STUDIES OF FUNGAL REMAINS FROM THE FLANDRIAN DEPOSITS IN THE WHITTLESEY MERE REGION, HUNTS., ENGLAND

VISHNU-MITTRE

Birbal Sahni Institute of Palaeobotany, Lucknow-226007

ABSTRACT

The paper gives an account of a qualitative and quantitative systematic enumeration of fungal spores and other remains from the Flandrian deposits at Holme Fen and Trundle Mere in the Whittlesey Mere region, Hunts., England. An attempt has also been made towards the correlation of populations of fungi with the various peat types, as a result of which it has been established that certain spore types have frequency variations that are correlated closely with the vegetation of given peat layers more particularly with the brushwood peat, the *Cladium* sedge peat and the *Phragmites* peat. It has indeed been found difficult to correlate the various fungal populations with the peat types of the raised bog for lack of knowledge of their hosts in the bog peats. The paper also discusses the prospects for the investigation of sub-fossil fungal spores particularly in regard to the role they play in the formation of peat types, their history and distribution in the various periods of the Quaternary era, and in regard to their ecological considerations.

INTRODUCTION

DURING the course of pollen-analytical investigations carried out during 1957-1959 of the Flandrian deposits from the Whittlesey Mere region in Huntingtonshire, England, it was found that besides sub-fossil pollen the material abounded in fungal spores. Although the bulk of the sub-fossil fungal spores and hyphae appeared beyond identification, yet there were some in varying proportions which could be identified without much difficulty with those of fungi which occur on plants from which peat is commonly derived. It was, therefore, tempting to undertake the statistical evaluation of the identifiable spores from long profiles at Holme Fen and Trundle Mere respectively. The chief object of the study was to understand the significance of the fluctuations in the population of fungi in relation to pollen zones and various peat types and to discover if they suggest any climatic indications, and to see whether their present distribution has been affected by the climatic fluctuation and human interference with vegetation and drainage of the fens.

METHODS

No special technique was adopted for the recovery of fungal spores beyond the usual method of acetolysis for the recovery of pollen. The present study is, therefore, based upon the fungal remains recovered along with pollen grains.

Considerable scanning of literature on fungi especially Fungi Imperfecti had to be undertaken in order to understand the morphology of fungal spores and assess the possibilities of their identification after dispersal. This necessitated a broad survey of British fungi especially of those found upon higher and lower plants from which the peat is derived. The results of the survey are given below.

Survey of British Fungal Spores — For the purpose of preliminary information on the morphology of spores of Fungi Imperfecti, a monograph on the Hyphomycetes of Europe by Lindau (1907, 1910) was first consulted. A study of the spores of the British fungi was made from comprehensive monographs and books on the British Fungi Imperfecti (Grove, 1935, 1937), British Smuts (Ainsworth and Sampson, 1950), British rusts (Grove, 1913) and Myxogastres (Massey, 1892), Archimycetes (Phycomycetes), Erysiphales, Discomycetales, Tuberales and other orders of Ascomycetes and Basidiomycetes, especially the Uredinales and the Ustilaginales. The spores of lichens and those of fungi growing on mosses and liverworts were also studied from the literature.

This detailed survey has shown that the possibility of identifying fungi from their dispersed spores is very much limited not only by lack of variety of the morphological characters but by a multiplicity of the species and even genera which, in the Fungi

Imperfecti, depends not only on the host but also on the individual organs of the same host so that the same fungus occurring on the leaf, stem, branch and flower of a plant may be described under four species and sometimes be placed in more than one genus. Further some fungi may be the imperfect stages of another, (*Aposphaeria fibricola* and *Diplodiella fibricola*), whereas some may be the imperfect stages of the same fungus and described under two different names, e.g. *Phoma subordinata* and *Diaporthe adunca* (Grove, 1935).

The difficulty in identification of isolated fungal spores is enhanced by variation found within the spores of one and the same species. A species may produce several entirely different types of spores, types that also occur in widely different genera and species. The genus *Phomopsis*, for instance, is characterised by 2 or 3 different types of spores. Several species of this genus occur in the fens. The nomenclature of fungal spores provides another difficulty because it is not possible to know if the sub-fossil spores are conidia, pycnidiospores, ascidiospores, basidiospores, amphispores, mesospores, uredospores or teleutospores.

Morphology of Fungal Spores — The structure of fungal spores is simpler than that of pollen in the higher plants. In most cases they have a single undifferentiated wall which is either smooth or bears protuberances directly on it, though in some an outer wall may also be present. More often fungal spores are aggregates of cells united with one another in several ways and producing a constant pattern. Fungal spores are often provided with pores, the number varying from one to many. In a few of them protuberances such as setae are present. All kinds of spores from spherical to cylindrical, septate or nonseptate, curved or straight, unicellular or multicellular, pyriform, smooth or sculptured are found and some may be furrowed. Their shape, size and occasionally structural details such as granulation, reticulation, spines etc., provide diagnostic features.

Identification of Sub-fossil Spores — Detailed survey of fungal spores in British fungi has revealed that a fairly large majority of the fungi can not be identified from their spores alone and the identification of the smooth walled, spherical or ovoid spores ranging in size from less than 5 μ to 20 μ is not possible through light microscopy. However, this detailed survey has brought out that there are some unique types of spores in modern fungi that are restricted to only a single species, a genus or to a few genera such for instance as *Helicosporium* and *Triposporium*. A few cases like *Clasterosporium caricinum* and *Meliolia* sp. are characterised by hyphopodia.

A working basis for identification of our sub-fossil spores was prepared by listing the spore types along with figures of them and morphological descriptions, for fungi on those hosts, whose remains have been discovered in bogs and fens. The outstanding forms of spore type were then sorted out from this array of spore types, and the sub-fossil spores were then identified by comparison with these assorted types. Quite a few sub-fossil spore types, the modern counterparts of which are found in a large genus or a group of genera, have been referred to the respective generic names and the identification in some of these is tentative. Some few spore types with distinct morphology could not be identified. The frequencies of these unidentified spore types that are restricted to particular levels in the profile and are of frequent or abundant occurrence have been determined.

The spore diagrams (Text-figs. 1-3) are constructed on the pattern of pollen diagrams. The arrangement of individual curves for spores is based on their frequencies in relation to depth in the profile. The frequency of each spore type is a percentage of the total spores counted in each sample of the profile. The zones indicated are the pollen zones. The C^{14} dates are only available (Radiocarbon Vol. III, 1961) for the Holme Fen profile and as shown below are entered on Text-figs. 1 & 3.

Q-403 Holme Fen, Site 1, 65 cm
3400 ± 120 B.P.
Q-404 Holme Fen, Site 1, 70 cm
3415 ± 120 B.P.
Q-405 Holme Fen, Site 1, 135 cm
4190 ± 130 B.P.
Q-406 Holme Fen, Site 1, 205 cm
4958 ± 130 B.P.

SUB-FOSSIL FUNGAL REMAINS

The necessary information about the morphology, indentification, frequency and the hosts of the fungal remains, in relation to stratigraphy and various peat types together with ecological inference is given below with each type. The names of the hosts are given in parenthesis.

A. Single-celled Spores

1. *Tubercularia* type 1

Pl. 1, fig. 1

The spores are unicellular, spherical and provided with fine hairs. No pores or apertures are noted. The spores range in diameter from about 5 μ to 10 μ. Such spores in the British fungi are restricted to a few genera such as *Zygodesmus, Periconia* and *Tubercularia,* a few species of which have spinulate or hairy spores. The spores of the genus *Periconia* are larger, about 12-17 μ and finely hairy as in *Periconia pycnospora* (on Gramineae). The spores of *Zygodesmus* spp., about 6·5-11 μ in size, are spherical, spinulate or tuberculate, i.e. *Z. fulvus* (*Quercus* and *Betula*), *Z. ferrugineous* (*Betula, Corylus, Quercus, Alnus*), *Z. violaceafuscus* (*Quercus*) and *Z. fuscus* (*Quercus, Betula* and *Corylus*). The spores in *Z. violaceafuscus* have irregular spines. The spores in *Tubercularia ciliata* (*Alnus*) with more or less the same range in size are hairy rather than spinulate. The fossil spores, too, appear to be hairy and are, therefore, referred to *Tubercularia* type.

Fossil spores of this kind in the Holme Fen spore diagram (Text-fig. 1) occur frequently at 100 cm where the profile shows *Eriophorum vaginatum* and *Sphagnum-Calluna* peat. They are comparatively more abundant between 125-130 cm in the *Phragmites* peat.

In Trundle Mere this spore type occurs frequently between 120-125 cm where *Sphagnum* (narrow- and broad-leaved)—*Calluna-Erica* peat with *Hypnum* and *Menyanthes* changes over to *Dicranum-Sphagnum-Drepanocladus-Thuidium-Erica-Calluna* peat.

2. *Zygodesmus* type

Pl. 1, fig. 2

Spores, 6-10 μ in diameter, minutely tuberculate, each provided with a distinct pore. Such spores are found in the genus *Zygodesmus* but whether the spores of *Zygodesmus* also have a pore each is not clear from their descriptions.

These spores were only seen in the Tundle Mere deposit and occur very rarely at 122·5 cm and 135 cm. These spores in the Trundle Mere spore diagram (Text-fig. 2) are shown under the name *Tubercularia* type 2.

Genus *Arthrinium* Kunze

The genus *Arthrinium* is well represented in marshes and fens (Ellis *et al.*, 1951, p. 497). In the present material it is represented by more than one species. The different British species are readily distinguished from one another by the shape and size of the conidia. The species occur parasitically on *Carex* spp., *Juncus* and *Scirpus* spp.

3. *Arthrinium sporophleum* type

Pl. 1, fig. 3

In all essential characters such as size and shape of conidia, the sub-fossil spores, 11-14×5-6 μ, approach those of *Arthrinium sporophleum*. The typical conidiophores are occasionally met with, though it is not possible to say to which of the species of the genus they belong. This species is known to occur on *Carex* (*acutiformis, hirta, paniculata, riparia*), *Eriophorum angustifolium* and *Typha angustifolia* in the British Isles, throughout Europe and in India. It also occurs on the other species of *Carex* and *Eriophorum* and on *Juncus effusus*.

This type has a more or less continuous distribution in the Holme Fen profile (Text-fig. 1) from 250 cm upwards and attains highest frequencies only below 150 cm in the *Cladium* sedge peat and the *Cladium-Phragmites* peat. High frequencies are also attained at 92 cm and 122·5 cm.

Its distribution in Trundle Mere (Text-fig. 2) is comparatively discontinuous but higher frequencies were obtained between 42·5-45 cm where the transitional stage is noted between *Sphagnum* peat with birch stem to *Eriophorum-Calluna-Sphagnum* peat.

4. *Arthrinium caricicola* type

Pl. 1, fig. 4

Though *A. caricicola* is known from Europe, it is not known from the British

Isles (Ellis *et al.*, *op. cit.*, p. 490-499). The characteristic boat-shaped spores of this type were matched with the modern spores obtained from the material kindly sent by Dr. M. B. Ellis of the Commonwealth Mycological Institute, Kew. The fossil spores are more variable in size than the living and the range in size over-laps in both.

This type is known to occur in Europe on species of *Carex* (*ciliata*, *ericetorum*, *praecox*, and *riparia*).

In Holme Fen (Text-fig. 1) it has a discontinuous distribution and low values. It occurs between 77·5 cm and 90 cm in *Sphagnum-Calluna* peat and from 115-125 cm at the transition between *Phragmites* peat and *Sphagnum* pool peat. The values in this region are slightly higher than those between 77·5-90 cm. In Trundle Mere (Text-fig. 2) its distribution is more discontinuous with low values except from 172·5-202·5 cm in moss peat, from 215-245 cm, and from 255-277 cm where the distribution is continuous.

5. *Papularia sphaerosperma* type

Pl. 1; fig. 5

Besides *Arthrinium*, the other genus of the "Bivalvae" found in marshes and fens is the genus *Papularia*, two species of which are known to occur in the fens. By their typical flattened nature, the spores are referred to *Papularia sphaerosperma*. The sub-fossil spores, 10-13 × 5-7 μ in size, are lenticular in shape and characterised by a furrow which gives them a two-valved shape.

This fungus is known to occur on *Phragmites communis*, *Calamogrostis canescens*, *Glyceria maxima*, *Cladium mariscus*, *Carex acutiformis*, *C. riparia*, *Phalaris arundinacea* and *Valeriana officinalis*. In other habitats it also occurs on *Pteridium aquilinum*.

It is of very rare occurrence in the Holme Fen profile (Text-fig. 1) at 22 cm, 55 cm and 80-82·5 cm in the bog peat. In Trundle Mere (Text-fig. 2) too it occurs in low values in the bog peat at 107·5-110 cm and at 117·5 cm.

6. ? *Volutella tristis* type

Pl. 1; fig. 6

The unicellular spindle-shaped spores with the proximal end truncate and upper end pointed are provisionally referred to *Volutella tristis* type, with which in range of size, 11-18 × 2-5 μ, the sub-fossil spores agree closely. The genus *Leptothyrium* has several species with spores approaching the sub-fossil type but in none of them is the proximal end truncate.

Volutella tristis is known to occur on *Erica arborea*, not a British native plant.

In Holme Fen (Text-fig. 1) this spore type is of abundant occurrence between 10-45 cm and 75-38 cm in the *Sphag-Calluna* peat and between 115-140 cm in the moss pool peat and *Phragmites* peat. It first appears at 192·5 cm at the transition between the *Cladium* sedge fen to the reed swamp stage.

It is of relatively more continuous occurrence in Trundle Mere (Text-fig. 2). With sporadic, frequent or abundant distribution at 42·5, 55, 70-72·5, 85 and 92·5 cm, its continuous distribution is seen between 97·5-192·5 cm in the moss peat. High values are obtained between 100-117·5 cm in the moss peat with poor *Sphagnum*, *Dicranum*, *Dicranella*, *Hypnum*, *Calluna*, *Erica* showing a transition to *Krioph-Calluna* peat.

7. *Meliolia* sp.

Pl. 1; figs. 7-9

Hyphopodia polygonal, squarish to rectangular in shape.

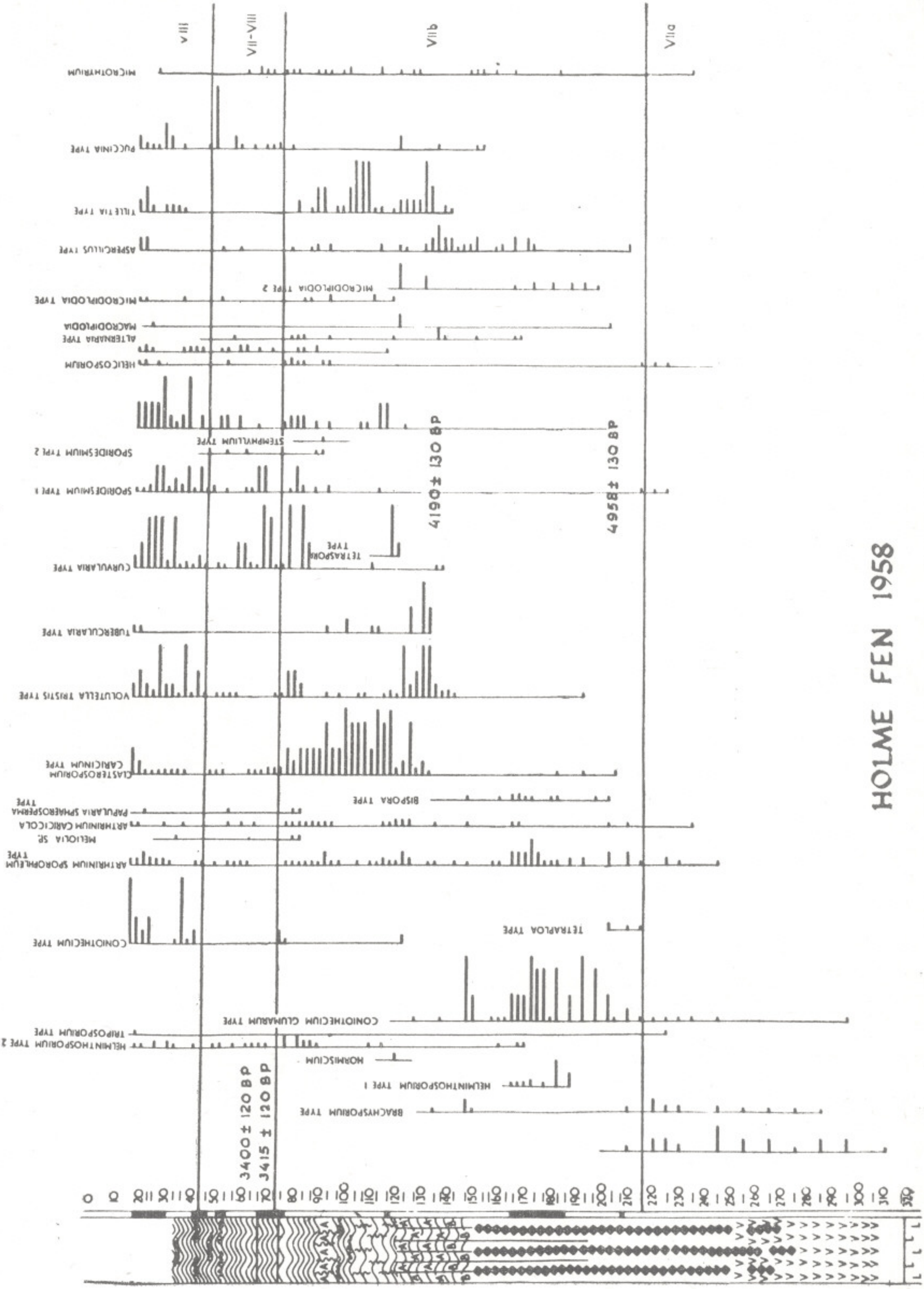
In Holme Fen Meliolia sp. occurs towards the top of Zone VIIb and in Zone VIII and maintains low and sporadic values (Text-fig. 1).

In Trundle Mere it begins from the upper middle part of VIIb and in Zone VII-VIII (Text-fig. 2). Though sporadic throughout it shows higher values in Zone VIIb and in VII-VIII than in Holme Fen.

8. *Clasterosporium caricinum* type

Pl. 1; fig. 10

Besides the lobed hyphopodia of this fungus, straight or curved polyseptate spores have also been found. In some samples this is the most dominant fungus with its mycelium also, to the hyphae of some of which the hyphopodia are seen attached in the fossil condition. The characteristic shape of the hyphopodia and their association with the conidia of this species confirm the



HOLME FEN 1958

TEXT-FIG. 1 — Spore diagram from Holme Fen.

identification of this fungus. *Clasterosporium caricinum* occurs in the Wheatfen Broad and Woodwalton Fen (Ellis *et al.*, 1951, p. 147) on *Carex* spp. (*acutiformis*, *elata* and *riparia*). After the death of the host the fungus survives as a saprophyte. The sedges on which this fungus grows are subjected to periodic flooding and the conidia of this fungus are often seen floating in the dikes.

In Holme Fen (Text-fig. 1) this fungus shows a continuous distribution from 132·5 cm upwards. Its high values are obtained between 70-132·5 cm while its abundant occurrence is seen between 92-135 cm in *Phragmites* peat and *Sphagnum* pool peat.

In Trundle Mere (Text-fig. 2) too its distribution is more or less continuous. With a sporadic occurrence before 97·5 cm, it is more continuous between 97·5-150 cm, and between 180-222·5 cm in *Sphag-Calluna* peat. It does not attain very high values except at 85 cm and between 102·5-107·5 cm and between 185-195 cm. Its distribution below 22·5 is more sporadic and values very low.

9. *Tilletia* type

Pl. 1; fig. 11

The spores, spherical and ellipsoid, about 5-14 μ, with prominent ridged-reticulation, meshes 2-4 with muri 1 μ thick, are referred to *Tilletia* type. This type of spore is also found in the genus *Ustilago*. The spores in the reticulate-spored species of British *Tilletia* (Table 1) are much larger in sizes than the sub-fossils. If *T. sphagni** is not considered, they might belong to the genus *Ustilago*. They seem to belong to more than one species of *Ustilago* and may be grouped into two classes.

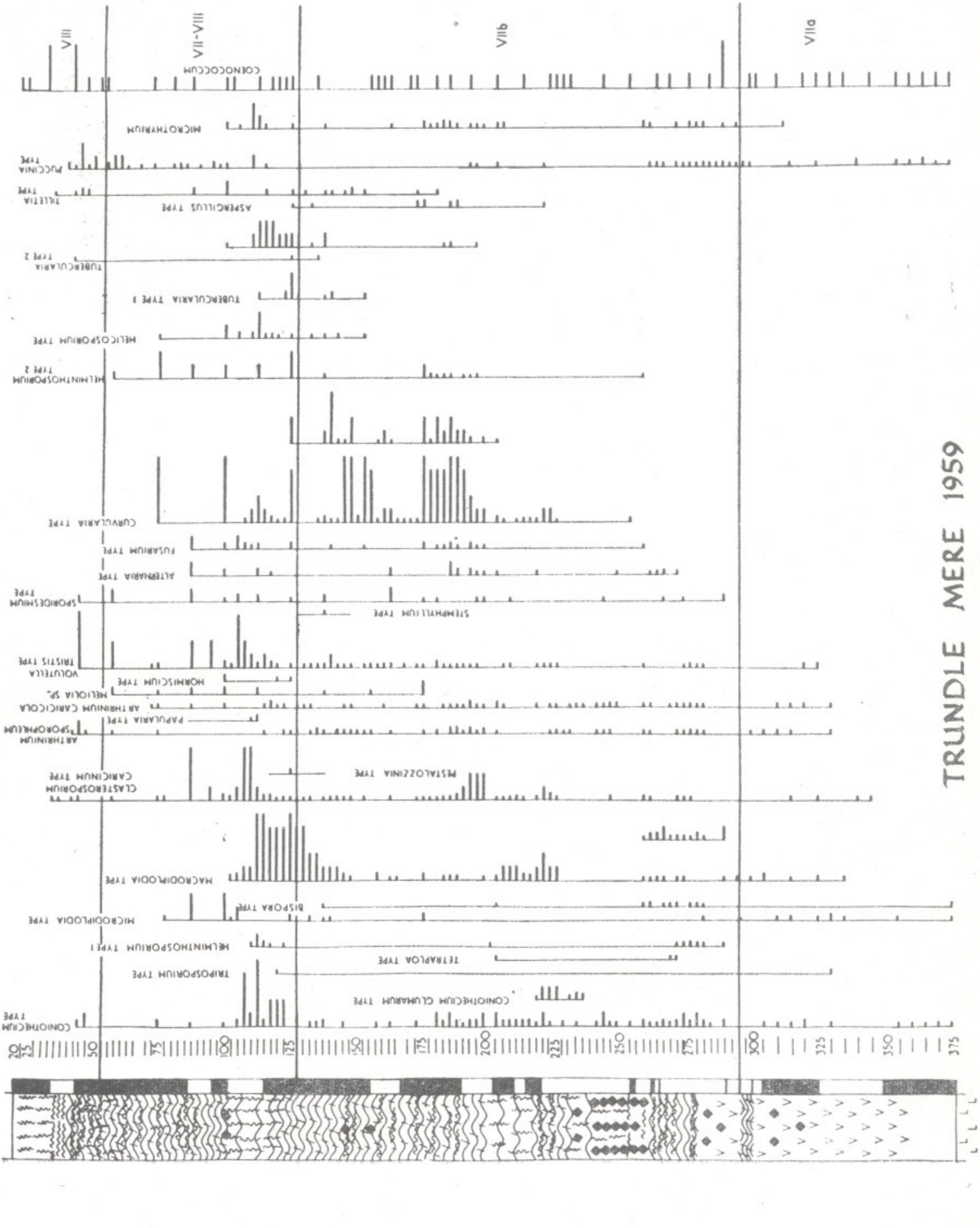
1. Spores between 5-10 μ with muri 1 μ thick.
2. Spores between 10-14 μ with muri 2 μ thick.

Further, in the genus *Tilletia* spores have muri much thicker than in *Ustilago*.

TABLE 1 — THE MORPHOLOGY OF TILLETIA-LIKE SPORES AMONGST THE BRITISH SMUTS*

SPECIES	HOSTS	SHAPE OF SPORES	SPORE DIMENSIONS		
			Size	No. of meshes	Thickness of muri
Ustilago vinosa	*Oxyria digyna*	Globose to sub-globose	6-10 (7-8 μ)	—	1 μ
U. violacea	*Caryophyll, Cerastium viscosum*	Spherical, sub-spherical or elliptical	5-12 (7-8 μ)	—	1 μ
U. succisae	*Succisa pratensis*	Globose to sub-globose	11-14 μ wall 2-3 thick	—	1 μ
U. utriculosa	*Polygonum* spp.	,, ,,	11-14 μ prominent reticulation	—	2-4 μ
U. anomala	,, ,,	,, ,, or ovoid	11-14 μ reticul. delicate	—	2 μ
U. kuehneana	*Rumex acetosa*, *acetosella* and *crispus*	Spherical	12-20 (13-16 μ)	—	—
Tilletia caries	Wheat and Rye	Globose to sub-globose	14-20 μ	2-9	2·5-3·5 μ
T. decipiens	*Agrostis* spp.	,, ,,	26-32 μ irregular meshes	—	,,
T. holci	*Holcus* spp.	,, ,,	22-28 μ	—	4-6 μ
T. lolii	*Lolium* spp.	,, ,,	18-22 μ	—	2-4×2-3 μ
T. menierii	*Phalaris arundinacea*	,, ,,	20-26 μ	—	2-4 μ

*Based on data in the literature.



TRUNDLE MERE 1959

TEXT-FIG. 2 — Spore diagram from Trundle Mere.

Some of these spores might as well belong to *Tilletia sphagni* but the status of this species in the British smuts still remains undecided*.

10. *Uromyces* type

Pl. 1; figs. 12, 13

The spores are spherical with a single pore. The spore wall is ornamented with granulation. The pores are thick-walled.

From their general characters they give the impression of being rust uredospores. The uredospores of the British rusts are either devoid of pores or with distinct or indistinct pores. The pores are always two or more than two with a single exception amongst the British rusts — *Uromyces geranii* in which the uredospores have one germ pore (rarely two). The species is of uncommon distribution in the British Isles and is parasitic on spp. of *Geranium* (Grove, 1913, p. 103-104). In size the sub-fossil spores do approach the uredospores of *U. geranii* but differ in ornamentation of the epispore. The thickened border around the germ pore in the sub-fossil is a typical character of the uredospores of *Uromyces* (Grove, *op. cit.*, p. 85).

Amongst the non-British rusts single-pored uredospores are produced by *Uromyces uniporulus* and *Puccinia monopora* (Grove, *op. cit.*, p. 33).

In both Holme Fen and Trundle Mere (Text-figs. 1 & 2) spores of this type are of extremely rare and sporadic occurrence, though frequent and continuous occurrence in Trundle Mere is seen only between 135-107·5 cm in the moss peat.

11. *Aspergillus* type

Pl. 1 ; fig. 14

The spores, 10-20 ×10-12 μ, are single-celled with a thick wall and provided with a pulley-shaped equatorial groove. There is another type with a few striations besides the groove. These spores are larger, 18·9-25 ×10-15 μ, and oval in shape.

The equatorial groove is only found in the ascospores of *Aspergillus*. Along with these spores the fungal fruiting bodies, the perithecia, are also found which are devoid of any appendages and without these their identification is not possible.

A more or less continuous distribution of the spores is noted in Holme Fen (Text-fig. 1) between 130-173 cm and their high frequencies correspond with the abundant occurrence of perithecia between 135-160 cm. At 210 cm both the spores and the perithecia are rare. These levels in the profile show *Cladium* sedge peat, *Cladium-Phragmites* peat and *Phragmites* peat. These spores also occur frequently in the *Sphagnum-Calluna* peat between 18-20 cm.

In Trundle Mere (Text-fig. 2) the remains of *Aspergilli* are of rare and very sporadic occurrence. They occur in low values at 23 cm, 217 cm, 200 cm, 182·5 cm, 170-172·5 cm, 122·5 cm and 130 cm, in the moss peat.

B. Two-celled Spores

12. *Unidentified* type

Pl. 1; figs. 15-16

The spores are small, 8-10 ×6-8 μ, thick-walled, the lower cell hyaline and the upper cell spherical with a pore.

In Holme Fen (Text-fig. 1) these spores show a more or less continuous distribution above 115 cm in the *Sphagnum-Calluna* peat. Very high frequencies are seen between 113-115 cm in the *Sphagnum* pool peat, between 75-80 cm in the region where the lower clay band is seen and between 50-58 cm a little above the level of second clay band. Abundant high values are noted between 18-38 cm in the *Sphagnum-Calluna* peat.

In Trundle Mere (Text-fig. 2) its continuous distribution is obtained between 200-172·5 cm with high values between 190-172·5 cm and between 150-135 cm in the moss peat.

13. *Puccinia* type

Pl. 1; figs. 17-20

The spores, 18-32 ×10-16 μ, are 1-3 celled, cells thick-walled each with a pore; septa fairly thick. The spores are reddish brown in colour. These spores approach the teleutospores of the rusts. Quite a few of them which are one-celled with an apical pore show a faint epispore pattern ranging from pits to a broad meshed reticulum

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*Ainsworth and Sampson (1950) have excluded this species from the British smuts.

with irregular muri. A distinct stalk is present in some of them while quite a few seem to be devoid of it.

A survey of the teleutospores in all the families of the British Uredinales shows that the sub-fossil spores compare with the teleutospores of Pucciniaceae. In Melampsoraceae the teleutospores are composed of 2-4 laterally adherent cells with the septa cruciately arranged or they are one-celled united into crusts; in Cronartiaceae they are sessile, single-celled and produced in chains and in Coleosporaceae the teleutospores are single-celled and later divide into 9 superimposed cells each. In shape and structure the teleutospores in Melampsoraceae, Cronartiaceae and Coleosporaceae are very much different from those of Pucciniaceae, in which the teleutospores range from one to two-celled, each cell provided with a pore. The position of the teleutospores in the family Pucciniaceae is as follows:

Single pore per cell	
spore one-celled (occasionally two-celled)	*Uromyces*
spores two-celled (occasionally three-celled)	*Puccinia*
spores radiately three-celled	*Triphragmidium*
Two or more than two pores in each cell	
spore two-celled	*Gymnosperangium*
linearly many-celled	*Phragmidium*, *Zenodochus*, *Kuehneola*

The sub-fossil teleutospores being 1-3 celled with a pore in each cell, seem to belong to both *Uromyces* and *Puccinia*. In the genus *Puccinia* one or several-celled teleutospores are rarely produced. Since it is not possible to distinguish amongst the sub-fossils the teleutospores of both the genera, all of them are here referred to *Puccinia* type. The smooth-celled teleutospores in the genus *Puccinia* can be grouped into the following 5 categories. The teleutospores of *Uromyces* are built on the same plan. No British *Puccinia* sp. is known with teleutospores of category 5, below.

In category 1 the apical cell is very much thickened distally and the thickening forms a conical protuberance at the apex.

In category 2 the apical thickening forms several distinct lobes.

In category 3 both the cells are uniformly thickened.

In category 4 the cells are equally thickened but the upper cell is truncate.

In category 5 a three-celled stage, thickening is moderate and the cells are more or less spherical.

Only two sub-fossil spores of the kind in category 1 were observed in the Holme Fen series, the rest of the sub-fossil teleutospores are of category 3 and a few of categories 4 and 5 (Text-fig. 1).

Out of 137 spp. of *Puccinia* in the British Isles as many as 22 have teleutospores which fall within the size range and characters of the sub-fossil spores. Of these very few are parasitic on such hosts as grow in the Fens and bogs and these are:

Puccinia phragmitis on *Phragmites communis*
P. umbilici on Umbelliferae
P. epilobii }
P. pulverulenta } on *Epilobium* spp.

The distribution of *Puccinia* type spores in Holme Fen (Text-fig. 1) seems to be more or less continuous between 18-75 cm in the *Sphagnum-Calluna* peat, very high frequencies are obtained between 75-55 cm and 18-30 cm. High values are also seen at 120 cm at the transition between the *Phragmites* peat and the raised bog peat. Values below this level are very low and sporadic.

In Trundle Mere (Text-fig. 2) a more or less continuous curve is seen between 112·5-37·5 cm with very high values between 45-60 cm in the moss peat.

14. *Macrodiplodia* type 1

Pl. 1; figs. 21-22

Macrodiplodia type 1 is one of the most common 2-celled types of the fungal spores. It shows a great range in size. Such sub-fossil spores are grouped into two categories,

One the *Macrodiplodia* type and the other **Microdiplodia* type. In both the ends are acute. The spores above 20 μ long and 10 μ broad are grouped under *Macrodiplodia* type while those below 20 μ

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*Not to be confused with the genera *Macrodiplodia* and *Microdiplodia* in which also these two spore types occur.

long and 10 μ broad are grouped under the *Microdiplodia* type. It seems extremely difficult to refer these spores types to any modern fungi unless some more characters are available.

The spores in *Macrodiplodia* type are 24-45 ×10-15 μ, with ends acute or broadly acute, occasionally eseptate, a few with round ends and 24-25 ×8-10 μ in size. These spores evidently belong to different genera and species.

In Holme Fen (Text-fig. 1) the *Macrodiplodia* type of fungal spores is extremely rare and of occasional occurrence at one or two levels. In Trundle Mere (Text-fig. 2) the *Macrodiplodia* type of spores shows a more or less continuous distribution between 97·5-225 cm with high frequencies between 97·5-145 cm, very abundant between 107·5-135 cm and very high values between 200-225 cm in moss peat.

15. *Microdiplodia* type

Spores from Trundle Mere (Text-fig. 2), about 10-14 ×5-6 μ, are with round ends. In Holme Fen the *Microdiplodia* spores are larger in size, 15-20 ×5-6 μ. *Microdiplodia* type in Holme Fen (Text-fig. 1) is very sporadic and of very low values, high values are only obtained at 120 cm at the transition between *Phragmites* peat into pool peat and at 130 cm in the *Phragmites* peat. Its low values are also seen in *Cladium-Phragmites* sedge peat.

In Trundle Mere (Text-fig. 2) it occurs in the moss peat at 75 cm, 85 cm, 97·5-102·5 cm and between 305-350 cm in wood peat. The values are very low throughout.

Some *Microdiplodia* type spores are very small in size, about 5-8 ×3-4 μ, Their frequencies are shown separately in the spore diagrams (Text-figs. 1 & 2) under the name *Microdiplodia* type 2.

16. *Pestalozziania* type

Fusoid two-celled spores about 48-50 × 4-5 μ, with each end tapering into a hyaline curved appendage. This type resembles the spores of *Pestalozziania uniseptata* parasitic on *Phragmites*.

This type of spore occurs only in Trundle Mere (Text-fig. 2) where very low frequencies are seen at 122·5 cm.

17. *Bispora* type

Pl. 1; fig. 23

Spores, 20-35 ×5-7 μ, with a thick septum and both ends truncate, resemble the spores of *Bispora monilioides* parasitic on *Salix, Quercus, Fagus* and *Corylus*.

This spore type occurs in low frequencies in Trundle Mere only (Text-fig. 2). Besides the more or less continuous distribution between 255-277·5 cm in the moss peat a little above the wood peat, low frequencies are also seen at 200 cm and 135 cm in the moss peat again.

C. Three to Many-celled Cylindrical Curved or Concentric Spores

18. *Unidentified* type

Pl. 1; figs. 24-26

Spores, 30-50 μ ×4-6 μ, 2-5 septate, usually 3 septate, all the cells except the apical, dark; apical cell prolonged, hyaline.

This type has more or less continuous distribution in Holme Fen above 90 cm and has low values in *Sphagnum-Calluna* peat (Text-fig. 1).

In Trundle Mere it has very discontinuous and sporadic distribution with very low values except between 195-172·5 cm in the moss peat (Text-fig. 2).

19. *Fusarium* type

Pl. 1; fig. 27

Spores 3-septate, 30-35 ×8-10 μ, slightly curved.

In Holme Fen more or less continuous distribution is noted between 18-90 cm with slightly higher values between 77·5-82·5 cm in *Sphagnum-Calluna* peat (Text-fig. 1).

In Trundle Mere (Text-fig. 2) it is of very discontinuous distribution with low values; a continuous distribution is only obtained between 172·5-195 cm. Comparatively higher values are seen at 55, 72·5, 85, 97·5, 110 and 122·5 cm.

20. *Curvularia* type

Pl. 2; figs. 28-30

Spores of the genus *Curvularia* are very characteristic in possessing one of the cells generally that next below the apical cell, larger and darker than the others which are hyaline. Sometimes the central cells are darker.

One of the species of the genus *Curvularia, C. crepini* is already known from Dernford Fen, Wheatfen Broads and Hickling Broads (Ellis *et al.*, 1951, p. 151) and has been found parasitic on *Ophioglossum vulgatum.*

The distribution of this fungus is continuous between 85-18 cm in Holme Fen (Text-fig. 1), abundantly high values are maintained at 80, 75, 70-72·5 and between 31 and 18 cm. Throughout it is distributed in the raised bog peat. It also occurs at 112 cm and in the *Phragmites* peat between 137-140 cm.

Comparatively more continuous distribution is noted in Trundle Mere (Text-fig. 2) between 132-225 cm, and between 105-122·5 cm in the moss peat. The values are sporadic but very high at 72·5 and 97·5 cm. Exceptionally high values with continuous distribution in Trundle Mere are obtained from 190-175 cm and between 152·5 and 142·5 cm in the moss peat.

21. *Helminthosporium* type 1

Pl. 2; fig. 31

The spores, about 20-28 × 11-13 μ, 3-4 celled, mostly 3-celled with the central one or two cells dark, the others hyaline, oval, long, cylindrical or ellipsoid. The corresponding form in modern *Helminthosporium* in the British Isles is noted in *H. velutinum*, with which the fossil spores resemble very much in essential characters. *H. velutinum* is parasitic on *Alnus, Salix* and *Betula*, while on upland it also occurs on *Corylus, Carpinus, Fagus* and *Tilia.*

This spore type has more or less continuous distribution in Holme Fen (Text-fig. 1) between 164-285 cm in *Cladium* sedge peat and wood peat. Above this it occurs sporadically in the *Phragmites* peat as well as in *Cladium-Phragmites* peat. Its values are very low throughout.

In Trundle Mere (Text-fig. 2) it occurs between 267·5-277·5 cm in very low values at the transition between wood peat and the raised bog peat.

22. *Helminthosporium* type 2

Spores 5-6 septate, 40-46 × 20-23 μ, all the cells except the outer ones dark, with very restricted distribution and low values in Holme Fen at 245 cm at the transition between wood peat and *Cladium* sedge peat (Text-fig. 1).

23. *Brachysporium* type

Pl. 2; figs. 32-33

Spores, 28-35 × 15-18 μ, cross-walls 3-6 with the upper cells very broad and the lower cells smaller, resemble the spores of *Brachysporium coryneoideum* but differ from them in having the outer cell darker while in *B. coryneoideum* only the two inner are darker. *B. coryneoideum* is parasitic on *Salix.* The species of *Brachysporium* parasitic on *Betula* and *Phragmites* have smaller spores.

In Holme Fen this type is present in low frequencies in the *Cladium* sedge peat at 215 and 220 cm (Text-fig. 1).

24. *Hormiscium* type

Pl. 2; fig. 34

The worm-like long and oval spores compare with those of *Hormiscium* spp. especially *H. antiquum* parasitic on *Salix* and *Betula.*

Hormiscium type of spores are of very rare occurrence in Holme Fen (Text-fig. 1) and only occur in very low values at 120 cm where transition from *Phragmites* peat to raised bog peat is noted. In Trundle Mere *Hormiscium* type spores are only seen in low frequencies at 97·5 and 122·5 cm (Text-fig. 2).

25. *Alternaria* type

Pl. 2; fig. 35

From the information extracted from the literature on the fungi which grow on hosts in the habitat of fens and marshes, it seems that no species of this genus occurs on the fenland species of higher plants.

These fossil spores joined end to end with the free ends longer appear to be like those of the genus *Alternaria*; in some cells the vertical septa are also present. Their very poor and discontinuous distribution in both Holme Fen and Trundle Mere (Text-figs. 1 & 2) suggests that they are derived from the upland.

26. *Helicosporium* type

Pl. 2; figs. 36-37

The characteristic spiral-shaped multiseptate spores, about 25-35 μ in diameter, can hardly be mistaken for anything other than the spores of *Helicosporium*. In the size and thickness of filaments and the number of septa these spores differ from *H. phragmitis* which is known from the fens and marshes (Ellis *et al.*, 1951, p. 163). In size they are smaller than those of *H. lumbricoides* and *H. pulvinatum* but resemble spores of *H. brunneum*. These species are parasitic on *Quercus*.

In Holme Fen (Text-fig. 1) the *Helicosporium* type spores occur at the transition between wood peat and *Cladium* sedge peat, and between 215-235 in *Cladium* sedge peat and between 77·5-92 and 18-25 cm in the *Sphagnum-Calluna* peat. They occur at these levels in very low frequencies.

In Trundle Mere (Text-fig. 2) they occur more or less continuously between 150-97·5 cm and sporadically above also in the moss peat.

D. Multicellular Spores with Both Parallel and Cross Walls

27. *Stemphylium* type 1

Pl. 2; figs. 38-40

Spores, about 20-35 × 6-14 μ in size, club-shaped ellipsoid or oval, with round ends and 1-7 vertical septa with smooth walls. These spores compare with those of the genus *Stemphylium* and seem to resemble the spores of *S. ericoctomum*. The spores in the genus *Alternaria* are different in having the upper cell very much elongated and occasionally truncate. Spores in the genera *Dichomera* and *Camarosporum* are much smaller. The spores in figs. 38, 39 might approach those of some species of *Camarosporum, C. pini* var. *major* in having only 1-3 medium cells with vertical septa, but the transverse septa are more than three. Besides, the spore type in fig. 40 might approach those of *Stemphylium piriforme*. All the three kinds of spores are included in *Stemphylium* type because of the variations which may be noted in the same species.

The species of genus *Stemphylium* are parasitic on *Betula, Alnus, Quercus, Gramineae*, and *Erica*. *S. piriforme* is parasitic on *Betula* and *S. ericoctomum* is parasitic on *Erica* spp.

In Holme Fen (Text-fig. 1) spores of this type are of very rare occurrence at 52·5, 60 and 90 cm in the *Sphagnum-Calluna* peat. In Trundle Mere (Text-fig. 2) low values are seen at 135 cm in the moss peat.

28. *Stemphylium* type 2

In Holme Fen spherical type of spores about 18-20 μ in diameter, with a few cross walls are seen with a very limited and rare distribution only at 52·5, 60 and 75 cm. These seem to compare with those of *S. magnusianum* parasitic on *Alnus*.

29. *Sporidesmium* type

Pl. 2; fig. 41

Spores oval, elongate ovate, spindle-shaped, about 50-60 × 30-90 μ, muriform seem to compare with those of *Sporidesmium cellulosum*. The spores of *Camarographium* too are very similar but not as broad as those of *S. cellulosum*. *Sporidesmium cellulosum* is parasitic on *Alnus* and *Quercus*. *Camarographium stephansii*, the spores of which are also similar to the sub-fossils, is parasitic on *Pteridium*. Spores in the genus *Macrosporum*, parasitic on *Erioph. vaginatum, Betula, Quercus, Epilobium* and *Sparganium* are very much different in size and structure.

Sporidesmium type spores have more or less continuous distribution in Holme Fen between 18-95 cm and high values are obtained between 46-23 and between 65-67·5 cm in the *Sphagnum-Calluna* peat (Text-fig. 1).

This type of spores in Trundle Mere has a very sporadic distribution and maintains low values in the wood peat, *Cladium* sedge peat and moss peat (Text-fig. 2).

30. *Steganosporium muricatum* type

Pl. 2; fig. 42

A single spore of this type has so far been observed and that in Holme Fen (Text-fig. 1) at a level of 140 cm where at the mesotrophic fen stage, *Phragmites* peat is formed. The spore about 40 × 16 μ in size, is pyriform, oblong ellipsoid, multilocular with five transverse and 3 vertical septa. The spore is typically attenuated below and resembles the spores of *Steganosporium muricatum* parasitic on *Betula*.

E. Stellate Spores

31. *Triposporium* type

Pl. 2; figs. 43-47

The stellate spores with three arms resemble in all essential characters the spores of the genus *Triposporium*. *Triposporium elegans* is known to occur on the dead stems of *Filipendula ulmaria* in Wheatfen Broad (Ellis *et al.*, 1951, p. 161). It is also known to occur on dead wood of *Betula* and *Quercus* and on other herbaceous stems. The sub-fossil spores seem to belong to more than one species.

It has very low frequencies both in Holme Fen and Trundle Mere (Text-figs. 1 & 2) and is of sporadic occurrence. In Holme Fen it occurs at 18 cm, and in the Trundle Mere at 117·5 and 120 cm in moss peat and at 325 cm in wood peat.

F. Spores with Setae

32. *Tetraploa* type

Pl. 2; fig. 48

The spores with four vertical and a horizontal wall dividing the spore body into 8 cells with four septate setae resemble in all essential characters, the spores of *Tetraploa aristata* which is parasitic on grasses. The ornamentation of the spore wall varies in some individuals while the setae in very rare cases are found to be eseptate suggesting the occurrence of more than one species amongst the fossils.

Of very rare occurrence both in Holme Fen and Trundle Mere (Text-figs. 1 & 2). In Holme Fen it occurs in low values at 202·5 cm in the *Cladium* sedge peat; high values are seen between 113·5-115 cm in the *Sphagnum* pool peat a little above the *Phragmites* peat.

In Trundle Mere it occurs between 265-267·5 cm in low values at the transition between the raised bog and the *Cladium-Hypnum* peat.

Genus *Coniothecium* Corda

The spores of *Coniothecium* are regularly or irregularly adherent together to form spherical and packet-like masses or variously heaped to form irregular elongate, ellipsoid spore masses. Quite a few species of the genus *Coniothecium* are expected to occur in fenland deposits. The sub-fossil spores are grouped together into the elongate type, *Coniothecium* type 1, and the spherical forms, *C. glumarum* type 2.

33. *Coniothecium* type 1

Packet-like elongate spore masses still attached to the woody tissues. Such longish spore masses are produced by several spp. of *Coniothecium*, parasitic on *Alnus*, *Salix*, *Betula*, such as *C. alneam*, *C. amentacearum*, *C. conglutinatum*.

In Holme Fen (Text-fig. 1) *Coniothecium* type 1 is seen more or less continuously present between 42·5-18 cm, very high values are obtained at 37·5 and between 18-25 cm and sporadic distribution is seen between 137·5 to 42·5 cm in the *Sphagnum-Calluna* peat.

In Trundle Mere (Text-fig. 2) this type shows a more or less continuous curve throughout with high values at 45, between 102-120 and between 177·5-217·5 cm in the moss peat.

34. *Coniothecium glumarum* type

Pl. 2; fig. 49

Spherical or globular spore masses resembling those of *C. glumarum* on *Phragmites communis*. The spore masses in *C. globiferum* and *C. applanatum* on *Salix* and *C. effusum* on *Alnus* though smaller in size are also not very much different.

This type has a more or less continuous distribution in Holme Fen (Text-fig. 1) between 145-245 cm in the *Phragmites* peat and the *Cladium* sedge peat. Low values of this type are seen at 295 cm in wood peat.

In Trundle Mere (Text-fig. 2) this type is restricted to the *Cladium-Hypnum* peat between 220-232·5 cm.

35. Unidentified type

Pl. 2; figs. 50-51

The specimens in figs. 50, 51 are here included in the Fungi although their identity remains uncertain.

The specimens are about 50-55 ×20-25 μ in size with both ends truncate: they are provided with 2-3 parallel and branched vertical ridges. Ridged spores are common in the Pezizaceae but they are very small in size. No corresponding form was noted in literature on British fungi.

In Holme Fen (Text-fig. 1) this type shows more or less continuous distribution between 210-310 cm in the *Cladium* sedge peat and wood peat. It is also seen at 150 cm at the transition from *Cladium* sedge peat to *Phragmites* peat and in *Phragmites* peat.

In Trundle Mere (Text-fig. 2) it is only seen continuously between 257·5-285 cm in the *Cladium-Hypnum* peat and the raised bog peat.

G. The Other Fungal Remains

36. *Microthyrium* spp.

The fossil ascomata or the thyriothecia of *Microthyrium* from the Flandrian deposits have already been reported by Godwin and Andrew (1951, p. 179). Similar fungal fruiting bodies have also been observed in the peat deposits of the Whittlesey Mere region. Three species of modern *Microthyrium* have been recorded from Britain since the fossils were reported (Webster, 1951, 1952). *M. nigroannulatum* and *M. culmigenum* has been recorded in Britain on wild and cultivated grasses (Webster, 1951, 1952). Godwin and Andrew (personal communication from Sir Harry Godwin) found fruiting bodies of *Microthyrium* on the flowers of living carices. Though it has not been possible to identify the species, it appears as if the sub-fossils represent the remains of more than one species. Those described by Godwin and Andrew (*op. cit.*) probably belong to *Microthyrium nigro-annulatum* Webster.

In the Whittlesey Mere region the fungal fruiting bodies resembling *M. nigro-annulatum* occur abundantly. There are also quite a few which seem to belong to *M. culmigenum.*

These fruiting bodies have a more or less continuous distribution in Holme Fen between 60-127·5 cm and between 147·5-165 cm in *Sphagnum-Calluna* peat, *Phragmites* peat, and *Cladium-Phragmites* peat (Text-fig. 1). In Trundle Mere their continuous distribution is seen between 172·5-202·5 cm in moss peat, between 97·5-112·5 cm and between 255-290 cm in *Sphagnum-Calluna* peat as well as in the wood peat (Text-fig. 2).

37. *Cenococcum graniforme* (Sow.) Ferdinandeen & Winge

Sclerotia round to ovoid, very small, black in colour and brittle like coal and hollow within. The sclerotia of *Cenococcum graniforme* have been found abundantly from both Holme Fen and Trundle Mere. They occur more abundantly in the wood peat than in the raised bog peat.

There is practically no recent record of the occurrence of *Cenococcum* in Britain, the only records known date back to the nineteenth century (Sowerby, 1800; Fries, 1829; Berkley, 1860). Sowerby found it in crusts of *Lecidea uliginosa*, Fries found it of common occurrence in woods on peaty soil.

Cenococcum graniforme, the single species known so far, has been recorded from various parts of Europe and of America. It has been known from the Pleistocene to the subrecent. It has been described from the Interglacial deposits of Germany (Weber, 1896, 1914), from the peat bogs of Finland (Andersson, 1898; 1902) and Sweden (von Post, 1906) and from the Dryas zone and the Diatom earth from Denmark (Hartz and Ostrup, 1899). It is of wide distribution in Norway (Holmboe, 1903). From the Late- and Post-glacial deposits Knud Jessen (1920) described it from North-eastern Zealand. He found it both from the Alleröd Period and from the younger Dryas Period.

It is of frequent occurrence in fresh water deposits of widely different character, rare in deeper waters, abundant in the moors and old forest peats, chiefly found in alder wood peat but also in bog peat. The kind of soils in which it is found range from sand and clay fresh-water chalk and gyttja, *Sphagnum* peat and *Carex* peat to wood peat of alder generally associated with *Betula* spp., *Pinus sylvestris, Empetrum nigrum, Quercus* and *Calluna.*

In the Flandrian peat bogs of Norrland in Sweden, von Post in 1906 found *Cenococcum* occurring most frequently and abundantly in strata of the bogs where the peat is rich in tree stumps or with fragments of birch and pine.

C. graniforme is found both in warm and partly in cold climates. From its distribution in the past it seems that it must have grown in varying ecological conditions from arctic to temperate. The sclerotia are smaller under cold and poor conditions.

This typical plant of the moors is also found in varying conditions of moisture, in woods, heaths, bogs, wet *Sphagnum* tufts, on *Calluna* heaths and is especially common in the rhizoidal felts of mosses. It has been found below *Dicranum scoparium*, *Hylocomium proliferum* and *Polytrichum*, under *Hypnum* in oakwoods, in *Sphagnetum*, *Sphagneto-Betuletum* and the "Lichen moors".

In Holme Fen (Text-fig. 1) it occurs abundantly in the alder wood peat, in the *Cladium* sedge peat, *Cladium-Phragmites* peat, *Phragmites* peat and then abundantly in the raised bog peat. In Trundle Mere too it occurs in all kinds of peat (Text-fig. 2).

THE SPORAE DIAGRAMS

The spore diagrams from both Holme Fen and Trundle Mere show the successional development of various fungi in the profiles. It is interesting to find that in the diagrams (Text-figs. 1-3) the fungi are very scarce in pollen zone VIIa (corresponding with the Atlantic Period), a great increase in the frequency and the variety of the fungi is seen especially in zone VIIb (corresponding with the Sub-boreal Period) and a part of the transition zone VII-VIII (transitional to the Sub-atlantic Period). While in Holme Fen higher frequencies of some of the species of fungi are again obtained in zone VIII, in Trundle Mere in the same zone fungi are again very scarce.

HOLME FEN (Text-fig. 2)

In Holme Fen the fungal population begins with the unidentified spore type no. 35 cf. descriptions above stated hereafter as unidentified spore type a which remains dominant throughout pollen zone VIIa. *Coniothecium glumarum* type has very sporadic values, *Brachysporium* type which commences later, maintains low values. Towards the top of zone VIIa *Helicosporium* type and *Arthrinium sporophleum* type appear and towards the extreme top of VIIa, *Brachysporium*-unidentified type a aggregate* includes besides *Helicosporium* and *Arthrinium sporophleum* type, low values of *Arthrinium caricicola*, *Microthyrium* and *Sporidesmium* type 1. *Triposporium* joins this aggregate little later.

The beginning of pollen zone VIIb marks the beginning of *Coniothecium-Arthrinium* aggregate in which *Coniothecium glumarum* type and *Arthrinium sporophleum* type remain codominant. *Aspergillus* and *Tetraploa* join this aggregate at the base of VIIb. The other members of the aggregate, the unidentified type a, *Brachysporium* type, *Arthrinium caricicola* type, *Sporidesmium* type 1 and *Helicosporium* type remain in very low values.

Coniothecium glumarum type gradually assumes dominance over all others. In the *Coniothecium glumarum* group *Helminthosporium* type 1, *Arthrinium sporophleum* type, *Aspergillus* type, and *Microdiplodia* type 2 maintain comparatively higher values than *Arthrinium caricicola*, *Bispora* type, *Clasterosporium caricinum* type and *Microdiplodia* type 2 while *Volutella tristis* type, *Macrodiplodia* type and *Microthyrium* are of rare occurrence. At 182·5 cm *Helminthosporium* type 1 falls to low values, and *Arthrinium sporophleum* type increases in its values. At 165 cm *Coniothecium glumarum* type too falls to low values and the fungal population on the whole is very much reduced and very low values of the other fungi such as *Helminthosporium* types, *A. sporophleum*, *Bispora* type, *Alternaria* type, *Puccinia* and *Microthyrium* type are maintained. Values of *Aspergillus* are higher at this level and continue increasing upwards. At 150 cm *Coniothecium* once again fluctuates to very high values and at this level *Aspergillus* type also achieves its maximum frequency. *Tilletia* type begins to appear from here. *Brachysporium* once again joins this aggregate.

With the decline in *Aspergillus* frequencies, the *Tilletia-Tubercularia-Volutella* aggregate

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*The terms 'aggregate' and 'group' are used to describe various fungal communities in the same sense as 'association' and 'consociation' are used to describe the communities of higher plants.

is formed, in which *Microthyrium*, *Microdiplodia*, *Alternaria*, *Curvularia*, *Arthrinium* is formed, in which *Microthyrium*, *Microcaricicola*, *A. sporophleum*, *Coniothecium glumarum* and *Brachysporium* types have very low values.

At 132·5 cm *Clasterosporium caricinum* joins the aggregate* and gradually assumes dominance. *Volutella tristis* type and *Tubercularia* type are reduced to very low values while *Tilletia* type, after a decline, once again attains high values. There is a brief phase of *Clasterosporium-Tetraspora* aggregate before the *Clasterosporium-Tilletia* aggregate is formed at 105 cm. The other fungi such as *Microthyrium* type, *Microdiplodia* type 1, *Sporidesmium* type 1, *Curvularia* type, *Arthrinium sporophleum* type, *Coniothecium* type, *Helminthosporium* type 2 and *Hormiscium* type maintain low and sporadic values.

The term 'aggregate' and 'group' are used to describe various fungal communities in the same sense as 'association' and 'consociation' are used to describe the communities of higher plants.

Towards the top of zone VIIb the *Curvularia* type suddenly assumes dominance but *Clasterosporium*, *Volutella*, *Sporidesmium* types and an unidentified spore type remain codominant in the group of the *Curvularia* type. The other fungi *Helminthosporium* type 2, *Coniothecium*, *Arthrinium* spp., *Papularia sphaerosperma*, *Helicosporium*, *Alternaria*, *Microdiplodia*, *Aspergillus* and *Microthyrium* types show low values.

During the transition zone VII-VIII the most frequent aggregate is the *Curvularia* group except towards the close of transition zone VII-VIII where the *Puccinia* type shows very high values. *Sporidesmium* type 2 attains very high values along with *Curvularia* type at 65 cm a little after the beginning of zone VII-VIII.

Zone VIII begins with the increasing values of *Sporidesmium* type 1, *Curvularia* type, *Volutella tristis* type, *Coniothecium* type and an unidentified type and soon the *Curvularia-Volutella* aggregate is formed and towards the top of the profile *Curvularia-Volutella-Coniothecium* aggregate is formed and here the frequencies of most other fungi, *Arthrinium sporophleum*, *Clasterosporium caricinum*, *Tilletia*, *Puccinia* and *Aspergillus* types also rise. Quite a few others maintain low values.

Thus, in Holme Fen the following sequential stages are noted:

14. *Curvularia-Volutella-Coniothecium* aggregate	VIII
13. *Curvularia-Volutella* aggregate	
12. *Curvularia* group	
11. *Curvularia-Sporidesmium* Type 2 aggregate	VII-VIII
10. *Curvularia* group	VIIb
9. *Clasterosporium-Tilletia* aggregate	
8. *Clasterosporium-Tetraspora* aggregate	
7. *Clasterosporium caricinum* group	
6. *Tilletia-Tubercularia-Volutella* aggregate	
5. *Coniothecium-Aspergillus* aggregate	
4. *Coniothecium glumarum* group	
3. *Coniothecium-Arthrinium* aggregate	
2. *Brachysporium-Unidentified* spore type aggregate	VIIa
1. Unidentified spore type group	

Consideration of the Population of Fungi with the Peat Types in Holme Fen

The unidentified spore type group is restricted to the brushwood peat which has been formed by the remains of alder-oak fen woods with cyperaceous rootlets and the Marsh Fern, *Dryopteris thelypteris* with a minor representation of *Salix*, *Betula* and *Pinus*. Towards the top of zone VIIa besides the above-mentioned plant remains frequent fruits of *Cladium mariscus* and *Hypnum* moss are present. *Osmunda* also increases to its maximum frequencies here. The fungal population is represented by *Brachysporium*-unidentified spore type aggregate. The genus *Brachysporium* is parasitic on *Salix* and *Betula*. The other members of the aggregate *Coniothecium glumarum* are parasitic on *Phragmites; Helicosporium* on *Phragmites* and *Quercus; Arthrinium sporophleum* on *Carex* spp., *Typha*, *Juncus* and *Eriophorum angustifolium; Microthyrium* on *Gramineae; Arthrinium caricicola* on *Carex* spp.; *Sporidesmium* on *Betula*, *Quercus*, *Epilobium*, *Alnus*, and *Sparganium* and *Triposporium* on *Betula* and *Filipendula ulmaria*. Thus the population of the fungi suggests those hosts whose remains are obtained by the micro and macroscopic analysis of the organic deposits.

Towards the top of the profile in zone VIIa the stratigraphy suggests the formation of the *Cladium* sedge-fen and swampy conditions. The Unidentified spore type shows higher frequencies here suggesting that the fungus to which these spores belong is characteristic of swampy situations. It is interesting to find the presence of two spp. of *Arthrinium*, *A. caricicola* and *A. sporophleum*, which first appear at this level. These two species are parasitic on spp. of *Carex*, *Eriophorum*, *Typha* and *Juncus*. The *Cladium* sedge-fen continues during the basal part of zone VIIb and then forms *Phragmites-Cladium* sedge-fen. The change over in the fungal population from *Coniothecium-Arthrinium* aggregate to *Coniothecium glumarum* group is quite significant. The presence of *Bispora* suggests the occurrence of *Quercus* and *Salix*, as *Helminthosporium* suggests that of *Alnus*, *Salix* and *Betula* spp. *Arthrinium* spp. and *Clasterosporium caricinum* suggest sedges in the vicinity. Thus both spore analysis and stratigraphy show the presence of oak-alder fen-woods and reed-swamp.

The establishment of the *Phragmites* fen due to flooding indicates conditions bringing about diminution in the population of the fungi. Between 135-150 cm only *Aspergillus* and *Alternaria* are seen, genera which thrive as saprophytes. At above 135 cm fungi again appear, probably due to decrease in water level. The *Tilletia-Tubercularia-Volutella* aggregate is seen, followed by a brief phase of *Clasterosporium-Tetraspora* aggregate and then by the *Clasterosporium caricinum* group. The stratigraphical and pollen analytical results show with lowered water levels the establishment of wet mesotrophic fen-wood with abundant birch and pine and *Phragmites* undergrowth. The occurrence of fungi such as occur on *Betula*, for example *Sporidesmium*, *Helminthosporium* and *Hormiscium*, is quite suggestive of that. Species of *Arthrinium* and *Clasterosporium caricinum* are parasitic on sedges.

The *Clasterosporium caricinum* group corresponds to the transitional stage between the mesotrophic fen-wood and the commencement of the raised bog. At this level numerous rootlets and fruits of Cyperaceae are encountered. The Cyperaceae pollen curve also shows high values.

It is difficult to correlate the populations of fungi in the raised bog peat since their hosts are not known. That carices have played a part in the development of the ombrogenous bog is evidenced by the presence of the spp. of *Arthrinium* and *Clasterosporium caricinum*. *Volutella tristis* is suggestive of Ericaceae and its high values corresponding to the *Eriophorum vaginatum-Sphagnum-Calluna* peat are quite striking.

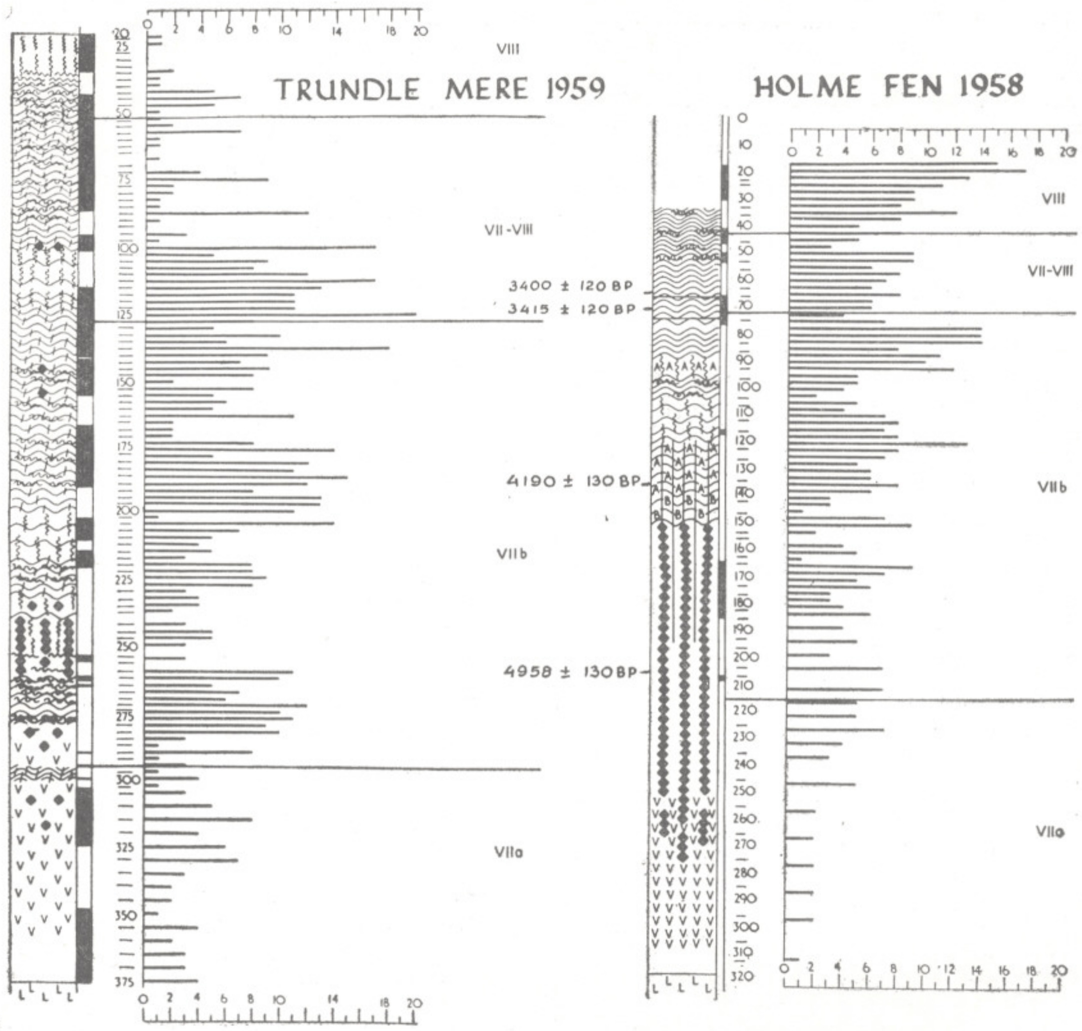
The occurrence of *Cenococcum graniforme* is not shown in the diagram, it does occur in fair abundance in the wood peat, *Cladium* sedge peat, *Phragmites-Cladium* sedge peat and the raised bog peat.

TRUNDLE MERE (Text-fig. 3)

The Trundle Mere spore diagram shows that during pollen zone VIIa *Cenococcum graniforme* remains abundant. In the group of *Cenococcum*, the population of *Coniothecium* type, *Microdiplodia* type, *Bispora* type and *Puccinia* type is very scarce. Towards the middle of zone VIIa *Clasterosporium caricinum* joins the population. At about 325 cm several more fungi appear such as *Triposporium*, *Macrodiplodia*, *Arthrinium sporophleum*, *Arthrinium caricicola*, *Volutella tristis* and *Microthyrium* types: all these fungi maintain low values.

The *Cenococcum* group continues until towards the middle of pollen zone VIIb. The population of fungi is not only increased after the beginning of VIIb by new members such as *Helminthosporium* types 1 and 2, *Sporidesmium* type, *Alternaria* type and an unidentified type, but some of the old members of the population show higher frequencies such as *Coniothecium* type. Quite a few others have a more continuous curve, such as *Puccinia*, *Tetraploa*, *Fusarium* and *Curvularia* types which join the population a little later.

At 232·5 cm *Coniothecium glumarum* type joins the population and soon attains high values. *Macrodiplodia* type attains high values after this level. A continuous curve is obtained by *Clasterosporium caricinum* and *Curvularia* types from above 225 cm. Above 200 cm *Curvularia* type shows ascending values until between 175 and 195 cm it achieves dominance over others



TEXT-FIG. 3 — Spore diagram showing the vertical distribution of the total number of the species of Fungi identified from their remains at Holme Fen and Trundle Mere.

and a *Curvularia* group is formed. A little before *Curvularia* type reaches its maximum, *Clasterosporium caricinum* shows a short maximum. The other members of the *Curvularia* group include besides two Unidentified spore types, *Cenococcum* which still maintains high values, *Microthyrium, Tilletia, Aspergillus, Helminthosporium* type 2, *Fusarium, Alternaria, Sporidesmium, Volutella tristis, Meliolia, Arthrinium caricicola, A. sporophleum, Clasterosporium caricinum, Macrodiplodia* and *Coniothecium* types. *Helminthosporium, Fusarium* and *Microthyrium* types maintain continuous values so long as the *Curvularia* group continues.

Above 177·5 cm values of *Curvularia* are very much diminished and a brief phase of *Cenococcum graniforme* dominance is noted again. The *Curvularia* type once again regains dominance after 157·5 cm.

Towards the top of pollen zone VIIb an unidentified fungus gradually attains high values and at 145 cm rapidly ascending values of *Macrodiplodia* type are also seen and before the end of VIIb the *Macrodiplodia* group is already established. The population of fungi at this level consists of several new members such as *Pestalozziania* type, *Hormiscium* type, *Stemphylium, Tuber-*

cularia types 1 and 2, *Puccinia* and *Tilletia* types.

At the beginning of the transition zone VII-VIII *Macrodiplodia-Curvularia* aggregate is formed.

At 112·5 cm with the sudden decline to low values of *Macrodiplodia*, the ascending values of *Coniothecium* type and *Clasterosporium* type become codominant and replace the *Macrodiplodia* group by an aggregate of *Coniothecium* and *Clasterosporium*. This is soon replaced by the *Coniothecium-Volutella* aggregate and then by the *Curvularia* group.

Towards the upper middle part of zone VII-VIII *Clasterosporium caricinum* once again dominates for a short while. At 87·5 cm *Microdiplodia*, *Volutella tristis*, *Sporidesmium*, *Alternaria* and *Fusarium* types maintain fairly high values.

In Zone VIIa *Volutella tristis-Cenococcum graniforme* aggregate is formed. *Puccinia maintains* high values here. The other fungi, *Coniothecium*, *Clasterosporium caricinum*, *Arthrinium sporophleum*, *Tubercularia* and *Tilletia* types have very low values.

The sequential stages of spore aggregates are as follows:

12. *Volutella-Cenococcum* aggregate	VIII
11. *Curvularia* group	
10. *Clasterosporium caricinum* group	
9. *Curvularia* group	VII-VIII
8. *Coniothecium-Volutella* aggregate	
7. *Coniothecium-Clasterosporium* aggregate	VII-VIII
6. *Macrodiplodia* group	
5. *Macrodiplodia-Curvularia* aggregate	
4. *Macrodiplodia* group	VIIb
3. *Curvularia* group	
2. *Cenococcum* group	VIIa
1. *Cenococcum* group	

Relation of the Population of Fungi to the Peat Types in Trundle Mere

At the Trundle Mere site the fungal population as a whole remains very low until towards the middle of zone VIIb probably because of the existence of a lake here. During this time the *Cenococcum* group persists. Besides other habitats it is of frequent occurrence in fresh-water deposits and also in alder wood peat, from which no doubt the lake sediments were partly derived. Towards the top of zone VIIa fruits of *Cladium mariscus* and cyperaceous rootlets are seen and here we find such fungi as spp. of *Arthrinium* and *Clasterosporium caricinum* which occur on sedges and *Triposporium* which occurs on *Filipendula ulmaria*.

A little after the beginning of zone VIIb the pollen analytical evidence shows open water in the lake and here we get *Sporidesmium* which also occurs on *Sparganium*, *Tetraploa* probably on *Phragmites*, and the unidentified type which in Holme Fen has been noted to be restricted to the swamp peat. *Coniothecium glumarum* type begins a little higher up.

After the establishment of the raised bog it is difficult to correlate the various fungal populations with the peat types, because several such fungal remains are discovered from the raised bog peat whose hosts are not definitely known, for example *Curvularia*, *Macrodiplodia* and *Microdiplodia* type. *Cenococcum* continues to have uniformly high values throughout the raised bog peat and is also known to occur frequently in the raised bog peat: as indicated already, it occurs in all kinds of communities in raised bogs.

Between 200-225 and 100-125 cm, *Hypnum* moss peat with fruits of *Cladium mariscus* especially between 100-125 cm suggests flooding. It is interesting to find that *Macrodiplodia* attains high values at each of these levels, followed by high values of *Clasterosporium caricinum*, showing that probably *Macrodiplodia* is parasitic on a plant species affected by the flooding. The absence of *Macrodiplodia* from the top of the profile and from the *Cladium-Hypnum* peat in VIIb where extensive flooding is indicated, shows that extensive flooding is probably detrimental to *Macrodiplodia*: very likely its hosts got submerged.

DISCUSSION AND CONCLUSION

Although very little is known of fossil microfungi the literature abounds in investigations of modern fungi in raised-bog peat, marshes and fens (Dale, 1914; Rudolph, 1917; Waksman, 1917; Waksman and Purvis, 1932; Jensen, 1931; Bisby *et al.*, 1935; Ellis, 1941; Ellis *et al.*, 1951; Boswell and

Sheldon, 1951; Moore, 1954; Huikari, 1956; Aartolahti, 1965; Mägdefrau, 1967; Wimstra *et al.*, 1971). These investigations are confined not only to the fungi, but to bacteria and Actinomycetes also.

Very few species of the fungi discovered by the above worker have been identified from the Holme Fen-Trundle Mere profiles while of those described by Ellis *et al.* (1951) as the British marsh and fen fungi, fifty per cent have been identified from this region. Some of the subfossil spore types described here are common with those reported recently by Van Geel (1972) through pollen analysis of the Wietmarscher Moor in West Germany. It has already been pointed out that spores of *Penicillia*, and several other Fungi Imperfecti are so undifferentiated that the identification on the basis of dispersed spores alone is impossible. The occurrence of such fungi in the region can not be excluded because extremely small spores 2-5 μ in size and devoid of any apertures or wall characters do occur, and might belong to *Penicillia* or other of the fungi so often met with in *Sphagnum* bogs. No evidence similarly can be adduced to show the presence of members of Mucoraceae, the genus *Trichoderma* and other members of Hyphomycetes which often make the bulk of the list of fungi isolated by the workers quoted above. It requires investigation, however, as to how far the differential production and dissemination of spores of fungi may be responsible for the absence of several kinds of fungal spores in the Fenland deposits.

Ecological considerations — An important fact that emerges from the study of literature mentioned above is that the proportion of Aspergilli isolated both from the British and the Danish soils and peat deposits is very small as compared with that of Penicillia and other fungi, while the proportion of Aspergilli in the soils of tropical countries is very large. This fact has also been pointed out by Waksman (1917) and Werkinthin (1916) in connection with American soils. Jensen in 1931 again draws attention to this fact in his studies on the microfungi in Danish soils and he looks upon Aspergilli as a group of thermophilic organisms more common in hot than in cold climates. It is interesting to find that the high values of the ascospores of *Aspergillus* with abundant perithecia in the Holme-Trundle Mere region are restricted to the period of the climatic optimum.

Modern investigations of microfungi in peat mostly concern the saprophytic fungi and the conclusions deduced from them can not be made use of in determining the ecology of the fungal remains in our deposits in which the bulk of fungi are parasites. The role of micro-organisms, i.e. fungi, Actinomycetes and bacteria in the formation of various types of peat has also been discussed by various workers (Waksman and Stevens, 1929; Waksman and Purvis, 1932, etc.), but here too the formation of various types of peat is attributed to the saprophytic fungi.

Prospects for the Investigation of Subfossil Fungal Spores

It appears that the prospects for identifying fungal spores are limited. It seems at present that the fungi which have played a major role in the formation of various peat types will never be identified from their isolated spores. There are, however, some interesting and encouraging results particularly in relation to the parasitic fungi, their history and distribution in the various periods of the Quaternary era. Further during the Quaternary era there have been climatic changes, the migration and extension of various species of higher plants and the extinction of others. Spore analyses may help us likewise to make out the former distribution of the fungi and to reconstruct the evolution of the modern fungus flora of the British Isles. During the Flandrian climatic optimum, when the climate was warmer than today, there are possibilities of finding some thermophilous fungi which might serve along with some higher plants additional indicators of climate. The present investigation has brought out some results in this direction:

1. *Arthrinium caricicola* of which spores have been found during the Flandrian period has no recent record in the British Isles.

2. None of the species of British *Puccinia* produces teleutospores of *Puccinia* spore type Category 5. The species of *Puccinia* producing such teleutospores are frequent in Central Europe.

3. *Meliolia*, a genus of tropical countries of some distribution during the pollen zone

VIIb and VII-VIII, and more restricted to VIIb has only once been recorded, from the field observations in the British Isles.

4. *Aspergillus* believed by mycologists to be thermophilous, is restricted in our two profiles to zone VIIb. In all tropical climates it is of abundant occurrence in contrast with Penicillia and Trichodermas which dominate in the temperate climates. The behaviour of *Aspergillus* and its known indicator value is similar to that of the thermophilous higher plants.

5. Some of the spore types such as *Triposporium* and *Tetraploa* suggest the occurrence of more than one species each in the Flandrian Period.

6. Quite a few characteristic spore types were also discovered and some of which are included in the spore diagrams too, the counterparts of which were not found in the known British fungi. If we have not overlooked them, they have not been discovered so far in the living state or they have become extinct. The European literature as a whole has been partly consulted and similar spores were not found there either.

7. It has been seen above that it is possible to correlate some peat types with the population of associated fungi such as the brush-wood peat, *Cladium* sedge peat and *Phragmites* peat. There are also indications of correlating the flood layers with the fungal populations. Thus the identification of fungal spores may well provide additional information about vegetational development in a region particularly where suitable organic deposits are prevalent.

It must be concluded that there is considerable promise in various directions of extended thorough investigation of subfossil fungal remains when suitably stratified organic deposits exist.

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EXPLANATION OF PLATES

All Figures × 750

PLATE 1

Single-celled spores

1. *Tubercularia* type 1
2. *Zygodesmus* type (*Tubercularia* type 2).
3. *Arthrinium sporopheleum* type
4. *A. caricicola* type
5. *Papularia sphaerosperma* type
6. *Volutella tristis* type
7- 9. Hyphopodia of *Meliolia* sp.
10. Hyphopodium of *Clasterosporium caricinum* Type
11. *Tilletia* type
12, 13. *Uromyces* type
14. *Aspergillus* type

Two-celled spores

15, 16. *Unidentified* type
17-20. *Puccinia* type
21, 22. *Macrodiplodia* type
23. *Bispora* type
24-26. Unidentified type
27. *Fusarium* type

PLATE 2

Three to many-celled, cylindrical, curved or concentric spores

28-30. *Curvularia* type
31. *Helminthosporium* type
32, 33. *Brachysporium* type
34. *Hormiscium* type
35. *Alternaria* type
36, 37. *Helicosporium* type

Multicellular spores both with parallel and cross walls

38-40. *Stemphylium* type 1
41. *Sporidesmium* type
42. *Steganosporium muricatum* type
43-47. *Triposporium* type
48. *Tetraploa* type
49. *Coniothecium glumarum* type
50, 51. *Unidentified type*


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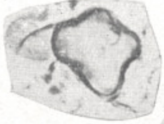
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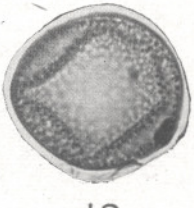
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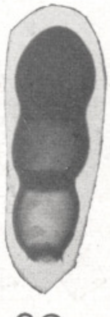
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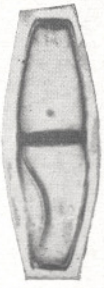
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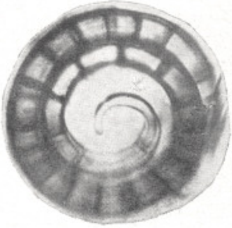
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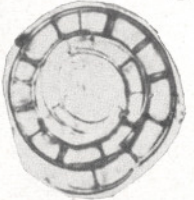
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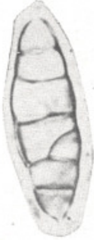
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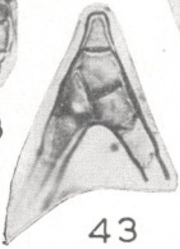
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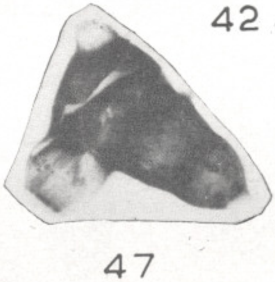
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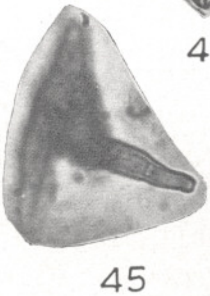
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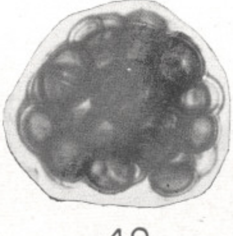
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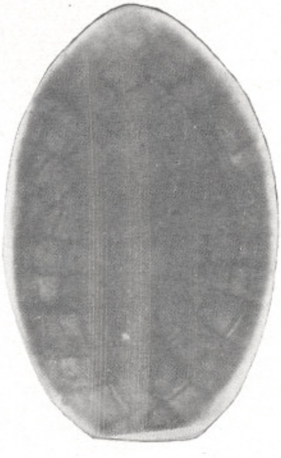
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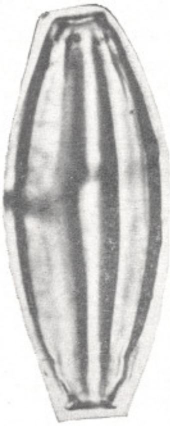
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