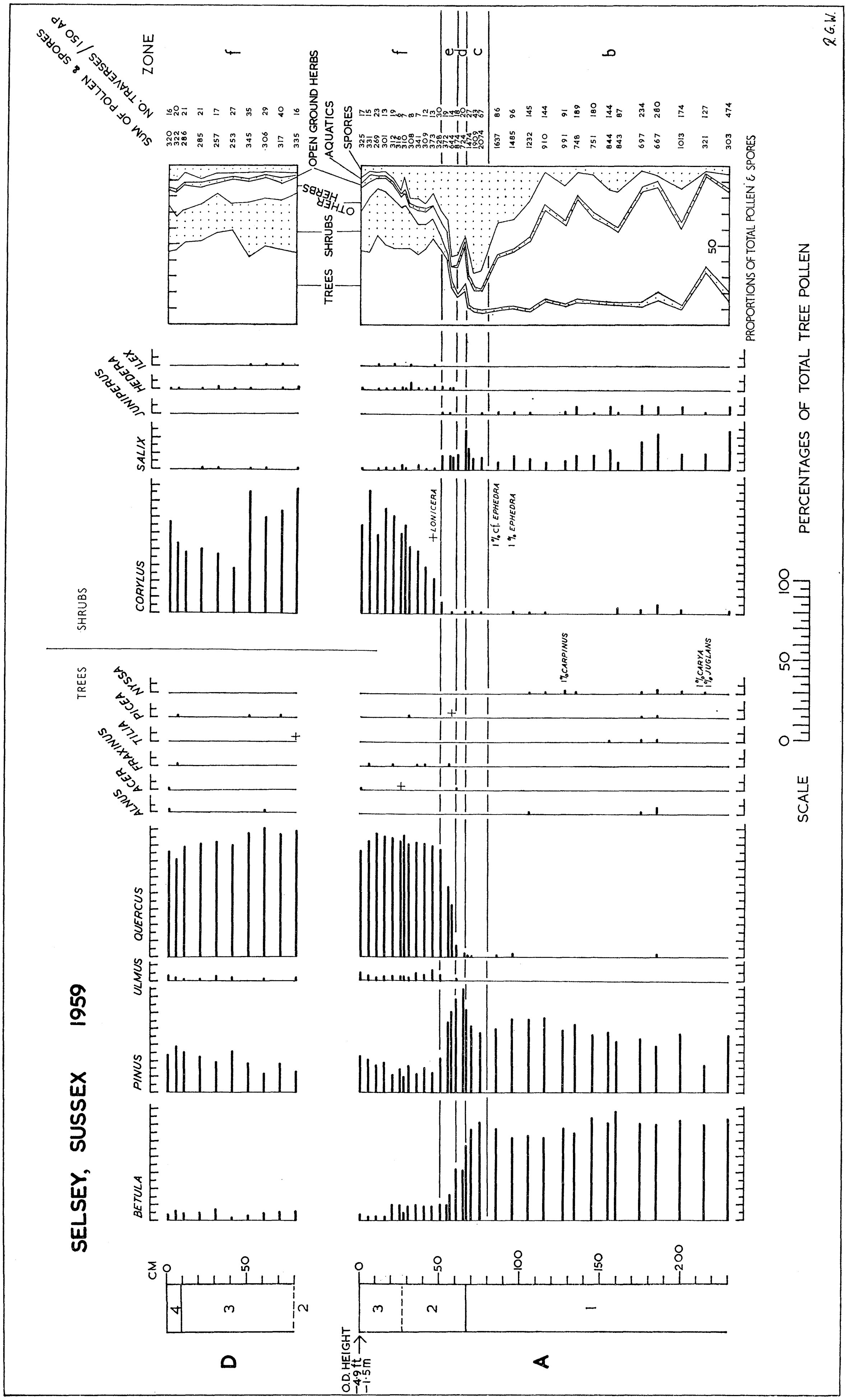


FIGURE 5. The tree pollen diagram from Selsey.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Zone *c*. Site A: 66 to 80 cm. Zone of *Betula* (dominant) and *Pinus*. The base of the zone is where the non-tree pollen (*NAP*) frequency falls sharply.

Zone *b*. Site A: 80 to 230 cm. Zone with high frequency of *NAP*. *Betula* and *Pinus* and abundant herbs present.

(iii) *Macroscopic plant remains*

The macroscopic plant remains identified and the numbers found are recorded in table 2. The nomenclature of the plants follows Dandy (1958).

The present-day distributions of the plants, of significance in considering the course of immigration of the flora and the climatic implications given by the presence of the plants, are taken chiefly from Hultén's (1950) *Atlas of the distribution of vascular plants in N.W. Europe*. Table 3 summarizes the process of immigration of the flora, as shown by the list of macroscopic remains. The same categories of plant distribution are used here as in the similar analysis of the plant remains of the interglacial deposit at Bobbitshole, Ipswich (West 1957). The assignment of each plant identified to its category is shown in table 2.

(iv) *Vegetational, environmental and climatic history*

Zone *b*

This zone is characterized by the high *NAP* frequency, indicating an open, relatively treeless regional vegetation. *Betula* and *Pinus* are the only trees represented by any quantity of pollen. *Betula* shows higher percentages of pollen than *Pinus*, and macroscopic remains of tree *Betula* sp. were not infrequent in the upper sediments of the zone. *Betula* must have been locally frequent during this time, and, to a less extent, *Pinus*. The continuous low frequencies of *Salix* and *Juniperus* indicate that these shrubs occurred infrequently in the locality. Pollen grains of the shrub *Ephedra* were found near the top of the zone.

The herbaceous pollen is divided in the pollen diagram into various categories of habitat. Apart from the aquatics, pollen of Gramineae and Cyperaceae is the most frequent of the herbaceous pollen types. The percentages of both vary between 100 and 200% of the total tree pollen. Several other herbaceous pollen types show relatively high frequencies throughout the zone. Of the plants of uncertain habitat, these include Caryophyllaceae, Compositae, Labiatae, *Ranunculus*, *Sium*-type and *Thalictrum*. These might belong to the local aquatic or marsh flora or to the terrestrial flora. Other herbaceous pollen types must probably belong to the regional terrestrial vegetation. Several are found in relatively high frequencies, including *Artemisia*, Chenopodiaceae, *Plantago maritima*, *P.* cf. *media* and *Polygonum bistorta*-type. *Armeria*, *Helianthemum*, *Sanguisorba officinalis*, *Scabiosa columbaria* and *Botrychium* also come within this group of plants.

Of the pollen of aquatics, that of *Sparganium*-type and *Typha latifolia* occurs abundantly. *Alisma*, *Caltha*, *Menyanthes* and *Equisetum* are also represented.

The macroscopic remains from zone *b* include both elements of the local aquatic and marsh vegetation and of the terrestrial vegetation. As might be expected, the former group is far more frequent than the latter, which includes only a few identifications: *Atriplex* cf. *hastata*, *A. glabriuscula*, *Chenopodium* Section *Pseudoblitum*, *Polygonum aviculare* (agg.) and *Potentilla* cf. *argentea*. Of the other species identified, seven are aquatics and eleven may be considered to belong to the shallower water or marsh vegetation. The former include three *Potamogeton* species, *P.* cf. *berchtoldii*, *P. crispus* (abundant) and *P. filiformis*, *Ceratophyllum demersum*, *Hippuris vulgaris* and *Menyanthes trifoliata*. Of the marsh species, these may be mentioned: *Alisma plantago-aquatica*, *Carex rostrata*, *Eleocharis palustris*, *Lycopus europaeus* (especially abundant), *Potentilla palustris*, *Ranunculus sceleratus*, *Rorippa islandica*, *Scirpus lacustris* (very abundant) and *Sparganium erectum*.

These pollen and macroscopic analyses give a clear indication of local and regional vegetational conditions. A rich aquatic and marsh flora lived in and bordered the water body—the sediments suggest a small lake or a river with slowly flowing water. In the surrounding region occurred low open vegetation with few trees and shrubs, with grasses and sedges (that the sedges are more than local is suggested by their high pollen frequency even when their macroscopic remains are scarce), and with many other herbaceous species, including for example, *Armeria*, *Artemisia*, *Helianthemum*, *Plantago* spp., *Sanguisorba officinalis*, *Scabiosa columbaria*, and the fern *Botrychium*. Some of these plants are characteristic of calcareous soils and open situations and they may have been present in the vegetation of the nearby chalk uplands.

In the Netherlands, van der Vlerk & Florschütz (1953) and Florschütz (1958) have described early Eemian or late Drenthian pollen diagrams which show the presence of open parkland vegetation at this time. They suggest that the vegetation may not have been wholly subarctic then, but mixed with 'steppe-elements', such as *Artemisia*, *Helianthemum* and *Thalictrum*. Our zone *b* vegetation, which must be about the same age as the Netherlands early Eemian or late Drenthian, also includes the same so-called 'steppe-elements', though plants definitely indicating an arctic or subarctic climate are lacking, as will be discussed later in this section.

The zone *b* vegetation also includes a number of species usually associated with saline conditions, e.g. *Armeria*, *Atriplex* spp., and *Plantago maritima*. It is not clear whether these species belong to vegetation associated with a neighbouring maritime climate or with the regional parkland. Halophilous plants have been found in the Tubantian (Last Glaciation) *Dryas*-floras of the Netherlands (van der Vlerk & Florschütz 1953; Florschütz 1958), and it is possible that our species in this category may similarly be associated with the regional vegetation.

Table 3 gives an indication of the present-day distribution of the thirty species identified macroscopically in zone *b*. The majority are found throughout Scandinavia, but certain species are more southerly in distribution. These include *Berula erecta*, *Carex acutiformis*, *Lycopus europaeus*, *Mentha* cf. *aquatica* and *Potamogeton crispus*. These species are all members of the local aquatic or marsh vegetation. The few land species have a wider distribution to the north. The occurrence of the more southerly plants indicates that the climate at this time cannot have been like the present arctic or subarctic climates, despite the parkland poor in trees. No plants of arctic or subarctic distribution type were found. The presence of high frequencies of pollen of *Typha latifolia* suggests the same. Iversen (1954) considers this plant to be distinctly thermophilous; in Scandinavia it is not found beyond the 14 °C July isotherm and in the Alps it rarely exceeds heights of 1000 m, well below the forest limit.

Perhaps there is some indication of winter temperatures in the presence of erratic boulders in the freshwater zone *b* sediment. If these were rafted by ice, then we may assume a winter temperature severe enough to produce substantial river ice.

We thus have the contrast between the thermophilous elements of the aquatic and marsh flora and the relatively treeless parkland. A similar contrast has been noted by van der Vlerk and Florschütz (1953) and Florschütz (1957) in the Tubantian (Last Glaciation) flora of the Netherlands. The *Dryas*-flora found at Velsen (North Holland) contains aquatic and marsh plants which cannot endure severe cold, and also plants that are characteristic of tundra and steppe. Florschütz (1957, p. 119) suggests that 'the former existence of these different elements in the neighbourhood of Velsen may have been due to the higher inclination of the sun. In arctic regions slopes turned towards the south can still offer adequate dwelling places for land-plants, whereas the flat surface of the water cannot catch sufficient warmth to enable the life of a water- and marsh-vegetation. At our latitude, on the contrary, this condition may have been fulfilled, even during the coldest phases of the last glaciation.' The same comment may apply to the contrasting elements of the zone *b* vegetation. It emphasizes that we cannot necessarily interpret past climates as equivalents of present climates.

It remains to consider in this section the infrequent occurrence of certain tree pollen types in zone *b*. *Carpinus*, *Carya*, *Juglans*, *Nyssa* and *Tilia* pollen all occur in sporadic and low or very low frequencies. It is very probable that this pollen, exotic to the type of vegetation we have described in this zone, is derived from older Early Pleistocene or Tertiary deposits, perhaps from the Tertiary deposits on which the interglacial deposits lie. All the genera concerned are commonly found in these older deposits.

Zone *c*

The increase in the *AP* frequency and the rise in the *AP*/*NAP* ratio which occur in this zone indicate that at this time the trees *Betula* and *Pinus*, already present in the previous zone, spread at the expense of the open grassland. The pollen of *Betula* is again more frequent than that of *Pinus*, The fruits of tree *Betula* species were found again in this zone, and also a stone of *Prunus avium*.

Most of the herbaceous pollen types found in the previous zone are also present in this zone, though their frequencies are much smaller. A noticeable change is the great frequency of the spores of Filicales (up to 933 % of the total tree pollen). The increase in their frequency began at the end of zone *b*, and may best be explained by the local abundance of ferns rather than by any regional vegetational change.

The macroscopic plant remains show that the aquatic and marsh vegetation of the zone remained much the same as in the previous zone. *Potamogeton acutifolius* and *Lysimachia vulgaris* are two new additions to it.

There is no indication of much change in climatic conditions since the previous zone. The increase in tree *Betula* pollen may suggest a slight amelioration of the terrestrial climate, and so may the find of the stone of *Prunus avium*, a small tree now more common in England and Wales than Scotland, and in Scandinavia only found in the southern part. Table 3 shows that the proportion of southern species in this zone exceeds that in zone *b*.

Zone *d*

The spread of *Betula* and *Pinus* which started in the previous zone is continued in this zone. The *AP* frequency rises, *Pinus* replaces *Betula* as the predominant tree pollen type,

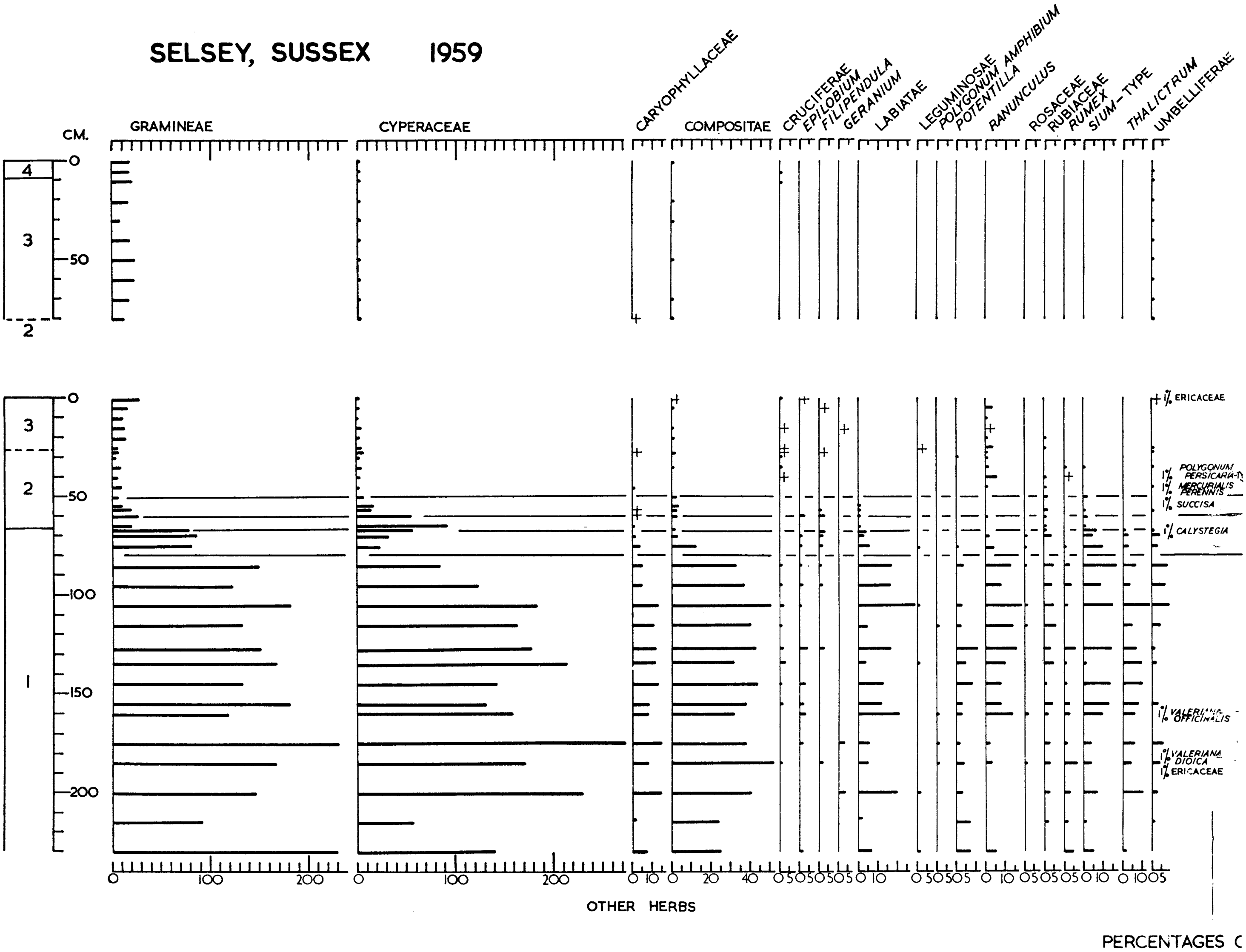
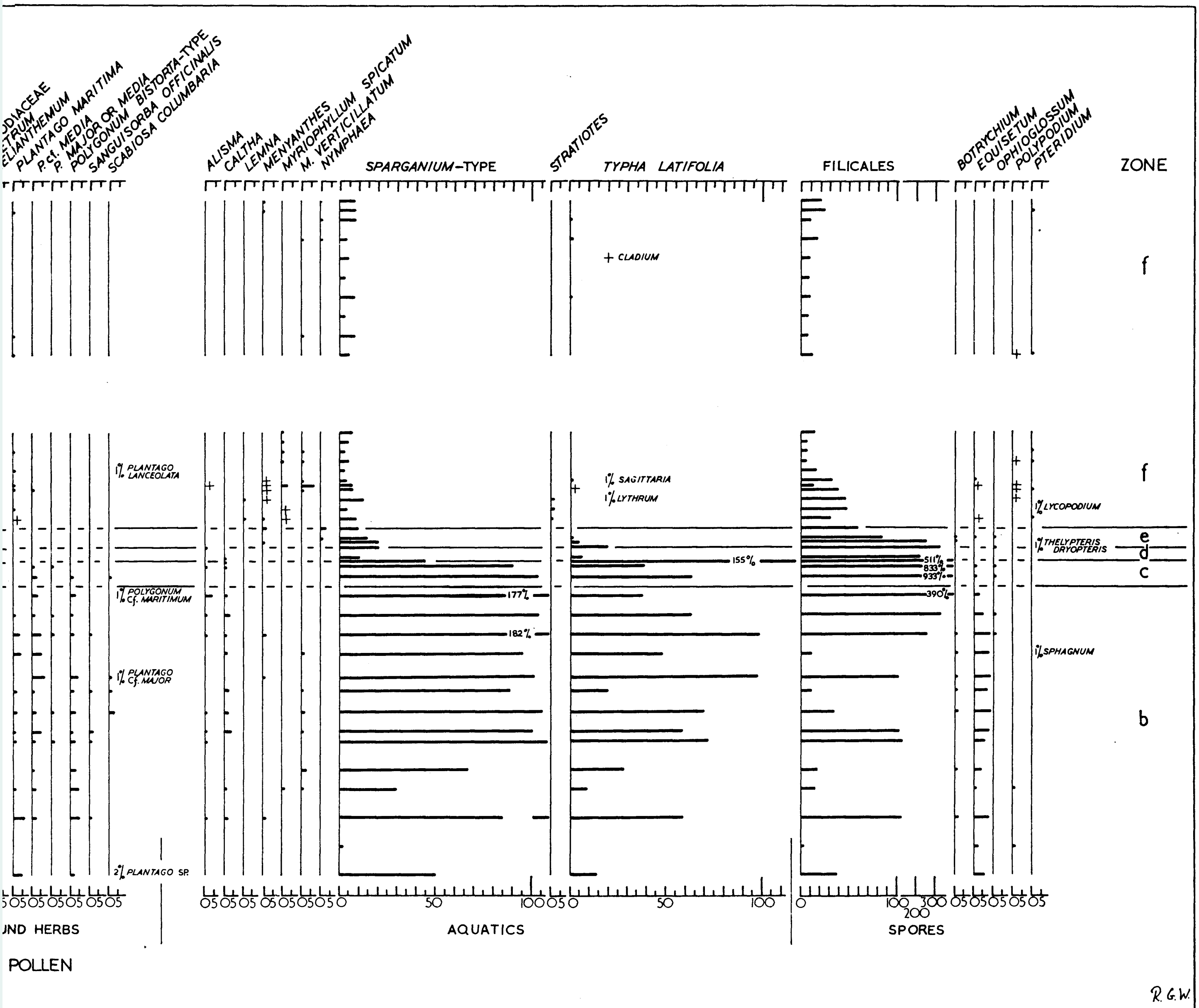


FIGURE 6. The non-tre

and the pollen of the thermophilous tree *Quercus* appears in significant quantity for the first time.

The *Salix* pollen in this zone shows a peak, probably associated with changes in the local environment. At the base of the zone the sediment suddenly becomes far more organic and contains many wood fragments (the change from bed 1 to bed 2). Here also the Cyperaceae pollen percentages show a rise, while *Sparganium* type and *Typha latifolia* show a sharp decrease. The aquatic species identified macroscopically are also reduced in number. The change in the sediment, the restriction of the aquatic environment and the spread of marginal carr communities, as suggested by the rise of *Salix* and Cyperaceae pollen, may be ascribed to a fall in the water level. A fluctuating water level at this time is also suggested by the unconformity between beds 1 and 2, described in §2 (*a*).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



gram from Selsey.

The pollen of herbs characteristic of zone *b* and, to a lesser extent, of zone *c* is either absent or at very low frequencies in zone *d*, as illustrated by the curves of Caryophyllaceae, Compositae, Labiatae, *Ranunculus*, Rubiaceae, *Sium*-type, *Thalictrum*, *Artemisia*, *Plantago* spp. and *Polygonum*. The restriction of these herbs must have followed the spread of the *Pinus–Betula–Quercus* forest and the changes mentioned above in the local conditions.

There is little indication of climatic change since the previous zone. The climate now allowed the expansion of *Pinus* and the increase in the number of southern species shown in table 3, but these changes may be successional and/or a reflexion of the rate of spread of species.

TABLE 2. LIST OF MACROSCOPIC PLANT REMAINS FROM SELSEY AND STONE

			SELSEY																					
		zone	...				*b*				*c*		*d*	*e*			*f*					*f*		
											site A											site D		
	distribution category	type of remains	200–230 cm	160–200 cm	130–160 cm	127–134 cm	120–127 cm	105–120 cm	90–105 cm	82–90 cm	75–82 cm	67–75 cm	56–67 cm	50–60 cm	40–55 cm	30–40 cm	20–30 cm	10–20 cm	0–10 cm	60–80 cm	40–60 cm	20–40 cm	10–20 cm	0–10 cm
Acer monspessulanum L.	6	*fr*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Ajuga cf. *reptans* L.	5	*n*	...	...	...	...	...	...	...	...	...	...	...	1	2	1	...	...	...	...	...	...	...	1
Alisma plantago-aquatica L.	3	*fr*	...	...	4	8	25	33	43	29	21	7	1	23	8	15	4	2	4	3	...	...	2	2
Aster tripolium L.	3	*a*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Atriplex glabriuscula Edmonst.	4	*s*	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Atriplex cf. *hastata* L.	2	*s*	...	...	...	...	...	...	...	1	...	...	...	...	1	...	...	...	...	...	...	...	...	...
A. patula L.	2	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...
Atriplex sp.	...	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Berula erecta (Huds.) Coville	5	*fr*	...	...	...	1	15	13	6	10	10	7	1	10	4	...	...	...	...	...	...	...	...	...
Beta vulgaris L.	5	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Betula cf. *pendula* Roth.	2	*fr*	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...
Betula cf. *pubescens* Ehrh.	2	*fr*	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...
Betula sp. (tree)	...	*fr, cs*	...	...	...	3	6	10	11	12	14	14	14	22	94	105	52	5	8	1	2	1	5	3
Bidens cernua L.	4	*a*	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Callitriche sp.	...	*d*	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...
Carduus sp.	...	*a*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...
Carex acutiformis Ehrh.	5	*n+u*	...	...	...	...	...	1	3	1	1	1	2	5	23	5	...	...	...	...	...	...	...	...
Carex cf. *rostrata* Stokes	2	*n+u*	...	...	...	...	1	2	1	2	1	...	1	...	...	...	...	...	...	...	...	...	...	...
Carex spp.	...	*n*	1	2	4	35	32	72	87	61	52	48	15	24	63	20	14	10	6	23	3	...	9	12
Ceratophyllum demersum L.	4	*n*	...	...	...	...	...	...	1	...	...	...	...	...	8	11	1	...	...	...	...	...	...	...
Ceratophyllum cf. *submersum* L.	5	*n*	...	...	...	...	...	...	...	...	...	...	...	1	...	1	...	...	...	...	...	...	...	...
Chenopodiaceae	...	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Chenopodium cf. *album* L.	2	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Chenopodium section *Pseudoblitum* Benth. & Hook. f.	3	*s*	...	...	...	3	1	2	2	2	1	...	...	...	...	...	...	...	...	...	...	...	...	...
Cirsium sp.	...	*a*	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...
Cladium mariscus (L.) Pohl	5	*n*	...	...	...	...	...	...	...	...	...	...	...	...	2	1	1	...	...	...	...	...	...	...
Eleocharis cf. *palustris* (L.) Roem. & Schult.	...	*n*	...	1	12	15	20	35	37	30	18	10	...	...	...	...	...	...	...	2	...	...	...	...
Epilobium sp.	...	*s*	...	...	...	...	6	1	4	3	...	...	...	...	...	...	...	...	...	...	...	...	3	...
Eupatorium cannabinum L.	5	*a*	...	...	...	...	...	...	...	...	...	...	3	58	63	45	12	...	2	...	...	...	1	8
Glaux maritima L.	2	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Hippuris vulgaris L.	2	*st*	...	...	...	...	1	...	1	...	...	2	...	1	12	6	2	1	...	...	...	...	...	...
Hydrocharis morsus-ranae L.	4	*s*	...	...	...	...	...	...	...	...	...	...	...	...	4	2	3	1	...	...	...	...	...	...
Juncus cf. *maritimus* Lam.	5	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Lapsana communis L.	3	*a*	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...
Lemna cf. *minor* L.	3	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...
Leontodon autumnalis L.	2	*a*	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...
Lycopus europaeus L.	4	*n*	1	1	49	65	206	263	373	288	228	203	52	50	50	23	17	2	3	2	1	1	1	3
Lysimachia vulgaris L.	3	*s*	...	...	...	...	...	...	...	1	...	...	...	1	3	1	2	...	...	...	...	...	...	...
Mentha cf. *aquatica* L.	5	*n*	...	...	...	1	12	8	21	7	24	48	127	162	87	32	7	3	2	2	...	1	...	3
Mentha spp.	...	*n*	...	...	...	1	3	...	14	2	6	17	60	21	8	5	1	...	3	2	...	2	...	7
Menyanthes trifoliata L.	2	*s*	...	...	...	...	7	4	6	10	10	27	1	3	5	1	...	...	...	...	...	...	...	...
Moehringia trinervia (L.) Clairv.	2	*s*	...	...	...	...	...	...	...	...	...	...	1	1	1	...	1	...	...	...	...	...	...	...
Myosoton aquaticum (L.) Moench	4	*s*	...	...	...	...	...	...	...	...	...	...	...	...	9	...	...	...	...	...	...	...	...	...
Myriophyllum spicatum L.	2	*n*	...	...	...	...	...	...	...	...	...	...	...	...	6	10	9	5	6	...	...	...	...	...

	distribution category	type of remains	221–234 cm	211–221 cm	200–211 cm	188–200 cm	176–188 cm	165–176 cm	153–165 cm	142–153 cm	130–142 cm	119–130 cm	104–119 cm	92–104 cm	80–92 cm	70–80 cm	58–70 cm	47–58 cm	44–47 cm	32–44 cm	28–32 cm	23–28 cm	16–23 cm	0–16 cm
			Stone																					
			zone …											f										
Acer monspessulanum L.	6	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	2	3	…	3	…	…	1
Ajuga cf. *reptans* L.	5	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Alisma plantago-aquatica L.	3	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Aster tripolium L.	3	*a*	…	…	…	…	…	…	…	…	…	…	…	…	4	6	6	5	3	…	…	…	…	…
Atriplex glabriuscula Edmonst.	4	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Atriplex cf. *hastata* L.	2	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
A. patula L.	2	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Atriplex sp.	…	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	1	…	…	…	…	…	…
Berula erecta (Huds.) Coville	5	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Beta vulgaris L.	5	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	2	…	…	…	…	…	…
Betula cf. *pendula* Roth.	2	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Betula cf. *pubescens* Ehrh	2	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Betula sp. (tree)	…	*fr, cs*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Bidens cernua L.	4	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Callitriche sp.	…	*d*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Carduus sp.	…	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Carex acutiformis Ehrh.	5	*n+u*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Carex cf. *rostrata* Stokes	2	*n+u*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Carex spp.	…	*n*	…	…	…	…	…	…	…	…	…	…	…	…	1	1	…	6	7	…	…	…	…	…
Ceratophyllum demersum L.	4	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	2	…	…	…	…	…	…
Ceratophyllum cf. *submersum* L.	5	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Chenopodiaceae	…	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	3	…	…	3	…
Chenopodium cf. *album* L.	2	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	1	…	…	…	…	…	…
Chenopodium section *Pseudoblitum* Benth. & Hook. f.	3	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Cirsium sp.	…	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Cladium mariscus (L.) Pohl	5	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Eleocharis cf. *palustris* (L.) Roem. & Schult.	…	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Epilobium sp.	…	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Eupatorium cannabinum L.	5	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Glaux maritima L.	2	*s*	1	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Hippuris vulgaris L.	2	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Hydrocharis morsus-ranae L.	4	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Juncus cf. *maritimus* Lam.	5	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	44	8	…	…	…	…	…
Lapsana communis L.	3	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Lemna cf. *minor* L.	3	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Leontodon autumnalis L.	2	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Lycopus europaeus L.	4	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	1	1	…	…	…	…
Lysimachia vulgaris L.	3	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Mentha cf. *aquatica* L.	5	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	1	…	…	…	…	…	…	…	…
Mentha spp.	…	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Menyanthes trifoliata L.	2	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Moehringia trinervia (L.) Clairv.	2	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Myosoton aquaticum (L.) Moench	4	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Myriophyllum spicatum L.	2	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…

		zone ...			b					c		d	e			f					f		
		site A																	site D				
	distribution category	type of remains	200–230 cm	160–200 cm	130–160 cm	127–134 cm	120–127 cm	105–120 cm	90–105 cm	82–90 cm	75–82 cm	67–75 cm	56–67 cm	50–60 cm	40–55 cm	30–40 cm	20–30 cm	10–20 cm	0–10 cm	60–80 cm	40–60 cm	20–40 cm	10–20 cm	0–10 cm
Myriophyllum spicatum or *verticillatum* L.	...	*n*	...	...	...	...	...	...	1	...	...	...	...	...	6	6	7	1	...	...	...	...	...	...
Naias marina L.	...	*fr*	...	...	...	...	...	...	...	...	...	...	...	2	34	153	257	35	17	7	...	...	...	1
N. minor All.	6	*fr*	...	...	...	...	...	...	...	...	...	...	...	1	12	38	19	...	2	...	...	...	...	...
Nuphar lutea (L.) Sm.	2	*s*	...	...	...	...	...	...	...	...	...	...	...	2	4	...	...	...	...	...	...	...	...	...
Oenanthe aquatica (L.) Poir.	5	*fr*	...	...	...	...	...	...	...	...	...	...	...	7	11	11	11	...	...	...	...	...	...	...
Polygonum aviculare L. *s.l.*	2	*n*	...	...	...	1	1	2	4	1	2	...	...	...	...	...	...	...	...	...	...	...	...	...
P. lapathifolium L.	2	*n*	...	...	...	...	1	1	...	...	...	...	...	2	...	...	...	...	...	...	...	...	...	...
Polygonum cf. *persicaria* L.	4	*n*	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...
Potamogeton acutifolius Link.	5	*st*	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...
Potamogeton cf. *berchtoldii* Fieb.	2	*st*	...	...	1	4	16	2	8	8	6	3	...	...	1	...	...	...	...	...	...	...	...	...
P. crispus L.	5	*st*	...	2	11	14	38	40	35	35	11	8	2	4	32	9	1	...	...	...	...	...	...	2
P. filiformis Pers.	2	*st*	2	4	...	6	4	7	2	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...
Potamogeton cf. *friesii* Rupr.	4	*st*	...	...	...	...	...	...	...	...	...	...	...	...	...	5	86	125	112	18	1	...	1	1
P. pectinatus L.	3	*st*	...	...	...	...	...	...	...	...	...	...	...	...	1	5	47	122	32	11	1	...	...	...
P. trichoides Cham. & Schlecht.	5	*st*	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...
Potentilla anserina L.	2	*a*	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Potentilla cf. *argentea* L.	2	*a*	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...
Potentilla cf. *erecta* (L.) Räusch.	2	*a*	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...
P. palustris (L.) Scop.	2	*a*	...	...	...	1	...	4	4	3	2	1	...	...	...	...	...	...	...	...	...	...	...	...
Prunus avium (L.) L.	5	*st*	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...
Pyracantha coccinea M. J. Roem.	6	*st*	...	...	...	...	...	...	...	...	...	...	...	...	...	1	3	1	1	...	...	...	...	...
Quercus sp.	4	*b, c*	...	...	...	...	...	...	...	...	...	...	...	1	1	...	...	2	...	1	...	...	...	...
Ranunculus cf. *flammula* L.	3	*a*	...	...	...	...	1	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...
R. sceleratus L.	3	*a*	...	...	1	9	6	11	25	19	9	5	8	252	23	10	5	3	2	...	2	1	6	5
Ranunculus section *Chrysanthe* (Spach.) L. Benson	...	*a*	...	...	...	1	3	1	2	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...
Ranunculus-Batrachium spp.	...	*a*	...	...	...	...	...	2	1	1	4	3	...	13	298	276	77	3	1	2	...	...	2	2
Rorippa islandica (Oeder) Borbás	2	*s*	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
R. microphylla (Boenn.) Hyland.	5	*s*	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...
Rosaceae	...	*th*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Rubus sp.	...	*st*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Rumex sp.	...	*n*	...	...	...	...	...	1	3	...	1	...	...	4	11	3	...	...	...	...	...	...	...	...
Ruppia maritima (agg.)	3	*fr*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	3	15	32	37	11	4	5	2
Salix sp.	...	*t*	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Scirpus lacustris L.	2	*n*	...	...	20	79	127	175	179	135	115	84	6	9	24	8	1	...	1	...	...	...	...	...
S. maritimus L.	4	*n*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Solanum dulcamara L.	4	*s*	...	...	...	...	...	...	...	...	...	...	...	1	3	1	1	...	1	...	...	...	...	...
Sparganium erectum L.	3	*st*	...	...	2	7	6	36	56	43	56	87	20	106	135	15	10	5	2	...	...	...	1	...
Stellaria neglecta Weihe	5	*s*	...	...	...	...	...	...	...	...	...	...	...	...	3	...	...	...	...	...	...	...	...	...
S. palustris Retz.	3	*s*	...	...	...	...	1	1	3	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Stratiotes aloides L.	3	*s*	...	...	...	...	...	...	...	...	...	...	...	...	10	3	1	...	...	...	...	...	...	1
Suæda maritima (L.) Dumort.	3	*s*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Thelycrania sanguinea (L.) Fourr.	5	*st*	...	...	...	...	...	...	...	...	...	...	...	2	5	...	...	2	...	...	...	...	...	...
Typha sp.	...	*s*	...	...	...	...	...	...	...	...	...	...	...	...	2	...	...	...	...	...	...	1	...	...
Umbelliferae	...	*fr*	...	...	...	...	...	...	...	...	...	...	...	...	1	1	...	...	...	...	...	...	...	...
Urtica dioica L.	2	*fr*	...	...	...	...	2	3	1	1	2	2	39	107	224	105	67	4	2	6	1	2	5	7
Viola sp.	...	*s*	1	2	...	...	...	...	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Zannichellia palustris L.	3	*a*	...	...	...	...	...	...	...	...	...	...	...	1	1	14	183	560	616	254	29	6	30	40
Characeae	...	*o*	...	...	...	...	...	...	...	...	...	...	...	...	2	...	...	...	1	6	...	...	...	...

Abbreviations: *a*, achene; *b*, bud; *c*, cupule; *cs*, cone scale; *d*, drupelet; *fr*, fruit; *n*, nut or nutlet; *o*, oospore; *s*, seed; *st*, fruit-stone; *t*, twig; *th*, thorn; *u*, utricle of *Carex*. The figures give the number of specimens of each plant at each level.

	distribution category	type of remains	221–234 cm	211–221 cm	200–211 cm	188–200 cm	176–188 cm	165–176 cm	153–165 cm	142–153 cm	130–142 cm	119–130 cm	104–119 cm	92–104 cm	80–92 cm	70–80 cm	58–70 cm	47–58 cm	44–47 cm	32–44 cm	28–32 cm	23–28 cm	16–23 cm	0–16 cm
zone …			f																					
Myriophyllum spicatum or *verticillatum* L.	…	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Naias marina L.	…	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	1	…
N. minor All.	6	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Nuphar lutea (L.) Sm.	2	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Oenanthe aquatica (L.) Poir.	5	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Polygonum aviculare L. *s.l.*	2	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
P. lapathifolium L.	2	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Polygonum cf. *persicaria* L.	4	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Potamogeton acutifolius Link.	5	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Potamogeton cf. *berchtoldii* Fieb.	2	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
P. crispus L.	5	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
P. filiformis Pers.	2	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Potamogeton cf. *friesii* Rupr.	4	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
P. pectinatus L.	3	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
P. trichoides Cham. & Schlecht.	5	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Potentilla anserina L.	2	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Potentilla cf. *argentea* L.	2	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Potentilla cf. *erecta* (L.) Räusch.	2	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
P. palustris (L.) Scop.	2	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Prunus avium (L.) L.	5	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Pyracantha coccinea M. J. Roem.	6	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Quercus sp.	4	*b, c*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Ranunculus cf. *flammula* L.	3	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
R. sceleratus L.	3	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	16	1	7	16	3	10	…	…	1
Ranunculus section *Chrysanthe* (Spach) L. Benson	…	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Ranunculus-Batrachium spp.	…	*a*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Rorippa islandica (Oeder) Borbás	2	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
R. microphylla (Boenn.) Hyland.	5	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Rosaceae	…	*th*	…	…	…	…	…	…	…	…	…	…	…	…	1	6	1	…	…	…	…	…	…	…
Rubus sp.	…	*st*	2	…	…	1	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	1
Rumex sp.	…	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Ruppia maritima (agg.)	3	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Salix sp.	…	*t*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Scirpus lacustris L.	2	*n*	…	…	…	…	…	…	…	1	…	…	…	…	1	1	…	…	…	…	…	…	…	…
S. maritimus L.	4	*n*	…	…	…	…	…	…	…	…	…	…	…	…	…	1	…	…	4	1	3	…	…	…
Solanum dulcamara L.	4	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Sparganium erectum L.	3	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Stellaria neglecta Weihe	5	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
S. palustris Retz.	3	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Stratiotes aloides L.	3	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Suæda maritima (L.) Dumort.	3	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	1	2	…	…	…	…	…	…
Thelycrania sanguinea (L.) Fourr.	5	*st*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Typha sp.	…	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	3	46	…
Umbelliferae	…	*fr*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Urtica dioica L.	2	*fr*	…	…	1	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Viola sp.	…	*s*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Zannichellia palustris L.	3	*a*	…	…	…	…	1	…	…	…	…	…	1	…	…	…	…	6	7	…	…	11	3	…
Characeae	…	*o*	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	1	…

Abbreviations: *a*, achene; *b*, bud; *c*, cupule; *cs*, cone scale; *d*, drupelet; *fr*, fruit; *n*, nut or nutlet; *o*, oospore; *s*, seed; *st*, fruit-stone; *t*, twig; *th*, thorn; *u*, utricle of *Carex*. The figures give the number of specimens of each plant at each level.

TABLE 3. ANALYSIS OF PLANT-GEOGRAPHICAL CATEGORIES IN THE LIST OF MACROSCOPIC PLANT REMAINS FROM SELSEY

The figures give the number of species (or genera) in each category in each zone; figures in parentheses are the percentages of the zone totals in each category.

	category					
zone	2	3	4	5	6	zone total
f	16 (33)	10 (20)	8 (16)	13 (27)	2 (4)	49
e	8 (26)	5 (16)	8 (26)	9 (29)	1 (3)	31
d	6 (40)	3 (20)	1 (7)	5 (33)	...	15
c	12 (50)	5 (21)	1 (4)	6 (25)	...	24
b	16 (53)	6 (20)	4 (13)	4 (13)	...	30

Definition of categories: 2, plants distributed throughout Scandinavia; 3, plants with northern limits in Scandinavia near the Arctic Circle; 4, plants with northern limits in Scandinavia about midway between those in categories 3 and 5; 5, plants with northern limits in the south of Scandinavia; 6, plants with northern limits in north-west Europe south of Scandinavia.

Zone *e*

The expansion of the forest in this zone is shown by the continued rise in the *AP/NAP* ratio. During this zone *Quercus* becomes the dominant tree, represented by over 50% of the total tree pollen at the end of the zone, while *Betula* and *Pinus* both decline in frequency. One bud of *Quercus* sp. was found in the sediment of the zone. *Fraxinus* and *Hedera* appear for the first time in this zone.

The frequency of herbaceous pollen is low in zone *e*. Of the non-aquatics, only Gramineae, Cyperaceae and Compositae are shown as continuously present. By this time the regional forest cover must therefore have been fairly complete.

The macroscopic remains include a high proportion of shallow water or marsh species, including *Ajuga* cf. *reptans*, *Alisma plantago-aquatica*, *Berula erecta*, *Carex acutiformis*, *Eupatorium cannabinum* (abundant), *Lycopus europaeus*, *Lysimachia vulgaris*, *Menyanthes trifoliata*, *Nasturtium microphyllum*, *Oenanthe aquatica* and *Ranunculus sceleratus* (very abundant). Aquatic plants are also well represented and include *Ceratophyllum demersum*, *C.* cf. *submersum*, *Hippuris vulgaris*, *Naias marina*, *N. minor*, *Nuphar luteum*, *Scirpus lacustris* and *Potamogeton crispus*. Remains of a number of terrestrial plants from this zone include these species and genera: *Betula* tree sp., *Thelycrania sanguinea*, *Lapsana communis*, *Moehringia trinervia*, *Quercus* (bud), and *Urtica dioica* (abundant).

By zone *e* the amelioration of the climate had continued far enough to permit the great expansion of *Quercus* and the growth of such thermophilous plants as *Thelycrania sanguinea* and *Hedera*. The rich lake flora, with *Ceratophyllum* cf. *submersum*, *Naias marina* and *N. minor*, also testifies to the summer warmth of the climate. Reference to table 3 will again show in this zone an increase in the proportion of the species of a southern distribution.

Zone *f*

Zone *f* is characterized by the high frequencies of the pollen of *Quercus* (up to 81%) and of *Corylus* (up to 78%). The regional vegetation at this time must have been dominated by *Quercus*, with *Corylus* as a prominent shrub. The pollen frequencies of *Pinus* remain between 10 and 30% throughout the zone, and this tree must also have been present in the forest. The only other trees consistently present are *Betula* and *Ulmus*. The pollen frequencies of the latter are rather greater at the beginning of the zone than at the end, and the frequency of *Betula* fruits is higher there also. The pollen of *Acer*, *Alnus*, *Fraxinus*, *Tilia* and *Picea* occur sporadically throughout the zone; these trees must have been rare or absent locally or distantly present. The pollen of *Hedera* occurs in substantial quantities through the zone, and *Ilex* pollen also occurs, though less frequently.

The herbaceous pollen continues to be at low frequency in zone *f*. The pollen of Gramineae and Cyperaceae accounts for a large proportion of it. Pollen of Chenopodiaceae is the most common of the other herbaceous pollen types and this must be related to the estuarine character of most of the zone *f* deposits. The change from fresh water to estuarine takes place at 27 cm at site A, and at this level the Chenopodiaceae pollen appears in some quantity, after its rarity since the end of zone *b*, where it was continuously present. *Armeria* and *Plantago maritima* show a similar distribution within the zones, being most abundant in zones *b* and *f*.

Of the other *NAP*, Filicales show a marked decline from the high frequencies reached during the previous zones; the spores show a minimum on the transition to estuarine conditions.

The macroscopic remains from zone *f* again reveal a rich aquatic and marsh flora, especially in the lower freshwater part. Here, in addition to the two *Ceratophyllum* species and the two *Naias** species also found in the previous zone, were found the remains of *Cladium mariscus*, *Hydrocharis morsus-ranae*, *Lemna* cf. *minor* and *Stratiotes aloides*. These four species were also found in the zone *f* deposits of the interglacial at Bobbitshole, Ipswich (West 1957). The last three fruit rarely or never in Britain today, and their presence indicates a considerable summer warmth, greater than that of the present day in the area. The presence of *Naias minor* gives a similar indication of summer warmth, and so do the records of the fruit-stones of *Pyracantha coccinea*, a native of southern Europe, found eastwards to the Caucasus and western Asia.

The high frequencies of *Corylus* and the presence of *Hedera* and *Ilex* suggest some degree of oceanicity in zone *f*. In particular the presence of *Hedera* gives some indication of winter temperatures. Iversen (1944) deduced the 'thermosphere' of *Hedera helix* from its present distribution, and he demonstrated that the plant will not tolerate an average temperature of the coldest month below $-1\cdot5$ °C. This is an indication that the winters in zones *e* and *f*, both with *Hedera* pollen present, were not colder than this.

In the estuarine part of zone *f*, at site D and above 27 cm at site A, the aquatic and marsh communities change considerably. The frequency table of macroscopic remains (table 2) shows how many species decrease their relative frequencies quickly;† for example, *Ceratophyllum demersum*, *Naias minor*, *Oenanthe aquatica*, *Ranunculus-Batrachium* and *Sparganium erectum*. Others increase their frequency rapidly as the change to estuarine conditions takes place, for example, *Potamogeton* cf. *friesii*, *P. pectinatus*, *Ruppia maritima*

* Reid (1899) also recorded *Naias graminea* Del. from the Pleistocene deposits at West Wittering, which are probably of the same age as the Selsey deposits. I re-examined his material (British Museum (Natural History) West Wittering, No. 1518) and find they resemble *N. flexilis* (Willd.) Rostk. & Schmidt in size and surface pattern far more closely than *N. graminea*. This interesting record should therefore be deleted from Reid's West Wittering list (R. G. W.).

† In the estuarine deposits at site D the absolute frequency of macroscopic plant remains declines, presumably because of the rapid estuarine sedimentation.

and *Zannichellia palustris*. *Naias marina* occupies an intermediate position, occurring in both freshwater and estuarine sediments; it is most abundant just after the water becomes brackish. The frequency of *Myriophyllum spicatum* hardly changes across the freshwater/estuarine boundary.

The brackish water communities represented are such that might be found at the present day at 1 to 2 m depth in quiet water on a sandy or muddy bottom. For example, all these species except *Potamogeton friesii* occur in such a habitat with a salinity of 5 to 7% in the Bay of Danzig (Kornaś 1958).

(v) *Comparison of the vegetational history*

The Selsey pollen diagrams, though of Ipswichian Interglacial age, show slight differences in detail from those at the type site at Bobbitshole, Ipswich (West 1957). They cover an earlier section of the interglacial than the Bobbitshole diagrams and do not extend so far into it. At Selsey *Pinus* shows considerably higher pollen frequencies in zones *b* and *c* and the *Pinus* maximum is reached earlier (in zone *d*) than at Bobbitshole. *Ulmus* reaches pollen percentages of between 5 and 10 in zone *d* at Bobbitshole, but at Selsey *Ulmus* does not appear in quantity until the beginning of zone *f*. The rise in *Quercus* is far more rapid at Selsey than at Bobbitshole, though the frequencies of *Corylus* rise in much the same manner.

These differences may probably be explained by the difference in latitude of the two deposits. The ice of the preceding glaciation, the Gipping Glaciation, reached the neighbourhood of Ipswich (West & Donner 1956), while Selsey was far south of the border of that glaciation. The distances of the glacial refuges of thermophilous plants from the two sites during the glaciation must have varied. It is probable that the rapid vegetational changes seen in zones *c*, *d* and *e* and the higher frequencies of *Pinus* at Selsey are a result of the closer proximity of glacial refuges, while the absence of early *Ulmus* may reflect a more easterly glacial refuge for this tree than for the others.

The records of macroscopic plant remains at Selsey and Bobbitshole are in many ways similar. Thermophilous aquatic and marsh plants occur in early zones at both sites; for example, the early appearances of *Carex acutiformis*, *Lycopus europaeus* and *Typha latifolia*. Many water plants of the later zones are also common to both sites; for example, *Hydrocharis morsus-ranae*, *Lemna* cf. *minor*, *Naias marina*, *N. minor* and *Stratiotes aloides*.

A comparison of the Selsey diagrams with continental diagrams from the same interglacial will not be made here. The vegetational character of this interglacial in southern England is now becoming clear (West 1960), and there are indeed considerable differences from the continental vegetational succession; these will be discussed elsewhere.

(*c*) *Mollusca*

The surface of the interglacial deposits betrays a quite exceptional richness in Mollusca, but, as a very comprehensive general collection of Mollusca was made by the late A. G. Davis, our attention was confined to analyzing the Mollusca from the bulk samples taken at sites A and D, which were used for the palaeobotanical study. Although the Mollusca are very interesting, they are not, unfortunately, present throughout the deposit, but only in site D and down to a depth of 60 cm in site A. Below that depth in site A, we recovered only single opercula of *Bithynia tentaculata* at 82 to 90 cm and at 120 to 127 cm, together with one specimen of *Agriolimax* cf. *reticulatus* at 82 to 90 cm. The Mollusca are listed in table 4.

Table 4. List of Mollusca from site A at Selsey

	zone *e*	zone *f*					
	50–60 cm	40–55 cm	30–40 cm	20–30 cm	10–20 cm	0–10 cm	total
Valvata cristata Müller	14	250	299	14	...	2	579
V. piscinalis (Müller)	22	392	454	28	1	1	898
Hydrobia ventrosa (Montagu)	21	67	377	5464	6253	7365	19547
H. ulvae (Pennant)	...	...	...	3	36	39	78
Bithynia tentaculata (Linné)	73	570	421	81	4	8	1157
B. leachi var. *inflata* (Hansén)	...	5	3	...	...	...	8
Carychium minimum (Müller)	...	3	1	...	...	...	4
Lymnaea peregra (Müller)	3	154	341	98	...	2	598
Physa fontinalis (Linné)	...	...	1	...	...	...	1
Planorbis carinatus Müller	...	1	3	...	...	...	4
P. planorbis (Linné)	...	3	3	3	...	...	9
P. (*Planorbis*) sp.	1	45	105	10	...	...	161
P. vorticulus Troschel	4	120	114	9	...	1	248
P. leucostoma Millet	...	...	1	13	...	...	14
P. laevis Alder	4	665	2019	180	3	6	2877
P. crista (Linné)	11	846	2147	1464	29	14	4511
P. contortus (Linné)	...	...	1	...	...	...	1
Segmentina complanata (Linné)	...	15	22	...	...	...	37
Acroloxus lacustris (Linné)	1	18	6	...	...	...	25
Succinea pfeifferi Rossmässler	...	...	?1	...	...	...	1
Succinea sp.	1	...	...	...	...	...	1
Vertigo angustior Jeffreys	...	3	...	...	...	...	3
Vallonia pulchella (Müller)	...	1	...	...	...	...	1
Punctum pygmaeum (Draparnaud)	...	...	1	1	...	...	2
Discus ruderatus (Férussac)	...	...	1	...	...	...	1
Vitrea sp.	...	1	...	...	...	...	1
Retinella radiatula (Alder)	...	2	...	...	...	...	2
R. nitidula (Draparnaud)	...	?2	...	...	...	...	2
Zonitoides nitidus (Müller)	...	2	1	...	...	...	3
Agriolimax cf. *reticulatus* (Müller)	1	2	...	...	...	...	3
Anodonta anatina (Linné)	...	...	4	...	...	...	4
Unio or *Anodonta* sp.	...	frag.	frag.	...	...	...	frag.
Corbicular fluminalis (Müller)	...	13	82	162	13	10	280
Sphaerium lacustre (Müller)	...	10	63	16	...	...	89
Pisidium obtusale (Lamarck)	...	1	1	...	...	...	2
P. milium Held	...	2	...	1	...	...	3
P. subtruncatum Malm	...	1	3	...	...	...	4
P. nitidum Jenyns	2	40	40	1	1	...	84
total	158	3234	6515	7548	6340	7448	31243

The usual care was taken in counting the Mollusca (see Sparks 1957), except that the *Corbicula* count is that of all recognizable pieces of hinge. Thus, its relative frequency is probably exaggerated even though it only just exceeds 2% of the total Mollusca at its maximum at 20 to 30 cm. This is a salutary corrective to the erroneous idea of its frequency one might obtain merely by looking at the deposit, when it appears to occupy a far higher porportion of the mollusc fauna.

Certain difficulties arose in identifying some of the species. The nature of the shells attributed to *Hydrobia ventrosa* and their relations with extinct Pleistocene species of *Hydrobia* are discussed in Appendix 1. Apart from this, the major difficulty was with the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

juveniles of the *Planorbis* species, *carinatus*, *planorbis* and *laevis*. Below a certain size it seems impossible to separate *planorbis* and *carinatus*, while very young specimens of *laevis*, of the order of size of one whorl, are very much like these other species at the same stage. Thus, the exact numbers assigned to each species may be a little uncertain, though it is believed that they are of the right order.

The most striking change shown by the fauna is the tremendous increase of the brackish water species (*Hydrobia*) in the 20 to 30 cm sample (figure 7). This coincides closely with the lithological change from brown detritus mud below to estuarine clay mud above

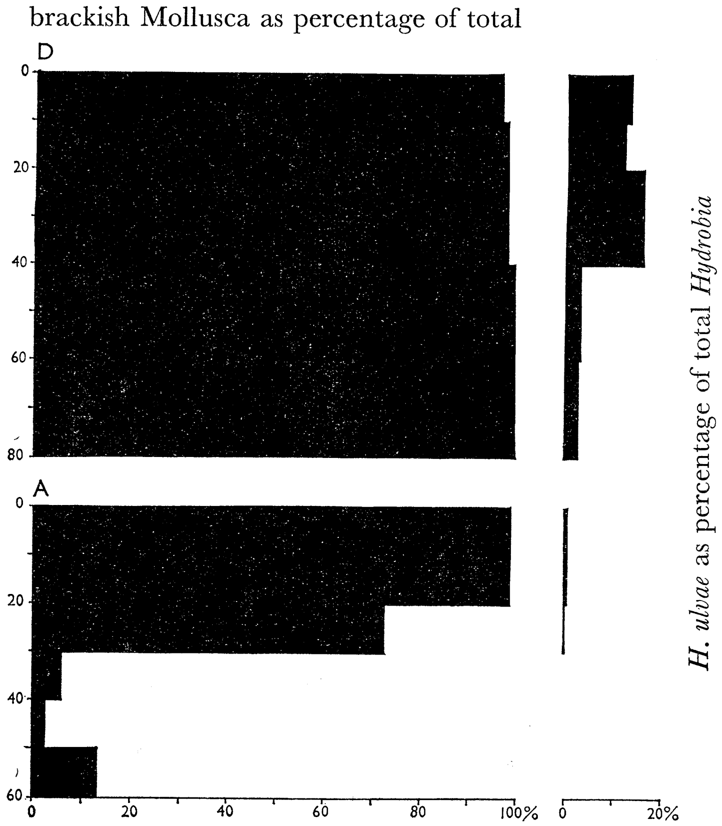


FIGURE 7. Percentage frequency of *Hydrobia* spp. in the Selsey deposit.

26 cm. The *Hydrobia* species which really flourished was *ventrosa*, usually considered to prefer less saline water than *ulvae*. The freshwater species present above 20 cm probably owe their existence not to survival in brackish water, but to being washed in by the stream as they belong to the most common species in the freshwater beds below.

Below 30 cm the freshwater fauna presents some peculiarities. The proximity of brackish water is shown by the presence of much smaller proportions of *H. ventrosa*. The combination of *Planorbis laevis* and *P. crista* as the dominant elements of the fauna is unusual. The former has been considered an inhabitant of low-level mountain lakes (Boycott 1936), but it is probably better to regard it as mainly living on water weeds in lakes and ponds (Ellis 1926), a situation favoured both by *P. crista* and *P. vorticulus*. It is difficult to escape the interpretation of a slowly moving body of water rich in plants, for *Bithynia* and *Valvata piscinalis* prefer running water while *V. cristata* is closer in ecology to the *Planorbis* species

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

mentioned above. The fauna is curiously like that from bed F of the Hoxne Interglacial deposit in its dominance by *P. laevis* and *P. crista*, though it possesses more southern species, especially *Corbicula fluminalis* and *Vertigo angustior*, not found at Hoxne. *Corbicula fluminalis* usually seems to indicate river deposits, but the shells are not particularly well developed in this organic deposit and the species may have lived in somewhat unsuitable conditions. Land species are few in number and consist almost entirely of those inhabiting damp marshy land: in true river deposits land shells are usually more abundant and include a high proportion of dry land species transported by the river. Thus, most of the evidence is consistent with a slowly moving stream or a lake rich in plants.

The fauna contains two species now extinct in Britain, *Corbicula fluminalis* and *Discus ruderatus*: the former is not known from the post-glacial and the latter only from its earlier parts. To these may be added *Bithynia leachi* var. *inflata* which is an interglacial variety, while the abundance of *Planorbis laevis* is a feature only recorded from a very few Pleistocene deposits.

The palaeobotanical evidence for the climatic conditions has already been discussed. The presence of *Corbicula fluminalis*, like the presence of seeds of *Stratiotes aloides*, is consistent with slightly warmer summers, while both species of *Hydrobia* and *Vertigo angustior* are not very northern in their present European distributions. Although there is only one sample, 50 to 60 cm, from pollen zone *e* and the number of Mollusca from that is small, it does seem that this deposit, like that at Bobbitshole (Sparks 1957), shows the appearance of the more southern species at the beginning of zone *f*. Especially interesting is the appearance of *Corbicula fluminalis* at this level and also *Vertigo angustior*, which also appeared at Bobbitshole at the same horizon.

The succession in Site A is extended upwards by site D, where the Mollusca listed in table 5 were found.

TABLE 5. LIST OF MOLLUSCA FROM SITE D AT SELSEY

	zone *f*					
	80–60 cm	60–40 cm	40–20 cm	20–10 cm	10–0 cm	total
Valvata cristata Müller	...	...	1	...	...	1
Bithynia tentaculata (Linné)	...	...	...	...	8	8
Hydrobia ventrosa (Montagu)	1291	488	127	305	501	2712
H. ulvae (Pennant)	44	17	24	43	74	202
Planorbis laevis Alder	...	...	...	...	2	2
P. crista (Linné)	1	...	...	2	5	8
Acroloxus lacustris (Linné)	...	...	...	1	...	1
Retinella radiatula (Alder)	...	...	...	1	...	1
Corbicula fluminalis (Müller)	...	...	2	2	3	7
Pisidium nitidum Jenyns	...	...	...	...	?1	1
Scrobicularia sp.	...	1	...	...	1	2
total	1336	506	154	354	595	2945

This section obviously represents a continuation of the brackish conditions found above 26 cm in site A. Conditions become more saline towards the top, as shown by the relative increase of *Hydrobia ulvae* (figure 7) and the appearance of *Scrobicularia*. Fragments of bivalve shells may indicate the latter genus at all levels at site D but hinge fragments could only be identified from 40 to 60 and 0 to 10 cm. In the deposit itself *Scrobicularia* seems quite common on the surface, but its relative abundance is not great. The sharp colour change between bed 3 (10 to 80 cm) and bed 4 (0 to 10 cm) does not seem to correspond to an ecological change, and this fact seems to confirm that suggestion made in the introduction that it is due to weathering.

(*d*) *Relative land- and sea-level changes*

The series of freshwater deposits overlain conformably by estuarine deposits clearly indicates a marine transgression. At site A the transgression is recorded in the early part of zone *f* at a height of −1·76 m O.D. At this time in the interglacial the high-tide level must have risen above this height. As indicated in §2 (*a*) the raised beach shingle seen in the cliffs at Selsey must have covered the interglacial channel deposits and they both seem to belong to one cycle of marine transgression. The height of this transgression is considered in §5.

3. Interglacial deposits at Stone, Hampshire

(*a*) *Stratigraphy*

In 1893 Clement Reid described an estuarine deposit on the foreshore at Stone, between Stone Point and the mouth of the Beaulieu River. The site was visited in 1957 and the deposit was found to be patchily exposed in the same area. Figure 8 shows the exact location of the deposit.

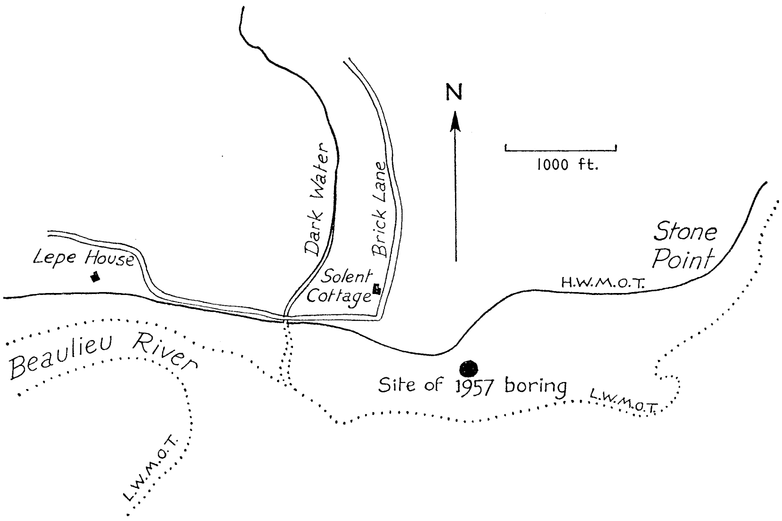


Figure 8. The coast at Stone, showing the location of the boring made in the interglacial deposit.

A detailed stratigraphical investigation could not be made, as the deposit was largely covered by recent marine deposits and was only visible at low tides. Even the relation with the local Oligocene rocks (Headon Beds) could not be made out. A single boring taking an 8 cm core was made; this penetrated to 230 cm, when sand was reached and water rose, so that the boring had to be abandoned at 257 cm.

The succession of deposits is shown in the stratigraphical column of the pollen diagram, figure 9. The deposits are all estuarine silty clays except for 34 to 44 cm, where freshwater detritus mud was found, and 16 to 34 cm, where silty clay seemed to be also freshwater.

The estuarine deposits were concealed on the landward side by recent beach deposits. The cliff behind the beach shows a degraded section of subangular flint gravel, a good section of which was illustrated by Reid (1893). As at Selsey, it appears that the deposits must pass under the cliff gravels. The origin of the gravels is not as clear as at Selsey. The flints are more angular and it is possible that, as suggested by Everard (1954), they are solifluction gravels reworked by marine action.

(*b*) *Palaeobotany*

The pollen diagram from the borehole samples is shown in figure 9. The tree pollen proportions remain much the same throughout the diagram. *Quercus*, *Pinus* and *Acer* are well represented and must have been the most frequent trees in the region. The pollen of *Betula*, *Ulmus*, *Alnus*, *Fraxinus* and *Picea* occur only in low frequencies, and these trees probably played an unimportant role in the local vegetation.

The changes in the *Corylus* and other non-tree pollen curves might be attributed to two causes other than regional vegetational changes. First, to local environmental changes resulting from the alternation of estuarine and freshwater conditions. Secondly, to differences in pollen sedimentation which are known to exist between estuarine-marine and freshwater environments, e.g. the over-representation of *Pinus* in estuarine-marine deposits. The rise in *Sparganium*-type pollen is undoubtedly associated with local ecological changes resulting from the freshwater sedimentation. The increase of *Corylus* and Gramineae might be a result of either of the two causes mentioned above or of a regional change in the vegetation. The correlation of their increase with the change to freshwater sediments suggests it is not a regional change.

It is difficult to assess the degree of regional forest cover. The *NAP* total rises in the freshwater part of the core. Whether this is a true reflexion of vegetational conditions rather than the low *NAP* values seen in the estuarine clay it is not possible to say.

The macroscopic plant remains from the borehole were few. They are listed in table 2. Some of the species found are characteristic of brackish waters, e.g. *Ranunculus sceleratus* and *Zannichellia palustris*. Others are characteristic of saltmarsh and foreshore communities, e.g. *Aster tripolium*, *Atriplex* sp., *Beta maritima*, *Glaux maritima*, *Juncus* cf. *maritimus*, *Scirpus maritimus*. This latter group was most commonly found from 45 to 90 cm, the level which contains a molluscan fauna indicating a height high in the intertidal zone or perhaps above it (see §3 (*c*) which also considers the significance of the fauna and flora for salinity changes). The seeds of *Typha* sp. were abundant in the freshwater sediments at 23 to 32 cm. Several fruits of *Acer monspessulanum* were also found in the upper samples of the borehole.

The climate indicated by the plant remains is a temperate one. Many of the species have a wide range in the temperate region. The presence of *A. monspessulanum*, which has a wide distribution in central and southern Europe, suggests a climate with summers rather warmer than at the present day.

(*c*) *Mollusca*

The core taken in the interglacial deposits at Stone yielded rather small numbers of Mollusca belonging to very few species. They are listed in table 6, which also shows frequencies of Foraminifera.

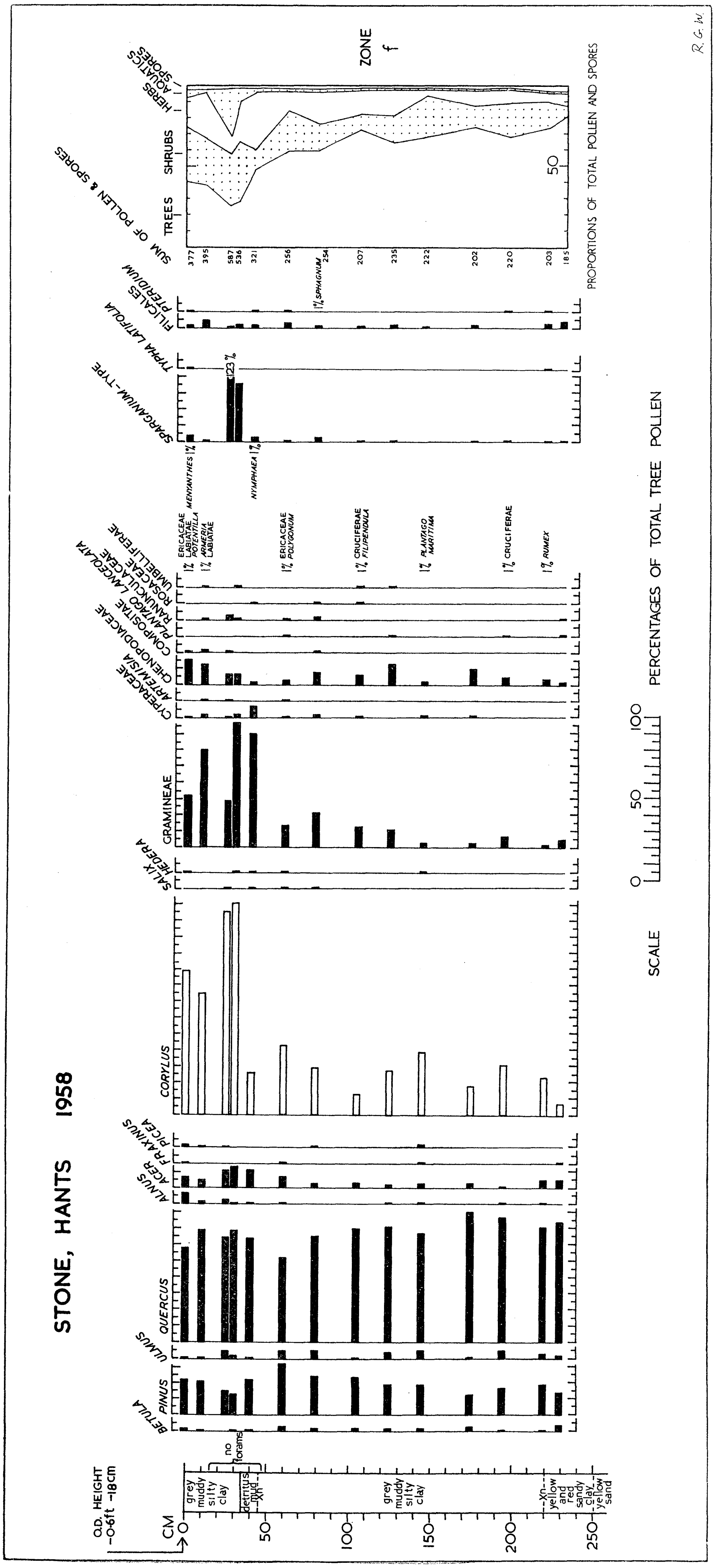


FIGURE 9. The pollen diagram from Stone.

The Mollusca are not well preserved, many of them being fragmentary. The *Hydrobia* species may usually be differentiated on the shape of the whorls, but this becomes very difficult when they are in the form of internal casts, for an internal cast of *H. ulvae* has well-rounded whorls like those of *H. ventrosa*. Indeed, it was only the discovery of specimens of *H. ulvae*, parts of which retained the shell and other parts of which were internal casts (plate 16, figures *j* and *k*), which prevented many more specimens being erroneously attributed to *H. ventrosa*. Not a single bivalve was recovered complete, but the fragments of hinges all seem to be those of *Scrobicularia* sp. and the shell fragments are consistent with this identification. *Phytia myosotis* is represented only by apices and by lip and columella fragments, but there seems little possibility of their belonging to any other species.

TABLE 6. LIST OF MOLLUSCA FROM STONE

zone *f* (cm)	*Hydrobia ventrosa* (Montagu)	*H. ulvae* (Pennant)	*Hydrobia* sp.	*Phytia myosotis* (Draparnaud)	bivalve fragments	Foraminifera	total
0–16	? 10	1	...	...	...	*vr*	11
16–47	...	...	...	...	...	...	...
47–58	9	13	...	5	...	*vr*	27
58–70	52	34	...	4	...	*r*	90
70–80	10	1	...	...	...	*rc*	11
80–92	66	25	...	8	...	*a*	99
92–104	1	10	2	8	...	*rc*	21
104–119	...	6	...	...	...	*r*	6
119–130	...	28	3	...	*r*	*a*	31
130–142	? 5	39	4	...	*c*	*a*	48
142–153	4	37	3	...	*c*	*a*	44
153–165	6	71	13	...	*c*	*a*	90
165–176	...	...	2	...	*c*	*c*	2
176–188	...	...	10	...	*c*	...	10
188–200	...	2	...	...	*c*	*a*	2
200–211	...	1	...	...	*r*	...	1
211–221	...	...	...	...	*r*	...	...
221–234	...	1	...	...	*r*	...	1
total	163	269	37	25			494

Abbreviations: *a*, abundant; *c*, common; *rc*, rather common; *r*, rare; *vr*, very rare.

Although only a limited number of species is present, the fauna is interesting. At all horizons where shells were found the fauna is a brackish water one, although the plant remains indicate freshwater conditions between 16 and 44 cm, from which section no Mollusca were recovered. Apart from the latter horizon, the deposit may be broadly described as intertidal, but variations within this zone may be noted from a detailed inspection of the distribution of Mollusca. Below 200 cm fossils are too few for any interpretation, but from about 200 cm up to 92 cm the relative abundance of Foraminifera,* of *Scrobicularia* and of *Hydrobia ulvae* suggests a position rather low down in the intertidal zone, for example *Salicornia* marsh. At about 92 cm, although all the changes are not precisely at the same level, the Foraminifera decrease strikingly, *Scrobicularia* disappears, *Hydrobia ventrosa* increases at the expense of *H. ulvae*, and *Phytia myosotis* appears. This last

* We are greatly indebted to Mr C. D. Ovey for the information that *Rotalia beccarii* (Linn.) is abundant, *Nonion depressulus* (W. & J.) occurs and *Elphidium umbilicatula* (Walker & Boys) is very rare in these deposits; the first and third tolerate low salinities and the second is littoral in ecology.

species, according to Ellis (1926, p. 96), 'lives on mud-flats and by brackish water in estuaries, under...plants such as *Obione portulacoides*'. All these features point to a position much higher in the intertidal zone, perhaps almost above it, and might be construed as the transition from more brackish conditions below to the freshwater conditions indicated by the plants above. At the very top of the section conditions change from freshwater back to brackish.

These changes could be interpreted as the development of a coastal marsh and its re-invasion by the sea. This probably took place on an open foreshore rather than in an estuary, for, curiously enough, there are no land nor freshwater species of Mollusca anywhere in the section, whereas a small proportion of such species is usually found in brackish water deposits (cf. Selsey), brought there presumably by local streams.

Very little can be inferred about the climate from so small a number of mollusc species. Both species of *Hydrobia*, however, seem to extend no farther north than the Gulf of Riga and southern Sweden, while *Phytia myosotis*, found at a very few localities on the German and Danish coasts, is very much southern European in its general distribution (Ehrmann 1933). These conclusions are consistent with those drawn from the presence of *Acer monspessulanum* in the deposit.

(*d*) *Correlation*

In the pollen diagram the proportions of the pollen of the different trees closely resemble those found in the zone *f* deposits of the Ipswichian Interglacial at Bobbitshole, near Ipswich (West 1957). In particular they resemble each other in the following points: the abundance of *Pinus*, *Quercus* and *Corylus*, substantial frequencies of *Acer* pollen, and low frequencies of *Betula*, *Ulmus*, *Alnus*, *Fraxinus* and *Picea* pollen. Corresponding to the *Acer* pollen curves at Stone and Bobbitshole, several fruits of *Acer monspessulanum* were found at Stone and one fruit of *A.* cf. *monspessulanum* at Bobbitshole.

This characteristic tree pollen assemblage of zone *f* of the Ipswichian Interglacial has so far not been found in interglacial deposits known to be of a different age. We must conclude that the Stone estuarine deposits were formed in zone *f* of the Ipswichian Interglacial, but at a later stage of zone *f* than is seen at Selsey, where *Acer* pollen is only sporadically found.

(*e*) *Relative land- and sea-level changes*

The presence of the freshwater mud intercalated in the estuarine clay near the top of the borehole at 0·5 m below O.D. shows that relative sea-level was slightly lower than at the present day. If we are correct in regarding the gravel in the cliff behind the deposit as a beach shingle, then the marine transgression of the interglacial must have reached a maximum later than the part of zone *f* represented in the pollen diagram.

4. Deposits on the Normandy (Calvados) coast

(*a*) *Location and stratigraphy*

(i) *Introduction*

A manuscript paper by the late Louis Guillaume gives an excellent account of Late-Pleistocene marine and freshwater deposits exposed from time to time on the foreshore at St Côme de Fresné and eastwards for a kilometre to Asnelles-Belle-Plage. The location of these deposits is shown in the map, figure 10.

The general succession described by Guillaume (see figure 11) may be summarized as follows:

	maximum thickness (m)
Limon and head	15
Green clay with *Elephas primigenius*	0·2
Compact peat with *E. primigenius*, the lower part with *Modiola* and *Mytilus*, the upper part with freshwater Mollusca	0·5
Sand with *Modiola*, passing laterally into beach shingle	3
Bathonian clays and limestones	

It is clear that the fossiliferous series was deposited in a marine regression, for the marine and freshwater parts of the peat are described as conformable. They also antedate the deposition of the limon and head.

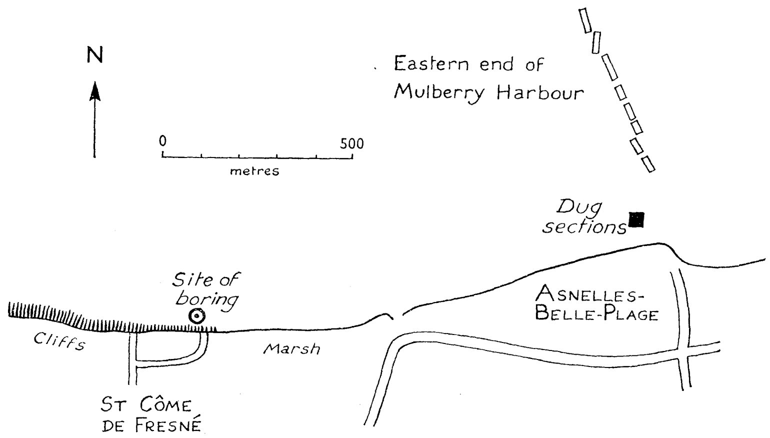


FIGURE 10. The coast near Arromanches (Calvados), showing the location of the sites investigated.

We visited the area in the summer of 1957, and with the aid of Guillaume's exact maps, were able to locate the deposits. A boring was made 1 m in front of the low cliff of limon, in the position shown in figure 10, as close as possible to a boring of Guillaume's which proved the peat below beneath the limon. In brief, the succession showed limon passing conformably below into detritus mud, below which was a silty clay with Foraminifera. The full record of the boring is shown in figure 11. Silt with marine shells overlain by silt with non-marine shells was found from 50 to 60 m in front of the promenade of Asnelles-Belle-Plage, just west of the eastern end of the line of 1944 Mulberry Harbour pontoons. Two sections dug here are illustrated in figure 11. The relative levels of the dug sections and the borehole at St Côme de Fresné are also shown in this figure.

The successions in the borehole and in the excavations may reasonably be supposed to be contemporary deposits both giving evidence of marine regression. Confirmation is provided by the description by Guillaume of marine deposits in a similar position to our excavations at Asnelles-Belle-Plage with a fauna typical of the sands with *Modiola modiolus*.

(ii) *St Côme de Fresné*

Though a gap of 30 cm unfortunately resulted from the difficulties of sampling the unconsolidated detritus mud, the sequence found in the borehole shown in figure 11 demonstrates clearly a marine regression. The estuarine silty clay is covered conformably by silty detritus mud, the transition from estuarine to freshwater conditions occurring in the mud itself, as demonstrated by the frequencies of Foraminifera and Entoprocta listed in table 7. Guillaume also found the transition to be in the detritus mud (see figure 11). The regression contact in the borehole occurs at about 90 cm above the present mean sea level.

The accumulation of the freshwater detritus mud came to an end with the deposition of silt or limon, a gradual transition between the two being clearly found in the borehole cores. The silt is probably of aeolian origin and represents the beginning of loess formation after the marine regression.

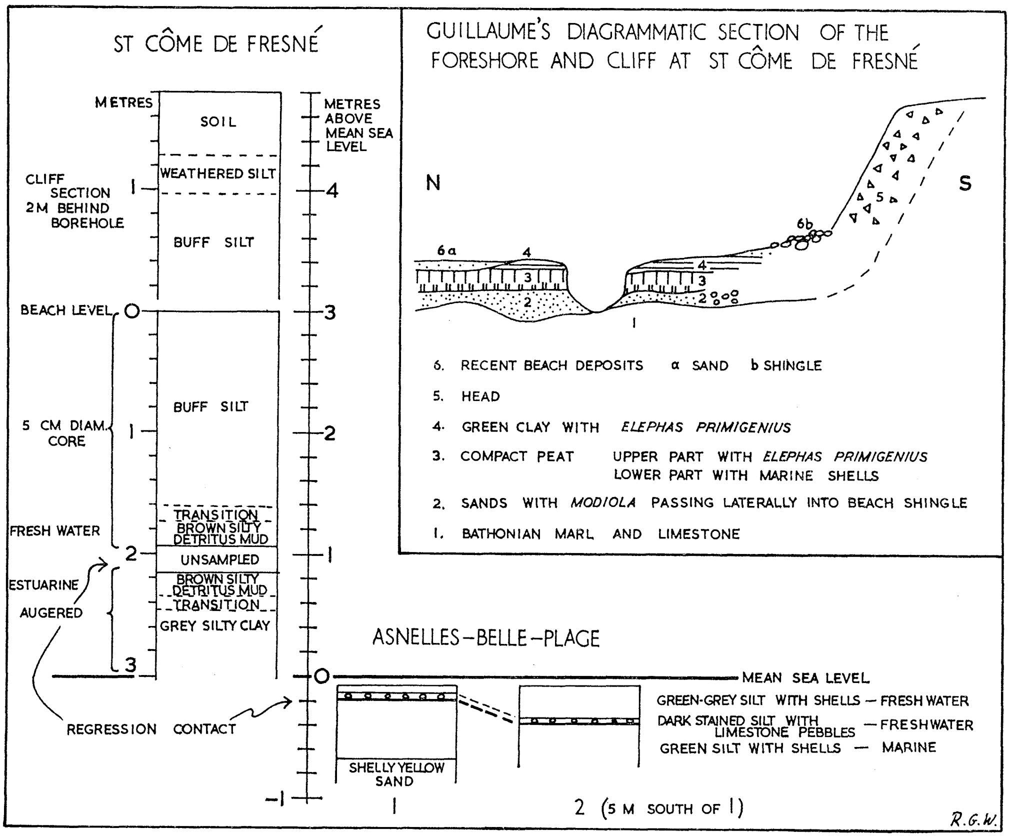


FIGURE 11. Stratigraphy of the deposits near Arromanches.

(iii) *Asnelles-Belle-Plage*

Here the regression was represented in silty deposits by a change in the molluscan fauna. Figure 11 shows the stratigraphy. In section 1 yellow shelly sand, probably equivalent to Guillaume's *Modiola* sand was found below the marine silt. The regression contact was marked in places by a line of limestone pebbles, and occurred at about 10 cm below mean sea level, a metre lower than at St Côme de Fresné. The regression here must have been somewhat later than at St Côme de Fresné, and it is very probable that the unweathered green silt of these sections is equivalent to the weathered buff silt found over the detritus mud at St Côme de Fresné, and to the green clay recorded by Guillaume on top of the same detritus mud.

(*b*) *Palaeobotany*

The silts of Asnelles-Belle-Plage, though rich in Mollusca, contained no plant remains apart from rare pollen grains of *Pinus*. The St Côme de Fresné deposits were richer in plant remains, especially pollen grains. The rare macroscopic plant remains are listed in table 7 and show nothing remarkable.

Table 7. Macroscopic remains from St Côme de Fresné

	170–180 cm	180–190 cm	230–240 cm	240–255 cm	280–290 cm
Carex sp. (nuts)	11	7	...	...	...
Ranunculus sceleratus L. (achenes)	4	1	1	...	...
Urtica dioica L. (fruit)	...	...	1	...	...
Foraminifera	...	...	rare	abundant	rare
cf. *Barentsia* Hincks* (Entoprocta)	...	...	common	...	...

* We are indebted for this identification to Mr R. G. Pearson of the Subdepartment of Quaternary Research. He reported that the finds were fragmentary remains of pedicels comparable with those of the marine entoproct genus *Barentsia*.

The pollen diagram from the borehole samples is shown in figure 12. *Pinus* is the dominant tree throughout the diagram. In the lowest three samples, taken from the estuarine deposits, it is accompanied by low percentages of *Betula*, by high frequencies of the pollen of Chenopodiaceae and by rising percentages of Gramineae and Cyperaceae. High frequencies of chenopodiaceous pollen are frequently found associated with brackish water deposits near transgression and regression horizons, and here they confirm the evidence of regression shown by the sediments.

In the freshwater upper part of the pollen diagram, the increase in *NAP* excluding Chenopodiaceae seen in the lower part of the diagram continues and averages 70 % of the total pollen. Pollen of *Pinus* accounts for over 95 % of the total tree pollen, and it is again accompanied by *Betula*, together with low frequencies of *Quercus*, *Alnus* and *Picea*, and also of the shrub *Ephedra*. High frequencies are shown by Gramineae and Cyperaceae, and several other herbaceous pollen types show considerable values, e.g. *Artemisia*, Caryophyllaceae, Compositae, Cruciferae and *Thalictrum*. The aquatics *Caltha* and *Sparganium* (or *Typha*) are also represented in the freshwater upper sediments.

In the lower part of the diagram the over-representation of *Pinus* which is common in estuarine and marine deposits may have distorted the *AP*/*NAP* ratio, but this ratio in the upper part of the diagram clearly indicates the prevalence of open vegetational conditions, even though some of the pollen may have been contributed by local aquatic or marsh plants, e.g. Cyperaceae, *Thalictrum*, Umbelliferae. Open conditions are also suggested by the presence of pollen of *Artemisia*, *Helianthemum*, *Plantago* and *Ephedra*. It will be recalled that many of these pollen types occurred in the zone *b* vegetation at Selsey.

Pollen sedimentation continued into the transition to the aeolian buff silt, and it is of interest to note that the evidence of open vegetation given by the pollen is compatible with the conditions of loess formation. The climatic indications of the plant remains also agree with the environment suggested by loess deposition. The absence of any quantity of pollen of thermophilous plants, with the dominance of *Pinus* and *NAP* suggests a rather severe and perhaps continental climate.

We may conclude that both the condition of deposition and the character of the vegetation suggest a cold steppe-like environment.

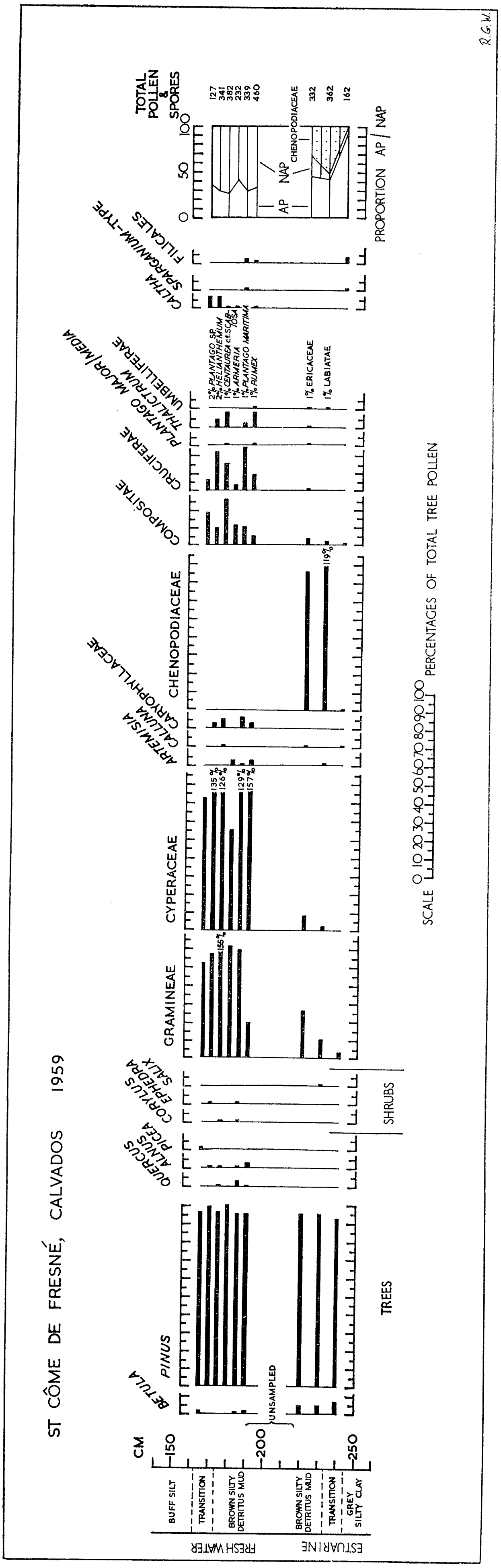


FIGURE 12. The pollen diagram from St Côme de Fresné.

(*c*) *Mammalia*

We have made no new records of mammals from the deposits. The following list is quoted from Guillaume's manuscript. The bones were found in the freshwater upper part of the detritus mud at St Côme de Fresné.

Elephas primigenius (an entire skeleton)
Rhinoceros tichorhinus (an entire skull)
Cervus sp.
Equus caballus, of large size.
Bison priscus
Bos sp.
Canis lupus

We must associate this fauna with the open steppe-like vegetational conditions suggested by the plant remains and the sediments of the freshwater horizon.

(*d*) *Mollusca*

(i) *St Côme de Fresné*

The core taken at St Côme de Fresné was very poor in Mollusca and those recovered were mostly badly broken. The species are listed in table 8.

TABLE 8. LIST OF MOLLUSCA FROM ST CÔME DE FRESNÉ

	190–180 cm	180–170 cm	170–165 cm	165–160 cm	160–145 cm	125–100 cm	100–75 cm	75–50 cm	50–25 cm	25–0 cm
Lymnaea sp.	...	...	...	...	...	...	2	1	...	...
Planorbis leucostoma Millet	...	...	...	...	...	...	2	1	...	...
P. laevis Alder	...	...	...	...	...	...	...	1	...	...
Succinea sp.	...	...	...	...	...	...	6	...	...	...
Pupilla muscorum (Linné)	...	...	...	...	...	...	?1	...	...	...
Vallonia sp.	...	...	...	...	...	...	2	...	...	...
Cecilioides acicula (Müller)	...	...	...	...	...	...	...	...	...	1
Hygromia sp.	...	...	...	...	...	frag.	frag.	frag.	frag.	1
Agriolimax cf. *agrestis* (Linné)	11	9	...	2	...	...	...	2	...	...
A. cf. *laevis* (Müller)	...	...	...	1	...	...	...	...	...	1
Agriolimax sp.	...	...	2	...	...	...	...	...	...	...
Pisidium sp.	...	...	...	...	...	...	1	...	1	...

Of the shells listed by genus only, the *Lymnaea* is probably *palustris*, the *Succinea* is *pfeifferi* and the *Hygromia* is probably *hispida*. The shell of *Cecilioides acicula*, a burrowing species, is probably modern.

Throughout this part of the core down to 190 cm the shells are land or freshwater and the freshwater ones are mainly tolerant of poor conditions. It is, as far as one can tell, a fauna similar to that found at Asnelles (see below), consisting of climatically tolerant species, most of which have been recorded from loess or similar deposits. Thus it is consistent with the lithology of the material.

Below this, between 230 and 290 cm, samples yielded only Foraminifera and a few broken pieces of marine Mollusca, some of which at 280 to 290 cm could be pieces of *Macoma balthica*.

(ii) *Asnelles-Belle-Plage*

Two holes were dug in the green silts exposed in the beach, one through the marine regression (AS 1) and the other in material above the regression (AS 2). The Mollusca found in each are listed in tables 9 and 10.

TABLE 9. LIST OF MOLLUSCA FROM ASNELLES-BELLE-PLAGE (AS 1)

	70–60 cm	60–50 cm	50–40 cm	40–30 cm	30–20 cm	20–13 cm	13–6 cm	6–0 cm	total
Lymnaea truncatula (Müller)	...	...	...	...	...	...	...	2	2
L. palustris (Müller)	...	...	...	...	...	2	...	18	20
L. peregra (Müller)	...	...	...	...	...	...	...	4	4
Lymnaea sp.	...	...	1	...	2	...	27	217	247
Planorbis leucostoma Millet	...	...	2	...	...	4	11	137	154
Succinea sp.	1	...	1	...	...	2	55	169	228
Pupilla muscorum (Linné)	...	...	...	1	1	2	5	4	13
Hygromia hispida (Linné)	...	...	...	...	...	...	2	1	3
Agriolimax cf. *agrestis* (Linné)	...	...	...	...	...	...	1	25	26
Agriolimax cf. *reticulatus* (Müller)	...	...	...	...	...	...	...	5	5
Pisidium sp.	...	...	...	...	...	...	1	11	12
Hydrobia ventrosa (Montagu)	...	...	...	...	2	5	...	...	7
H. ulvae (Pennant)	8	...	? 1	6	6	4	...	...	25
Hydrobia sp.	...	1	...	...	...	...	...	...	1
Macoma balthica	4	...	...	...	...	...	...	...	4
marine juveniles	*c*	*rc*	*r*	*r*	*a*	*a*	*a*	*vr*	...
Foraminifera	...	*rc*	*r*	*vr*	*a*	*a*	...	*vr*	...
total	13	1	5	7	11	19	102	593	751

The symbols for the degree of rarity are the same as those used in table 6 on page 121.

TABLE 10. LIST OF MOLLUSCA FROM ASNELLES-BELLE-PLAGE (AS 2)

	30–27 cm	27–20 cm	20–10 cm	10–0 cm	total
Lymnaea truncatula (Müller)	...	4	2	5	11
L. palustris (Müller)	5	33	28	5	71
L. peregra (Müller)	1	...	...	...	1
Lymnaea sp.	36	233	184	61	514
Planorbis planorbis (Linné)	...	? 1	...	...	1
P. leusostoma Millet	10	183	191	70	454
P. laevis Alder	...	2	...	...	2
Succinea pfeifferi Rossmässler	...	...	1	...	1
Succinea sp.	12	181	334	94	521
Pupilla muscorum (Linné)	2	2	14	70	88
Vallonia costata (Müller)	...	...	1	...	1
Hygromia hispida (Linné)	frag.	4	3	9	16
Agriolimax cf. *agrestis* (Linné)	...	25	31	24	80
Agriolimax cf. *reticulatus* (Müller)	...	6	4	2	12
Agriolimax sp.	1	...	26	10	37
Pisidium obtusale (Lamarck)	? 1	6	...	...	7
Pisidium sp.	4	12	11	...	27
marine juveniles	2	5	4	4	15
Foraminifera	...	...	*vr*	*vr*	...
total	74	697	834	354	1859

The *Lymnaea* sp. are in all probability mainly *palustris*, while the *Succinea* are either *pfeifferi* or *putris*. The same is true in the section AS 2, the Mollusca of which are listed in table 10. The marine juveniles include *Littorina*, *Mytilus*, and *Cardium*.

Up to and including the 20 to 13 cm sample of AS 1, marine forms make up at least 90 % of the total Mollusca, while above that level non-marine species exert a similar dominance. The change is quite abrupt and extremely great. The few non-marine species below 13 cm should probably be considered to be washed in from nearby streams. The Foraminifera and marine juveniles which, although rare, do occur above 13 cm, were probably blown into shallow depressions from drying marine alluvium. The non-marine fauna at the top probably lived in shallow marshy depressions and pools, subject to periodic drying, between slightly higher swells of emerged marine silt.

The succession is continued in AS 2. Table 10 lists Mollusca from this section.

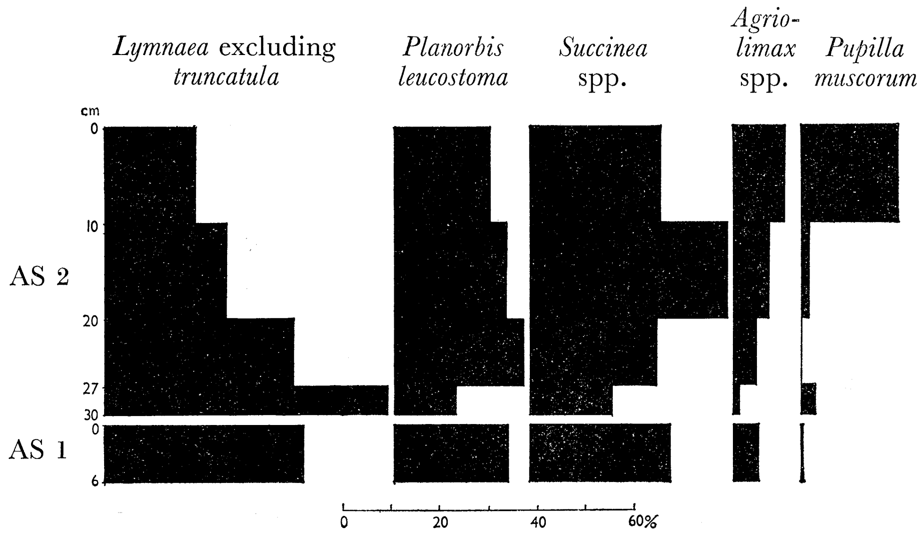


FIGURE 13. Percentage frequency of selected Mollusca in the Asnelles deposit.

This section represents the continuation of the conditions of AS 1 with appreciable drying of the environment becoming apparent towards the top. If the main species and groups of species of Mollusca are graphed (figure 13) *Lymnaea* spp. and *Planorbis leucostoma*, all freshwater species though mostly tolerant of poor conditions, decrease towards the top; *Succinea* and *Agriolimax*, marsh snails and slugs, increase towards the top except for the drop in the former genus at the very top, while *Pupilla muscorum*, a xerophile probably living on dry swells between marshy slacks, increases strikingly at the very top.

Unfortunately no trace was found of the cold Mollusca, *Pupilla alpicola*, *Pisidium vincentianum* and *P. obtusale lapponicum*, reported by Guillaume in his unpublished paper, but all the species found are highly tolerant of cold conditions, while a profusion of *Pupilla muscorum*, such as occurs at the top of AS 2, is typical of cold dry conditions in the Pleistocene.

(*e*) *Correlation*

The absence of any marked changes in the pollen diagram makes it impossible to put forward a good correlation of the deposits. The conditions of deposition—a marine regression, followed by loess deposition—suggest the end of an interglacial period, and the pollen diagram in fact resembles pollen spectra from zone *i*, the *Pinus* zone, at the end of the Eemian Interglacial. The overlying loess would then belong to an early phase of the Last Glaciation. Alternatively, if we allow a sea-level higher than the present during interstadial periods, the deposits could be interstadial in the Last Glaciation, as the pollen diagram can be matched by Last Glaciation interstadial pollen diagrams from north-west Europe. In this instance, the loess and head overlying the organic deposit would belong to a later phase of the last glaciation. The former correlation seems to us to be the more satisfactory.

5. Relative land- and sea-level changes in the English Channel

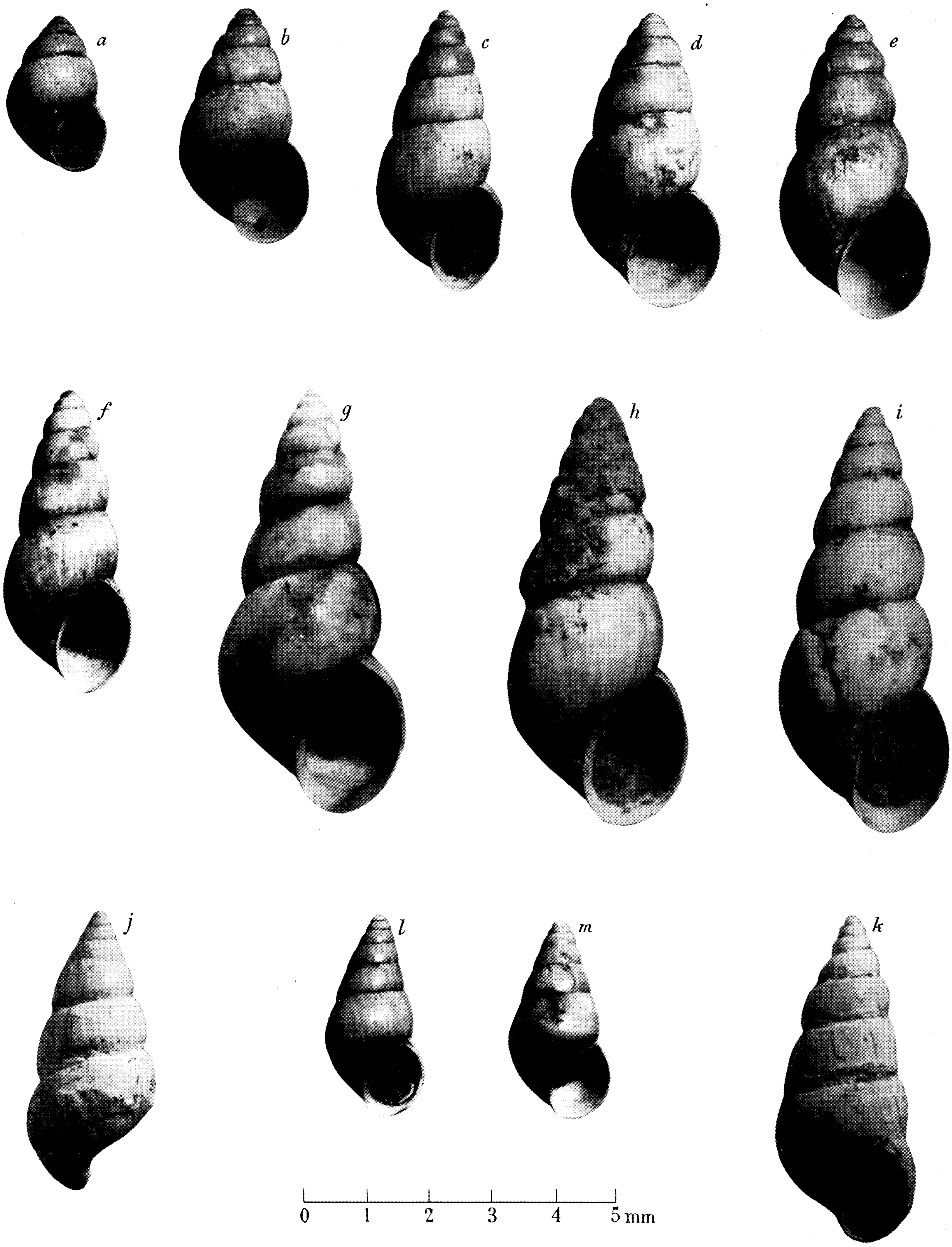
At Selsey the fossiliferous deposits lie below the raised beach shingle exposed in the low cliffs in several localities at or near Selsey and mapped inland by the Geological Survey (Sheet 332). This raised beach shingle reaches an elevation of 23 ft. o.d. on the coast west of Selsey Bill. Raised beach shingle is known from many neighbouring localities, mostly in the east between Littlehampton and Brighton, at about this elevation in the Sussex coastal plain, and is usually described as the '15-feet' beach, for example by Palmer & Cooke (1923) and by Martin (1938). But most of the localities where the raised beach shingle is known are probably not near the former shoreline, which is to be found near Black Rock, Brighton, where Smith (1936) has recorded maximum elevations of 38 ft. o.d. for the top of the shingle and 29·5 ft. for its base. Smith observed that as the cliff was worn back, the beach and its underlying platform both rose in elevation, but the notch at the foot of the cliff was not seen by him. Therefore, the maximum height of wave activity may be taken as about 40 ft. o.d., this representing probably an elevation of about 4 ft. above high spring tide level. At present Brighton has a maximum tidal range of about 22 ft. so that mean sea level during the formation of the beach was probably about 25 ft. above the present one.

It seems reasonable to attribute all these low raised beaches of Sussex to one period, partly because of their similarity in height and partly because of their usual situation beneath deposits of brickearth and/or coombe rock. The variations in height between the different beach deposits are explicable by attributing them to different phases of the transgression and regression.

The gravel of the low cliffs behind the interglacial deposit at Stone was probably deposited in the same cycle of transgression and regression. Lithologically this gravel is less like the normal raised beach shingle, for it is far less rounded, but Everard (1954) has suggested that in the Solent, where fetch is restricted, the sea may have done little more than re-sort gravels of terrestrial origin moved down by solifluction. Modern beaches of this sort, composed mainly of gravel derived from coombe rock deposits, may be seen in parts of the Sussex and Hampshire coasts.

The pollen-analytical evidence shows that this transgression was taking place during zone *f* of the Ipswichian (Eemian) Interglacial, so that we may conclude from the English side that sea level rose above its present level in this interglacial some time during zone *f*, which, judged from the homogeneity of the deposits, both lithologically and palaeontologically, at Selsey and Stone, was a period of rapidly rising sea level.

In Normandy two raised beaches have been described by Dangeard & Graindor (1956) and Elhaï (1958). The lower of these, Normannien II or Bas-Normannien, is represented by shingle found from present sea level up to 5 to 8 m (i.e. 16 to 26 ft.) above. This shingle is recorded by Guillaume from St Côme de Fresné and is considered to be associated with



a	*Hydrobia ventrosa* (Montagu). Selsey.	*h*	*H. deani* (Kendall). Co-type. Woodston, near Peterborough.
b	*H. ventrosa* (Montagu). Selsey.	*i*	*H. deani* (Kendall). Co-type. Woodston, near Peterborough.
c	*H. ventrosa* (Montagu). Selsey.	*j*	*H. ulvae* (Pennant). Stone. Badly weathered.
d	*H. ventrosa* (Montagu). Selsey.	*k*	*H. ulvae* (Pennant). Stone. Badly weathered.
e	*H. ventrosa* (Montagu). Selsey.	*l*	*H. ulvae* (Pennant). Selsey.
f	*H. ventrosa* (Montagu). Selsey.	*m*	*H. ulvae* (Pennant). Selsey.
g	*H. ventrosa* (Montagu). Selsey.		

(*Facing p.* 131)

the fossiliferous deposits on the foreshore in a cycle of transgression and regression. The height of the Normannien II marine shingle is very similar to that of Sussex and suggests a correlation with the Eemian Interglacial. As pointed out in §4 (*e*) above, the pollen diagram suggests zone *i* of the Eemian Interglacial as a possible date and, if this is correct, we may conclude that during the marine regression of the Eemian Interglacial sea level fell below its present level during zone *i*.

If our correlations are correct it follows that the brickearth over the deposits at Selsey and the loess over the deposits in Normandy are roughly contemporaneous and were formed during the Last Glaciation.

This dating of the marine transgression and regression of the Ipswichian (Eemian, Last) Interglacial in the English Channel agrees reasonably well with its dating in the Netherlands and North Germany. Von der Brelie (1954) has shown that in that region the transgression generally took place during zones *d* to *f* and the regression in zone *h*, the spruce zone preceding zone *i* in continental Eemian deposits. However, the evidence of the Eemian transgression and regression on the continent is found in areas which are known to be downwarped so that, although the present elevations of the deposits are known, their original elevations are difficult to determine. For example, Sindowski (1958) has described transgression and regression contacts many metres below mean sea level in Ostfriesland. The general similarity of elevations of the low raised beaches of Normandy and Sussex suggests that this central part of the English Channel has been much more stable during the Late Pleistocene, so that the dating in terms of pollen zones of the height of sea level in the last Interglacial may be made much more accurately here.

Finally, if the 7 to 8 m 'Monastirian II' shoreline of southern Europe is equated by its height with the raised beaches described above, it should then be correlated with the Ipswichian (Eemian) Interglacial of northern Europe.

We are indebted to Dr K. P. Oakley for drawing our attention to the deposits at Selsey, and to Dr A. T. Sutcliffe and the late Mr A. G. Davis for their help on the site. The deposits on the Normandy coast were brought to our attention by Professor W. B. R. King, F.R.S., and we are very grateful to him for his interest and help with the investigation, and to the University of Cambridge for financial aid which enabled us to carry out the field work in Normandy. We thank Miss C. A. Lambert for her valuable assistance with the preparation of samples.

Appendix 1. *Hydrobia ventrosa* from Selsey (B.W.S.)

A considerable variation in form is shown by the thousands of *Hydrobia* shells from the Selsey deposit, and at an early stage the possibility of there being two or more species involved was considered. This idea was rejected when it was found that it was virtually impossible to find any discontinuities in the variation. A number of typical specimens of *H. ventrosa* from Selsey are shown in plate 16, where the variation from a rather broad spire, figures *a*, *b*, *d* and *e* to a narrow spire, figures *c* and *f*, can be clearly seen. Similarly, the degree of roundness of the aperture varies quite considerably, the extremes being shown by figures *c* and *d*. But however much *H. ventrosa* varies, it seems always to be easily distinguishable from *H. ulvae* from the same deposit, figures *l* and *m*, which has a characteristic spire and whorl shape and which is separable from *H. ventrosa* even in a very immature or broken state.

Some specimens of *H. ventrosa* attain a large size, figure *g*, but apart from the size they seem to be perfectly normal *H. ventrosa* with an extra whorl (cf. figure *f*). They appear to be identical with co-types of *H. deani* (Kendall) from the Sedgwick Museum, figures *h* and *i*, and the question arises whether they should be recorded as that species. Kendall's species was founded on specimens from what is probably an Ipswichian Interglacial deposit comparable in age with that at Selsey. He stated that *H. deani* was regarded as a distinct species by all the leading conchologists to whom he submitted shells, but he does not give a comparative description. However, I am inclined to regard *H. deani* merely as a large form of *H. ventrosa*, one to be regarded perhaps as an Ipswichian Interglacial race, though this is merely a tentative opinion based upon very few occurrences. Whether *Paladilhia radigueli* Bourguignat, the other extinct Pleistocene *Hydrobia*, is to be included in *H. ventrosa* is less certain for specimens from Swanscombe lent to me by M. P. Kerney seem rather different.

Appendix 2. Mammalian remains from Selsey

By A. T. Sutcliffe
British Museum (Natural History)

Remains of the following have been found in the interglacial deposits:

Bed 2 (zones *d*, *e* and *f*):

- Rhinoceros, *Dicerorhinus hemitoechus* (Falconer). An almost complete skeleton.
- Large cervid, elk, *Alces* sp., or giant deer, *Megaceros* sp.
- Fallow deer, *Dama* sp.
- Hippopotamus, *Hippopotamus* sp.

Bed 1 (zones *b* and *c*):

- Horse, *Equus* sp.
- Rhinoceros, *Rhinoceros* sp.

The correlation with the vegetational zones is shown.

A further detailed description of the *Rhinoceros* skeleton will be given elsewhere.

References

Boycott, A. E. 1936 The habitats of freshwater mollusca in Britain. *J. Anim. Ecol.* **5**, 116.

Dandy, J. E. 1958 *List of British vascular plants*. London: British Museum (Natural History) and the Botanical Society of the British Isles.

Dangeard, L. & Graindor, M. 1956 L'étage normannien et ses divisions. *C.R. Acad. Sci., Paris*, **242**, 1744.

Elhaï, H. 1958 Le littoral du Nord du Cotentin. *Norois*, **17**, 5.

Ehrmann, P. 1933 *Die Tierwelt Mitteleuropas II (i) Mollusken (Weichtiere)*. Leipzig: von Quelle und Meyer.

Ellis, A. E. 1926 *British snails*. Oxford: Clarendon Press.

Everard, C. E. 1954 The Solent river: a geomorphological study. *Trans. Inst. Brit. Geogr.* **20**, 41.

Florschütz, F. 1957 The excavation at Velsen. 4. The flora of the Eemian and Tubantian. *Verh. Kon. Ned. Geol.-Mijn. Gen. Geol. Serie*, **17**, no. 2, 119.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Florschütz, F. 1958 Steppen- und Salszumpfelemente aus den Floren der letzten und vorletzten Eiszeit in den Niederlanden. *Flora*, **146**, 489.

Guillaume, L. Les formations quaternaires de la plage du débarquement brittanique de Saint Côme de Fresné—Asnelles-Belle-Plage (Calvados). Unpublished manuscript, undated but probably about 1950.

Hultén, E. 1950 *Atlas of the distribution of vascular plants in N.W. Europe*. Stockholm: Generalstabens Litografiska Anstalts Förlag.

Iversen, J. 1944 *Viscum*, *Hedera* and *Ilex* as climate indicators. *Geol. Fören. Förhdl.* **66**, 463.

Iversen, J. 1954 The Late Glacial flora of Denmark and its relation to climate and soil. *Danm. Geol. Unders.* (II Raekke), **80**, 87.

Jessen, K. & Milthers, V. 1928 Stratigraphical and palaeontological studies of interglacial fresh-water deposits in Jutland and north-west Germany. *Danm. Geol. Unders.* (II Raekke), **48**.

Kendall, C. E. Y. 1913 Notes on some Pleistocene Mollusca in north Huntingdonshire. *J. Conch.* **14**, 83.

Kornaś, J. 1958 Sea bottom vegetation of the Bay of Gdańsk off Rewa. *Bull. Acad. Polon. Sci.*, Cl. II, **7**, no. 1, 5.

Martin, E. C. 1938 The Littlehampton and Portsdown Chalk inliers and their relation to the raised beaches of West Sussex. *Proc. Geol. Ass.* **49**, 198.

Palmer, L. S. & Cooke, J. H. 1923 The Pleistocene deposits of the Portsmouth district and their relation to man. *Proc. Geol. Ass.* **34**, 253.

Reid, C. 1892 The Pleistocene deposits of the Sussex coast, and their equivalents in other districts. *Quart. J. Geol. Soc. Lond.* **48**, 344.

Reid, C. 1893 A fossiliferous Pleistocene deposit at Stone, on the Hampshire coast. *Quart. J. Geol. Soc. Lond.* **49**, 325.

Reid, C. 1899 *The origin of the British flora*. London: Dulau and Co.

Sindowski, K. H. 1958 Das Eem im Wattgebiet zwischen Norderney und Spiekeroog, Ostfriesland. *Geol. Jb.* **76**, 151.

Smith, B. 1936 Levels in the raised beach, Black Rock, Brighton. *Geol. Mag.* **73**, 423.

Sparks, B. W. 1957 The non-marine Mollusca of the interglacial deposits at Bobbitshole, Ipswich. *Phil. Trans.* B. **241**, 33.

van der Vlerk, I. M. & Florschütz, F. 1950 *Nederland in het Ijstijdvak*. Utrecht: W. de Haan N.V.

van den Vlerk, I. M. & Florschütz, F. 1953 The palaeontological base of the subdivisions of the Pleistocene in the Netherlands. *Verh. Akad. Wet. Amst.* (1st series), **20**, 2.

von der Brelie, G. 1954 Transgression und moorbildung im letzten Interglazial. *Mitt. geol.* (*St*) *Inst. Hamburg*, **23**, 111.

West, R. G. 1956 The Quaternary deposits at Hoxne, Suffolk. *Phil. Trans.* B, **239**, 265.

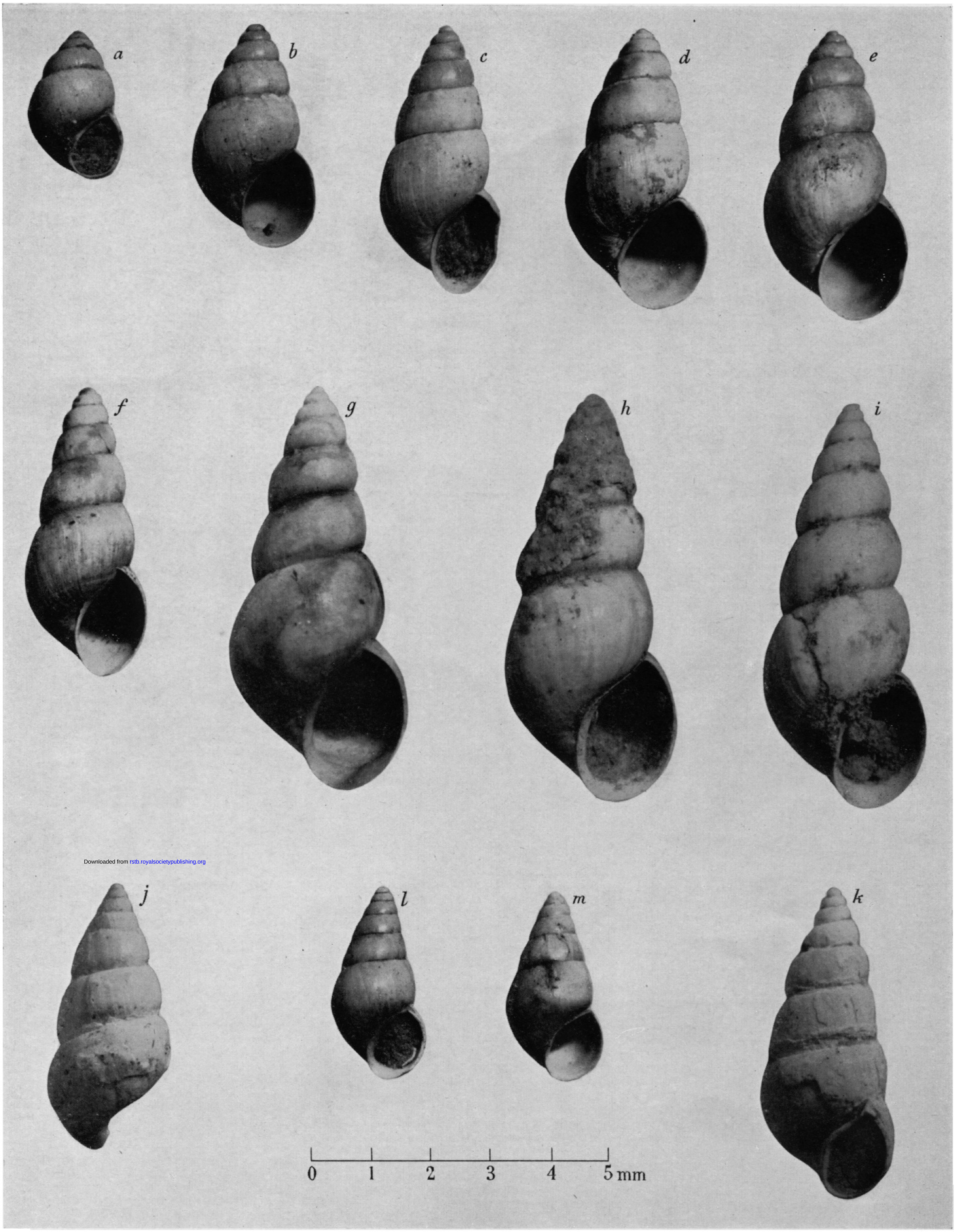
West, R. G. 1957 Interglacial deposits at Bobbitshole, Ipswich. *Phil. Trans.* B, **241**, 1.

West, R. G. 1960 The Ice Age. *Advn. Sci., Lond.* No. 64 (March 1960), 428.

West, R. G. & Donner, J. J. 1956 The glaciations of East Anglia and the East Midlands: a differentiation based on stone orientation measurements of the tills. *Quart. J. Geol. Soc. Lond.* **112**, 69.

Woldstedt, P. 1950 Das Vereisungsgebiet der Britischen Inseln und seine Beziehungen zum festländischen Pleistozän. *Geol. Jb.* **65**, 621.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



a *Hydrobia ventrosa* (Montagu). Selsey.
b *H. ventrosa* (Montagu). Selsey.
c *H. ventrosa* (Montagu). Selsey.
d *H. ventrosa* (Montagu). Selsey.
e *H. ventrosa* (Montagu). Selsey.
f *H. ventrosa* (Montagu). Selsey.
g *H. ventrosa* (Montagu). Selsey.
h *H. deani* (Kendall). Co-type. Woodston, near Peterborough.
i *H. deani* (Kendall). Co-type. Woodston, near Peterborough.
j *H. ulvae* (Pennant). Stone. Badly weathered.
k *H. ulvae* (Pennant). Stone. Badly weathered.
l *H. ulvae* (Pennant). Selsey.
m *H. ulvae* (Pennant). Selsey.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES