FOSSIL FUNGI FROM EARLY TERTIARY DEPOSITS

OF SOUTHERN ENGLAND

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"Following the finding of sporopollenin in fungal spores it is to be expected that the structures of such spores should have survived to be recognised in fossiliferous rocks. Unfortunately, the fossil fungus spore is the Cinderella of palynology, and usually is ignored or at least at best assessed in a footnote to the main descriptions of microfossils of a particular sediment" (Gooday, 1981).

ABSTRACT

A selective review of fungi in the fossil record is given, special consideration being given to the more dubious and perhaps extravagant claims for Precambrian occurrences of fossil fungi. The various taxonomic and nomenclatural methods that are used and have been proposed for both epiphyllous remains and dispersed fossil fungal spores are detailed and some alternative procedures are suggested. Especial emphasis is placed upon the necessity for population study techniques to establish taxonomic limits for variability within taxa for dispersed fossil fungal spores irrespective of which classification and nomenclatural system is followed.

Two early Tertiary deposits, one Palaeocene (Newbury) and one Eocene (Hordle Cliff) have yielded extremely diverse fossil fungal floras, encompassing epiphyllous forms and dispersed spores. After a brief description of the geology of the two sites, the epiphyllous forms are studied in detail. Specimens attributable to the following form-taxa are reported for the first time from British Tertiary deposits: Callimothallus, Cribrites, Meliolinites, Trichothyrites, and Stomiopeltites and the creation of a new form-genus Actinopeltites is proposed. The modern affinities of these form-taxa in relation to taxonomic revisions of the living ascomycete families concerned is discussed.

The epiphyllous forms, in conjunction with 'germlings' are used as palaeohabitat indicators. This is the first attempt to apply criteria established for Southern Australian Tertiary fossil fungi to Northern Hemisphere material.

From the broad range of dispersed fossil fungal spores within the deposits, several forms have been chosen for population studies. These include the first European record of two morphologically bizarre form-genera <u>Ctenosporites</u> and <u>Pesavis</u>, and suggestions made for possible affinities to _recent fungal taxa. A new form-genus of dispersed fungal spores, <u>Trochophorisporites</u>, is proposed; and two other spore populations are used to illustrate the difficulties inherent in delineating specific boundaries within proposed taxa.

DIRECTIONS TO READERS

The reprints presented as appendices should be read as an adjunct to the thesis. The arguments developed in the papers are restated and expanded in the text of the thesis. Tables and Figures are located opposite the pages on which they are first cited. Tables and Figures are numbered according to chapter and Plates are numbered consecutively.

ACKNOWLEDGEMENTS

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1. FUNGI IN THE FOSSIL RECORD

Fossilized remains of a wide range of fungal structures including hyphae, fruiting bodies (fructifications), rhizomorphs and, most frequently, dispersed spores occur throughout the geological record. Seward (1898), Meschinelli (1902) and Pia (1927) were amongst the earliest to catalogue described taxa and their geological distribution. This early interest in fossil fungi was not sustained however and was only revived in the 1950's. This resurgence in interest can be attributed to the rapid advancement in palynological techniques and the extensive application of palynology in the exploration for fossil fuels, resulting in the discovery of large numbers of fungal spores in palynological preparations. These spores were found to have, in many cases, extremely distinctive morphologies. Graham (1962) compiled data on 204 genera of fossil fungi, recording both their stratigraphic and geographic distribution. He argued that dispersed fungal spores, with their resistant walls, have an equal chance of preservation to that of any pollen grain or higher plant spore. Modern air spora counts demonstrate that the morphological variety and numerical abundance of fungal spores can often far outnumber those of pollen grains.

Graham (1962) used 32 species of basidiomycete spores to show the size range and morphological variability found in living fungal spores. This group of fungi are characterized by spores of fairly uniform morphology and, due to the less resistant nature of their walls, are liable to destruction by treatments such as acetolysis.

	MYXOMYCOTA	MASTIGOMYCOTINA & ZYGOMYCOTINA	ASCOMYCOTINA	BASIDIOMYCOTINA	DEUTEROMYCOTINA
QUATERNARY					
TERTIARY					
CRETACEOUS					
JURASSIC					
TRIASSIC					
PERMIAN					
CARBONIFEROUS					
DEVONIAN					
SILURIAN					
ORDOVICIAN					
CAMBRIAN					
PRECAMBRIAN					

TABLE 1.1   Occurrence of fungi in the geological record
(after Tiffney and Barghoorn, 1974).

DIVISION	SUB-DIVISION	CLASS
MYXOMYCOTA		
	MASTIGOMYCOTINA	CHYTRIDIOMYCETES
		HYPHOCHYTRIDIOMYCETES
		OOMYCETES
	ZYGOMYCOTINA	ZYGOMYCETES
		TRICHOMYCETES
EUMYCOTA	ASCOMYCOTINA	HEMIASCOMYCETES
		LOCULOASCOMYCETES
		PLECTOMYCETES
		LABOULBENIOMYCETES
		PYRENOMYCETES
		DISCOMYCETES
	BASIDIOMYCOTINA	TELIOMYCETES
		HYMENOMYCETES
		GASTEROMYCETES
	DEUTEROMYCOTINA	BLASTOMYCETES
		HYPHOMYCETES
		COELOMYCETES

TABLE 1.2   Classification of the higher taxa of fungi (from Ainsworth, 1973).

Graham (1962) acknowledged the possible destruction of spores of this group from fossil deposits but recognised that spore variability within other fungal groups with more resistant spores could be of great value in stratigraphic studies. Fossil fungal spore data could also be applied to palaeoecological and palaeoclimatological studies if the often very narrow ecological amplitude or the host-specificity of many extant fungi could be safely extended to fossils of the same generic character.

Tiffney and Barghoorn (1974), Pirozynski (1976a, 1976b), Elsik (1978) and Locquin, Pons and Salard-Cheboldaeff (1981) have all reviewed the geological record of fossil fungi. Tiffney and Barghoorn (1974) record the geological distribution and comment upon the taxonomic assignment of some 500 taxa of fossil fungi (see Table 1.1, p.16). Pirozynski (1976a, 1976b) examined the record of fossil fungi from the standpoint of modern mycology, linking form-genera of fossils to extant genera of fungi wherever possible. Elsik (1978) and Locquin, Pons and Salard-Cheboldaeff (1981), dealt with more circumscribed material, reviewing the geological history of the fructifications of microthyriaceous (Ascomycotina) fungi. Papers subsequent to these reviews, and some not cited by these authors, warrant further comment as to their bearing on the geological history of the fungi. These will be dealt with in the framework of the classification of higher taxa of living fungi of Ainsworth (1973) as summarized in Table 1.2 (p.17).

Although Graham (1971) considered the spores of Myxomycota sufficiently resistant and characteristic to be of stratigraphic

value, the fossil record of the Myxomycota is extremely fragmentary and the following discussion will be restricted to the Eumycota.

1.1   MASTIGOMYCOTINA AND ZYGOMYCOTINA

(PHYCOMYCETES sensu Tiffney and Barghoorn, 1974)

Within the Eumycota, the great majority of extant taxa are terrestrial, reproducing by means of airborne spores. Ingold (1975) gives the figure of 2% of extant taxa as being aquatic, the majority of these belonging to the classes Chytridiomycetes and Oomycetes. It is to the Oomycete fraction of this small aquatic percentage that the geologically earliest fossils thought to be fungi have been assigned.

PRECAMBRIAN RECORDS

Aseptate or infrequently septate filaments from late Precambrian deposits of Central Australia were described by Schopf (1968) as Eomycetopsis. A tentative determination of affinity with the Oomycetes was suggested mainly on the basis of the occurrence of the filaments in mycelium—like mats. This similarity in growth form coupled with the thick but brittle walls of the filaments, which appeared to resist compression of the filaments, were advanced as reasons to suggest that the wall forming material was chitinous in nature rather than the gelatinous sheath characterizing many blue-green algae. This tentative alliance of Eomycetopsis with the Oomycetes has been questioned by Hofmann (1976). Whilst accepting that the original attribution acknowledged the lack of reproductive structures, Hofmann (1976) demonstrated that the filaments were

FIGURE 1.1

10 μm

A

50 μm

B
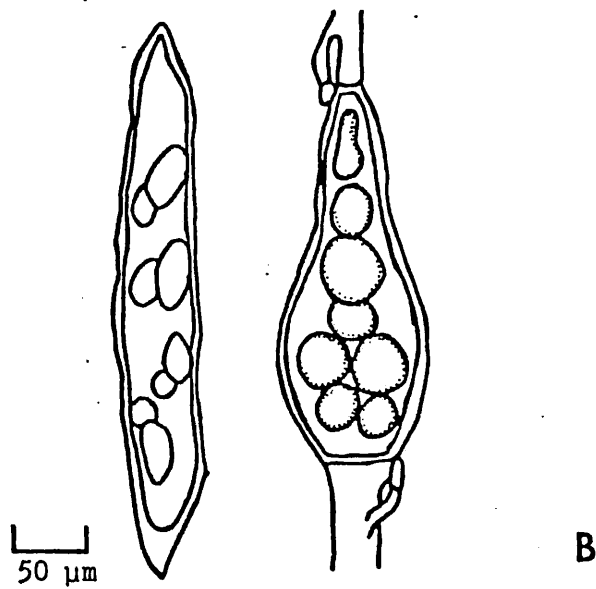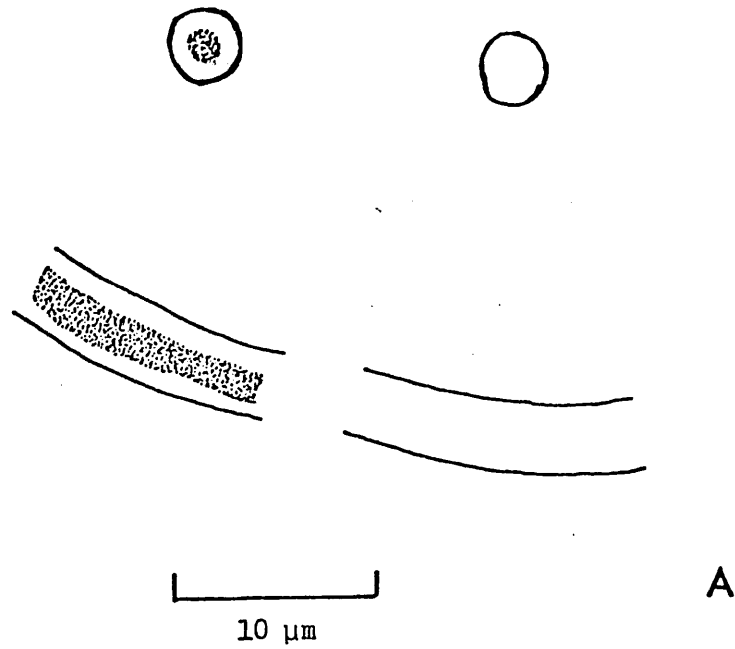
A.   Diagrammatic representation of filaments of _Eomycetopsis_ with

      and without cell contents. T.S. above (after Knoll & Golubic, 1979)

B.   Diagram showing comparison of the 'ascus-like' fossil (left) and

      the intercalary oogonium of _Saprolegnia_ (right) after Pirozynski,

      1976b).

definitely aseptate, the infrequent 'septa' mentioned by Schopf
(1968) were shown to be due to folding and deformation of the
filaments prior to silicification. On this basis it was suggested
that Eomycetopsis is better allied either to trichobacteria such as
the iron-bacterium Leptothrix, or alternatively to be interpreted as
sheaths of Phormidium-like oscillatorian blue-green algae. These
alternatives were advanced after re-examination of Schopf's (1968)
material from Central Australia and from further Canadian Precambrian
stromatolite deposits. The cyanophycean interpretation has been
greatly strengthened by Knoll and Golubic (1979) again working on the
Bitter Springs, Central Australian stromatolites. Eomycetopsis-type
filaments have been found as densely packed and monospecific sheets
oriented perpendicular to the bedding planes. This would suggest
Eomycetopsis to be an integral part of the stromatolite-forming
flora, its spasmodic dense occurrence being governed by some
unspecified environmental change. Knoll and Golubic (1979) suggested
variations in water level during stromatolite growth as a possible
explanation. The recognition of Eomycetopsis as an unequivocal
cyanophyte is further strengthened by the observation of shrunken
cylindrical cytoplasmic contents within the filaments (see Fig. 1.1A,
p.20). Eomycetopsis is thus now regarded as a blue-green alga
morphologically very similar to the extant genera Lyngbya and
Phormidium.

Other Precambrian fossils, however, offer stronger evidence of
fungal affinity. Schopf and Barghoorn (1969) figured such a specimen
from the Skillogalee dolomite of Adelaide, South Australia. Although
reluctant to give a formal diagnosis because of the lack of

substantiating evidence, Schopf and Barghoorn (1969) catalogue the specimen as an "ascus-like micro-fossil of uncertain systematic position". Pirozynski (1976b), although not totally discounting a possible algal origin for the specimen, has commented on the similarity of the specimen with the intercalary oogonium of the extant oomycete genus Saprolegnia (see Fig. 1.1B, p.20). On this basis he interpreted the eight 'ascospore-like' structures contained within the specimen as resistant zygospores.

Hallbauer and van Warmelo (1974) reported the occurrence of 'fungus-like' structures, hyphae, conidia, conidiophores and sclerotia from gold-bearing Precambrian strata from South Africa. Carbonaceous material obtained by hydrofluoric acid extraction from these deposits was described as occurring in three forms; columnar, spherical 'fly-speck' nodules and coaly material. The spherical 0.2-1.0 mm diameter nodules were compared to fungal sclerotia on no firmer evidence than that of the irregularity and pitting of the surface and "remarkable resemblance to living fungal sclerotia". No microscopic evidence of internal structure is presented to support this statement. Complete oxidation, at temperatures above 500°C, of the columnar structures revealed features leading to the description of an external membrane-like structure. This was said to contain bundles of "parallel septate fibres", exhibiting true branching; the authors claimed that these had been preserved by the replacement of original biogenic material by radioactive uranium oxide. Gold and other materials were thought to have been extracted from the environment and deposited by the living organisms both inter- and intra-cellularly. Citing results of Prashnowski and Schidlowski

(1967) for carbohydrate analyses of the columnar carbonaceous material, Hallbauer and van Warmelo (1974) reconstructed a

"symbiotic relationship which had evolved in Precambrian times similar to existing lichens ...... which probably consisted of an algal partner and a fungal organism occupying areas ranging from a few square centimetres to a few square metres on bare rock or gold-bearing heavy mineral sand".

In the reconstruction the 'sclerotia' of the spherical nodules are interpreted as possible reproductive structures.

Hallbauer and van Warmelo (1974) have alluded to the evidence for mineral accretion in extant lichens and some fungi to support their suggestion of fungal affinity for their South African material. Pirozynski and Malloch (1975) have argued, independently, that fungal symbiosis may have been an important factor of early land plant evolution. The credibility of Hallbauer and van Warmelo's (1974) interpretation however must rest on the evidence of the material itself. The fact that no organic matter remained after the drastic preparative treatment leaves grave doubt as to whether their 'fossils' actually represent remains of fungi, lichens, or indeed living bodies of any kind. One can only conclude that this claim for a lichen-like association in the Precambrian is based to a large extent upon supposition and a readiness to translate supposed points of external morphological similarity into criteria suggesting affinity with scant regard for the extreme length of geological time separating the taxa under comparison. Hallbauer and van Warmelo (1974) also report the presence of solid, or occasionally hollow tubes of silica interpreted as 'branched septate hyphae' after total

combustive oxidation of the coaly carbonaceous material. These they observe bear a "strong suggestive affinity to extant Deuteromycotina" on the basis of putative conidiophores and conidia; these authors suggest that they represent fungal attack upon organic debris during its transport to the deposition site. The suggested preferential silicification of these 'fungal hyphae' coupled with the total absence of any silicification in the coaly matrix appears very implausible. It would seem reasonable to expect that if 'hyphae' and coaly material truly represent fungus and substrate, deposited contemporaneously, that some silicification of the substrate material would also occur. This would allow a more definite identification of these silica tubes as hyphae of saprophytic fungi, or at least make it possible to demonstrate an intimate connection between 'fungus' and 'host' as in other permineralized deposits such as the Devonian Rhynie Chert. Retallack (1981) while accepting that the carbon is biogenic in the Witwatersrand deposits, has dismissed the claims for the presence of terrestrial fungi made by Hallbauer and van Warmelo (1974). He preferred to interpret the structures reported as probable artefacts of the preparation procedures employed. Retallack's (1981) interpretation seems to be the more tenable, because of highly destructive preparative techniques employed by Hallbauer and van Warmelo (1974).

PALAEOZOIC RECORDS

Despite most Precambrian fossils having for the most part only tenuous connections with extant forms of fungi, Cambrian, Ordovician and Silurian deposits do reveal evidence of both marine Oomycetes and Chytridiomycetes. Shell-borings and attacks to arthropod cuticle and

fish scales cited by Taylor (1971) have been attributed to fungal origins. Oomycetes and Chytridiomycetes have also been advanced as putative parasites of early corals (Duncan, 1876) and have been recorded in association with Bryozoans (Elias, 1966). With the advent of the land flora, the variety of habitats available for fungi diversified greatly and as a result the fungus-land plant associations that developed can be catalogued as endophytic-symbiotic, saprophytic and parasitic. The endophytic-symbiotic type of association can best be illustrated with reference to the Lower Devonian Rhynie Chert association. Kidston and Lang (1921) described six species within the form-genus Palaeomyces from fungi found within the tissues of Rhynia, Asteroxylon and Horneophyton. The generic name Palaeomyces was employed "as a useful and comprehensive designation under which to place fossil fungi of the precise systematic position of which there is insufficient evidence".

Establishing the mode of nutrition for any fossil fungus can only be a highly uncertain exercise. Some possible indications may be gained by comparison with living fungi, but the exact nutritional relationship of any fossil fungus must often only be conjectural. Although the fungi were predominantly endophytic, Kidston and Lang (1921) concluded that the majority were in fact saprophytic. Boullard and Lemoigne (1971) have also suggested a saprophytic mode of existence for at least some of the Rhynie endophytes; a view further supported by Harvey et al. (1969) for a Palaeomyces-like fungus found in association with Prototaxites. A close morphological similarity in both reproductive and vegetative features is evidenced in this instance with the extant oomycete Apodachlya pyrifera.

Attribution of these endophytic fossil forms to the Oomycetes, especially those genera involved in mycorrhizal associations, has been accepted for a considerable time. Butler (1938) has commented upon the similarity of the Rhynie fungi and later fossil forms to modern genera of fungi involved in endomycorrhizal associations with living plants. Nicolson (1981) also noted the similarity of many of the Rhynie fossil forms to modern endomycorrhizal genera, many of which are placed in the family Endogonaceae. Although the occurrence of oomycete-type fungi has been adequately demonstrated, such certainty of identification and affinity cannot be claimed for all the purported fungi reported in association with early land plants. Both Tiffney and Barghoorn (1974) and Pirozynski (1976a, 1976b) give ample documentation of the geological history and occurrence of this group of fungi after the Devonian.

1.2   ASCOMYCOTINA

Whilst Tiffney and Barghoorn (1974) record occurrences of ascomycete fossil remains from the Carboniferous they do not totally preclude the possibility of pre-Carboniferous occurrences of Ascomycotina. Several attributions to Ascomycotina, more especially those specimens which have been linked with ascomycete families of the class Loculoascomycetes (see Table 1.2, p.17) which possess thyriothecia need to be treated with extreme caution. The term thyriothecium is used to describe a type of fructification (ascocarp) characterized as being inverted, with the hyphal cells of the wall being more or less radially oriented (see Fig. 1.2, p.27). Although

FIGURE 1.2

20 µm
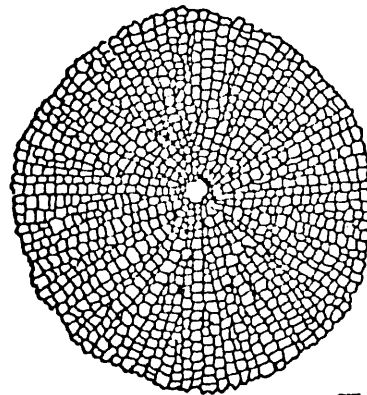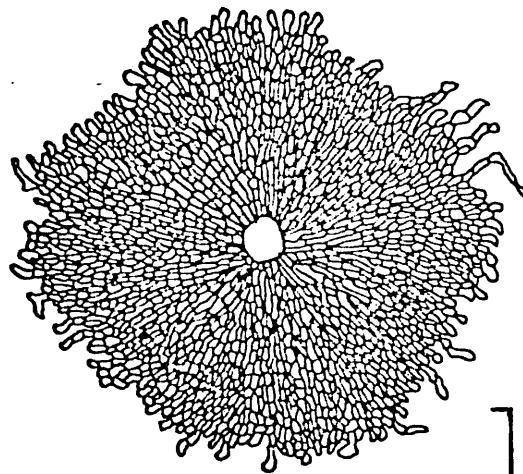
40 µm

Thyriothecia of Microthyrium microscopicum (upper) and
Arnaudiella genistae (lower) to show appearance of this
type of structure (after Germeraad, 1979).

being produced by a number of ascomycete families this type of fructification is often described somewhat loosely in palaeomycological and palynological works as a microthyriaceous fructification. Tiffney and Barghoorn (1974) and Elsik (1978) both accept the Lower Cretaceous occurrence of Stomiopeltites (Alvin & Muir, 1970) as the earliest undisputed fossil microthyriaceous fungus exhibiting this type of fructification. In view of these statements it is of interest to note claims in two recent papers for the occurrence of thyriothecia in Silurian and Devonian deposits. Pons and Locquin (1981) described what they take to be an ostiolate ascomycete ascocarp from the Rhynie Chert deposits of the Lower Devonian. Similarly Krassilov (1981) reported the presence of thyriothecium-like structures found on the cuticle of the Lower Devonian terrestrial plant Orestovia. Both of these reports are however pre-empted by the genus Trematophora described by Eisenack (1965) from Silurian deposits from Sweden. Eisenack (1965) himself made no attempt to attribute this genus to anything other than 'Problematika' with the remark that the specimen could be a plant structure. Locquin, Pons and Salard-Cheboldaeff (1981) and Pons and Locquin (1981) have however, on the basis of the original diagnosis and the accompanying two illustrations of Eisenack (1965), unhesitatingly accepted this fossil as the earliest example of an ascomycete thyriothecium. There is no further justification for their claim or even evidence that they have re-examined Eisenack's (1965) original material; rather that from the meagre published information they have extrapolated a firm affinity on the basis of nothing more than the morphological similarity with extant forms. No reference is made to the alternative proposition that several

heterotrichous green algae have an exceedingly similar morphology, a point raised by Hansen (1980) in considering present day affinities of some Tertiary specimens which had been loosely classified as microthyriaceous fungal fructifications. The third, and probably the most plausible interpretation of Trematophora, from the examination of Eisenack's (1965) illustrations, is that the figured specimen is nothing more than a modern contaminant, misinterpreted as being synchronous with the Silurian Hystrichosphaerids which form the major part of the paper. This interpretation is further reinforced by the figures from the same source attributed to the family Linotolypidae by Eisenack (1965) which appear to be very similar to the 'fly-ash' particles as figured by Gregory (1973). These particles are a highly distinctive by-product of iron smelting processes and thus would appear to be a clear indication of Recent contamination of Eisenack's (1965) Silurian material.

Pons and Locquin (1981) have described as Mycokidstonia sphaerialoides a single specimen identified as an ostiolate ascocarp from a petrological thin section from the Lower Devonian Rhynie Chert. While not attributing this specimen to the loose grouping of microthyriaceous fructifications, the specimen is placed as a definite member of the Synascomycetes (sensu Gäumann, 1949). Gäumann (1949) regarded this group as extremely primitive Ascomycotina distinguished by the formation of the haploid spores, not in asci, but in a compound spore sac known as a synascus. This group of fungi are accomodated in the class Hemiascomycetes (see Table 1.2, p.17). However, apart from the presence of the structure interpreted as an ostiole, the single specimen bears more than a superficial

resemblance to the reticulate spores recorded by Kidston and Lang

(1921) as a specimen of <u>Palaeomyces</u>. This is, in my opinion, a more

readily tenable hypothesis.

From cuticle preparations of the enigmatic Lower Devonian

thalloid plant <u>Orestovia</u>, Krassilov (1981) recorded structures which

he interpreted as stages in the development of a microthyrialian

fructification. These stages range from structures interpreted as

haustorial hyphae penetrating stomata of <u>Orestovia</u> through to almost

mature fructifications. On the basis of the reticulate construction

of the 'thyriothecial' wall and the apparent lack of mycelial hyphae

Krassilov (1981) had no hesitation in placing the putative

fructification in the family Hemisphaeriaceae (<u>sensu</u> Stevens &

Manter, 1925). Once again, no possible alternative such as an algal

affinity (<u>vide</u> Hansen, 1980) was countenanced. Morphological

resemblances were accepted as homologies with extant fungal

structures and the Devonian material was regarded as contaxic, at

least at family level, with present day highly modified ectoparasitic

ascomycete fungi. This claim based as it is on the arguments stated

above appears to me to be over-optimistic.

It is of interest to contrast these somewhat exuberant claims

for the occurrence of Palaeozoic ascomycete fungal genera originating

from palaeobotanical and palaeontological sources, with the much more

cautious and conservative approach of mycologists. Pirozynski and

Weresub (1979a) briefly review the fossil record of the Ascomycotina,

and comment upon advances over those reviewed in Pirozynski (1976a,

1976b). Eisenack (1965) is not mentioned in any of these reviews and

FIGURE 1.3
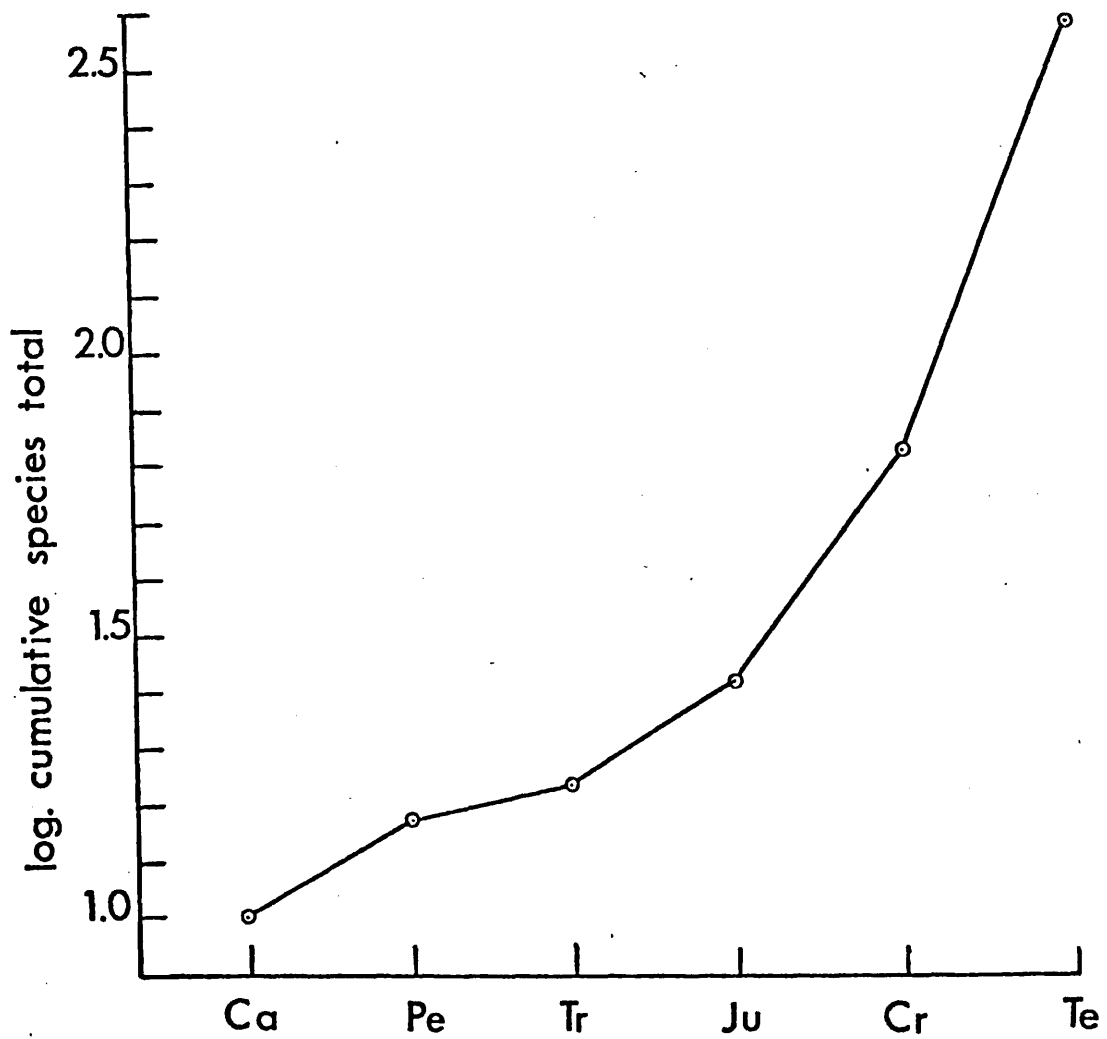
Graphical representation of the increase in ascomycete fossil
fungi from the Carboniferous (Ca) to the Tertiary (Te);
data from Tiffney and Barghoorn (1974).

Pirozynski and Weresub (1979a) placed the first fossil records of Ascomycotina in the Carboniferous; but questioned the fungal affinities of the genera such as <u>Sporonites</u> and <u>Chaetosphaerites</u> regarded by certain authors as belonging to this group. Similarly they queried the attribution "on evidence that would not however convince most mycologists" of sclerotinites as fungal. Sclerotinites is the term coined by Stach (1956) to describe a petrological coal type in which a rich diversity of fungal bodies is claimed to occur (<u>vide</u> Benes, 1956, 1978). Coal petrologists are however divided as to the origin of sclerotinites; many authors (e.g., Taylor & Cook, 1962) regard these structures as fusinized resins. Pirozynski and Weresub (1979a) suggested an origin for the Ascomycotina within the Mesozoic but considered that unequivocal fossil ascomycete fungi first occur in the Potomac group of rocks investigated by Doyle (1977). A representative selection of these spores are illustrated and their morphological similarity to extant genera is used to relate these Cretaceous spores to genera existing today. Singh (1971) and Krassilov (1967) recorded examples of Lower Cretaceous microthyriaceous fructifications, the host plants in the case of the assemblage illustrated by Krassilov (1967) being exclusively gymnospermous. The rapid upsurge and diversification of the Angiosperms in the Cretaceous-Tertiary period, is mirrored by a similar increase in the diversity and number of ascomycete fossil forms encountered (see Fig. 1.3, p.31).

1.3   BASIDIOMYCOTINA

As previously stated, apart from the thick-walled spores of the rusts, the majority of the spores of Basidiomycotina are characterized by very thin walls. This is presumably the reason for the rarity of fossil spores that can be attributed to this fungal group. Tertiary palynological assemblages do however contain spores that can be compared with those of extant Basidiomycotina. Other fossil remains which can be regarded as of unequivocable basidiomycete origin range from the Carboniferous hyphae described as Palaeancistrus by Dennis (1970) which exhibit the definitive basidiomycete character of clamp connections, to the occasional report of fossil basidiomycete fructifications (vide Tiffney & Barghoorn, 1974). These fossil fructifications are usually of the more 'woody' and hence more resistant polypore or bracket fungus type, and are frequently found in association with fossil wood, as instanced by the Miocene genus Archeterobasidium (Koeniguer & Locquin, 1979).

1.4   DEUTEROMYCOTINA

Paralleling the Cretaceous-Tertiary diversification of the Ascomycotina and to some extent resulting from it, is the increase in frequency of occurrence of the large fungal division, the Deuteromycotina. The genera allocated to this division are known only from the non-sexual, imperfect, or anamorphic state (Hennenbert & Weresub, 1977). Luttrell (1979), Kendrick and Discomo (1979),

Kendrick and Watling (1979) all deal with the advances made in linking these anamorphic Deuteromycotina with the sexual, perfect, or teleomorphic state (Hennenbert & Weresub, 1977) of either ascomycete or basidiomycete fungi. The asexual propagules or conidia of the Deuteromycotina are often the most diagnostic feature of these fungi and, as emphasized by Pirozynski (1976a, 1976b, 1978) and Pirozynski and Weresub (1979b), the conidia found in Tertiary and latter deposits can often be readily matched with conidia of extant Deuteromycotina.

2. NOMENCLATURE AND CLASSIFICATION OF FOSSIL FUNGI

Seward (1898), Meschinelli (1892, 1902) and Pia (1927) all show in their treatises the nomenclatural and classification system available to the early workers concerned with palaeomycology. In all cases the modus operandi was to incorporate the newly described fossil material into the hierarchical classification for extant fungi. The nomenclatural alternatives at their disposal to achieve this were:-

1) to describe the fossil material as conspecific with an extant
   fungus;

2) to describe the fossil material as a new, fossil,
   species of an extant fungal genus;

3) to describe the material as a new fossil genus.

This course took the form of combining the suffix -ites with the name of an extant fungal genus. This procedure was considered by the earlier authors as a way of implying phylogenetic relationship to extant genera, in so far as this can be construed simply from morphological similarities. Felix (1894) is quoted by Pirozynski and Weresub (1979b) as follows:

> "Unter dem Namen Chaetosphaerites fasse ich diejenigen fossilen
>
> Pyrenomyceten-Reste zusammen, welche mit der lebendem gattung
>
> Chaetosphaeria so übereinstimmen dass sie möglicherweise zu
>
> ihr gerechnet werden können".

Similar views were expressed by Meschinelli (1892) in a footnote

stating that the suffix -ites distinguished the fossil from the living "with which they are linked for very obvious reasons, yet cannot be equated absolutely" (vide Holm, 1959).

From the comparative simplicity of the early treatments, the fields of nomenclature and classification have become fraught with a variety of alternative and often conflicting approaches. The confusion is due in large part to the availability of two methodologies based upon different philosophies of nomenclature and classification.

2.1   FORM- AND ORGAN- GENERA

From the outset of palaeobotanical studies there has been the necessity to have a method capable of dealing with the fragmentary plant remains preserved as fossils. Since the time of Brongniart (1828) there has been the acceptable alternative of the form-genus available. The form-genus is a purely artificial but extremely useful generic concept for those fossils where there is insufficient evidence of botanical affinity. Brongniart (1828) maintained that in cases such as this, descriptions of the fossils must be drawn entirely from direct observation of characters present in the fossils themselves. Ideally these observations should not be coloured by speculative correlation of these features with those of living plants. At the same time however Brongniart (1828) recognised the immense value of comparative anatomical and morphological studies in clarifying the taxonomic relationships of fossil plants. The ideal

outcome would be the eventual elucidation of the status of these artificial or form-genera and their inclusion into the existing phyletic or natural classification.

The emphasis on anatomical investigations of fossil plants in the early part of this century by workers such as Scott (1920) and Seward (1898) led to the establishment of a second artificial category, the organ-genus. The features of this taxon were based upon the characteristics of a particular plant organ. The significance of the organ-genus being that it was possible to place such a genus in a family, whereas the form-genus is not referable to a family but may be referable to a higher taxonomic grouping. The concept of the organ-genus has been, and still is, a cause of considerable debate, generating a vast and lengthy argument both for its retention (Schopf, 1963; Jansonius, 1974) and its abolition (Faegri, 1963; Stafleu, 1967). The abolitionists gained the ascendancy at the 1975 Botanical Congress in Leningrad and the organ-genus was deleted from the International Code of Botanical Nomenclature (I.C.B.N.). The organ-genus can of course still be used as a designation. It is not however given formal status and is not regarded as differing from a 'genus' (as distinct from a 'form-genus') in the revised edition of the I.C.B.N. agreed to at the 1981 Botanical Congress in Sydney. The debate is however far from finished (Meyen & Traverse, 1979; Boulter, 1979). The main point of contention centring on the procedural niceties of referring the form-genus to a natural taxon of family or higher rank. Despite the legalistic manoeuverings the necessity for both natural and artificial or form-taxa has been an accepted facet of palaeobotanical

nomenclature and classification and is likely to remain so.

2.2   ARTIFICIAL CLASSIFICATIONS

The recognition that palynological investigations are of enormous value to stratigraphic and palaeobotanical studies, plus the emphasis placed upon palynology in the search for fossil fuels has resulted in an information explosion. The results of this upsurge in palynology were twofold.   The vast amounts of data rapidly accumulated on fossil spores and pollens demanded an approach to classification and nomenclature that allowed both the efficient retrieval of data plus ease of communication by the investigators. Secondly, and perhaps more importantly, palynology drew workers from various scientific disciplines all of whom were not cognisant with the strictures and requirements of the natural hierarchical classification as applied to the study of recent and fossil plants. The end result of the interaction of these factors has led to a plethora of alternative approaches to nomenclature and classificaton. The majority of these alternatives are strictly utilitarian in which taxonomic considerations, in the phylogenetic sense, have been dispensed with entirely.   Many however cling to the binomial nomenclatural approach, and are thus to be considered within the ambit of the rules of nomenclature as set down in the I.C.B.N.

FIGURE 2.1
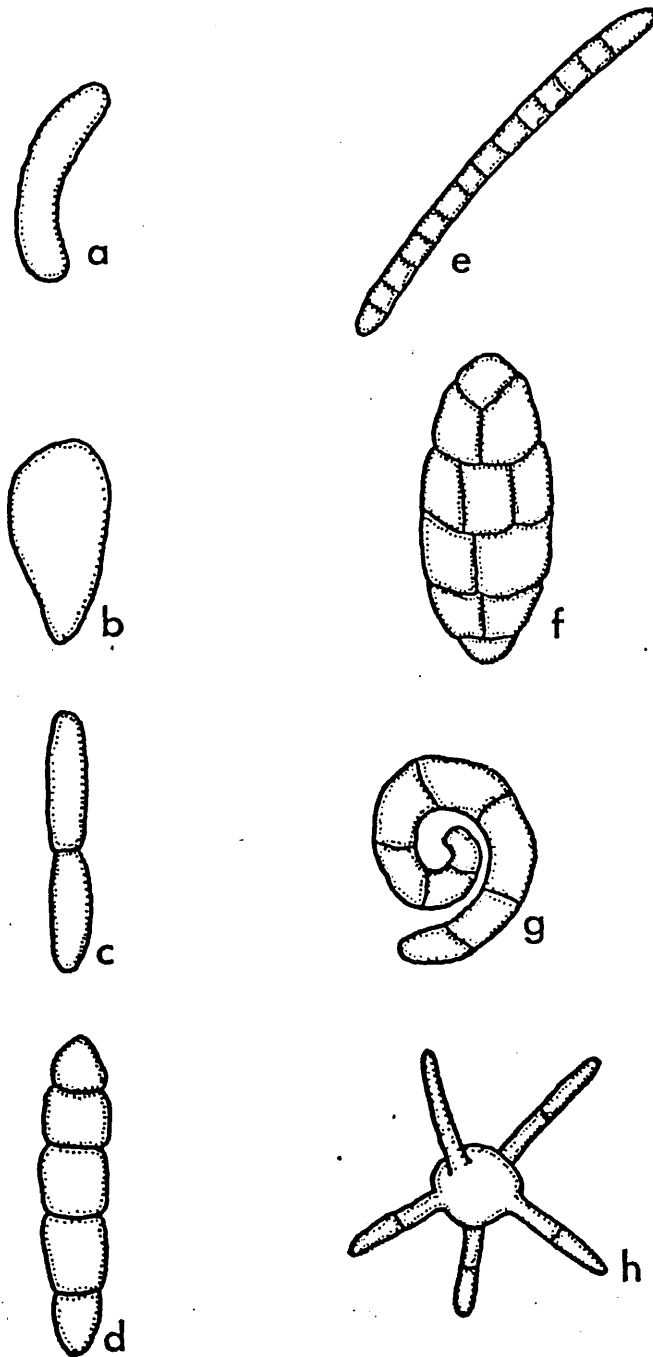
Saccardoan spore groups:

a. allantospore   b. amerospore   c. didymospore

d. phragmospore   e. scolecospore   f. dictyospore

g. helicospore   h. staurospore

TYPES OF ARTIFICIAL CLASSIFICATION

Pirozynski and Weresub (1979b) have given an extremely cogent

and concise review of the development of the alternative artificial

classification and nomenclatural systems in palynology and

palaeomycology. The types of classification system available to the

palaeobotanist can be either natural, in the phyletic sense, or

artificial. Within this latter category certain subdivisions of

taxonomic approach can be drawn. First of these is the anatomical as

instanced by the system used by mycologists for the Deuteromycotina

(Fungi Imperfecti). Second is the morphographic in which

architectural features of the spores such as the number and type of

apertures, ornamentation and in the case of fungal spores, number of

cells are of paramount importance. And finally there is the

catalogue (Lange & Smith, 1971) in which the fossil spores are

grouped into broad and large categories based upon the overall spore

morphology groups erected by Saccardo (1882-1926) for fungal spores

(see Fig. 2.1, p.39). No taxonomic conclusions are drawn in this

cataloguing process, it is simply an ordering and illustration of

information made available for other workers, and is as such outside

the I.C.B.N. Perhaps those more familiar with living fungi and their

taxonomy will be able to recognise at least some of the spores thus

catalogued in terms of affinity with living genera.

The anatomical type of artificial classification used for the

Deuteromycotina by mycologists has often been used to justify

artificial classifications in toto. Pirozynski and Weresub (1979b)

emphasize the point that this classification is deemed to be

artificial because taxa of Deuteromycotina are based upon anamorphic rather than holomorphic states. Hence although these fungi exhibit an independent existance, reproduction is solely by asexual methods. The taxa therefore cannot be regarded as holomorphic (i.e., with both sexual and asexual stages) and thus ipso facto can only be artificial or form-genera. All other taxonomic workers are at liberty to describe and erect taxa based on either teliomorphic or holomorphic states from fragmentary type material. These fragments are taken as representing the entire organism even if the fragments are of one organ alone. There would appear to be no restriction in describing either a living or fossil plant solely on the basis of leaf material or say pollen material as the representative portion of the organism in its holomorphic state. Only the mycologists working with Deuteromycotina cannot exercise taxonomic judgements and utilize his experience in erecting such holomorphic taxa; rather the nomenclatural formality of the artificial taxon must be used until such time as the teliomorphic state of the organism is isolated and demonstrated to link with the anamorphic form-taxon.

Classification and nomenclatural approaches to fossil fungi depend to a large extent upon the background of the investigator. Although a small minority (Dilcher, 1965; Selkirk, 1975) employ the natural classification, many (Elsik, 1968; Elsik & Jansonius, 1974; Elsik & Dilcher, 1974; Sheffy & Dilcher, 1971; Ramanujam & Rao, 1978) follow the artificial classification system of van der Hammen (1954a). This system is, for entirely fortuitous reasons, the only valid portion of a much wider classification system designed to cover all fossil pollens and spores, with however no taxonomic implications

Hyphomycetes		
Coelomycetes		
	Cellae*	
Mycelia Sterilia	Hyphae*	
	Peltae*	
	Indeterminae*	
	Sporae Monocellae	
	" " Monodicellae	
	" " Dicellae	
Fungi Sporae Dispersae**	" " Tricellae	
	" " Tetracellae	
	" " Multicellae	
	" " Cellae Indeterminatae	

TABLE 2.1   Additions proposed by Elsik (1976a) to the

classification of the Deuteromycotina.

* additions to pre-existing 'form-order'

** erection of new 'form-order'

whatsoever as to the relationships of the fossils to living plants. Nomenclaturally van der Hammen's (1954a) system is a collection of terms descriptive of the morphology of the fossil pollen or spore into which the specimen can be placed. The major divisions of his pollen classification was invalid as these divisions were typified by using examples of living taxa and their binomial nomenclature. The small group of fossil fungal taxa are however based solely on fossil material with no 'typification' by living genera and are hence regarded as validly published names.

Elsik (1976a) has suggested an amalgamation of those fossil fungal form-genera based on morphological features into the Deuteromycotina. He proposed the erection of a new supra-familial taxon for fossil fungal spores, the 'form-order' Fungi Sporae Dispersae. Other fossil fungal material, apart from spores, could be incorporated into the existing 'form-order' Mycelia Sterilia (see Table 2.1, p.42). Elsik (1976a) does however acknowledge that much fossil fungal material is readily assignable within the other subdivisions of the Eumycota and expresses the opinion that in time, even more will be moved into the natural system of classification.

Whilst agreeing with the assignation of fossil fungal spores to extant genera, Pirozynski and Weresub (1979b) do not see any cause for the new 'form-order'. In cases where taxonomic judgements cannot be made at once, they prefer the incorporation of such fossil fungal spores into the taxonomically non-committal Saccardoan spore groupings (see Fig. 2.1, p. 39). Comparison of the fossil fungal spores with those of similar morphology from living fungi would, in

their opinion, best facilitate identificaton and eventual taxonomic treatment.

The attempt at a synthesis between artificial and natural classification systems by Elsik (1976a) and the suggestions by Pirozynski and Weresub (1979b) concerning the treatment of fossil fungal spores in the context of living genera, can be regarded as one extreme in the spectrum of approaches available. The other, diametrically opposed method, is exemplified by the treatment of all dispersed fungal spores - Mycota Sporae Dispersae - whether fossil or living advanced by Locquin (1980). This classification is strictly morphological, based loosely on the Saccardoan spore groupings to which has been married a variety of features which the mycologist would tend to regard as palynological. These include features concerned with spore wall ornamentation, presence and number of septa, presence, number and type of aperture and/or appendages. On the basis of combinations and permutations of these characters Locquin (1980) has constructed an hierarchical classification of 4 classes, 28 orders and 137 families, each with a new type genus which he claims conforms entirely with nomenclatural rules. That this is in fact the case is highly questionable. Terminologically Locquin (1980) has devised a series of phonetic abbreviations each of which is descriptive of a particular morphological feature used in the proposed classificaton (vide Stafleu, 1967). These are used in various combinations but in a strictly regimented order to define each of the over three hundred new taxa proposed.

The four new classes are erected as follows:-

I   INAPERTUROSPOROMYCETES: all inaperturate spores.

II APERTUROSPOROMYCETES: all porate or lirellate spores. (Lirella
    is the term used to describe a type of lichen fruit body which
    is long and narrow with an elongate central furrow or groove,
    Ainsworth & Bisby, 1963). Locquin (1980) however, would appear
    to misuse this special term to describe a crack or fissure
    caused by germination of the spore. Thus all fossil fungal
    spores showing fissures in their walls, would perforce be deemed
    lirellate. This is despite the fact that these fissures would
    in many instances be ruptures caused by compression of the
    specimen during fossilization.

III HILOSPOROMYCETES: for all spores exhibiting either a hilum or an
    apiculus. A hilum as defined by Ainsworth and Bisby (1963) is a
    mark or scar on the spore at the point of attachment to the
    conidiophore or sterigma upon which the spore was borne
    initially. Similarly an apiculus is defined by Ainsworth and
    Bisby (1963) as a projection on the spore by which the spore was
    originally attached to the conidiophore or sterigma.

IV APERTUROHILOSPOROMYCETES: aperturate or lirellate (sensu
    Locquin, 1980) spores which also exhibit a hilum or an apiculus.

It is however with the creation of ordinal, familial and genetic epithets that the proposed system gives full rein to phonetic permutations and combinations. In categorizing single-celled dispersed fungal spores (amerospores) Locquin (1980) distributed them within seven separate and distinct orders. Family numbers within each order are indicated below but details of how families are segregated and their description follow shortly.

O.   AMESPORALES (21 families)

> Order for inaperturate amerospores.

O.   AMEPOSPORALES (8 families)

> Order for porate amerospores.

O.   AMESASPORALES (6 families)

> Order for porate amerospores with an equatorial germination
> furrow, giving the spore a bivalvate appearance.

O.   AMELISPORALES (1 family)

> Order for porate amerospores exhibiting a lirellate fissure
> (sensu Locquin, 1980).

O.   AMEPIOSPORALES (12 families)

> Order for inaperturate amerospores bearing either a hilum
> or an apiculus.

O.   AMEPOPIOSPORALES (8 families)

> Order for porate amerospores with either a hilum or an
> apiculus.

O.   AMELIPIOSPORALES (1 family)

> Order for hilate or apiculate amerospores with a lirellate
> fissure (sensu Locquin, 1980).

FIGURE 2.2
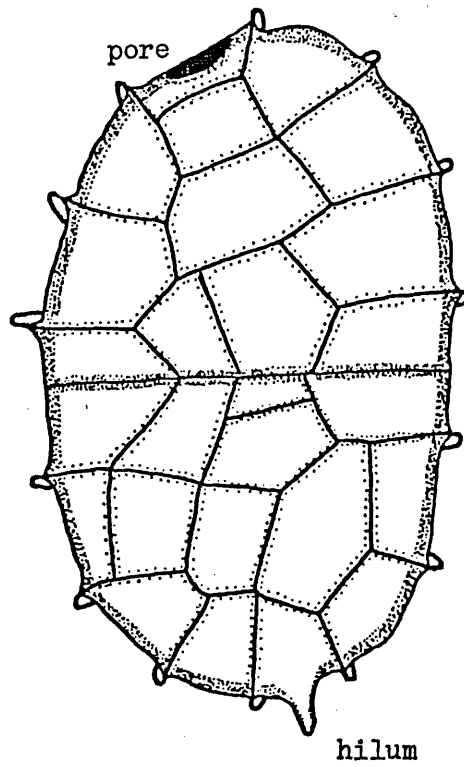
Diagram to show the morphological features circumscribing
the family Redimopopiosporaceae (sensu Locquin, 1980).

The ritual for construction of familial names is even more complex, and the rubric to be observed is quoted (in translation):-

"The name should always end with the suffix -sporaceae. If the spore has one or more apertures the syllable (phoneme) denoting their presence is placed before this suffix. This is in turn preceded by the phoneme denoting their number. If the spore is either porate or hilate/apiculate this phoneme is placed next to that denoting aperture number. If both porate and hilate/apiculate the order should be porate previous to hilate/apiculate. These in turn must be preceded by the phoneme denoting the degree of septation of the spore. Ornamentation and/or appendages of the spore should be denoted by the requisite phoneme or phonemes at the beginning of all these terms. It is essential that all these previous terms must be preceded by a prefix indicating the general form or type of spore."

Thus the familial epithets are self-defining terms, which in practise can have up to six phonemes preceding the family suffix. Redimopomopiosporaceae thus denotes the family for didymospores with reticulate ornamentation having a single pore and a hilum (see Fig. 2.2, p.47).

Under this system of classification and nomenclature, the highly characteristic Tertiary fossil fungal genera Ctenosporites and Pesavis (Elsik & Jansonius, 1974; Lange & Smith, 1975a, 1975b; Smith, 1978; Smith & Crane, 1979; see Fig. 2.3, p.49) would be accomodated

FIGURE 2.3

A

B
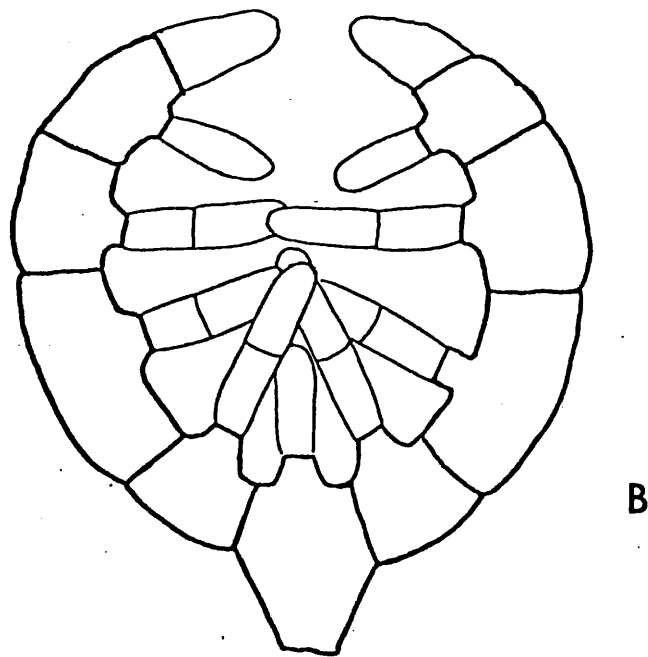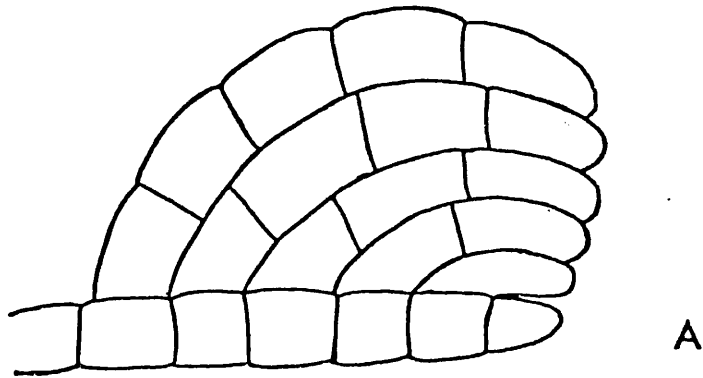
Diagrammatic representations of:

A. Ctenosporites

B. Pesavis

as follows:

	Ctenosporites	Pesavis
Class	Hilosporomycetes	Hilosporomycetes
Order	Bopiosporales	Bopiosporales
Family	Asyboplosporaceae	Multaeboplosporaceae
Genus	Asyboplospora	Multaeboplospora

However, despite Locquin's (1980) claim that these proposals agree entirely with nomenclatural rules, none of the type genera designated for each of the 137 proposed families can be deemed to be validly published in accordance with the I.C.B.N. rules. Although each of the new families is regarded as being self-defined in the poly-syllabic epithet proposed, this cannot be transferred to the description of the genus. None of the proposed genera have a formal diagnosis either in the vernacular or in Latin therefore satisfying neither the mycological or the palaeobotanical requirements for valid publication under the I.C.B.N. rules of nomenclature. Coupled with this invalidation, no attempt has been made to designate either a type species or type specimen for any of the proposed genera, both of which are further requisites of the I.C.B.N. rules of nomenclature. Similarly in no case has any attempt been made to indicate synonymies between the proposed new type genera and those genera, both of living and fossil fungal spores, that have already been validly published and accepted and are in current usage. The entire proposal can perhaps therefore be best regarded as an interesting terminological

(vide Stafleu, 1967) exercise of extremely doubtful value in bridging the gap between artificial and phyletic classifications. A potentially more damaging result however could be the further distancing of palaeomycology from neomycology.

It is heartening to recognise that advances have been proposed by Pirozynski and Weresub (1979b), both eminent mycologists, aimed at lessening this latter schism, or at least allowing for a more meaningful dialogue between workers in the fields of palaeomycology and neomycology. Of course, due to their grounding in modern mycology these two authors are predisposed toward incorporating fossil fungi into the natural classification used for living fungal taxa, and using with some modification the I.C.B.N. rules of nomenclature governing the naming of living fungi. After very careful scrutiny and detailed consideration of the special provisions of the I.C.B.N. in the naming of fossil plants as revised by the Leningrad Congress, Pirozynski and Weresub (1979b) make a series of ten proposals to be considered for adoption by all mycologists,

"in the hope that a full discussion among us can bring about a consensus on the ways in which we can avoid the obvious dissatisfaction and chaos that prevails in other botanical studies that try to make taxonomic and evolutionary sense out of inadequately integrated information about living and fossil forms."

If these proposals were to be adopted, there would be widespread consequences to those palaeomycologists who attempt to adhere to the natural system of classification. The end result of these proposals

would appear to be the removal of palaeomycological nomenclature from the special provisions of the I.C.B.N. for all other aspects of palaeobotany and their submersion into the specifically mycological provisions of the I.C.B.N. As the advantages appear to be heavily biassed toward the neomycologist a closer study of the proposals is called for, and they are quoted in their entirety from Pirozynski and Weresub (1979b) as follows:

"1) All modern genera, on publication, to be automatically prepared for fossil members, the generic name modified by means of an -ites suffix and treated as an autonym. The autonym requires no separate validation, being typified by the type species of the root name. All modern species, on publication, to be similarly prepared, the epithet requiring no change (except perhaps in gender), the generic name indicating the autonymic fossil member by its -ites modification.

2) The starting-point date for the names of fossil fungi to coincide with the starting-point dates for the names of modern fungi.

3) Validation of the names of fossil fungi to be re-incorporated in Art. 36, which rules on the names of modern fungi, requiring the publication of a description or diagnosis in Latin, as of 1 Jan. 1935.

4) If a fossil shows characters diagnostic of one species of the modern mycota, identification to be made with the modern

species, under the modified name of the modern genus, as in 1) above.

5) If a fossil shows characters diagnostic of a modern genus, but not of any known species therein, the fossil to be described as a new species in the modern genus (its name modified as in 1) above); if the fossil is teleomorphic (or both teleomorphic and anamorphic), in a holomorphic genus; if anamorphic alone, in an anamorph-genus.

6) If a fossil shows characters diagnostic of a modern family, but inadequate for distinguishing among its genera, "a new species to be described in the type genus", its name modified as in 1) above.

7) If a fossil is not immediately recognizable as referable to a modern species, genus or family, or not distinctive enough to be judged extinct without further study, formal taxonomic naming is not recommended, the fossil to be given informal designation within a Saccardoan group.

8) If the fossil represents only part of a phase of a fungus (e.g., spores), and is distinctive enough to be judged extinct but not referable to a modern genus or family, it is to be published as a fossil form-species restricted to e.g., spores alone, in a fossil form-genus for spores. It is recommended that indication be given of the lowest-level taxon (among higher categories) to which the form-genus can be referred.

9) If the fossil comprises enough of (a) a teleomorphic phase, and is distinctive enough to be judged extinct but not referable to a modern genus or family, it is to be published as a fossil holomorphic species in a fossil holomorphic genus; or (b) an anamorphic phase and is distinctive enough to be judged extinct but not referable to a modern anamorph-genus or -family, it is to be published as a fossil anamorph-species in a fossil anamorph-genus.

10) Names for new genera of living or fossil fungi are to be formed as for other botanical groups (Art. 20) except that (a) the -ites suffix is to be reserved for the fossil autonyms of the names of living genera; and (b) a construction of the name such that it can be confused with the names of informal morphographic categories is to be abjured."

Several of these proposals need only brief comment, for example, Proposal 3), validation of fossil fungal names by reincorporation into Article 36, thereby necessitating a Latin diagnosis. Pirozynski and Weresub (1979b) argue that in the interests of integration of fossil and living fungi, although there is at present no necessity for a Latin diagnosis for valid publication of fossil fungal genera, this is a small price to pay. In their opinion the number of existing fossil fungal taxa requiring revalidation is relatively small, singling out Cookson (1947a), Dilcher (1965), and Selkirk (1975) as workers worthy of this accolade. There are other post-1935 taxa that would warrant similar treatment but the main justification of this suggestion is the "review of forms published under invalid

names, ... a proper redescription (in mycological terms) and redisposition (among other fungi) of adequately diagnosable and identificable material ...... before chaos descends on palaeomycology in the form of hundreds of useless but indestructible morphographic names". Whilst applauding the palaeobotanical requirement embodied in Article 38 whereby for valid publication any new taxon must be illustrated, no such requirement is presently called for in respect to the valid publication of living fungal taxa. No such requirement is presently demanded, and Pirozynski and Weresub's (1979b) proposals make no suggestion for such a reciprocal gesture.

Proposal 6 in conjunction with Proposal 1 could be interpreted as producing an extremely messy treatment, resulting in the formation of catch-alls for any ill-defined fossil. However the methodology indicated in these proposals has been successfully attempted by several authors, for example Selkirk (1975), in dealing with fossils similar to the modern family Meliolaceae, and Doubinger and Pons (1973) dealing with fossils attributable to the modern family Asterinaceae. A fuller discussion of these genera follows in Chapter 4.

Perhaps the more immediate consequences of these proposals would result from those concerned with the dictates dealing with nomenclature and those relating to the placing of any new taxon within the hierarchical classification. Whilst admitting that a contrary view is widely held by authorities such as N.F. Hughes (1976a) and Doyle (1977), Pirozynski and Weresub (1979b) regard the addition of the suffix -ites to a modern generic name as an

indication of at least a close relationship between the fossil and
the living genus. Justification for this is grounded in the earlier
accepted usage of the suffix in this manner by Felix (1894) and by
Meschinelli (1892). However, Pirozynski and Weresub (1979b) extend
this implication of close morphological similarity to a living genus
(Wolf, 1969) into a postulation of phyletic connection between fossil
and living genus, and thus in their view, the suffix would recognise
the fossil as an autonymic member of the extant genus. In which case
their proposed system would be using names constructed in such a
manner to imply a phylogenetic relationship between fossil and living
forms. Such a procedure would seem to grant greater import to the
name than that recognised by the I.C.B.N. which in its preamble
states:

> "The purpose of giving a name to a taxonomic group is not to
> indicate its character or history, but to supply a means of
> referring to it and to indicate its taxonomic rank".

However the use of the suffix -ites in this manner would not
appear to be greatly at variance with Recommendation 20A(e) of the
I.C.B.N. which states:

> "To indicate, if possible, by the formation or ending of the
> name the affinities or analogies of the genus."

There would also appear to be a certain amount of internal
contradiction within the suggestions of Pirozynski and Weresub
(1979b) concerning the autonymic status of their proposed fossil
fungal genera. The identification of a Miocene ascospore from
Western India is cited as Pleosporites farlowianus Rehm "in

accordance with the postulation that the fossil ascospore belongs to the same species with the type specimen of the name of _Pleospora farlowiana_". Now if this postulate is correct and is accepted, the proposed name can hardly be regarded as an autonym but more exactly it is a synonym of _Pleospora_, and therefore, following the rules of priority is an invalid name. The suffix -_ites_ could therefore lose its significance as an indication of the fossil nature of the material described using this proposed method.

Palaeobotanical nomenclature is already bedevilled by far too many paired generic names (e.g., _Ginkgo_ and _Ginkgoites_, _Equisetum_ and _Equisetites_). Use of the living generic name e.g., _Ginkgo_ carries with it the tacit acknowledgement that the fossil material is congeneric, and in theory exhibits a definite phylogenetic relationship with the living genus. _Ginkgoites_ may be used, perhaps more cautiously, for a fossil showing close morphological similarity with the living genus in perhaps leaf structure alone, but where there is inadequate information available on other parts of the plant to justify assigning the fossil to the living genus. However, the certainty and degree of acceptance by each individual worker of this relationship, is inevitably based upon a subjective interpretation of the facts available. This personal interpretation could not fail to be strongly influenced if the suggestion of Pirozynski and Weresub (1979b) concerning the nomenclatural status is not questioned _viz à viz_ autonymy or synonymy and is adopted. This is due to the corollary of their Proposal 1), that fossil material accomodated in the suggested manner needs no further validation, typification of the fossil material being the same as that for the type of the root name.

One would hope that description or diagnosis, would be given of the fossil material but, reductio ad absurdam, this is not mandatory if these proposals are followed explicitly. Assessment of the accuracy of taxonomic judgements made in such a manner would therefore be much more difficult and could open the exercise to criticism on the grounds of 'uncritical matching' Doyle (1976), or 'prejudgement' (N.F. Hughes, 1976b). Pirozynski and Weresub (1979b) however are firmly committed to the 'backward extrapolation' from living to fossils on the grounds that it is more logical to start with a potential living descendant than with an arbitrary hypothetical ancestor. This emphasises once again the dichotomy between the approaches of the neo-taxonomists and palaeo-taxonomists. Both are striving towards a common goal but with very disparate methods of attaining it.

A possible middle path for the treatment of dispersed fossil fungal spores is given in the following chapter.

3. A PROPOSED METHOD FOR THE DESIGNATION OF DISPERSED

FOSSIL FUNGAL SPORES

N.B.   Parts of the argument developed in this chapter have been published previously, see Smith (1978), Smith and Crane (1979) and Smith (1981); Appendices I, II and IV.

Although much merit may be seen in the system proposed by Pirozynski and Weresub (1979b), caution must be exercised in its acceptance and use.   Despite their proposed modifications of the I.C.B.N. to accomodate fossil fungal taxa, any fossil genus must at present be accepted as being typified by fossil specimens of a specified morphology and not on some imagined extrapolation of a living genus.   It is this necessity to rely upon spore morphology, the single diagnostic feature available that allows comparison and possible correlation with living fungi.   Within the living fungi the morphology of their propagules, both sexual and asexual, plays a prominent role in the systematic treatment of many groups.   Happily this correlation between spore morphology and taxonomic treatment can, to a large degree, be extended to fossil fungal spores; especially to those of Tertiary origin.   This is because it has been found that Tertiary deposits contain an extremely high percentage of genera that can be accomodated within either the Ascomycotina or the Deuteromycotina.   The placement of any given fossil fungal spore in one or other of these major groupings is still however dependent upon the taxonomic expertise of the individual workers.   Ascomycete fungi have the ability to produce both sexual spores (ascospores) and asexual spores (conidiospores) whilst the deuteromycete fungi are

FIGURE 3.1
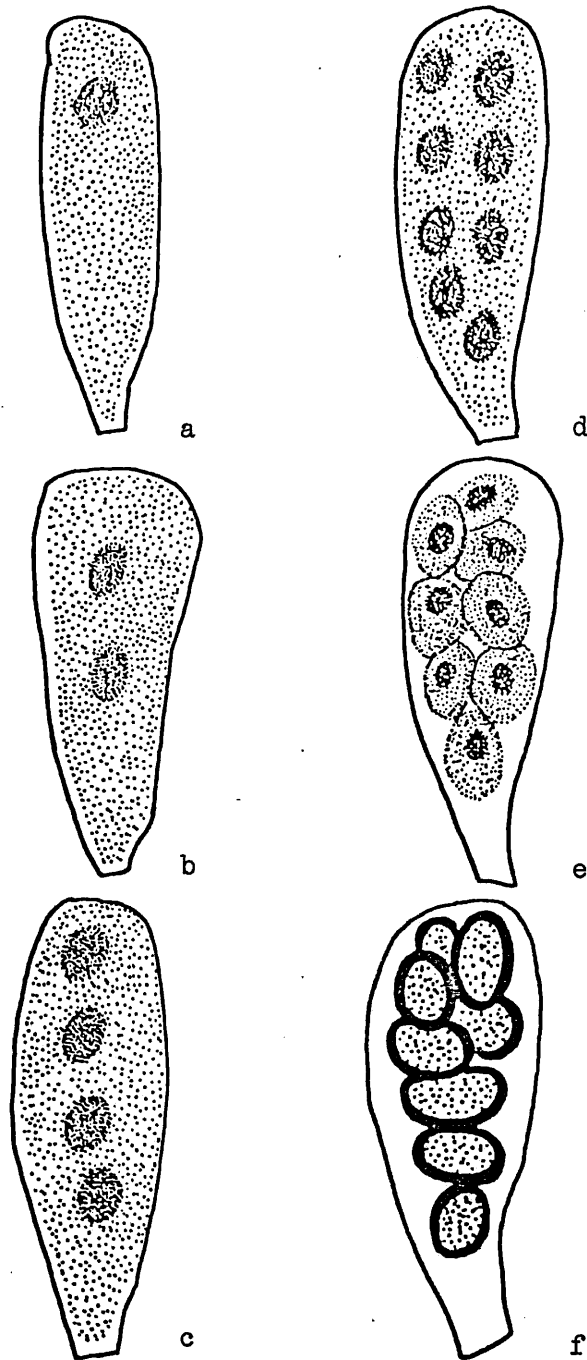
Diagram showing generalised stages in
ascospore development (a - f).

FIGURE 3.2
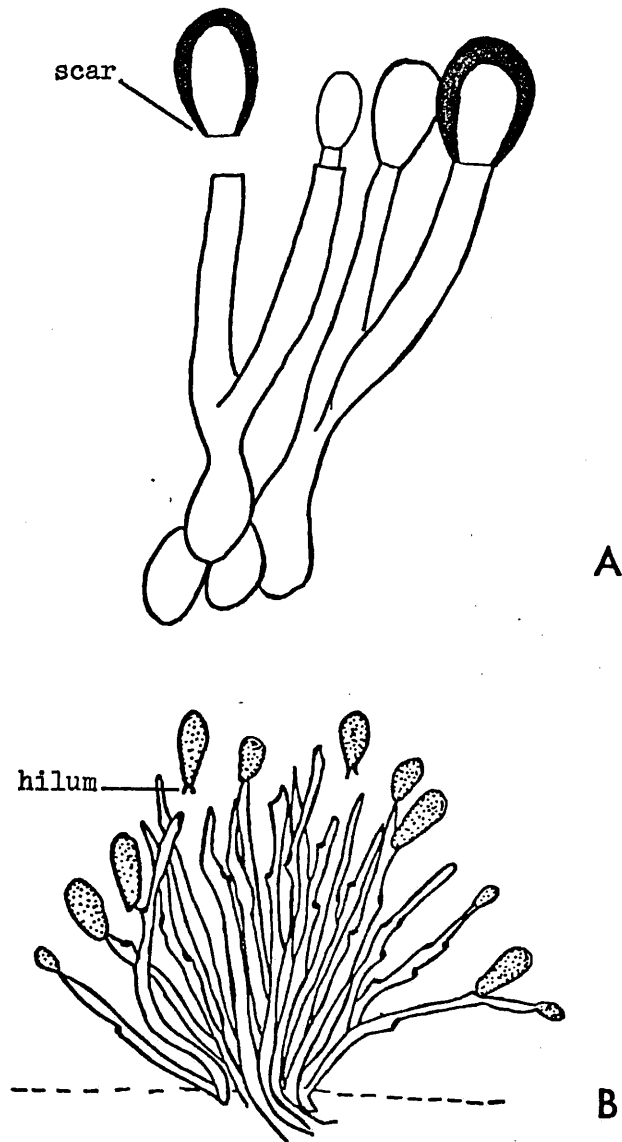
A. Conidiophores and conidiospores of <u>Melanconium</u>

B. Conidiophores and conidiospores of <u>Ramularia</u>

(not to scale)

FIGURE 3.3
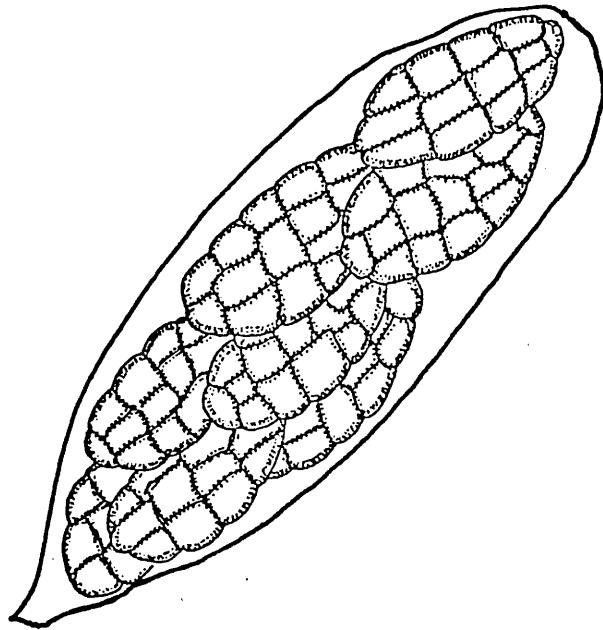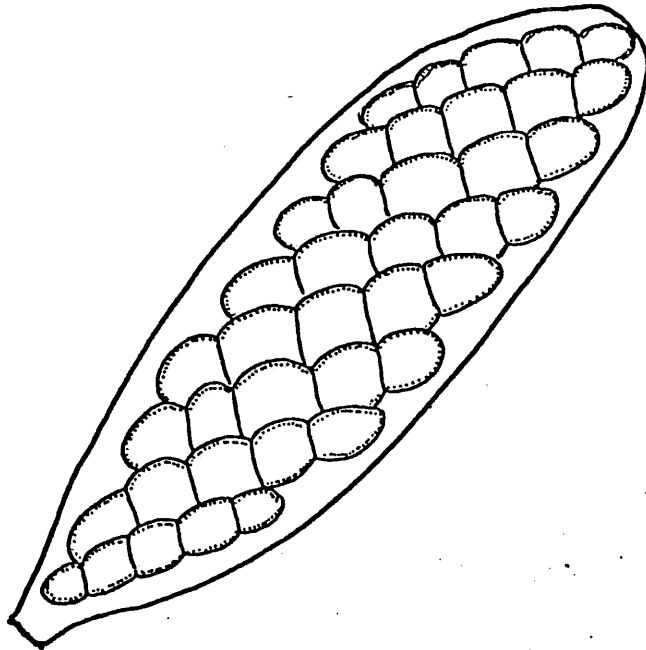
Diagrammatic representation of the multicellular ascospores of:

A. Pleosporales   B. Meliolales

known only from conidial states. The ability to recognise and distinguish between these two spore types is based to a large extent upon an understanding of the ontogenetic differences which separate the formation of the ascospore from the formation of the conidiospore. Ascospores are formed by a developmental process which results in the production of a set of usually 8 spores that have no aperture or hilum (see Fig. 3.1, p.60). In contrast conidiospores are recognised by the presence of either an aperture or a scar (hilum) denoting the point of attachment of the conidiospore to that part of the fungus specialised to produce these asexual spores, the conidiophores (see Fig. 3.2, p. 61). Some ascospores and conidiospores have sufficient morphological characteristics to make them of very great value, allowing neo-mycologists to place a heavy diagnostic emphasis upon them. Examples of this are the multicellular ascospores of the orders Pleosporales and Meliolales (see Fig. 3.3, p.62). However in the case of conidiospores, with the availability of no other characters to strengthen the taxonomic decision to be made, the designation of the conidiospore as ascomycetous or deuteromycetous will often eventually depend upon first hand knowledge of the morphology of the conidiospores of possible modern equivalents. Despite the contention of some mycologists that, given the necessary background, most Tertiary fossil fungal spores could be linked to modern genera, it must be realised that few people dealing with these fossils have the necessary expertise. Thus it is not at all surprising that in most instances fossil fungal spores have been described using the morphographic method of classification rather than attempting to incorporate the spores into the natural classification.

Nomenclaturally there is debate concerning the validity of erecting a genus of living fungi on the sole basis of spore morphology. In theory a genus of fungi could thus be erected, with the more likely case being for a genus based on the sexual (meiospore) spore morphology. Most mycologists however would tend to condemn this practice as 'bad' taxonomy. Within the Deuteromycotina great emphasis has previously been placed upon conidiospore morphology. The systems of classification now being used to categorise and order the large number of deuteromycete genera place far more emphasis upon the method of conidiogenesis, (spore formation and production) (S.J. Hughes, 1971; Kendrick and Carmichael, 1973). This set of criteria, available to the mycologist through culture techniques etc., are of course rarely if ever at the disposal of the palaeomycologist or palynologist confronted with a suite of dispersed fossil spores. Consequently it would seem to be appropriate to be able to distinguish the genera of fossil fungal spores from those for fossil remains of other fungal structures such as fructifications and mycelial hyphae where the designation of these genera may be based on stronger, or at least clearer evidence. Thus rather than following the proposal of Pirozynski and Weresub (1979b) whereby all fossil fungal genera should end with the suffix -ites, an alternative strategy is suggested.

It is advocated that the common practice of including the suffix -sporites as part of the name be generally adopted for any fossil fungal genus based solely upon spore characters. The reasons for this are twofold. Firstly in order to minimise the number of new generic name pairs that could otherwise be introduced into

palaeobotanical literature, especially in view of the possible
uncertainty concerning the proposed autonymic status of the proposed
Pirozynski and Weresub (1979b) procedure. It would seem, after study
of Article 22.1 of the I.C.B.N. (1978), that the procedure for
autonyms (automatically established names) suggested by Pirozynski
and Weresub (1979b) could result in all such fossil fungal genera
being regarded as sub-genera or sections of the extant genera upon
which their names are based. Although this may well satisfy the
intention of demonstrating that the fossil material is contaxic with
the living genus, it is likely that it would also result in a new set
of nomenclatural problems to cloud the fossil/living fungus relation-
ship that the procedure was meant to highlight and clarify.

Secondly, if the diagnosis is based upon morphological features
of the dispersed spores, similarity of these spores with those of a
living genus is suggested by combining the suffix -sporites with the
name of the living genus. Such a procedure could equally well be
taken as having an implicit phylogenetic connotation. However, the
suffix -sporites is indicative of the basis for the morphological
comparison and consequently any inferred phylogenetic connotation
would of necessity be extremely circumspect due to the very small
range of attributes available to establish such a phylogenetic
relationship.

The alternative proposal advanced here has a certain mnemonic
value as well as drawing attention to morphological similarities and
possible relationships. Also whilst following the spirit of the
Pirozynski and Weresub (1979b) proposal it circumvents the

METHODS PROPOSED BY PIROZYNSKI AND WERESUB (1979b)	ALTERNATIVE TREATMENT AS ADVOCATED HERE
1. ALL FOSSIL FUNGAL GENERA TO END IN THE SUFFIX -ites	1. FOSSIL FUNGAL SPORE GENERA TO HAVE SUFFIX -sporites
2. GENERIC NAMES BASED ON THE CONCEPT OF AUTONYMY	2. GENERIC NAMES ERECTED de novo AS REQUIRED
3. ALL GENERA BASED ON LIVING TYPES WHERE POSSIBLE	3. GENERA BASED ON FOSSIL TYPES
4. AUTONYMIC GENERIC NAMES IMPLY CONTAXIC NATURE WITH LIVING FUNGI	4. GENERIC NAMES MNEMONIC, BASIS FOR MORPHOLOGICAL COMPARISON WITH LIVING FUNGI; AND ACKNOWLEDGES POSSIBILITY OF AFFINITY
5. VALIDITY OF AUTONYMIC STATUS QUESTIONABLE UNDER PRESENT I.C.B.N. RULES	5. FOSSIL GENERIC NAMES WOULD BE VALID UNDER PRESENT I.C.B.N. RULES
6. FOSSIL FUNGAL GENERIC DESCRIPTIONS SHOULD FOLLOW NOMENCLATURAL RULES APPLIED TO LIVING FUNGI	6. FOSSIL FUNGAL GENERIC DESCRIPTIONS FOLLOW NOMEN- CLATURAL RULES APPLIED TO ALL FOSSIL PLANTS

TABLE 3.1   Summary of differences between the proposals of Pirozynski and Weresub (1979b) and the treatment adopted in this work.

possibility of further nomenclatural difficulties as each taxon erected following my proposal would have to follow the requirements for typification as laid down in the I.C.B.N., totally separate and divorced from that of the modern genus used as the root name. It must further be emphasised that assignment of spores to a genus erected in the manner proposed here would depend solely upon structural agreement with the diagnosis regardless of any hypothesis of relationship. The points of difference between the proposals of Pirozynski and Weresub (1979b) and the treatment adopted here are summarized in Table 3.1 (p.66).

As well as the nomenclatural aspects of this alternative proposal there are the taxonomic considerations. Regardless of the classification used, either natural or artificial, any worker on dispersed fossil fungal spores must depend upon characters displayed by the spore. This means, of necessity, that the number of features that can be used as taxonomic criteria are limited, and consequently undue emphasis can often be placed upon small morphological variation. The relatively few characters available to serve as diagnostic features and the often undue emphasis, or taxonomic 'weighting', placed upon such minor variations in the morphological features has in many cases led to the creation of many taxa of fossil fungal spores based on a single, or very few specimens. In these instances concentration on the minutiae necessary to establish such quasi-taxonomic distinctions appear to have obscured and often supplanted the broad underlying principles applicable in any exercise in defining taxonomic limits. These limits are usually drawn as a result of analysis of several correlated characters and encompass the

variability found to occur within the population under study.

3.1   VARIABILITY AND TAXONOMIC CIRCUMSCRIPTIONS

It is axiomatic that any population thought to be of a single species will show a certain amount of genetic variability. For example pink-flowered and white-flowered forms of Rosa canina L. occur in nature yet the colour of the flower is not regarded as an important taxonomic criterion, except perhaps at varietal level. Similarly, even the most cursory examination of the illustrations in a treatise such as that of Ellis (1971) highlights the intraspecific variability that can occur in extant fungal spore morphology. There is no reason to suggest that this wide inherent variability in spore morphology is not a point to be taken into account when dealing with fossil fungal spores also.

The problem of spore morphology variability is however not restricted to the inherent, or genetic factors, but is compounded by the observations that spores of living fungi are often extremely susceptible to changes in external factors. The influence of these factors is usually expresssed in the very features of the spore that are used as the basis for species distinction in fossil fungal spore genera.

Browne and Horne (1926) using strains of a single species of Fusarium, in culture, were able to demonstrate that length of the spore, and degree of septation could be altered by a large number of external factors. These included:

1) the concentration of nitrogenous material in the culture

FIGURE 3.4
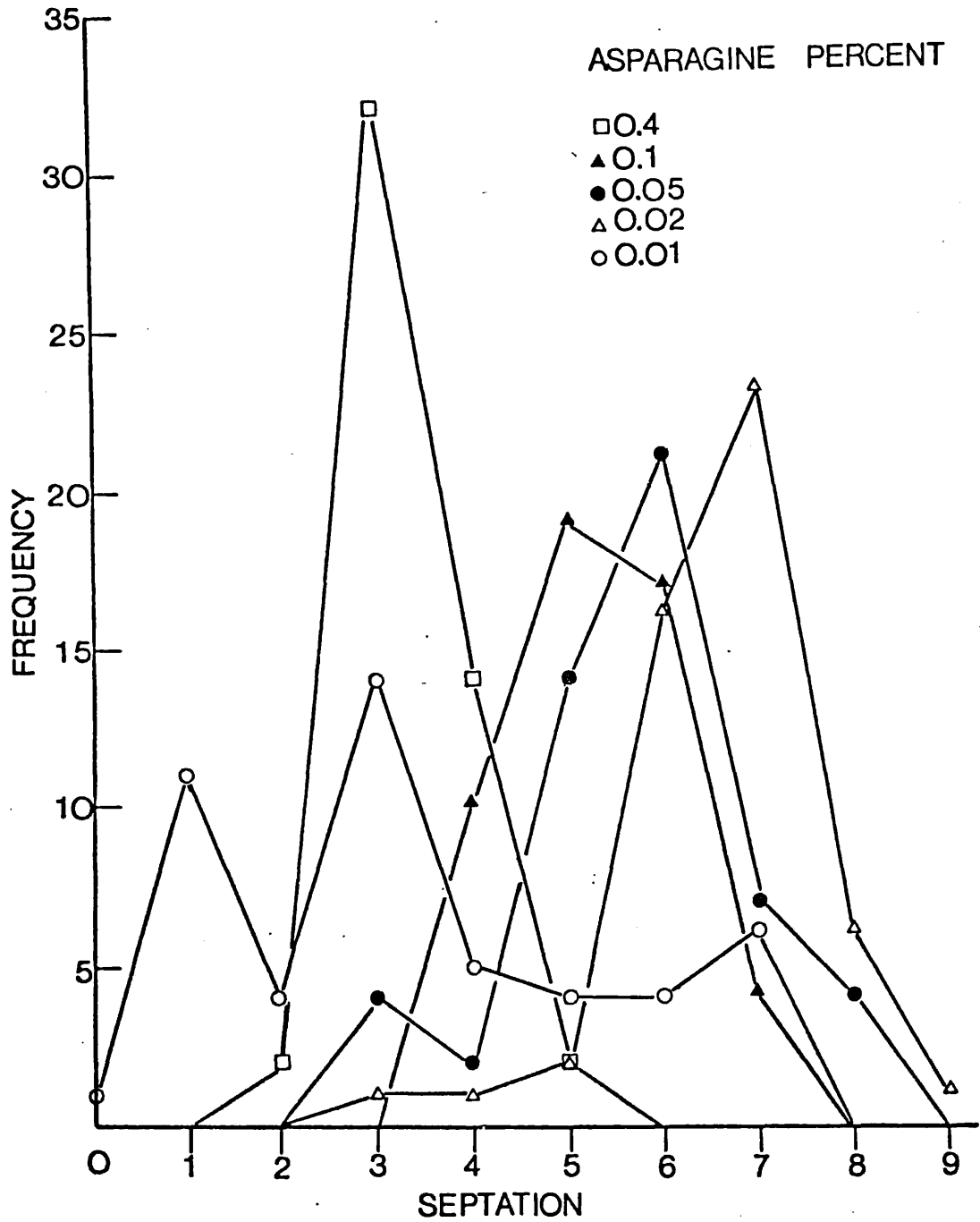
Variation in the degree of septation in _Fusarium_ spores caused by differing levels of asparagine in the culture medium (after Browne & Horne, 1926).

FIGURE 3.5
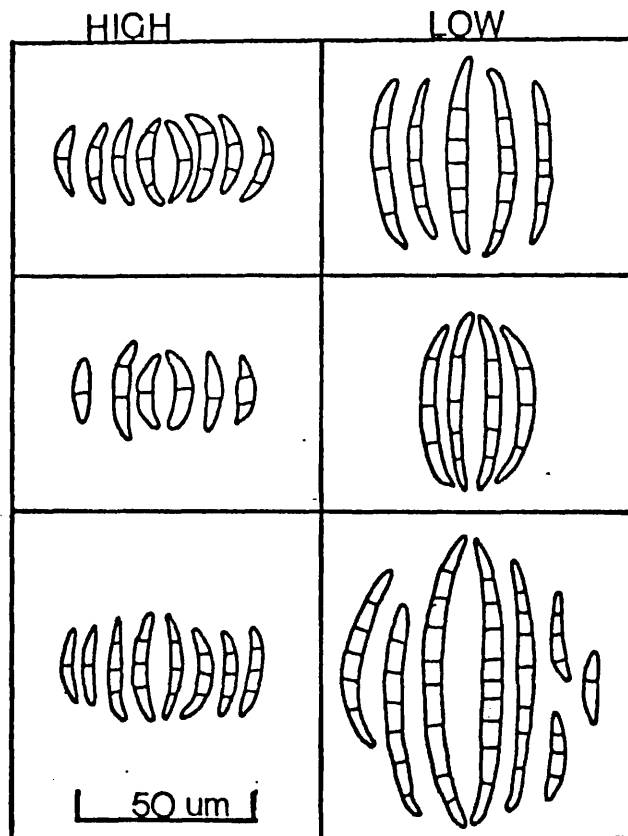
ASPARAGINE LEVEL

Variation in spore morphology in Fusarium due to different
levels of asparagine in the culture medium (after Browne &
Horne, 1926).

FIGURE 3.6
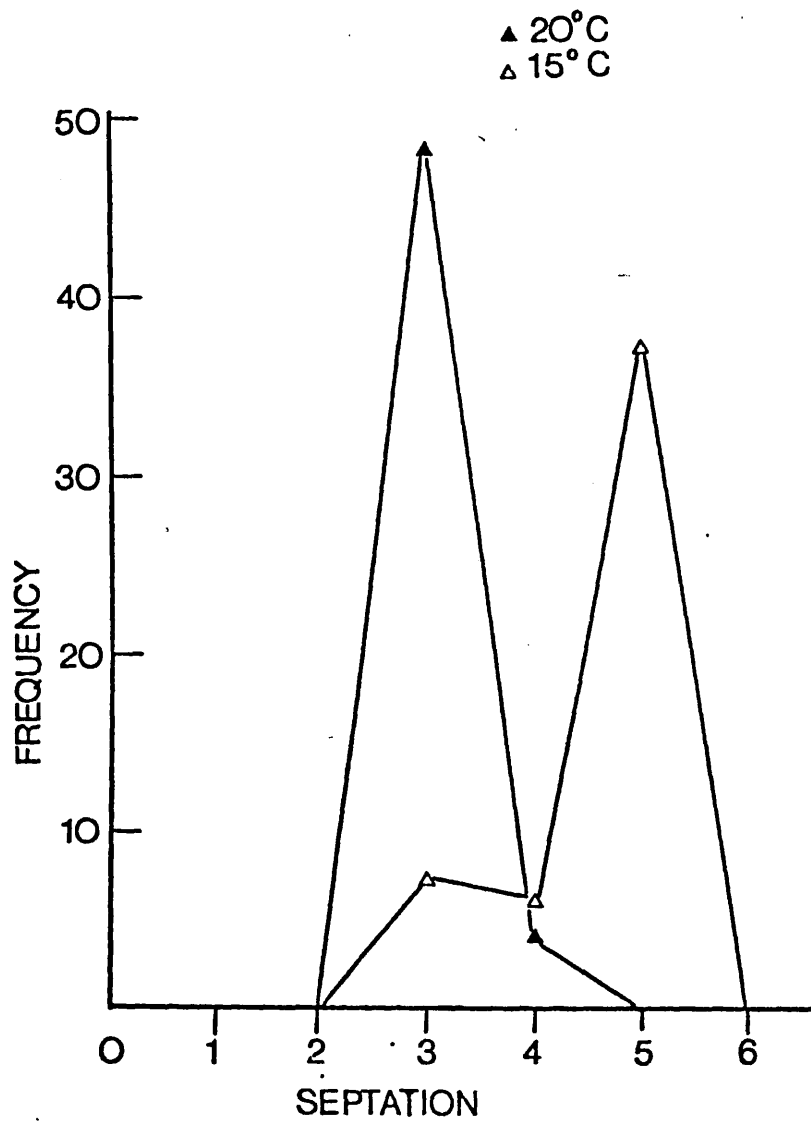
Effect of temperature on the degree of septation of
Fusarium spores (after Browne & Horne, 1926).

medium especially asparagine,

2) the pH balance of the medium,

3) the temperature at which the cultures were incubated.

Alteration of the level of the amino-acid asparagine caused the alteration of the carbon-nitrogen (C/N) ratio of the medium. This alteration of the C/N ratio is reflected in the degree of septation produced in the conidiospores produced on these media as seen in Figure 3.4 (p. 69). The significance and implications of this range of variation, in a palaeomycological context, are emphasised more fully if the overall morphology of the spores produced in conditions of extreme asparagine supply or deprivation are illustrated as in Figure 3.5 (p. 70). If this range of spore morphology were encountered in a sample of fossil fungal spores the most likely result would be to separate these forms into any of three or four existing form-genera viz Dicellaesporites, Dyadosporites, Multicellaesporites and Pluricellaesporites. The extreme morphological diversity resulting from variation in one external factor could therefore cause the separation of one highly variable genus into a number of artificial genera.

A similar situation is encountered if the effect of temperature on septation of Fusarium spores is considered. As can be seen from Figure 3.6 (p.71), changes in temperature that can in no way be regarded as extreme, can have marked effects upon spore septation and hence spore morphology. Browne and Horne (1926) and Horne and Mitter (1927) have shown that large changes in spore morphology are to be found in many species of Fusarium as a result of manipulating external factors. Kakkar and Mehotra (1971a, 1971b) have shown

FIGURE 3.7
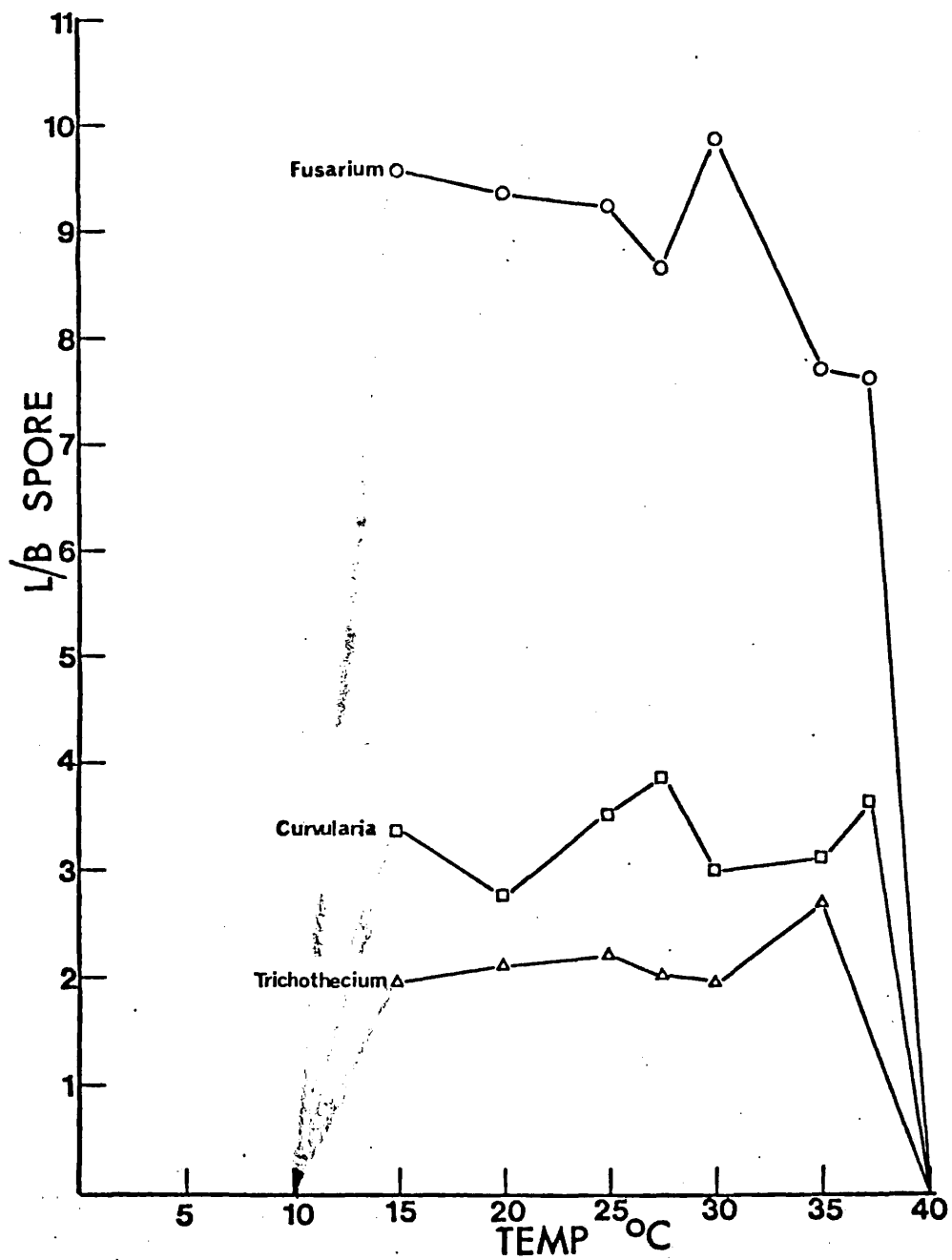
Variation in length/breadth ratio of spores of Fusarium

semitectum, Curvularia lycopersi, and Trichothecium roseum

cultured under differing temperature regimes, calculated

from Kakkar and Mehotra (1971b).

FIGURE 3.8
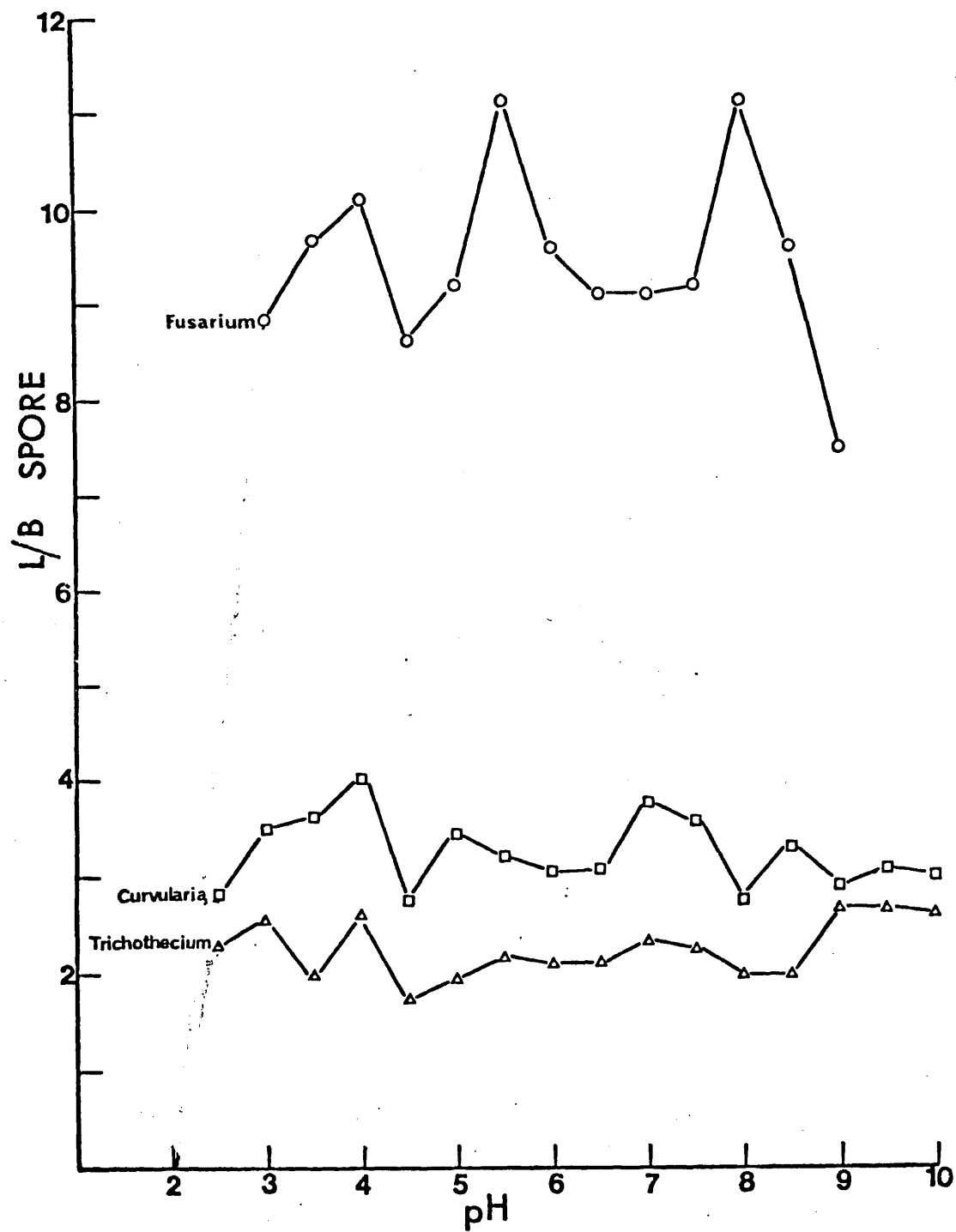
Variation in length/breadth ratio of spores of <u>Fusarium</u> <u>semitectum</u>, <u>Curvularia</u> <u>lycopersi</u> and <u>Trichothecium</u> <u>roseum</u> cultured in media of differing initial pH, calculated from Kakkar and Mehotra (1971a).

similar effects occur in spores of genera other than Fusarium. From their data, length/breadth ratios of the spores have been calculated and are used here as a measure of the variation encountered. The three species used were Fusarium semitectum, Curvularia lycopersi and Trichothecium roseum. Kakkar and Mehotra (1971b) extended the range of temperatures studied for their influence on spore morphology and the variation in length/breadth ratio have been represented graphically in Figure 3.7 (p. 73). Again the Fusarium species used showed the greatest variations in length/breadth ratio, however no mention was made of the effect of temperature on septation, if any, although considering the data of Browne and Horne (1926) in Figure 3.6 (p.71) variation in the degree of septation must occur. Both Curvularia and Trichothecium also exhibit quite marked variation in the length/breadth ratio over the range of temperatures at which sporulation could occur, and these variations would be reflected in the gross morphology of the spores produced in each temperature regime. Kakkar and Mehotra (1971a) also showed that the initial pH, either acid or alkaline, of the culture medium also had an effect upon the morphology of spores, as reflected in the length/breadth ratios calculated from their data. Although the fungi under consideration could, to some extent ameliorate the pH of the culture medium upon which it grew, there is no doubt that the morphology of the spores will be influenced by the pH of its substrate as shown in Figure 3.8 (p.74).

Although in studying fossil fungal spores there is virtually no meaningful conclusions that can be drawn as to the maturity of the parent mycelium, there is evidence from the study of living fungi

FIGURE 3.9
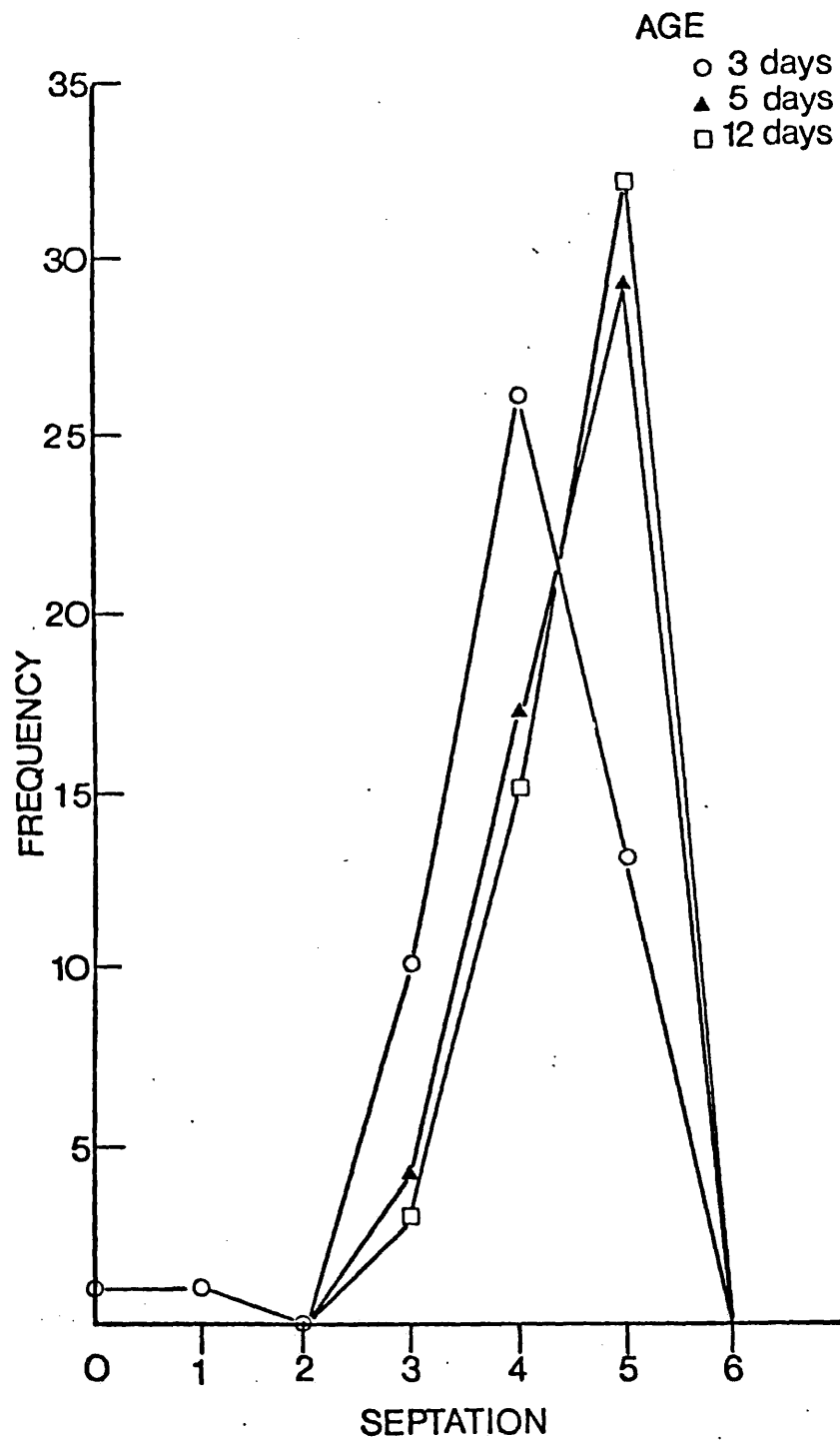
Variation in septation in spores of _Fusarium_ from samples
of different ages, after Browne and Horne (1926).

FIGURE 3.10
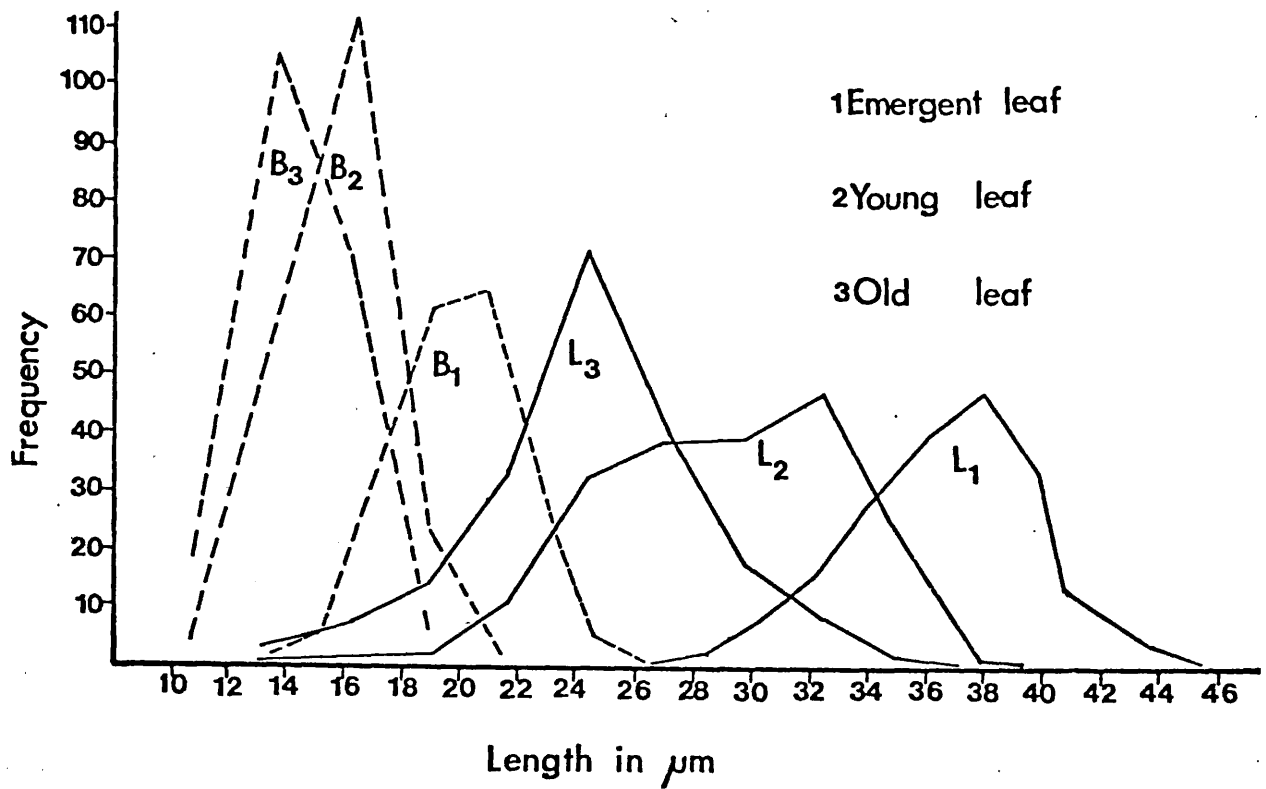
Variation in length and breadth measurements of spores of <u>Oidium</u>

collected from leaves of <u>Laburnum</u> of different age, after Fischer

(1957).

that mycelial age can influence spore morphology. Browne and Horne (1926) have shown (see Fig. 3.9, p. 76) that septation of Fusarium spores can vary with the maturity of the parental mycelium. Working with the single-celled (amerosporous) conidiospores produced by the genus Oidium on leaves of Laburnum, Fischer (1957) has shown on the basis of length and breadth measurements that spore morphology will vary during the life cycle of the parent fungus and the degree of maturity of the host substrate (see Fig. 3.10, p.77). In this case however it would be unwise to discount the possible contributions of the effect of other external factors. As already mentioned, temperature and nutritional status of the host could well be playing some part in the variation recorded. Morphological expression of the effects of alterations and fluctuations in environmental parameters is no doubt widespread throughout all branches of palaeobotany and is not the sole province of fossil fungal spore taxonomy. Nevertheless if this likelihood of wide variation in the morphology of living fungal spores is accepted as being an equally probable occurrence in fossil fungal spores, the taxonomic consequences would be far-reaching indeed. If the possibility of variability of morphology is not considered, any attempt at a taxonomic treatment with an over emphasis on minor morphological differences as taxonomic criteria will result in the erection of taxa of dubious validity. Lange (1978a) has clearly demonstrated this in his critical re-examination of the species erected by Sheffy and Dilcher (1971) in the two form-genera Inapertisporites and Monoporisporites. The diagnosis for Inapertisporites van der Hammen (1954b) as emended by Sheffy and Dilcher (1971) is as follows:

"Fungal or algal spores unicellate, nonseptate and

inaperturate. Shape globular or subglobular, outline smooth or often uneven because of wrinkles or folds. Ornamentation variable. Size range 5-11 µm."

The type species is taken to be I. pseudoreticulatus Rouse (1959). Sheffy and Dilcher (1971) recorded the occurrence of 35 specimens of fossil fungal amerospores which they regarded as congeneric with Inapertisporites. Two of these specimens were identified as being conspecific with previously described species, I. minutus van der Hammen (1954b) and I. elongatus Rouse (1962). The remaining 33 specimens are then disposed into 17 new species, 12 of these being established on the basis of a single specimen, one on two specimens, three on three specimens and one on ten specimens. Monoporisporites van der Hammen (1954b) has the following diagnosis as emended by Sheffy and Dilcher (1971):

"Monoporate, nonseptate, psilate to finely punctate fungal or algal spores. Shape spherical to subspherical, hilate or monoporate."

The type species is M. minutus van der Hammen (1954b). Sheffy and Dilcher (1971) recognise five species, of which all save M. annulatus van der Hammen (1954b), are new species, erected in each case on the basis of a single specimen. However the major diagnostic feature separating these two genera of amerospores is essentially the presence or absence of an aperture. Even this however is questionable as the diagnosis for Monoporisporites has been emended to include hilate as well as porate amerospores within the generic circumscription. Sneath and Sokal (1962) when considering the generalised theory of numerical taxonomy, state "no single attribute is in theory sufficient or necessary for membership in the group so

long as the members share a high proportion of characters". Lange (1978a) therefore analysed each of the species of Inapertisporites and Monoporisporites erected by Sheffy and Dilcher (1971). This analysis involved scoring each of the described species for a series of features: maximum dimension, degree of opacity, degree of turgidity, ornamentation, aperturation, pore outline curvature, longitudinal symmetry, transverse symmetry and presence of a hilum, and performing a principal components analysis upon the data thus generated. If Inapertisporites and Monoporisporites are indeed separate and distinct taxa, the expected result of such a numerical taxonomic exercise would be the formation of two clusters, one for all Inapertisporites species and one for all Monoporisporites species investigated. Lange's (1978a) investigation did not produce this result, rather all the species analysed aggregated into a curved band ordered on spore outline from elliptical through circular and ovoid to oblong. It is of extreme interest to note that the type species I. pseudoreticulatus Rouse is outside the perimeter of this band and is only approached closely by I. minutus van der Hammen (1954b) and I. scabridus Sheffy and Dilcher (1971), both of which have clearly ornamented walls. Lange (1978a) concludes that the majority of Sheffy and Dilcher's (1971) Inapertisporites species are not closely related to the type species and that these species are generally heterogeneous.

This example serves to emphasize the commonest pitfalls in the field of fossil fungal spore taxonomy. Lange (1978a), Lange and Smith (1971), Smith (1978, 1981) and Smith and Crane (1979) have all emphasized that any attempt at a meaningful taxonomic treatment of

dispersed fossil fungal spores must be based upon population studies rather than a small number of specimens. In this way it is possible to establish with some degree of certainty the range of both inherent and environmentally induced morphological variability. Acceptance of the population study method would in some way obviate the prevalent tendency to create taxa de novo with extremely narrow taxonomic circumscriptions due to insufficient acknowledgement of probable variation. This would also lessen the chance of any proposed new taxa degenerating into little more than terminologic niches, which at specific level are separated on the basis of criteria of debatable taxonomic value. These criteria are really nothing more than foci within the continuous variation which exists between individual members of a species. These foci are therefore often mistakenly interpreted, due to the lack of supporting evidence, as being equivalent to the complete discontinuities occurring in a number of correlated features which allow whole-plant taxonomists to determine species boundaries. This set of correlated features available to the whole-plant taxonomist are however usually not at the disposal of the workers dealing solely with dispersed spores. With a minimal number of characters upon which to base their taxa, these workers have, as previously mentioned, tended to separate spores into species very readily. Perhaps the population study method is equally open to criticism on the grounds that species recognised under this type of investigation are larger and contain much more morphological variability than other species of fossil spores. This sort of criticism can best be answered by referring to the situation in modern fungal spores as shown by the data previously cited in this chapter. Although more cautious than the alternative approach,

population studies tend toward the situation found by mycologists dealing with extant taxa and hopefully will result in closer co-operation between the two branches of mycology.

4. FOSSIL EPIPHYLLOUS FUNGI

There is an entire suite of fossil fungal materials, distinct from dispersed spores, which is best described as epiphyllous. In the broadest sense the term epiphyllous describes a variety of ecological niches which can be occupied by a broad spectrum of fungal genera. These often unrelated groups of fungi, usually from within the Ascomycotina, have all evolved superficially similar fructifications as a response to their folicolous mode of life. Pirozynski (1978) lists leaf-parasitism, parasitism of other leaf-dwelling fungi, and commensalism, existing on leaf or insect exudates, as variants within the ambit of this epiphyllous mode of existence. J.P. Ellis (1976) further extended the range by citing ascomycete fungi with similar fructifications saprophytic on dead leaves, stem, wood and bark.

Seward (1898) wrote in rather disparaging fashion of the early fossil epiphyllous fungal descriptions:

".... there are numerous recorded species of fungi, founded on dark coloured spots and blotches on the impression of a leaf. Most of such records are worthless, the external features being usually too imperfect to allow an accurate identification."

Berry (1916) whilst echoing these misgivings gives justification for their description and study:

"The presence of spots of different shapes on the leaves of fossil plants is exceedingly common and a very large number of

so-called species of fossil leaf-spot fungi have been described
.... These determinations are based entirely on superficial
similarities between the fossil and some modern leaf-spot fungus
.... The identification of these fossil forms obviously rests
on very insecure foundations .... Nevertheless large numbers of
undoubted fungi are preserved in this manner and it is the
legitimate duty of the palaeobotanist to describe and illustrate
them."

As Dilcher (1965) commented the advent of improved
palaeobotanical techniques for maceration of sediments and also for
clearing fossil leaves and cuticle preparation, have enabled much
more detailed and accurate comparisons of fossil epiphyllous fungi
with extant forms to be made. Many of the specimens which have been
attributed to this very large grouping of fossils have the form of
more or less circular discs of radially arranged cells. These are at
least superficially similar to the discoid fructifications, i.e.,
thyriothecia, (see Fig. 1.2, p. 27) of fungi belonging to the
Loculoascomycetes within the Microthyriales (see Table 1.2, p.17).

The systematic position of many of these radiate structures has
been questionable for some considerable time. Köck (1939) and
Kirschheimer (1942) both argued strongly that there were good
morphological grounds to distinguish both an algal and a fungal
contribution to this group of fossils. Kirschheimer (1942) suggested
that those fossil fructifications lacking a central opening, or
ostiole, but with pores present in the individual cells of the
fructification, are in fact algal. Those fructifications with a

distinct ostiole and lacking porate cells were regarded by Kirschheimer (1942) as being fungal in origin. Both Köck (1939) and Kirschheimer (1942) attributed purported algal forms to the living green algal genus Phycopeltis. Kirschheimer (1942) erected the species P. microthyrioides for the forms he described, i.e., a fossil species in an extant genus. Dilcher (1965) however restored the concept that all of the fossil radiate structures, under consideration were of fungal origin. Part of Dilcher's (1965) argument rested upon the interpretation of smaller structures, deemed both by Köck (1939) and Kirschheimer (1942) to be Phycopeltis, as immature stages in the development of the fructification and termed 'microthyriaceous germlings'. 'Germlings' constitute a separate and distinct suite of fossils and this part of the argument will be returned to and dealt with more fully later in the chapter. Dilcher (1965) fastened on the statement by Kirschheimer (1942) that the major constituent of living Phycopeltis walls was cellulose rather than fungal chitin. The nature of the wall would thus be such as to be unlikely to survive normal processes of fossilization. A strong case for a fungal origin was also made by Dilcher (1965) from the lack of specialized globose gametangial cells within the radiate construction of these fossil thalli. Dilcher (1965) therefore erected a new form-genus Callimothallus within the loculoascomycete order Microthyriales which he stated to be congeneric with Phycopeltis microthyrioides Kirschheimer, although he was not aware of any extant microthyriaceous fungus which possessed the characteristic porate cells in its thyriothecium Germeraad (1979) drew attention to just such a fungus, Mycoleptodiscus terrestris described and illustrated by Gerdemann (1953, fig. 7) in McVey and Gerdemann

(1960), apparently overlooked by Dilcher (1965) but which would have done much to strengthen his argument. Nevertheless Callimothallus has been attributed to the Microthyriales by most workers since 1965. Two papers since that of Dilcher (1965) need to be considered however as their results tend to resurrect the algal origin theory. Good and Chapman (1978) have demonstrated that the cell walls of the extant alga Phycopeltis epiphyton do not contain cellulose, chitin or lignin but react chemically and physically like sporopollenin. This would appear to support Kirschheimer (1942) that Phycopeltis would be capable of undergoing fossilization. Hansen (1980) has advanced the most radical restatement of the algal theory of origin to date. Hansen (1980) studied specimens found not attached to cuticles although cuticle fragments were frequent in the marine shale investigated. Hansen (1980) contended that neither Kirschheimer (1942) nor Dilcher (1965) made mention of such unattached palynomorphic forms in the sediments associated with their leaf fossils. Hansen's (1980) argument is extremely detailed but hinges on a perceived close morphological resemblance between the fossil structures and the Recent radiate green micro-alga genus Ulvella. Culture studies by Nielsen (1977) on two species U. lens and U. setchellii have demonstrated that in contact with a firm substrate, the thallus of these algae develops into a radiate discoid form. Callimothallus is borne on a wide range of host cuticles namely Symplocos, Engelhartia and Litzia (Kirschheimer, 1942), and Sapindus (Dilcher, 1965). Hansen (1980) regards this as suggesting a non-microthyrialian nature for Callimothallus since very few parasitic fungi have such a wide host range. Hansen (1980) proposed that the leaf cuticles were utilized by Ulvella as substrates upon which to

form thalli in the depositional environment. All bar one of the known recent species of Ulvella are marine and usually grow as epiphytes on large benthic algae. Hansen (1980) therefore merges Callimothallus and another genus Microthallites (Dilcher, 1965) into synonomy with Ulvella, and consequently transfers them from fungal origin to algal affinity. Despite Hansen's (1980) carefully presented arguments there are several points that place his conclusion in doubt. Firstly, the blanket acceptance of a parasitic mode of existance for all Microthyrialian fungi by Hansen (1980) is not substantiated by Luttrell (1973) who, like Pirozynski (1978), widens the concept of existance from leaf parasites to include hyperparasitism of other superficial fungi, and ectocommensals growing on exudates from cuticles and stomata. This in turn would decrease the importance of Hansen's (1980) contention based upon the apparent lack of host-specificity of Callimothallus (sensu Dilcher, 1965). Richter (1981) throws doubt upon Hansen's (1980) conclusion that Callimothallus (sensu Dilcher, 1965) is in fact a marine encrusting green alga by reporting that the maw contents of the artiodactyl fossil Messelbunodon schaeferi contained many badly preserved leaves. Many of these leaf fragments bore fructifications that Richter (1981) had no hesitation in identifying as Callimothallus (sensu Dilcher, 1965). However the crux of this report by Richter (1981) is that this leaf material was thought to have been "devoured not fresh but in a state of decomposition. These leaves and the abundant sand grains in the maw contents - both absent in the surrounding sediments - are considered as involuntarily devoured during the search for food." Similarly Hansen (1980) seems to have overlooked the occurrence of 'callimothalloid shields' in

EDWARDS 1922

    Phragmothyrites*

ROSENDAHL 1943

    Trichothyrites*

COOKSON 1947a

    Asterothyrites*

    Euthythyrites*

    Microthyriacites*

    Notothyrites*

    Plochmopeltinites*

    Trichopeltinites*

DILCHER 1965

Asterothyrites

Brefeldiellites*

Callimothallus*

    <u>Phycopeltis</u>

Dictyopileos*

Pelicothallos*

Microthallites*

Trichopeltinites

SELKIRK 1975

    Phragmothyrites**

        <u>Asterothyrites</u>

        <u>Microthyriacites</u>

        <u>Microthallites</u>

    Callimothallus

    Dictyopileos

    Plochmopeltinites

    Trichopeltinites

KAR and SAXENA 1976

    Phragmothyrites**

        <u>Phycopeltis</u>

        <u>Callimothallus</u>

        <u>Microthyriacites</u>

        <u>Microthallites</u>

        <u>Pseudosphaerialites</u>

ELSIK 1978

    Asterothyrites

    Brefeldiellites

    Callimothallus**

        <u>Pseudosphaerialites</u>

    Euthythyrites

    Microthyriacites

    Microthallites

    Phragmothyrites

    Plochmopeltinites**

        <u>Stomiopeltites</u>

    Trichopeltinites**

        <u>Pelicothallos</u>

    Trichothyrites**

        <u>Notothyrites</u>

TABLE 4.1   Commonly cited form-genera of epiphyllous fungi with their treatments by various authors.

* diagnosis of form-genus

** emendation and/or synonymies

Asterinaceae

    <u>Asterina</u>

    <u>Asterothyrites</u>

    <u>Euthythyrites</u>

Microthyriaceae

    <u>Paramicrothallites</u>

    <u>Phragmothyrites</u>

Trichothyriaceae

    <u>Trichothyrites</u>

Trichopeltinaceae

    <u>Trichopeltinites</u>

    <u>Brefeldiellites</u>

Micropeltidaceae

    <u>Stomiopeltis</u>

    <u>Stomiopeltites</u>

    <u>Plochmopeltinites</u>

Parmulariaceae

    <u>Callimothallus</u>

    <u>Microthallites</u>

TABLE 4.2   Attribution of form-genera to extant families

                  within the order Microthyriales (from Pirozynski, 1978).

modern Australian leaf-litter samples as reported by Lange (1976, 1978b) although the mycological identification was not pursued or clarified. More importantly Lange (1978b) illustrates a species, <u>Callimothallus</u> <u>australis</u>, from South Australian Tertiary deposits attached at the centrum to knotted hyphae of a fungus mycelium which infects the host leaf. On balance therefore, although the theory that some of these peltate structures are in fact algal cannot be totally disregarded, there seem to be equally tenable arguments to maintain the <u>status</u> <u>quo</u> and accept all of the structures as fungal.

The literature on microthyriaceous fructifications is extremely wide and diverse. Dilcher (1965) and Elsik (1978) give fairly full reviews of the literature. Elsik (1978) concentrates upon those genera that have been reported as palynomorphs, i.e., not attached to the leaf cuticle of the host plant. Elsik (1978) uses a strictly morphological classification to separate and distinguish between twelve of the form-genera to which palynomorphic microthyriaceous fructifications have been attributed to most frequently (see Table 4.1, p.88). Pirozynski (1978) uses many of the same morphological features of the fructifications to construct a key to the seven extant families within the Microthyriales to which the majority of the form-genera cited by Elsik (1978), Dilcher (1965), and many other workers can be accomodated (see Table 4.2, p.89). It is of interest to note the tentative linkage by Pirozynski (1978) of the fossil genera <u>Callimothallus</u> and <u>Microthallites</u> to the family Parmulariaceae. The taxonomic and nomenclatural treatments of this assemblage of fossils, often loosely determined as 'microthyriaceous fructifications' has resulted in a veritable morass of synonymies.

O. MYRIANGIALES

Atichiaceae, Myriangiaceae, Saccardiaceae, Saccardinulaceae

O. DOTHIDIALES

*Trichothyriaceae, Chaetothyriaceae, Pseudosphaeriaceae,

Parodiopsidaceae, Dothioraceae, *Capnodiaceae, Dothidiaceae

O. PLEOSPORALES

Dimeriaceae, Venturiaceae, Mesnieraceae, Botryosphaeriaceae,

Lophiostomataceae, *Sporormiaceae, *Pleosporaceae, Mycopoaceae

O. HYSTERIALES

Hysteriaceae, Arthoniaceae, Opegraphaceae, Phillipsiellaceae,

Patellariaceae, Lecanactidaceae

O. MICROTHYRIALES

*Micropeltidaceae, *Munkiellaceae, *Microthyriaceae,

*Trichopeltinaceae, *Parmulariaceae, *Aulographaceae,

*Asterinaceae, *Brefeldiellaceae, Leptopeltidaceae,

Stephanothecaceae, Schizothyriaceae

TABLE 4.3   Classification of Loculoascomycetes after Luttrell (1973).

* signifies families to which fossil epiphyllous fungi

have been attributed by various authors.

The problem is exceedingly large and complex and the following example is only one of many that need to be resolved if this type of fossil fungal structure is to be given a firm taxonomic and nomenclatural grounding.

The group of genera that I wish to consider centres round the genus _Phragmothyrites_ erected by Edwards (1922) for fossil fructifications of Eocene age, which resemble those of the living genus _Phragmothyrium_ as defined by von Höhnel (1912). Edwards (1922) refers to earlier descriptions of fossil fungal fructifications including Pampaloni (1902a, 1902b) but queries this as a doubtful record (Engelhardt & Kinkelin, 1908; Nathorst, 1915; Krausel, 1920). Rosendahl (1943) highlights one of the problems involved by commenting that the living genus _Asterina ilicis_ to which Engelhardt and Kinkelin (1908) attributed their fossil specimens had since been transferred from the Microthyriales to the Discomycetes by Theissen (1913). This of course means that any attempts to link fossil forms with extant genera requires a knowledge of the latest treatments in any taxonomic revisions of the extant genera. To this end the taxonomy of recent groups followed here is that of Luttrell (1973) (see Table 4.3, p.91). Cookson (1947a, 1947b) described a series of fossil fructifications as 'microthyriaceous' within the order Hemisphaeriales Theissen (synonym Microthyriales). Cookson (1947a) maintained that three of the six families, as defined by Ainsworth and Bisby (1963) were represented, namely Microthyriaceae Saccardo, Trichopeltaceae Theissen, and Micropeltaceae Clements and Shear. Cookson (1947a) made the point that spore characters are a valuable criterion for distinguishing between living genera in these families,

Microthyriaceae

    Microthyrieae

        <u>Notothyrites</u>

    Asterineae

        <u>Asterothyrites</u>

        <u>Euthythyrites</u>

    Incertae Sedis

        <u>Microthyriacites</u>

Trichopeltaceae

    <u>Trichopeltinites</u>

Micropeltaceae

    <u>Plochmopeltinites</u>

TABLE 4.4   Form-genera erected by Cookson (1947a) and their incorporation into living taxa.

as are the form of the asci and the presence or absence of paraphyses. Edwards (1922) recorded the presence of two phragmospores and stated that these spores probably belonged to the same species as the fructification described as Phragmothyrites. Cookson (1947a) concluded that due to the absence of spores associated with the Australasian material, comparisons with Phragmothyrites could not be made, and consequently erected six new form-genera (see Table 4.4, p.93). However no works other than Edwards (1922) and Nathorst (1915) dealing with fossil fungal fructifications appear in her bibliography. It must therefore be assumed that she was unaware of the striking similarity between the forms she described as Notothyrites with the previously published Trichothyrites of Rosendahl (1943). This similarity also seems to have escaped Selkirk (1975) who maintained Notothyrites as a valid genus but also described other somewhat similar fructifications as possibly those of Trichothyriaceae. Jansonius and Hills (1976) however deemed that Notothyrites and Trichothyrites are in fact identical and have submerged Notothyrites into synonomy; a view that was followed by Elsik (1978). Smith (1980) commented on the similarity between these two fossil genera. No attempt to submerge either of these generic names into synonomy was made because of the differences in thyriothecial construction that exist between Microthyriaceae and Trichothyriaceae (Smith, 1980). As far as can be established, no detailed comparison of thyriothecial construction was made by Jansonius and Hills (1977). Their opinion was apparently based upon the overall morphological similarity of the two fructification types.

Cookson (1947a) in her treatment of fossil fungal

fructifications followed the classification of Stevens and Ryan

(1939) for the Microthyriaceae. This further subdivided the family

into two subfamilies, Microthyrieae and Asterineae, largely on the

basis of the presence or absence of persistent free mycelial hyphae

in association with the mature fructification (see Table 4.4, p.).

Genera with persistent superficial mycelial hyphae were placed in the

subfamily Asterineae, whilst those genera lacking or with evanescent

mycelial hyphae were placed in the subfamily Microthyrieae. Selkirk

(1975) has shown the differences which result from basing taxonomic

conclusions primarily upon this diagnostic character for extant

fungi. Firstly there is the problem associated with the fact that

fossil thyriothecia are discovered both attached to fossil cuticles

and also as palynomorphs. The difficulty of establishing the

presence or absence of hyphae associated with palynomorphic forms is

self-evident, consequently the palynomorphic forms cannot be ascribed

to either of the sub-families with any degree of certainty. Cookson

(1947a) was aware of this problem and followed this dictum:

> "In order to minimize their number, generic descriptions are
>
> made as broad as possible; distinction which amongst living
>
> species would be certainly considered of generic rank, being
>
> regarded as only of specific value."

To this end Cookson (1947a) erected the form-genus <u>Microthyriacites</u>

(basionym Microthyriaceae) for palynomorphic forms where no evidence

of the presence or absence of free hyphae was available. Dilcher

(1965) found thyriothecia attached to cuticles which were very

similar to those forms described as <u>Microthyriacites</u>. The specimens

described by Dilcher (1965) gave no evidence of possessing free

hyphae; they were consequently deemed to belong with the sub-family Microthyrieae, and placed in the form-genus Microthallites. Selkirk (1975) advanced three possible reasons for the absence of free hyphae in fossil thyriothecia:

1) absence of free hyphae at any stage of the living organism (prior to fossilization);

2) preservation of fruiting bodies in which free hyphae had degenerated (i.e., evanescent free hyphae); and

3) non-preservation of free hyphae, or destruction of these free hyphae during maceration processes involved in isolating the specimens.

The problem of evanescent hyphae is also emphasised by Selkirk (1975), for the nature of the hyphae could only be determined from a study of developmental stages which, in a study of fossil specimens, is impossible to establish in practice. Selkirk (1975) also stressed that preservation may well vary from specimen to specimen and that a decision can only be made after examining a large number of individual specimens. On the basis of these factors, Selkirk (1975) maintained that hyphal characters can not be used with any degree of certainty in classifying fossil microthyriaceous fungi; and thus the most important character available is the shape or structure of the fruiting bodies. Selkirk (1975) therefore concluded that on similarity of fruiting body structure, Microthyriacites Cookson and Asterothyrites Cookson, should be merged and that, coupled with Microthallites Dilcher, all these forms should be regarded as synonyms of Phragmothyrites Edwards, which has priority. In this he supported the contention of Sah (1967) that Microthyriacites and Phragmothyrites are synonymous. Kar and Saxena (1976) came to

similar, but not identical, conclusions to those of Selkirk (1975) whereby Phycopeltis microthyrioides Kirschheimer, Microthyriacites Cookson, Microthallites Dilcher, Pseudosphaerialites Venkatachala and Kar (1969) all were submerged into synonymy. On a nomenclatural nicety, that Edwards (1922) failed to designate a holotype for Phragmothyrites eocenica, and a contention that some of Edwards' illustrations (1922, figs. 2 and 4 of plate 8) demonstrate that some of the cells are in fact porate, Kar and Saxena (1976) emend Edwards' (1922) diagnosis in such a way that Callimothallus is also submerged into synonymy with Phragmothyrites. Jansonius and Hills (1977) include the following statement by Jansonius on this decision.

"It appears to me that the illustrations of Edward's type material do not show cell pores, as well as an entire, smooth outline, with no evidence of setose cells. The broadening of the generic and specific concept by Kar and Saxena seems premature to me. J.J."

Elsik (1978) follows the opinion of Jansonius and Hills (1977) and that of Selkirk (1975) in maintaining Callimothallus as a separate and distinct form-genus but does regard Pseudosphaerialites Venkatachala and Kar as contaxic with Callimothallus. Elsik (1978) does not however cite Selkirk (1975) and would seem to be unaware of the cautionary approach advocated concerning dehiscence of fossil fructifications. Selkirk (1975) was concerned that apparent dehiscence could be caused by mechanical damage; therefore dehiscence should only be used as evidence of maturity with great caution. If mechanical damage could account for apparent dehiscence in some fossil fructifications, it must follow that the shape of the rupture caused by this process would be variable. Thus the maintenance by

Elsik (1978) of several of the form-genera submerged by Selkirk (1975) would appear to be questionable (see Table 4.1, p.88) if the primary aim of the classification used is to show relationships both between fossil genera and to extant genera. Elsik (1978) however emphasized that the classification he employed was for palynomorphic occurrences only. As a consequence of this Elsik (1978) would accomodate all microthyriaceous fructifications found as palynomorphs within the Sphaeropsidales of the Fungi Imperfecti, in direct contrast to Cookson (1947a), Dilcher (1965) and Selkirk (1975) all of whom have endeavoured to incorporate the fossil fructificaton into the loculoascomycete order Microthyriales.

Not withstanding the inexactitudes that exist in formalizing the nomenclature and taxonomic treatments of these fossil fructifications, many workers have accepted their presence, either on fossil leaf cuticles or as palynomorphs, as a good climatic indicator. From the predominantly tropical distribution of modern Microthyriaceae, an often uncritical transference to the fossil forms of similar climatic requirements has been made. Cookson (1947a), Selkirk (1975) and Elsik (1978) all caution against a too ready acceptance of this transference of similarities. Unless the fossil forms can be shown to be identical with extant genera and species, one cannot validly state they could have had similar ecological requirements. These workers also follow Edwards (1922) in noting the much higher correlation of incidence of modern genera with high humidity rather than with high temperature. Selkirk (1975) and Elsik (1978) especially used this point to explain the wide geographical distribution of the fossil forms. Dilcher (1965) also concluded that

FIGURE 4.1
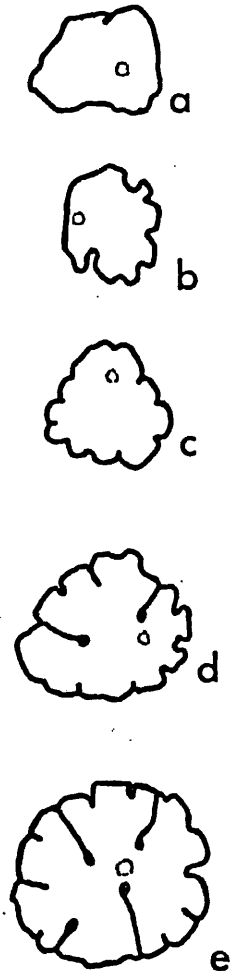
.Outline diagrams of the morphology of 'germlings'. They are
ordered a - e to correspond with Lange's (1976) grades 1 - 5.

generalized ecological arguments should not be based on isolated fructifications alone. However information from fossil fungi could be useful if used in conjunction with evidence derived from associated macrofossils and pollen.

4.1   'GERMLINGS'

To return to the suite of fossils often loosely described as 'microthyriaceous germlings' a similar confusion as to their true taxonomic position can be demonstrated. The specimens which can occur either as palynomorphs or on fossil cuticles have an extremely characteristic morphology (see Fig. 4.1, p. 99). They are often discoidal with deep centripetal grooves of varying depth, the lobes between the grooves may be notched, giving the impression of dichotomising growth. Dilcher (1965) reviewed the descriptions of occurrences of this type of fossil and dealt with the early attempts at taxonomic treatments. Davis (1916) and Bradley (1929, 1931) described specimens from Eocene shales from the Green River, Colorado. Davis (1916) related the specimens to the green algal genus Pediastrum a free-floating planar coenobial (colonial) form; Bradley (1931) related the same material to Coelastrum, a free-floating hollow spherical coenobial algal form. Kock (1939) and Kirschheimer (1942) both described specimens of 'germlings' and in each case related them to the algal genus Phycopeltis. Both Kock (1939) and Kirschheimer (1942) illustrate developmental series from 'germlings' (sensu Dilcher, 1965) to mature fructifications. Edwards (1922) similarly described stages from stigmocysts ('germlings' sensu Dilcher, 1965) to mature fructifications of Phragmothyrites. Dilcher (1965) cautioned that such developmental series can only be

constructed on the basis of an indirect relationship, namely their intimate association together on the same cuticular preparations. Thus such reconstruction may in fact be based upon 'germlings' of various species and/or genera of microthyriaceous fungi. Dilcher (1965) regarded fossils of this type as fungal, but following the admirable dictum of Seward (1898) to refrain

"from converting a possibility into an apparently recognised

fact by the application of definite generic and specific names"

applied to them all, the broad nomenclatural cover of 'microthyriaceous germlings'. Lange (1976) re-examined the disagreement concerning the taxonomy of 'germlings' especially those subsequent to Dilcher (1965). Chief amongst these is the alternative advanced by Bradley (1967), who after reviewing the literature available to Dilcher (1965), came to the conclusion that these fossils should be assigned to a fossil species of the living genus Entophlyctis. This genus is a member of the aquatic fungi of the class Chytridiomycetes (see Table 1.2, p. 17). Bradley (1967) was struck by the close overall similarity between the fossil specimens and the sporangia of the living species Entophlyctis lobata described by Willoughby and Townley (1961). Bradley (1967) concluded that

"the fossil Entophlyctis sporangia became commonly mixed with

epiphyllous fungi entirely by accident and after the 'host'

leaves had fallen into shallow water."

Lange (1976) in an appraisal of Bradley's (1967) findings, levels four strong points of criticism for transferring these fossils from the Microthyriaceae to the Chytridiomycetes:

1.a) Extant Microthyriaceae do possess structures like the microfossils.

   b) Extant Microthyriaceae are epiphyllous.

   c) Fossil Microthyriaceae are well documented.

2. _Entophlyctis_ _willoughbyi_ Bradley has not been demonstrated to occur on leaves, neither have living specimens of _Entophlyctis_ which are usually parasitic, although E. _lobata_ Willoughby and Townley is saprophytic and chitinophilic.

3. The range of morphological variation of the sporangial structure exhibited by E. _lobata_ Willoughby and Townley did not extend to structures similar to the complex invaginated and lobed fossil forms.

4. There is no necessity for leaves to fall into water for them to acquire a spectrum of structures akin to the fossil forms. Living leaves and leaves of herbarium specimens can exhibit a wide range of such epiphyllous structures.

However as Lange (1976) was at pains to stress this, ultimate point is not totally conclusive. He cites the work of Ruinen (1961) demonstrating that in tropical rainforest, conditions, at least for organisms living within a few micrometres of the leaf cuticle, could be regarded as aquatic. However it would appear that Bradley (1967) had not sought any evidence that would suggest that _Entophlyctis_ could be epiphyllous. Lange (1976) also queried whether the 'germlings' are solely Microthyriaceous, as claimed by Dilcher (1965), but concluded that whilst Microthyriaceae are thoroughly implicated, that other epiphyllous fungi probably are as well, and that exclusion of algal and other groups is not entirely

FIGURE 4.2

Mean   Annual   Rainfall (dm)
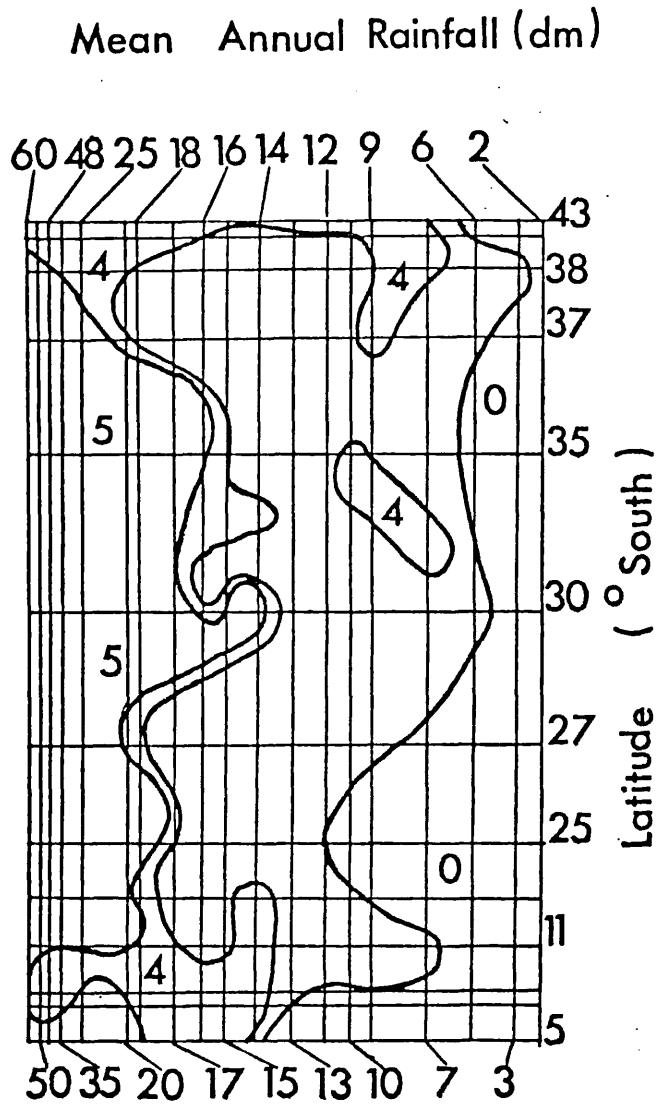
Habitat-range chart from Lange (1976). The most complex
morphologies of 'germling' correspond to 5, the least
complex to 0.

conclusive. Lange (1976) concluded that irrespective of whether 'germlings' are monophyletic or polyphyletic in origin and composition, they do constitute a coherent group for palaeontological purposes. The major part of Lange's (1976) investigation was concerned with an analysis of the use of 'germlings' as ecological and habitat indicators parallelling the claims for fossil microthyriaceous fructifications. Present day leaf litter samples were obtained from 72 sites within the Australasian plant geographical region, including New Britain, New Guinea, New Hebrides, mainland Australia, Tasmania and New Zealand. Cuticle preparations were prepared from each site and the epicuticular 'germlings' counted and scored using a ranking system based upon morphological complexity. Associated site data were tabulated and latitude and regional annual average precipitation used to construct a habitat-range chart (Fig. 4.2, p.103). Similarly the 72 collection sites were grouped into seven vegetation types of the Australasian region (Wood, 1949). Statistical analysis showed a very highly significant association between source vegetation-type and highest grade of 'germling' present. The most complex 'germling' morphologies were detected from leaf litter samples from "rainforest lacking Eucalyptus but with a wide variety of plants of affinities common north of Australia, often mesomorphic with stem buttresses, twiners and epiphytes; also vine-forest and some miscellaneous broad-leaf mesomorphic vegetation." With reference to the habitat-range chart "highest grade of 'germling' detected" partly indicates regional annual average precipitation. The most complex forms (grade V) occur from sites where precipitation exceeds 14-15 dm per annum, the least complex (grade 0) occur only from sites with precipitation less than

8 dm per annum. Lange (1976) concluded that 'germlings' do show some promise as palaeohabitat indicators but recommended extreme caution in basing interpretations solely on the presence of the highly complex morphological forms. As Lange (1976) stated, the presence of these forms may imply that "a wet site also donated leaves to this deposit masking the contribution from drier sites". Lange (1978b) extended his search for palaeohabitat indicator value to include a variety of other recognised fossil epiphyllous fungal structures, and their living counterparts. The fossil form-genus <u>Callimothallus</u> Dilcher and <u>Cribrites</u> Lange (1978b), fossil hyphae termed manginuloid, rangiferoid setae and melioloid fossil spores were all shown to have living equivalents amongst the leaf litter samples. Several of these groups will be examined from a taxonomic stand point later in this chapter. Lange (1978b) found that the living callimothalloid or cribritoid shields occurred from sites ranging from equatorial wet broad leaf vegetations south through tropical swamp and vine forest to subtropical rainforest. Rainfall values for the habitats range from 6000-1600 mm per annum. Manginuloid hyphae, rangiferoid setae and melioloid spores were found generally to occur in association with the living equivalents to the callimothalloid and cribritiform fructifications. Lange (1978b) used the combination of these fossils plus the presence of 'germlings' from two separate South Australian Eocene floras to infer conditions similar to those of present day wet tropical vegetation. The Golden Grove flora has, on the basis of these comparisons, no counterpart south of New Guinea. The Maslin Bay Eocene flora (Lange, 1970; Lange & Smith, 1971; Lange & Smith, 1975a) has no modern Australasian counterpart south of the MacPherson-MacLeay overlap, i.e., sub-tropical rainforest (Burbridge,

1960). It would appear therefore that there is a high probability that the previously widely accepted indicator value of fossil epiphyllous fungal structures has a strong factual basis.

4.2 OTHER EPIPHYLLOUS FOSSIL FUNGI

A third, and quite sizeable group of fossil epiphyllous fungal genera have also to be considered. The group consists of those genera which clearly demonstrate an affinity to extant genera from families other than Microthyriaceae; plus those fossil genera in which affinities to extant taxa are far more tenuous and more difficult to establish. Of these fossil genera with clear affinities to extant taxa, some can be linked with ascomycete taxa within the order Microthyriales as shown in Table 4.3 (p.91). Others can be accomodated within the recent family of Pyrenomycetes, Meliolaceae; placed either within the order Meliolales (Müller & von Arx, 1973) or the order Erysiphales (Yarwood, 1973). Meliolaceae are parasitic fungi mostly occurring as epiphytes on leaves, and have a number of criteria, both vegetative and reproductive that can be used in identification of fossil examples, equally effectively as for living examples. Yarwood (1973) lists six characteristics of the family:

1) <u>Mycelium</u> : characteristic differences in length, diameter and branching of hyphal cells between species.

2) <u>Capitate hyphpodia</u> : short, commonly two-celled branches from the main hyphae; closely adpressed to the host leaf. Terminal cell usually swollen, functioning as an appressorium from which an haustorium arises.

3) <u>Mucronate hyphopodia</u> : one-celled commonly flask-shaped

FIGURE 4.3
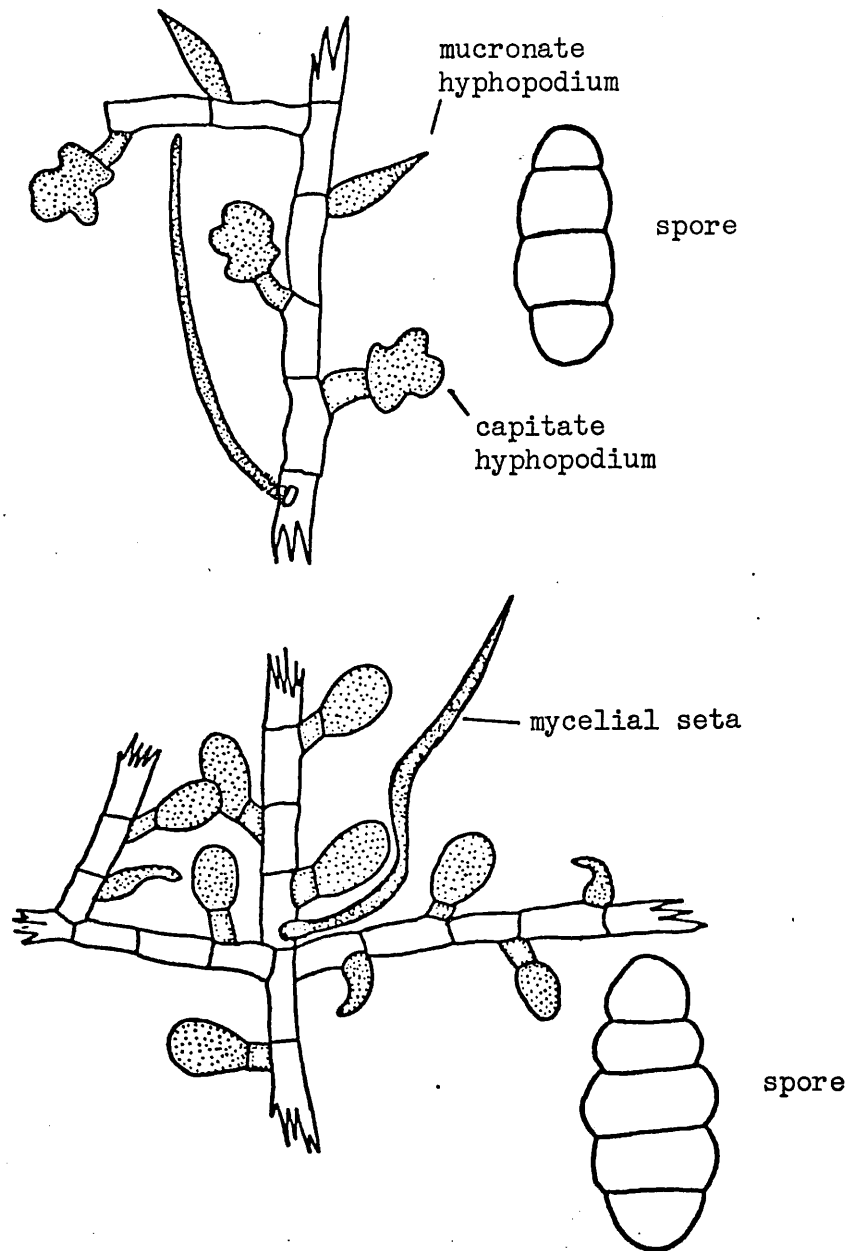
Diagrammatic representation of two living species of <u>Meliola</u>
to show mycelial features: capitate and mucronate hyphopodia,
mycelial setae and nature of spore (after Hansford, 1953).

> branches arising from the main hyphae, usually at
>
> right angles to the host surface.

4) <u>Mycelial setae</u> : found only in the genus <u>Meliola</u>. Long
erect hyphae formed over the surface of the
mycelium and/or only from around the base of the
fructification.

5) <u>Fructification</u> : usually smooth or verrucose globose
perithecia. [Some genera possess flattened
fructificatons, frequently non-ostiolate or
possessing only a rudimentary ostiolar neck
(Müller & von Arx, 1973)].

6) <u>Ascospores</u> : highly characteristic, very dark in colour and
usually multicellular, varying from 2-5 cells
(see Fig. 4.3, p.107).

Distinction of living species within the family Meliolaceae is
commonly made by using an eight digit numerical formula, (Beeli,
1920) which designates qualitative limits for the characters listed
above, and includes spore size. The highly distinctive morphology of
the vegetative mycelium (see Fig. 4.3, p. 107) enables a ready
identification of fossil forms at least to family level. Kock (1939)
and Dilcher (1965) had no hesitation in describing fossil material as
contaxic with the living genus <u>Meliola</u>. Selkirk (1975) however was
more circumspect concerning identification to generic level; and
followed Hansford (1961) who separated <u>Meliola</u> from all other living
melioloid genera on the basis of the presence or absence of setae on
the mycelium. Species in which mycelial setae were absent were
placed in different genera. Both Yarwood (1973) and Müller and von
Arx (1973) used the same criterion for the isolation of <u>Meliola</u> from

all other melioloid genera, which in turn have been separated largely on characters associated with the fructification. Selkirk (1975) concluded therefore that only fossil specimens in which the presence of mycelial setae is incontrovertable can be assigned to the living genus Meliola. Selkirk (1975) further stated that unless well-preserved fructifications are present in the fossil material, no placement in any of the other living melioloid genera could be possible. This is due to the fact that with living specimens a major criterion for disposition into genera, other than Meliola, is the presence or absence and type of appendage associated with the fructifications. Selkirk (1975) therefore created the form-genus Meliolinites in which fossil material lacking mycelial setae and/or fructifications, but possessing close vegetative similarities with extant melioloid fungi, can be accomodated. Dilcher (1965) described two fossil species Meliola anfracta from the cuticle of Sapindus and Meliola spinksii from cuticle preparations of Chrysobalanus. Meliola anfracta, by virtue of the presence of mycelial setae, and four-celled (three-septate) ascospores has been regarded as an acceptable fossil species of the genus Meliola by Selkirk (1975). Meliola spinksii was regarded as having insufficient characters to justify maintaining this as a valid species and Selkirk (1975) used Meliola spinksii as the generitype for his form-genus Meliolinites as Meliolinites spinksii (Dilcher) Selkirk. Meliolinites nivalis Selkirk was described from a putative myrtaceous cuticle, together with species of Meliolinites with no specific epithet, from the cuticle of a lauraceous leaf from Miocene deposits at Kiandra, New South Wales, Australia. Daghlian (1978) followed Selkirk (1975) and described a fossil melioloid fungus as Meliolinites dilcheri (note
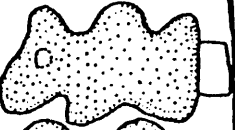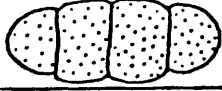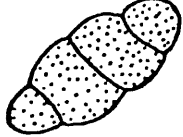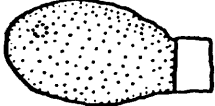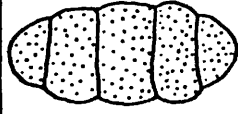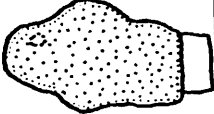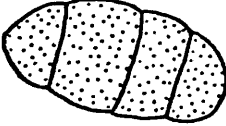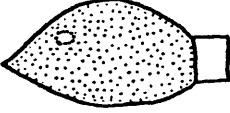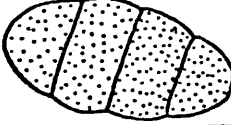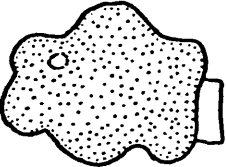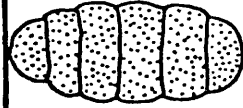
orthographic correction of the specific epithet in accordance with recommendation 73C1(a) of I.C.B.N., 1978). This species was located on a cuticle of a leaf tentatively identified as lauraceous (cf Nectandra). Selkirk (1975) does not however consider the nomenclatural status of the two other reports of Meliola, or material similar to Meliola, recorded by Dilcher (1965). Colani illustrated a specimen borne on the cuticle of a Taxus species leaf (1920, plate XXIX, fig. 5 and fig. 20, p. 412), and described it as a "thallophyte" with possible affinity to the dematiaceous Deuteromycotina. Despite the minimal degree of photographic magnification (90X) of Colani's (1920) illustration, Dilcher (1965) concluded:

> "close examination of his illustrations reveals that the 'thallophyte' has two-celled lobed hyphopodia and sinuate hyphae similar to M. anfracta .... not enough is known about it to justify a generic designation".

However the generic diagnosis for the form-genus Meliolinites has been erected by Selkirk (1975) so as to require the presence of the characteristic melioloid spores. This record of Colani (1920) at present must remain in a state of nomenclatural limbo. Kock (1939) described material from the German Eocene brown coal as a Meliola with no specific epithet. Dilcher (1965) concluded that several features of the material were similar to his Meliola anfracta and other features reminiscent of his Meliola spinksii (sensu Dilcher, 1965). From Kock's (1939) illustrations (Taf. II 2 & 3, Taf.VI 1-14, Taf. VII, Taf. VIII 9-12) it is clear that on the basis of the separation of Meliola and Meliolinites as drawn by Selkirk (1975) the material is definitely to be regarded as contaxic with the recent

FIGURE 4.4

		Hyphopodia	M.Setae	Spore
Meliola anfracta	a		+	
Meliola sp	b		+	
Meliolinites spinksii	c			
Meliolinites nivalis	c			
Meliolinites sp	c			
Meliolinites dilcheri	d			

Fossil species of Meliola and Meliolinites to show features used in their descriptions; + indicates that mycelial setae are present.

Authors of species: a. Dilcher (1965) b. Köck (1939)

c. Selkirk (1975) d. Daghlian (1978)

genus _Meliola_. In Tafel VI, figures 9 and 10 Köck (1939) illustrated "hyphen mit Borsten". These bristles could better be interpreted as mycelial setae, as could Tafel VI figure 14, which Köck (1939) had interpreted as the conidiophore of some dematiaceous fungal parasite such as _Helminthosporium_ or _Arthrobothyrum_. Coupled with this point, the statement by Köck (1939) that, although difficult to clearly discern detail, there was evidence of "borsten" (setae) borne on the fructification, seems sufficient to permit the assignment of this material to the extant genus _Meliola_. There is therefore the availability of two nomenclatural alternatives for the treatment of fossil melioloid fungi. However _Meliolinites_, with the diagnosis based on vegetative mycelial features and associated spores, is a much broader taxonomic concept than that encompassed by the living genus _Meliola_ (see Fig. 4.4, p.111).

This tendency to rely predominantly on vegetative mycelial characters for the definition of taxa in fossil melioloids is inevitable and could well result in many taxa of fossils having a partial overlap of concept with living taxa. There is ample evidence (Luttrell, 1973) to show that in living epiphyllous fungi a considerable degree of morphological convergence is evident between the pyrenomycete order Meliolales and certain families within the loculoascomycete order Microthyriales. The microthyrialian family most likely to be confused with the family Meliolaceae is probably the Asterinaceae. Features that are helpful to neo-mycologists in distinguishing between these two families are fructification (ascocarp) form and structure and spore characters. But even within the family Meliolaceae both globose perithecia (ascocarps), as in

<u>Meliola</u>, and flattened radiate ascocarps as in <u>Amazonia</u> are to be found. The ascocarp in the Asterinaceae, in common with most Microthyriales is a flattened disc-like fructification (ascostroma). This distinction concerning the morphological differences in ascocarp construction is one that is not readily obvious in fossil forms. Due to flattening, and frequently rupture of the ascocarp during fossilization, this distinction is easily confused, provided of course that the fossil material had mature ascocarps which could be examined. Daghlian (1978) has described stages in ascocarp development in <u>Meliolinites dilcheri</u> and figures a cupulate structure interpreted as the lower half of a mature globose ascocarp. A similar cupulate structure was described by Selkirk (1975) associated with <u>Meliolinites nivalis</u>. Again whilst most living genera of Meliolaceae produce ascospores characterized by more than one septum such that the spores can be described as phragmospores, the living genus <u>Armatella</u> possesses uni- or bi-celled spores in common with the uni-septate (bi-celled) ascospores found in genera of the Asterinaceae. Conversely Luttrell (1973) uses the criterion of possessing two- and three-septate, i.e., three- and four-celled spores in his key to the genera of Asterinaceae e.g., <u>Halbania</u>, <u>Batistinula</u>, <u>Patouillardina</u> and <u>Kriegeriella</u>.

Palaeomycologists, due to the often fragmentary and incomplete nature of their fossil material, can therefore face a virtual taxonomic impasse. Clear illustration of this is given if the work of Doubinger and Pons (1975) is considered. They described and named a fossil epiphyllous fungus from a dicotyledonous leaf cuticle from Maestrichtian deposits in Colombia. The presence of two-celled

capitate hyphopodia, and an ascocarp interpreted as being globose could both suggest taxonomic affinity within the family Meliolaceae, although the material had no indication of the presence of mycelial setae and thus the genus _Meliola_ is excluded. Conversely the presence of bi-celled spores found in close proximity to the mycelium would exclude all genera of the Meliolaceae bar _Armatella_ and could suggest a closer affinity is to be found within the Asterinaceae. Doubinger and Pons (1975) therefore erected the form-genus _Molinaea_ however they did not assign the genus to any specified order or family within the Ascomycotina. Their material was described as _Molinaea asterinoides_, the specific epithet chosen perhaps to suggest a preference toward a closer taxonomic affinity with the Asterinaceae than with the Meliolaceae.

Within previously described fossil fungi attributed to the living family Asterinaceae Dilcher (1965) described two fossil species _Asterina eocenica_ and _Asterina nodosaria_ within the extant genus _Asterina_. Pirozynski (1976a) however regards _A. nodosaria_ as being contaxic with the extant genus _Asterolibertia_. Selkirk (1975) followed the same practice when describing the fossil species _Asterina kosciuskensis_. Hunger (1952) illustrated but gave no formal diagnosis for an hyphopodiate mycelium from the Tertiary brown coals of Germany. Hunger (1952) did however comment upon the close morphological similarity of the material with the living genus _Asterina_. Dilcher (1965) also described a fossil asterinoid fungus as ?_Parasterina plectopelta_, a tentative identification on the basis of the similarity of the mycelia and hyphopodia to the extant species _Parasterina implicata_. Doubinger and Pons (1973) on the other hand

erected the genus <u>Asterinites</u> for fossil epiphyllous fungi from the early Tertiary of Colombia (see Fig. 4.5, p.116). Krassilov (1967) had previously used this name but as Cookson (1947a) is cited as its author, this is clearly an orthographic confusion with <u>Asterothyrites</u> Cookson, and therefore if Selkirk (1975) is followed, the three species described by Krassilov (1967) would be placed in synonymy with <u>Phragmothyrites</u> Edwards. Doubinger and Pons (1973) described two species <u>Asterinites</u> <u>tellezii</u> and <u>Asterinites</u> <u>colombiensis</u> from cuticular preparations of the Colombian material. After a very careful consideration of the morphological characteristics of the previously described fossil specimens attributed either to Meliolaceae or Asterinaceae, Doubinger and Pons (1973) made no definite assignment of their form-genus to any specific ascomycete order or family. The diagnosis of the genus <u>Asterinites</u> is based upon the presence of intercalary stigmocysts (hyphopodia) and/or uni-cellular and bi-cellular lateral capitate hyphopodia. Mucronate hyphae and mycelial setae are absent. No information concerning the fructification or spores was given. The etymology of the generic epithet was explained by Doubinger and Pons (1973) as follows:
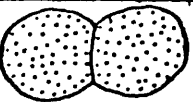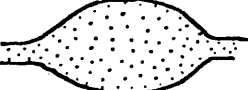
" .... genre de forme <u>Asterinites</u> qui définit des champignons parasites ayant un mycélium externe très differencié spécialisé et caractéristique d'une adaption à un climat chaud et humide ('climat astérinéen')".

One of the species described, <u>A. tellezii</u>, was found to be associated with two bi-cellular spores. Doubinger and Pons (1973) did not link these spores with the vegetative mycelium of <u>A. tellezii</u> but assigned them to the form-genus <u>Dicellaesporites</u> that Elsik (1968) erected for

FIGURE 4.5

Fossil fungi attributed (with various degrees of certainty) to the family Asterinaceae showing capitate hyphopodial (left column) and spore characters (right column). Authors of species:

a. Doubinger and Pons (1975)   b. Dilcher (1965)

c. Selkirk (1975)   d. Doubinger and Pons (1973)

dispersed fossil fungal spores. <u>A. tellezii</u> was compared with <u>Asterina nodosaria</u> Dilcher; however, despite some close morphological agreement, the setal structures and characteristic setal bases described by Dilcher (1965) for <u>Asterina nodosaria</u> were not present. Here there is another example of two genera with an overlap of concept, due in large part to the non-availability of sufficient diagnostic features in the fossil specimens (see Fig. 4.5, p.116). Another contributing factor is the understandable reluctance on the part of many of the authors of such fossil genera to imply a degree of agreement with an extant taxon difficult to justify; and thus the basionym for the form-generic epithet is often taken from higher hierarchical levels within the natural classification (cf Pirozynski & Weresub, 1979b; Proposals 1 and 6 discussed in Chapter 2).

The decision whether fossil material is contaxic, or is to be regarded as contaxic, with living examples is that of the individual workers describing the fossils, and their interpretation of the taxonomic criteria available to them. Despite the lack of spores, Dilcher (1965) felt justified in describing a fossil species of the living genus <u>Stomiopeltis plectilis</u> (Microthyriales family Micropeltidaceae) from cuticle preparations of <u>Sapindus</u> leaves. The criteria that Dilcher (1965) relied upon for this determination were the sinuous nature of the hyphae of the fruiting body and the organization of the mycelial hyphae. However, Alvin and Muir (1970) placed very similar fructifications found on conifer shoots resembling <u>Frenelopsis</u> from the English Wealden, as <u>Stomiopeltites cretacea</u>. Although careful morphological comparisons with the extant <u>Stomiopeltis citri</u> were made, Alvin and Muir (1970) did not feel

that, in the absence of associated spores, the fossil material could be attributed to the living genus. Genera within the Micropeltidaceae are separated largely on ascospore characters listed by Batista (1959) and Luttrell (1973). Alvin and Muir (1970) questioned Dilcher's (1965) inclusion of his material in the living genus, when spores were not found. Pons and Boureau (1977) follow Alvin and Muir (1970) in attributing to Stomiopeltites cretacea fossil fructifications from cuticles of Frenelopsis alata from the Cenomanian of Anjou.

The final example of form-genus/extant genus coupling has as its starting point the description of Shortensis memorabilis by Dilcher (1965). This form-genus was erected as the perfect state of the genus Manginula described by Arnaud (1918). Lange (1969) demonstrated from fresh material that Arnaud (1918), working entirely from dried herbarium material, had mistakenly classed disintegrated ascospores as asexual stylospores. Lange (1969) therefore reduced Shortensis memorabilis to Manginula memorabilis (Dilcher) Lange and erected two further fossil species Manginula osbornii and Manginula magdefravii, after emending the generic diagnosis for Manginula. Lange (1969) based his diagnosis primarily on the exceedingly distinctive septation patterns of the vegetative mycelium. Both his species showed connection of the mycelial hyphae to fructifications, however the spores that were present could not "be attributed unequivocably to the fruiting bodies and were therefore discounted". Selkirk (1972) did not accept the argument advanced by Lange (1969) that Manginula was other than an imperfect fungus and followed S.J. Hughes (1953) in regarding Vizella as the perfect state of Manginula.

Selkirk (1972) therefore categorized fossil material with ascospores as fossil species of the living genus _Vizella_; thus _Manginula memorabilis_ (Dilcher) Lange became _Vizella memorabilis_ (Dilcher) Selkirk and a new species for the Kiandra, New South Wales material _V. discontinua_ was described. Pirozynski (1976a) however considered _V. memorabilis_ to be conspecific with the living species _V. oleariae_. Selkirk (1972) suggested the retention of _Manginula_ for those imperfect species which exhibit only pycnidiospores, but as both Lange's (1969) species were based only on the mycelial and fruiting body characters, these cannot be accomodated in this genus. Selkirk (1972) therefore erected the form-genus _Entopeltacites_ and placed the two fossil species of Lange (1969) as _E. osbornii_ and _E. magdefravii_. Therefore in this case, in spite of the highly individual mycelial construction common to all of the three possible genera, two extant and one form-genus, the final disposition of any given fossil will depend upon either the presence and type of spore, ascospore or pycnidiospore, or the absence of any spore. If spores are present, the generic choice is between _Vizella_ and _Manginula_ whilst _Entopeltacites_ can be used for specimens lacking spores; _Vizella_ for material showing (sexual) ascospores, _Manginula_ for material exhibiting (asexual) pycnidiospores. In this instance therefore, the overlap of taxonomic concept, i.e., _Vizella_ and _Entopeltacites_ is further complicated by the nomenclatural considerations necessitated by the occurrence of the extant genus in either the perfect or imperfect state, _Vizella_ and _Manginula_.

FIGURE 5.1
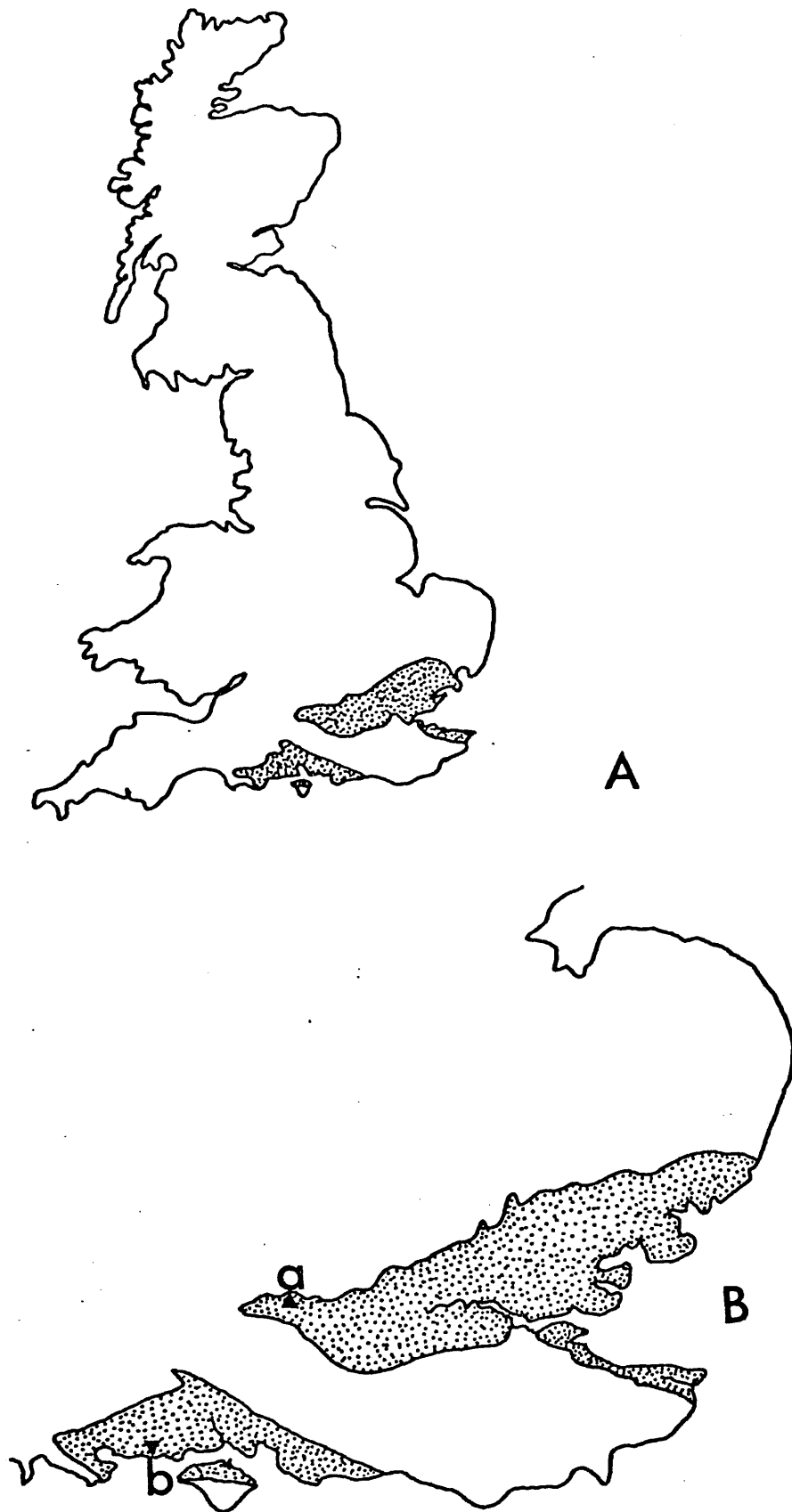
A. Occurrence of Tertiary sedimentary deposits in England.

B. Location of study sites: a. Cold Ash Quarry near Newbury (London

Basin), b. Hordle Cliff (Hampshire Basin).

CENOZOIC	Quaternary		Holocene
			Pleistocene
	Tertiary	Neogene	Pliocene
			Miocene
		Palaeogene	Oligocene
			Eocene
			Palaeocene

TABLE 5.1   Recommended terminology for Cenozoic era
(after Curry et al, 1978).

FIGURE 5.2
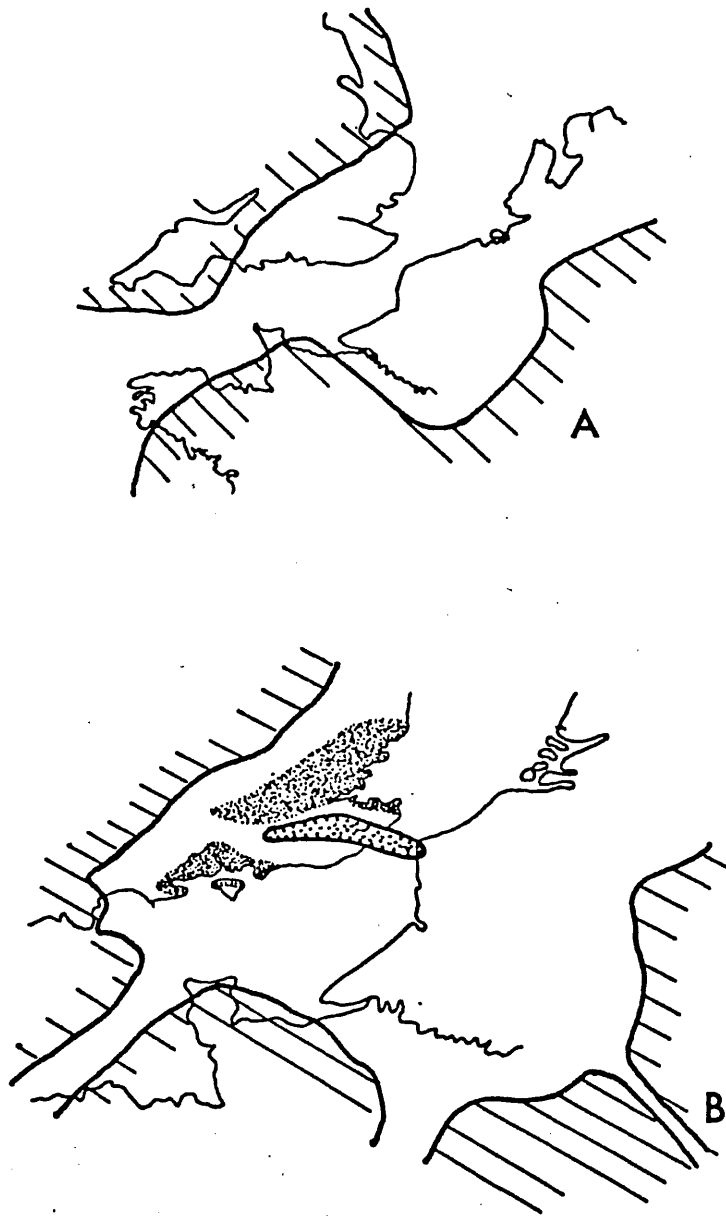
A. Extent of Anglo-Parisian-Belgian Basin in the Early Tertiary.

B. Proposed position of 'Wealden Island' separating London and

Hampshire Basins (after Stamp, 1957).

5. GEOLOGY AND PALAEOCLIMATOLOGY OF THE STUDY SITES

The terminology recommended by Curry et al (1978) for the Tertiary portion of the Cenozoic era will be followed here (see Table 5.1, p. 121).

Two separate early Tertiary (Palaeogene) sites from Southern England have been shown to possess large and diverse fossil fungal floras. Both of the floras contain elements from each of the suites of fossil fungal remains previously detailed in Chapters 1 and 4. The two sites investigated are located each within one of the major outcroppings of Tertiary strata in Southern England, the London and Hampshire Basins (see Fig. 5.1, p.120). These two synclinal basins are but small portions of the much larger depositional basin the Anglo-Paris-Belgian basin (see Fig. 5.2A, p.122). Curry (1965) provided an excellent historical review of the development of geological and palaeontological researches dealing with the London and Hampshire Basins. Prestwick (1852) and Stamp (1957) held that these two basins have been at least partially distinct from early Palaeogene time. The separation was attributed to the exposure of Cretaceous beds during early Palaeogene times to form the 'Wealden Island' or 'Shoal' (see Fig. 5.2B, p.122). More recent opinion (Curry, 1965; Rayner, 1967; Bennison & Wright, 1969) tends to discount this view, and regard the uprise of the Wealden anticline separating the two basins as having occurred in the Mid-Tertiary (Miocene) at the time of the Alpine Orogeny. Both the London and Hampshire Basins exhibit complex and cyclic sequences of marine

		HAMPSHIRE	LONDON
Oligocene	7 ̄ ̄ ̄6	U Hamstead ↑ M&U Headon	———
Eocene	5 ̄ ̄ ̄4 ̄ ̄ ̄3	Lr Headon & Barton	———
		U Bracklesham	U Bagshot
		Lr Bracklesham	M Bagshot
			Lr Bagshot
		London Clay	
Palaeocene	2 ̄ ̄ ̄1	Woolwich & Reading	
		———	Thanet
		———	———

TABLE 5.2   Stratigraphic sequences in the London and Hampshire Basins in the Palaeogene (after Rayner, 1967; Bennison and Wright, 1969). 1-7 represent cycles of sedimentation and their suggested extent.

FIGURE 5.3
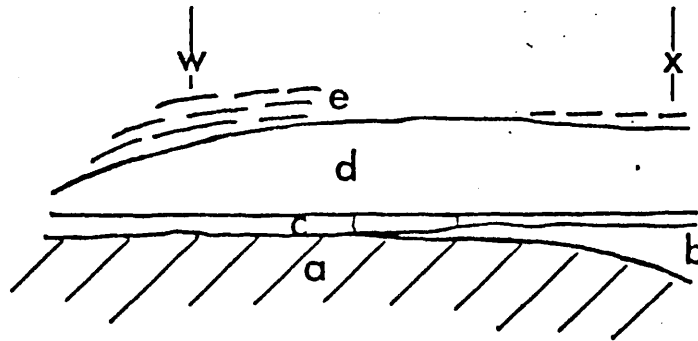
Stratigraphic sequence in the London Basin (after Rayner, 1967).

a. Chalk   b. Thanet Sands   c. Woolwich and Reading Beds

d. London Clay   e. Bagshot Beds   w. Reading   x. East Kent
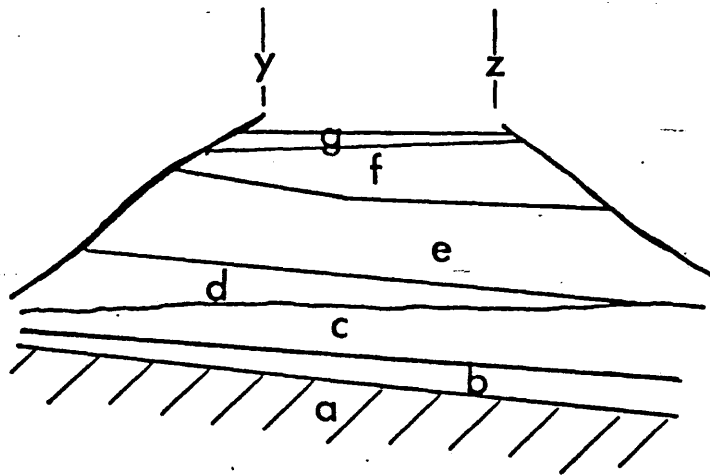
Stratigraphic sequence in the Hampshire Basin (after Rayner, 1967).

a. Chalk   b. Reading Beds   c. London Clay

d. Bagshot Beds   e. Bracklesham Beds   f. Barton Beds

g. Lower Headon Beds   y. Alum Bay   z. Whitecliff Bay

TABLE 5.3   Placement of the Palaeocene/Eocene boundary (after
Crane and Jarzembowski, 1980).

1. Morley Davis et al (1975)   2. Cooper (1976)

3. Curry (1958)   4. Curry (1966)

5. Anonymous (1969)   6. Davis and Elliott (1957)

7. Curry et al (1969)   8. Gurr (1962)

9. Pomerol et al (1977)

transgressions of Palaeocene strata. The earliest Palaeocene strata
are not represented in either of the basins (see Table 5.2, p.124),
although present in both the Paris and Belgian Basins. Similarly the
later Palaeogene strata are not represented in the London Basin
having been removed by post-Palaeogene erosion (see Figs. 5.3A, 5.3B,
p.125).

From the London Basin a flora has been isolated from the Reading
Beds at Newbury, near Reading. The age of these beds has been
variously put either as upper Palaeocene or Lower Eocene. The latter
interpretation being that of a minority of workers (see Table 5.3, p.
126). The second flora has been isolated from the Lower Headon Beds
of the Hampshire Basin at Hordle Cliff, Hampshire. These deposits
are generally accepted as being of Upper Eocene age (Curry et al,
1978).

5.1   READING BED DEPOSITS

The late Palaeocene Woolwich and Reading Beds have been dated,
using both radiometric methods (Odin et al, 1978) and planktonic
foraminiferal zones (Hardenbol & Berggren, 1978) at circa 5.5 million
years b.p.

Within the stratigraphic sequence of the early Tertiary (see
Fig. 5.3A, p.125) of the London Basin, the Woolwich and Reading Beds
are to be found underlying the London Clay. The Woolwich and Reading
Beds occur as three distinct facies. Sherlock (1947) described these

FIGURE 5.4

Diagram showing Wooldridge's (1926) interpretation of the lagoonal

and marine conditions of the London Basin in Late Palaeocene times.

Hatched area - lagoonal.   Solid area - marine.

facies in relation to their geographic distribution within the London Basin. To the extreme eastern edge of the basin (i.e., in East Kent) the beds are predominantly marine fossiliferous glauconitic sands. In North Kent, South-east London, East Surrey and Essex the marine sands are replaced by grey lagoonal and estuarine clays with occasional intercalations of freshwater limestones. However at the extreme western edge of the London Basin, as at Newbury, the glauconitic sands are overlaid by red and variegated clays, and sands of fluviatile and deltaic continental origin. Wooldridge (1926) suggested that during Upper Palaeocene times there had been a considerable retreat of the sea from the western limit of the London Basin leaving a lagoonal situation (see Fig. 5.4, p.128).

Hawkins (1946) suggested a set of conditions under which the Reading Beds were deposited. He envisaged a low-lying country of fresh-water marshes interspersed with sand dunes and temporary pools. Climatic conditions were probably semi-arid with much of the deposited sediment being wind-borne. The overall picture of the Woolwich and Reading Beds site of deposition as proposed by Hawkins (1946) and supported by Curry (1965) is of a shallow eastern sea fringed by brackish mud-flats which in turn are backed by low-lying marshy country to the north and west. This interpretation does not differ radically from those of Wooldridge (1926) and Sherlock (1947).

Collinson and Crane (1978) listed the articles dealing with fossil plants from the Woolwich and Reading Beds, and to these can be added Crane and Jarzembowski (1980), Crane (1981a, 1981b) and Smith and Crane (1979). However the collections are, on the whole,

FIGURE 5.5

A. NEWBURY (64009)

B

C
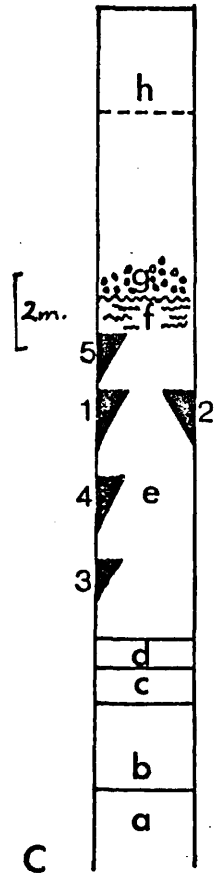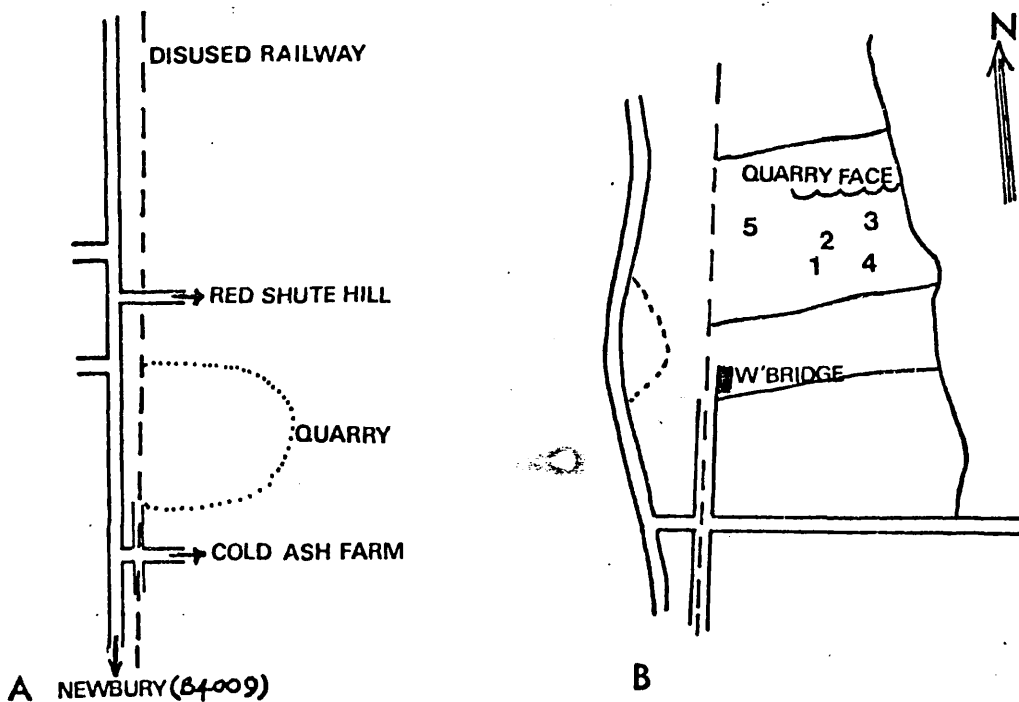
A. and B. Location maps of Cold
Ash Quarry (from cyclostyled field
maps of Crane, 1979, unpublished).

C. Stratigraphic sequence at Cold
Ash Quarry (after Crane and
Jarzembowski, 1980).

1-5 Fossiliferous deposits.

a. chalk   b. glauconitic sandy clays   c. sands

d. lenticular beddings with burrows   e. cross-bedded sands

f. contorted bedding   g. conglomerates of clay clasts

h. mottled clays

fragmentary; and the parent flora is not well understood. Davis and Elliott (1957) have suggested that the fossils of the Reading Beds represent a lateral extension of the flora which produced the London Clay flora. Chandler (1964) concluded that all the lower Tertiary floras from British deposits "are merely representatives of a single characteristic Eocene-Oligocene vegetation".

5.2 PALAEOCENE DEPOSITS AT NEWBURY

Small clay and silt lenses have been revealed as temporary exposures during 1976 and 1977 amongst cross-bedded sands from Cold Ash quarry 6 km north-east of Newbury, Berkshire (national grid reference SU 501713). Crane (1978), Collinson and Crane (1978), Crane and Jarzembowski (1980) and Crane (1981a, 1981b) all deal with the stratigraphy and geology of the deposits.

. The fossil fungal remains were isolated from the silty clay of sites 1 and 2 (see Fig. 5.5, p.130). Although these sites were exposed at different times during quarrying activity, their similarity of plant remains (Assemblage 1; Crane, 1978) spatial juxtaposition and lithology suggest that the two exposures are both from the same bed (Crane 1978, 1981b).

5.3   LOWER HEADON BED DEPOSITS

The upper Eocene (Curry et al, 1978), Lower Headon Beds have

been dated using both radiometric methods (Odin et al, 1978) and by

correlation with planktonic foraminiferal zones (Hardenbol &

Berggren, 1978) at circa 35-40 million years b.p. From Table 5.2 (p.

124) it can be seen that the later Palaeocene beds, of which the Lower

Headon Beds are a representative, are to be found only in the

Hampshire Basin (see Figs. 5.3A, 5.3B, p.125). Their absence from the

stratigraphic sequence of the London Basin is thought to be due to

post-Palaeocene removal by erosion (Rayner, 1967; Bennison & Wright,

1969).

The complex sequence of marine transgressions and regressions

initiated in the Palaeocene continue into the Eocene and Oligocene

(see Table 5.2, p.124). The Barton Beds which underlie the Lower

Headon Beds are predominantly marine sands with abundant molluscan

fossils. The uppermost sediments of the Barton Beds indicate a

gradual shift to less saline water, with the Lower Headon Beds being

laid down in fresh or only very slightly brackish water.

The flora of the Lower Headon Beds is far better documented than

that of the Reading and Woolwich Beds previously dealt with. Reid

and Groves (1921), Chandler (1925, 1926, 1961), Fowler et al (1973)

and Crane and Plint (1979) have all contributed to extending the

macrofossil flora.

Chandler (1961) recorded a wide variety of fossil fruit and

seeds, several of which are interpreted as indicating an aquatic and

FIGURE 5.6
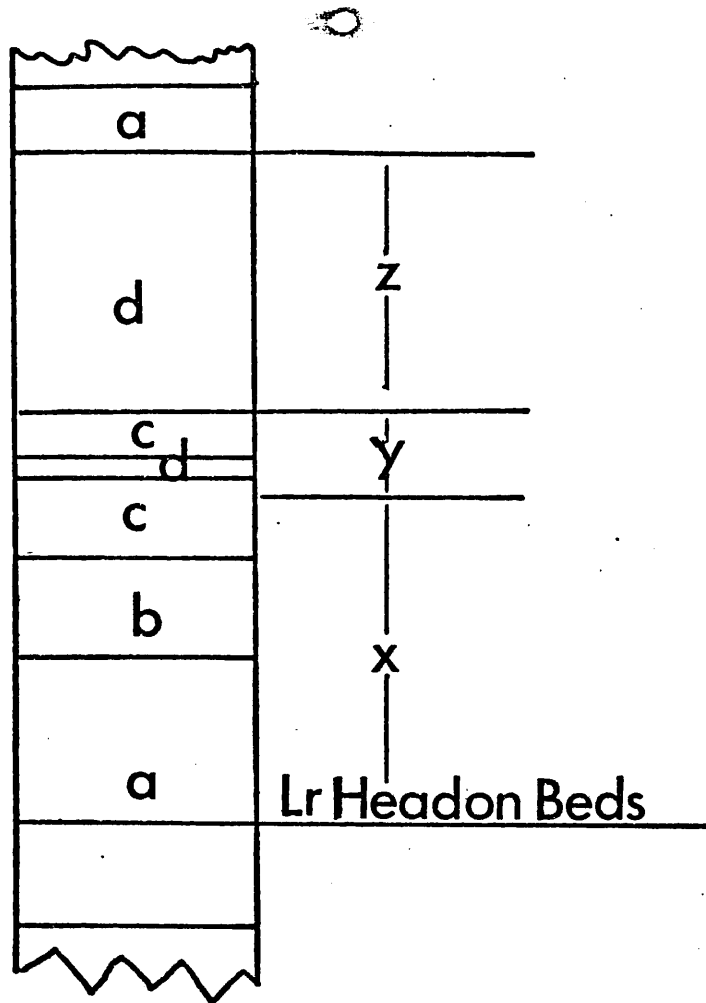
Stratigraphic sequence of Lower Headon Beds (after Fowler et al, 1973)

x. MAMMAL BED   y. LEAF BED   z. CROCODILE BED

a. clay   b. sandy clay   c. silty clay   d. sand

semi-aquatic environment. Coupled with this has been the discovery of _in situ_ Taxodiaceous tree stumps and roots by Fowler et al (1973). The Lower Headon palaeoenvironment has been envisaged as a coastal alluvial flood plain, with open water and swamp forest. The Lower Headon floral assemblage has been likened to that of the deciduous and evergreen swamp vegetation of present day Southern Florida (Fowler et al, 1973). Crane and Plint (1979) have interpreted as a shallow fresh-water lake, the environment from which calcified hydrophytic angiosperm roots have been isolated.

5.4   LOWER HEADON DEPOSITS AT HORDLE CLIFF

Chandler (1961) in her description of the Hordle flora of fruit and seeds, gave a vivid account of the extreme variation in exposure of the Lower Headon Beds at Hordle Cliff. Tawney and Keeping (1883) divided the Lower Headon Beds exposed at Hordle Cliff near Milford-on-Sea (national grid reference SZ 262923) into 33 beds. Of these it is Bed 10 'the Leaf Bed' from which matrix material was examined for fossil fungi (see Fig. 5.6, p.133). It was from Bed 10 that Fowler et al (1973) described the _in situ_ coniferous stumps and roots. Crane and Plint (1979), described the hydrophytic angiosperm roots from the Mammal Bed (Bed 9; Tawney & Keeping, 1883) which immediately underlies the Leaf Bed.

6. EPIPHYLLOUS FUNGI COMMON TO THE READING AND LOWER HEADON BEDS

Despite the difference in geological age between the two sites examined (see Chapter 5) there is sufficient similarity in the types of fossil epiphyllous fungi represented in these two floras to justify treating them together. The physical state of the fossil fungi to be described in this chapter varies according to the site from which they were isolated. Those from the Reading Beds, of Palaeocene age, at Cold Ash Quarry, Newbury (see Fig. 5.5, p.130)are often found in situ at least in the sense that they are still attached to their host leaf cuticles. However those from the Lower Headon Beds, of Eocene age (see Fig. 5.5, p.130), can generally be classified as palynological, because they are usually not still attached to the host leaf cuticle.

6.1 MELIOLALES

As has been shown in Chapter 4, a range of fossil epiphyllous fungi that have been described previously. But the separation of the fossil fungi from the host cuticle will have some effect upon the rigour with which certain taxonomic criteria can be applied. This is especially so when considering material comparable with that which has previously been described within the Meliola/Meliolinites genus pair from the Pyrenomycete order Meliolales. The main differences between these two genera have already been indicated in Chapter 4 (p.83 -122). In order to make critical comparisons with previously

described fossil material however, it is as well to re-examine the bases of the classification process for both these genera. Hansford (1961) places great emphasis upon the identity of the host plant in his key to the species of <u>Meliola</u>. This criterion is however totally unuseable in the case of fossil specimens represented solely as palynological fragments, separated as they are from host cuticles, or of such a small size as to make taxonomic determinations of the minimal amount of host cuticle well nigh impossible. The size of these dispersed fragments are usually so small that no mycelial setae can be detected, let alone fructifications. Thus assignment to the extant genus <u>Meliola</u> is not possible. Use of the fossil genus <u>Meliolinites</u> as erected by Selkirk (1975) is also precluded if the diagnosis is followed closely:

> "Fossil fungal colonies. Mycelium and spores with general characteristics of members of the Meliolaceae. Mycelial setae absent. Information regarding perithecial structure and nature of perithecial appendages uncertain or lacking".

Thus for a fossil specimen to be considered for possible inclusion within the form-genus <u>Meliolinites</u>, not only must there be mycelial remains but also 'spores with general characteristics of members of the Meliolaceae'. This requirement can only be fulfilled when the fungal mycelium is still attached to the host cuticle and, by happy coincidence, spores can be shown to occur in close proximity with the mycelium. In palynological preparations such demonstrations of 'similarity through contiguity' are virtually impossible. Even if spores and mycelial fragments both showing 'characteristics of the Meliolaceae' are present, these must be regarded as two separate and distinct entities. There can be no possible justification for

PLATE 1   Mycelial remains (cf. <u>Meliolinites</u>) from the Hordle Cliff
            and Newbury Deposits. Magnification X1,500.

            Figure 1. Mycelial hyphae with capitate hyphopodia and
                        possible mycelial seta (arrowed).

            Figure 2. Mycelial fragment with alternate capitate
                        hyphopodia.

            Figure 3. Mycelial fragment with possible unilateral
                        capitate hyphopodia.

            Figure 4. Mycelial hyphae to show capitate hyphopodia
                        and their disposition and variation in head-
                        cell shape.

1

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4

regarding them as two aspects or facets of the single form-genus Meliolinites. Selkirk (1975) having carefully circumscribed the diagnosis for Meliolinites was content to catalogue and describe vegetative mycelial material still attached to host cuticles as 'sterile mycelia, probably Meliolaceae'. Rather than create yet another form-genus to accomodate such vegetative mycelial fragments from palynological preparations from the Eocene material, Selkirk (1975) will be followed. Despite the greater availability of leaf cuticle material, and as a consequence, the possibity of more complete specimens of their epiphyllous fungi, similar strictures concerning assignation to either Meliola or Meliolinites apply in the case of the Palaeocene material also. Unless mycelial setae and fruiting bodies and spores are present, the genus Meliola will be excluded.

VEGETATIVE MYCELIAL REMAINS (PROBABLY MELIOLACEAE)
FROM HORDLE CLIFF DEPOSITS

Of the three specimens found, only one (see Plate 1, fig. 1) shows a structure which could feasibly be interpreted as a mycelial seta. This thinner hyphal filament appears to overlay the distinctive Meliola-type vegetative mycelium; however, it is not easy to show any connection between the putative mycelial seta and the mycelium. No mucronate hyphopodia, spores, or any indication of a fructification can be seen. The bi-celled capitate hyphopodia have a predominantly alternate distribution. The head cells of the capitate hyphopodia appear to have an obovate shape. The remaining specimens are little more than minute fragments. One of these, specimen 2

(Plate 1, fig. 2), appears to have an alternate arrangement of bi-celled capitate hyphopodia; the head cells having a globose to ovate shape. There is no indication of any of the other features which characterise the genus Meliola. The third specimen (Plate 1, fig. 3), although small, is similar to specimen 1 (Plate 1, fig. 1), in the morphology of the head cells of the capitate hyphopodia. The arrangement of the capitate hyphopodia appears to be unilateral rather than alternate as in specimen 1. However the size of this third specimen is such that even the arrangement of capitate hyphopodia cannot be stated with any certainty.

VEGETATIVE MYCELIAL REMAINS (PROBABLY MELIOLACEAE)
FROM NEWBURY DEPOSITS

In contrast to the material described above, from the Hordle Cliff deposits, the Newbury material has been found on the host plant leaf cuticle. Preparations of leaf cuticles from the Newbury deposits are of variable quality but in this case, the host leaf is probably related to the Cercidiphyllaceae (Crane, 1981a). The fungal mycelium is borne on the upper cuticle but, as in the Hordle Cliff specimens, there are insufficient criteria available to consider placing the material either in Meliola or Meliolinites.

The portion of the vegetative mycelium still attached to the host leaf cuticle, shows only the typical bi-celled capitate hyphopodia (see Plate 1, fig. 4), with a predominantly alternate arrangement. The shape of the head cell appears to vary from ovoid to undulate in outline. However this variability may well be due to the methods of preparing the cuticles rather than being an inherent

character of the mycelium under examination.

Despite the lack of sufficient features to enable these specimens to be placed in either the extant genus Meliola or the fossil genus Meliolinites, the mere presence of these fossils, with their characteristic vegetative structure is of great interest. Dilcher (1965), Daghlian (1978) and Selkirk (1975) all comment upon the predominantly tropical to subtropical distribution of present day Meliolaceae. Dilcher (1965) further comments upon the close specificity, or obligate nature of the parasitic relationship between the fungus and the host plant, and cites Stevens (1925) who maintained that the relationship was "a long, even very ancient, association with these hosts, or even their progenitors".

Hansford (1953) showed that although best developed in the tropics and subtropics, the Meliolaceae do extend into temperate regions. Nevertheless fossil meliolaceous fungi have generally been accepted as indicating tropical to subtropical conditions. Goos (1978) has made one of the few ecological studies of living Meliolaceae and showed that, on the island of Oahu (Hawaii), distribution of at least one species, Meliola argentina, has its ecological distribution determined primarily by rainfall, rather than by the geographical distribution of the host plant. Goos (1978) found that M. argentina occurred only in those regions of Oahu where the average annual rainfall is in excess of 250 cm. Germination of the ascospores and their continued development into the vegetative mycelium on the host appears to depend to a very large degree upon the retention of a film of moisture upon the surface of the host

Species		Author	Diameter
Callimothallus pertusus	E*	Dilcher (1965)	to 250μm
C. quilonensis	P**	Jain and Gupta (1970)	to 65μm
C. assamicus	P	Ramanujam and Rao (1973)	to 80μm
C. raoi	P	Kar, Singh and Sah (1972)	to 75μm
C. australis	E	Lange (1978b)	to 50μm
C. corralesense	E	Doubinger and Pons (1975)	to 90μm

*E fructifications on host leaves

**P fructifications as palynomorphs

TABLE 6.1   Described species of Callimothallus.

FIGURE 6.1
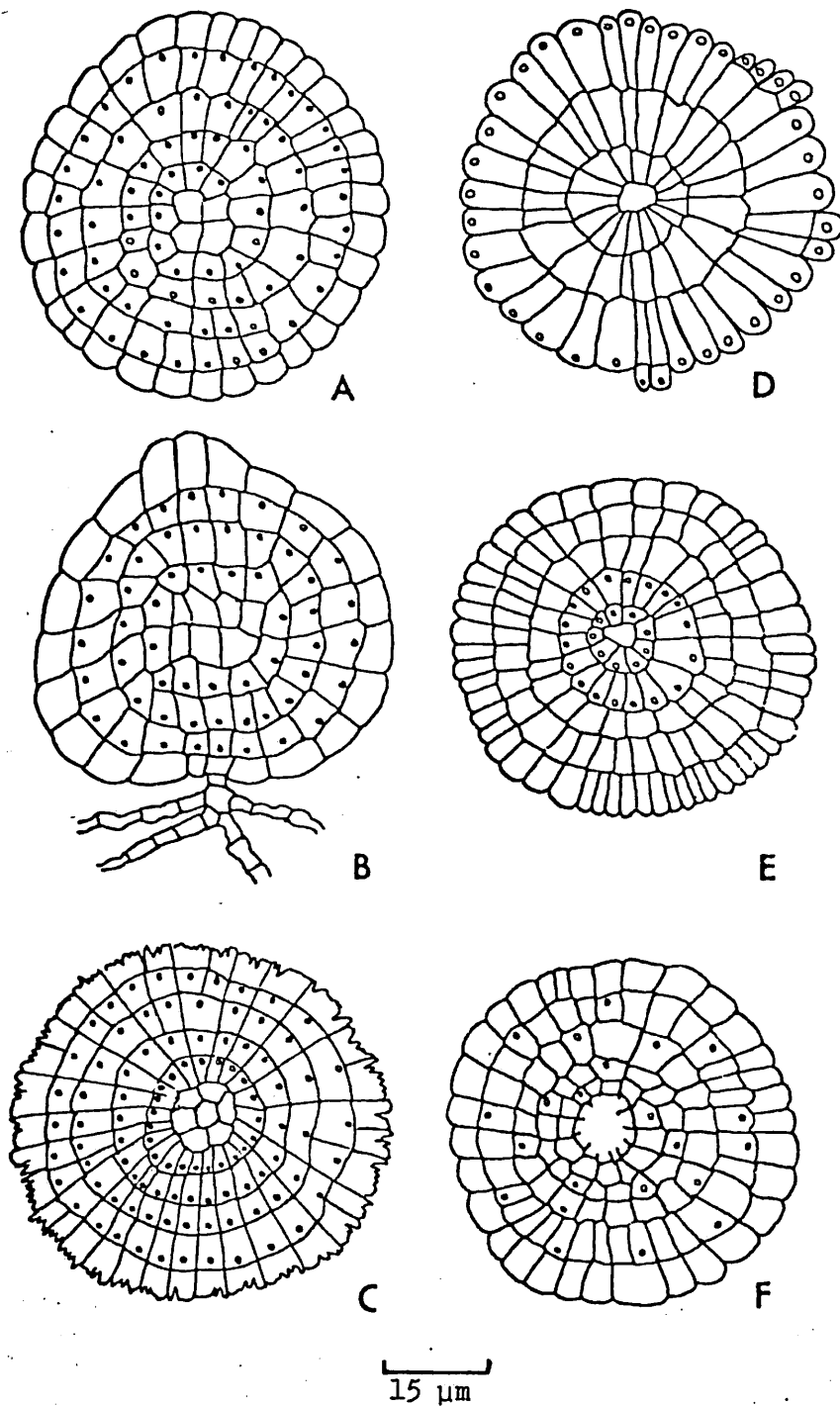
Diagrammatic representation of <u>Callimothallus</u> species described in
the literature: A. <u>C. pertusus</u>   B. <u>C. australis</u>

C. <u>C. corralesense</u>   D. <u>C. quilonensis</u>   E. <u>C. assamicus</u>

F. <u>C. raoi</u>

leaf. It would therefore seem reasonable to infer that humidity may very well be an important factor also. Lange (1978b) had also shown the importance of rainfall in governing the distribution of modern equivalents of Tertiary fossil epiphyllous fungi. In this case however only germinated 'melioloid' spores were included in the spectrum of epiphyllous fungi considered (see Chapter 4, p.83-122).

The general consensus therefore, would indicate that the presence of fossil mycelial remains of putative meliolaceous affinity can be regarded as a pointer toward conditions of high rainfall and probably of high humidity as well. This use of meliolaceous epiphyllous fungi as climatic indicators is perhaps more firmly based when the fungi are still attached to the host leaf. In these cases identification of the host leaf could reinforce the conclusions drawn from the fungal material alone. Nevertheless the extremely characteristic mycelial structure is readily recognisable, even if fragmentary, and its presence should not be discounted as a possible climatic indicator.

6.2   MICROTHYRIALES, PARMULARIACEAE

Despite the confusion as to whether the genus Callimothallus is to be regarded as algal or fungal (see Chapter 4, p.86), I follow the general consensus of Dilcher (1965), Selkirk (1975), Lange (1978b), Elsik (1978) and Pirozynski (1978) and accept this genus as one for fossil epiphyllous fungal fructifications. To date there have been six species described within this genus (see Table 6.1, p.142 and Fig. 6.1, p.143) of which three, C. pertusus, C. corralesense and C.

australis are not known detached from cuticle. The distinction between these species, is in essence, the presence or absence of attached mycelial hyphae. C. pertusus lacks any evidence of mycelial hyphae; whereas Lange (1978b) described, as C. australis, "callimothalloid shields indistinguishable from flabelliform C. pertusus except by attachment at the centrum to knotted hyphae of a mycelium which infects the host leaf". The host leaf was not identified by Lange (1978b) whereas Dilcher (1965) stated that his species, C. pertusus, was borne by a _Sapindus_ leaf. C. corralesense described by Doubinger and Pons (1975) is separated from C. pertusus basically upon the smaller diameters of the pores found in the cells and by the fact that the peripheral cells tend to have a fimbriate or crenate outer margin. No such crenation is to be found in the Newbury material. The three palynological forms have all been decribed from Indian Tertiary deposits. The authors of all three species comment upon the overall similarity of their material with Dilcher's (1965) type-species C. pertusus. Their species are separated from C. pertusus chiefly upon the number and distribution of pores in the cells of the fructification. Elsik (1978) dealt solely with palynological forms of this genus, and whilst he accepted Callimothallus as a valid genus of dispersed epiphyllous fungal fructifications, he made no mention of species other than C. pertusus. Selkirk (1975), despite finding delicate superficial hyphae in association with such fructifications, described from putative lauraceous leaves from Kiandra, New South Wales, did not regard this as a sufficiently important difference to warrant the formation of a new species. Selkirk (1975) therefore placed his material in the type-species C. pertusus. Selkirk (1975) in

contrast to Kar and Saxena (1976), was content to retain Callimothallus as a separate and distinct genus from Phragmothyrites (see Table 4.1, p.88).

Multiperforate shields with all the morphological features of the genus Callimothallus have been isolated fom the matrix of the Palaeocene deposits from the Cold Ash Quarry near Newbury. These specimens, being strictly palynological, with no indication of the host leaf cuticle to which they were originally attached, should perhaps first be compared with the three species of palynological forms. C. quilonensis Jain and Gupta (1970) can be discounted from the outset, because pores are to be found in this species only in the outermost peripheral ring of cells. In contrast the material from the Cold Ash Quarry does not have the perforations restricted to the peripheral cells. C. raoi Ramanujam and Rao (1973) is distinguished from C. pertusus on the basis of the presence of an irregular central cavity in the fructification. Ramanujam and Rao (1973) were uncertain as to whether the central cavity is a regular feature of the species or not. However the presence of pores in some ('a few') of the cells in the fructification, was regarded as sufficient justification to treat the material as a species of Callimothallus. This decision must be questioned however, due to the presence of five to six layers of smaller thicker walled cells surrounding the central cavity. Dilcher (1965) in his purported ontogeny of the Callimothallus fructification from the single-celled 'germlings' does mention the occurrence of some thick-walled cells in the centre of the fructification but suggested that such clusters of thick-walled cells, may be a form of vegetative reproduction. Dilcher (1965) in

PLATE 2 <u>Callimothallus</u> fructifications from the Newbury Deposit.

Magnification X1,500.

1

2

3
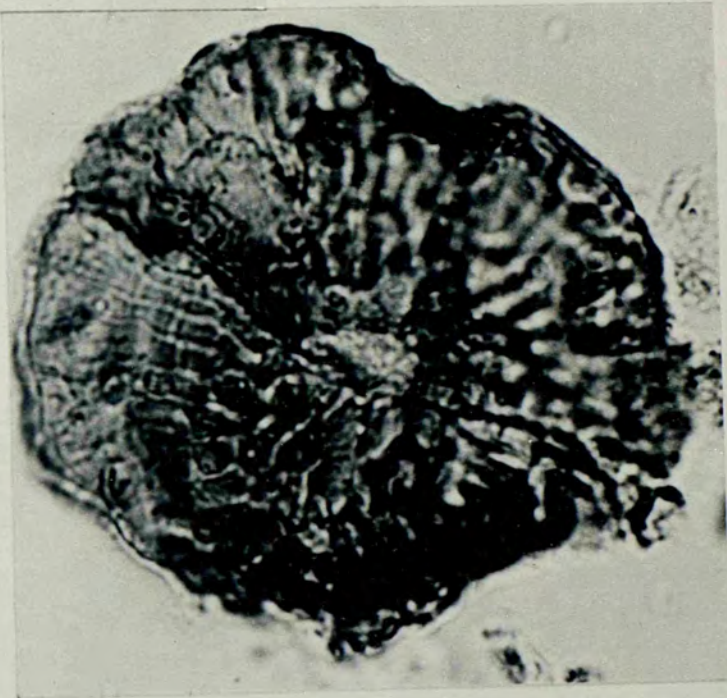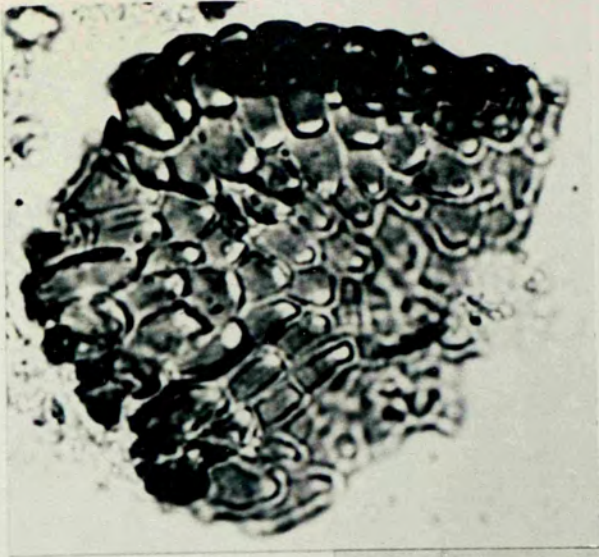
his diagnosis of the genus and the description of the type species comments only that the central cells of the fructification may often be darker than those of the rest of the cells. No mention is made of a marked difference in wall thickness between central and peripheral cells. The attribution of the material by Ramanujam and Rao (1973) to Callimothallus is further called into question if cell diameter measurements cited are compared with those given by Dilcher (1965):-

	CENTRAL CELLS	PERIPHERAL CELLS
Ramanujam & Rao (1973)	1.25-3.00 µm	2.5-6.0 x 2.0-4.0 µm
Dilcher (1965)	3.0-5.0 µm	2.0-8.0 x 3.0-12.0 µm

Irrespective of the validity of C. raoi, the Cold Ash Quarry material lacks any indication of a central cavity in the fructifications. C. assamicus Kar, Singh and Sah (1972), the third palynological species, has the pores or perforations restricted to the central cells of the fructification, pores not being observed in the outer peripheral cells. This is in distinct contrast to the material from Cold Ash Quarry where the central cells of the fructification are not perforate (see Plate 2, fig.1).

As the Cold Ash Quarry specimens are incomplete, there can be no comparison of this form with the species described as C. australis by Lange (1978b). It would seem that the outline of the complete fructification was circular rather than flabelliform, which was one of the major features used by Lange (1978b) to distinguish his species from C. pertusus. The diameter of the fructification from

PLATE 3   Fructifications (cf. <u>Cribrites</u>) from the Hordle Cliff

Deposit. Magnification X1,500.
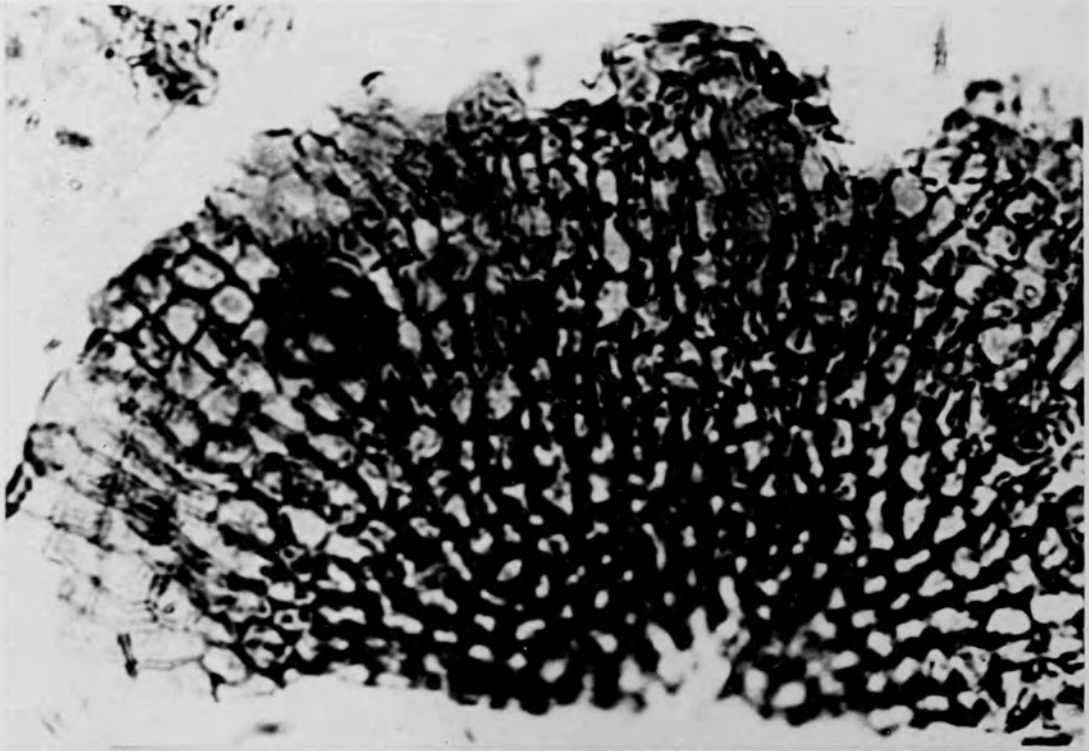
1
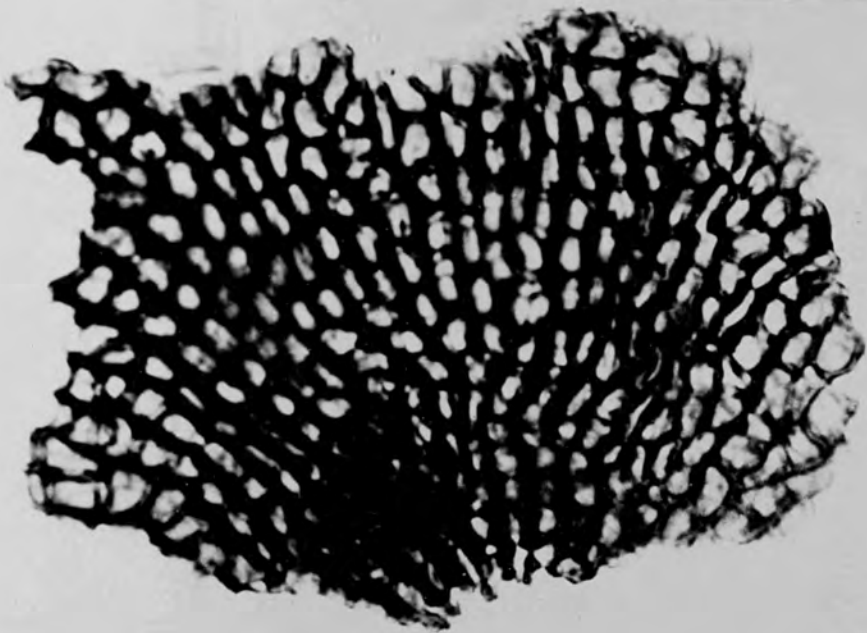
2

Cold Ash Quarry is estimated to be of the order of 40 μm, slightly

smaller than the size range 50-250 μm given by Dilcher (1965) for C.

pertusus. Due to this incomplete nature, identification is therefore

taken no further than Callimothallus sp. (cf. C. pertusus Dilcher).

The Eocene deposits from Hordle Cliff have not shown the

occurrence of this highly distinctive morphological form of

fructification. There are however a very small number of fragments,

found as palynological forms, which are of perforate or porate

fructifications (Plate 3, fig.1-2). Dilcher (1965) described a

multiporate epiphyllous fructification as Microthyriella fungosa.

This is a fossil species within an extant genus. The fructification

was typified as consisting of pseudoparenchymatous cells, many of

which are porate. However when the illustrations (Dilcher, 1965, Pl.

15, figs. 118-120) are compared with the Hordle Cliff palynological

fragments it is evident that there is little or no morphological

similarity and that affinities must be sought elsewhere. Lange

(1978b) has erected Cribrites aurea for a fossil epiphyllous

fructification in which

> "every cell exhibits a large pore that occupies the bulk of the
>
> cell and seems to perforate the cell entirely. In mature
>
> specimens the pores are arranged in more or less radial lines."

Morphologically the Hordle Cliff material bears a very close

resemblance to C. aurea except that the extreme peripheral cells do

not have the marked thickening of the walls shown in the specimens

illustrated by Lange (1978b, figs. 5, 7 and 8). The complete

fructifications of C. aurea were cited by Lange (1978b) as being up

to 150 μm in diameter, although one specimen figured (Lange, 1978b,

fig. 7) is only 25 μm in diameter. The palynological fragment from the Hordle Cliff material, although incomplete, has a maximum radial measurement of 80 μm which would, by extrapolation, give a diameter of 160 μm. This would place the Hordle Cliff fragment extremely close to the upper observed limit of the size range for C. aurea. As in the case of the Newbury examples of Callimothallus, the Hordle Cliff occurrence is far too fragmentary for a definite assignation to Cribrites aurea, however the general similarity of observable features is such that assignation to the form-genus Cribrites is warranted, as Cribrites sp. (cf. C. aurea Lange).

It is interesting to note that Lange (1978b) commented that Cribrites occurred commonly on leaves from Middle Eocene deposits in South Australia, both with Callimothallus and separately, yet these two genera have not as yet been found in close association in either the Palaeocene or Eocene deposits from Southern England. Lange (1978b) has used both 'callimothalloid' and 'cribritoid' shields from modern leaf litter samples as habitat indicators to establish geographic, climatic and vegetational types, and on this basis endeavours to reconstruct both palaeoclimate and palaeoecology of the fossil forms (see Chapter 4, p.105).

Lange (1978b) used the occurrence of 'callimothalloid' and 'cribritoid' shields together in a fossil flora as indicative of an equivalence with present-day wet tropical forest. Although these two forms have not been found in conjunction in either of the deposits studied here, it is very tempting to couple the dual occurrence of Meliolinites-like vegetative hyphae with Callimothallus in the

Palaeocene deposits of Newbury and with <u>Cribrites</u> in the Eocene deposits at Hordle Cliff, and thus conclude that the source vegetation for both these deposits were analogous to present-day wet tropical forest.

6.3 MICROTHYRIALES, MICROPELTIDACEAE

A further type of epiphyllous fructification found in both the Palaeocene and Eocene deposits under consideration can be compared with forms previously described either as <u>Stomiopeltis</u> or <u>Stomiopeltites</u>. Some of the nomenclatural complications brought about by ascribing fossil material either to a living genus or alternatively by erecting a new fossil form-genus have already been dealt with (see Chapter 4, p.90). Discussion here will be restricted to a brief taxonomic survey of previously described forms and a comparison with the fructifications isolated from the Newbury and Hordle Cliff deposits.

Luttrell (1973) recognised 11 families within the loculoascomycete order Microthyriales (see Table 4.3, p.91). Of the many features available for separation of recent fructifications only two of these are readily available for fossil fructifications. Firstly, the nature of the mode of spore liberation; either the fructification possesses a round ostiole, or the fructification opens by crumbling or splitting to form a broad pore, longitudinal slit, or irregular clefts. Secondly, the construction and appearance of the surface of the fructification. The fructification either gives the appearance of a radiate construction, as the individual cells are straight-walled and either square or rectangular in outline or,

FIGURE 6.2

10 μm

A.

10 μm

B.
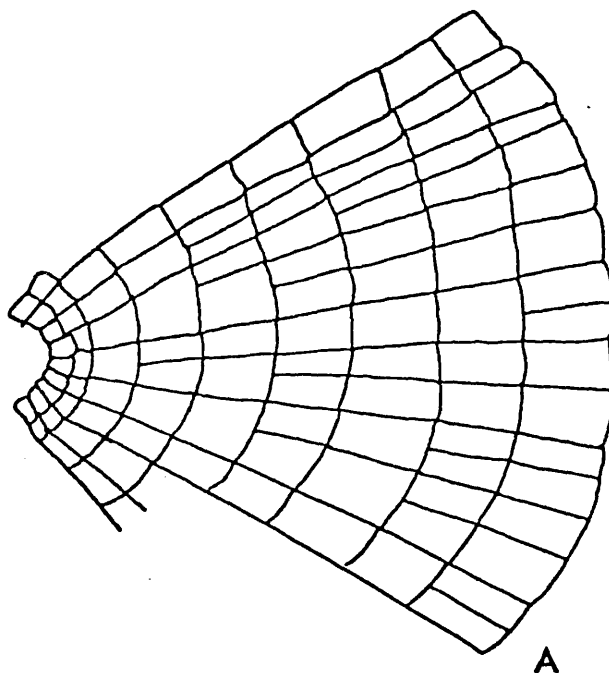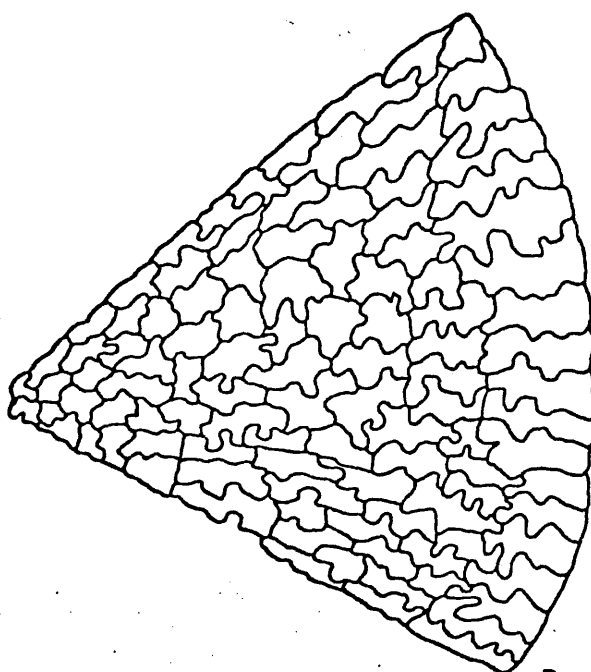
Diagrammatic representations of thyriothecial cell patterns in
Microthyriaceae and Micropeltidaceae.

A. Microthyrium macrosporum (after Ellis, 1976)

B. Stomiopeltis cupressicola (after Ellis, 1977b)

alternatively, the fructification is composed of a hyphal reticulum of sinuous irregularly lobed cells which do not have a regular radiate arrangement (see Fig. 6.2, p. 155). Luttrell (1973) distinguished between Microthyriaceae and Asterinaceae on the one hand and Micropeltidaceae on the other on the basis of the nature of the fructification wall. Microthyriaceae and Asterinaceae have radiating files of cells, Micropeltidaceae possess a fructification wall composed of sinuous meandering hyphae. Pirozynski (1978) has used the nature of spore liberation, fructification construction plus the shape of the fructification to construct a key which places fossil epiphyllous fructifications into modern families of the Microthyriales (see Table 4.2, p.89).

Elsik (1978) has made a very similar 'classification' for dispersed (palynological) fossil fructifications of Microthyriales in which 13 form-genera are distinguished and separated on the basis of their observable morphological features but Elsik (1978) made no attempt to suggest affinities to living microthyrialian families. It is of interest to note that Elsik (1978) regards the form-genus Stomiopeltites as being unavailable for dispersed palynological specimens since its diagnosis by Alvin and Muir (1970) includes details of fructifications, pycnidia, and mycelium. Elsik (1978) regards such palynological forms as being assignable to the form-genus Plochmopeltinites erected by Cookson (1947a) for fructifications 'of a dimidiate form with ascostomatal membranes of sinuous plectenchyma'. Cookson (1947a) attributed these predominantly palynological forms to the sub-family Plochmopeltineae (= Stomiopeltoideae) of the family Micropeltaceae (sensu Clements and

Shear, 1931). Alvin and Muir (1970) queried this attribution on the basis that the fructification is composed of 'sinuous but radiating cells and is not therefore classifiable in the Micropeltidaceae', a conclusion supported by Selkirk (1975) who described similar fructifications to those described by Cookson (1947a) as P. masonii Cookson emend Selkirk from Kiandra, New South Wales. After re-examination of Cookson's (1947a) type material, P. masonii was placed in the family Microthyriaceae. Although Alvin and Muir (1970) and Selkirk (1975) maintain that Plochmopeltinites should be attributed to the Microthyriaceae, this is based solely on their interpretation of the hyphae making up the fructification being radiate in construction. This criterion is extremely hard to distinguish in many fossil fructifications, equally the recognition that the fructification is composed of more than one layer of sinuous cells (cf. Stomiopeltis/Stomiopeltites) necessary to prove affinity with Micropeltidaceae is extremely difficult. Thus a subjective decision as to what constitutes 'radiate' and 'sinuous' construction must be made by each individual worker.

The occurrence of 'light brown, conglobate, 1-septate spores constricted ca 14 μm long x 8 μm wide ...... lying on the outer face of the fructifications close to the ostiole and scattered on the cuticle' was reported by Selkirk (1975). As none were observed attached to hyphae or within a fructification, Selkirk (1975) did not assign them definitely to P. masonii.

Mariusia andegavensis was erected by Pons and Boureau (1977) as a new microthyriaceous form-genus for epiphyllous fossil fructifications from Cenomanian deposits from Anjou, France. Their attribution to the Microthyriaceae of this type was based on the presence of 3-septate phragmospores, sinuous hyphae arranged radially and the occurrence of intercalary hyphopodia producing coralloid haustorial processes in the host epidermal cells. Pons and Boureau (1977) list the following extant genera of Microthyriaceae as those with morphological similarities to the fossil material: _Asterinema_, _Caudella_, _Maublancia_ and _Platypeltella_. Of these _Platypeltella_ has the closest vegetative similarity but the ascospores of _Platypeltella_ do not have a close morphological similarity with those found in association with _Mariusia_. Ascospores of _Platypeltella_ are 3-septate, hyaline becoming brown at maturity, not constricted at the septa, fusoid and slightly curved in shape. The spores found in association with _Mariusia_ were described by Pons and Boureau (1977) as tetracellate (3-septate), the two central cells being larger than the two terminal cells. The terminal cells differ in shape, one being much more globular, the other more elongate, also the spore outline is not smooth due to constrictions at the septa.

Selkirk (1975) made no comparison of _Plochmopeltinites masonii_ with extant microthyriaceous genera. However the occurrence of 'light brown conglobate, 1-septate spores constricted _ca_ 14 µm long x 8 µm wide ..... lying on the outer face of the fructifications close to the ostiole and scattered on the cuticle' were reported. As none were observed attached to hyphae or within a fructification Selkirk (1975) did not assign them definitely to _Plochmopeltinites masonii_.

However of the genera listed by Pons and Boureau (1977), two deserve closer examination in this context. Asterinema, Caudella and Maublancia all produce bicellular (1-septate) ascospores. Caudella can be dismissed as the ascospores in this genus have the lower end drawn out into a long slender appendage. However Luttrell (1973) groups both Asterinema and Maublancia into the group of microthyriaceaous genera in which lateral hyphopodia are consistently present, a feature not mentioned either by Cookson (1947a) or Selkirk (1975) in describing Plochmopeltinites masonii.

The taxonomic position of the Recent genus Plochmopeltis has been re-evaluated by von Arx (1959) and Luttrell (1973); von Arx (1959) concluded that the fructifications in the living genus are

".......flattened ascomata which are not covered with a perithecial wall. The asci are surrounded by paraphysoids which are brown and furcate into short branches at their apices. ....

.. The genus Plochmopeltis is related to Schizothyrium and Phillipsiella and should be placed in the order Dothiorales."

Luttrell (1973) re-introduced the ordinal name Hysteriales for the group of families grouped within the order Dothiorales (sensu von Arx, 1959) and placed Plochmopeltis in the family Phillipsiellaceae. It would appear therefore that the contention of Elsik (1978) admittedly on apparent morphological similarity only, that Stomiopeltis/Stomiopeltites are assignable to Plochmopeltinites if found as palynological forms, is valid if Plochmopeltinites is regarded as a form-genus for micropeltidacean-like fructifications. Pirozynski (1978) has stressed that Plochmopeltinites, although a fossil member of the Micropeltidaceae, bears no relation to the

FIGURE 6.3
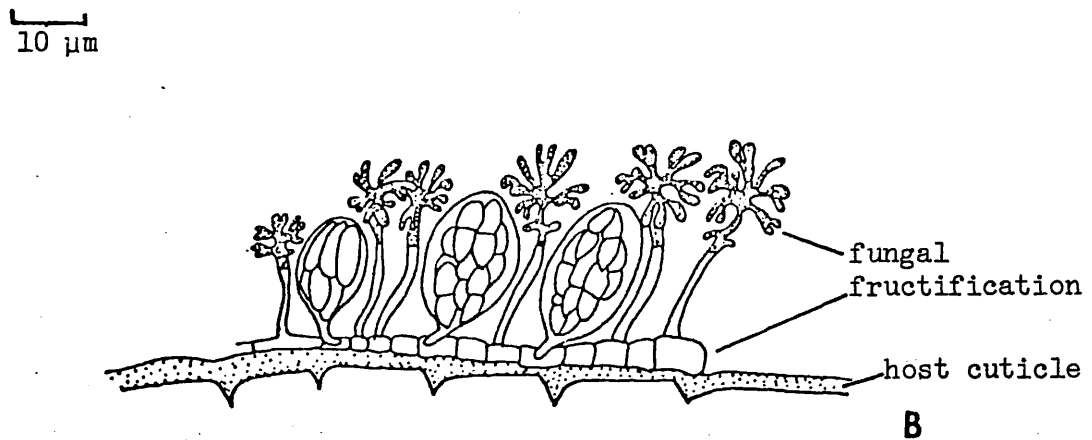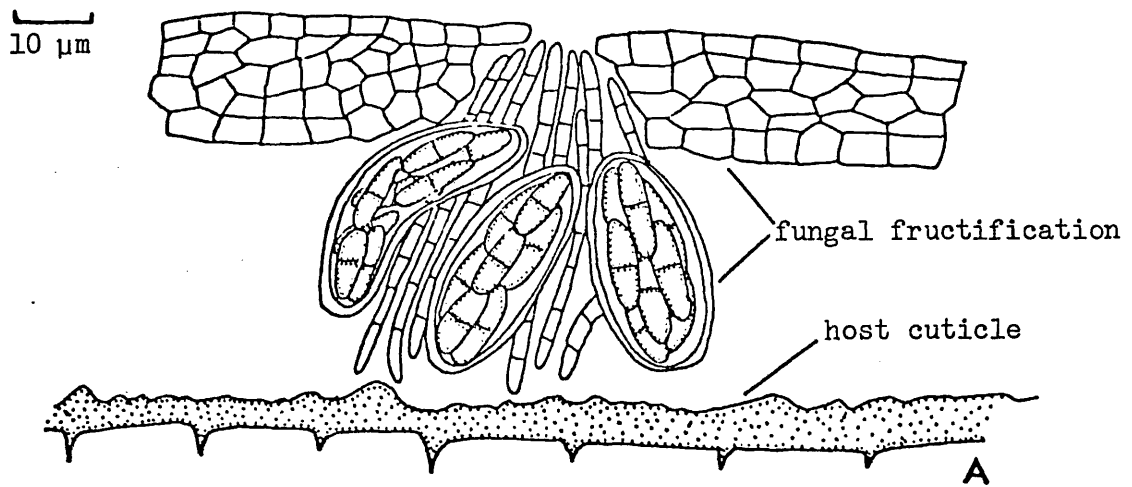
Vertical sections of fructifications of _Stomiopeltis_ and _Plochmopeltis_

to show different constructions.

A. _Stomiopeltis_ _polyloculatis_ (after Luttrell, 1946)

B. _Plochmopeltis_ _intricata_ (after von Arx, 1959)

living genus <u>Plochmopeltis</u> which he placed in the family Schizothyriaceae (=Hysteriales, Phillipsiellaceae <u>sensu</u> Luttrell, 1973) on the basis of differences in the construction of the fructification (see Fig. 6.3, p.160).

Some of the nomenclatural complications and the different treatments of epiphyllous fructifications attributed to the <u>Stomiopeltis</u>/<u>Stomiopeltites</u> complex were raised in Chapter 4 (p. 117). Dilcher (1965) was of the opinion that his fossil material showed sufficient essential features in common with extant material to be regarded as contaxic with the living genus <u>Stomiopeltis</u> as the fossil species <u>S. plectilis</u>. Dilcher (1965) found no spores, either sexual (ascospores) or asexual (pycnidiospores) associated with his material. He was at pains to compare his material with the descriptions of living species given by Luttrell (1946). <u>Stomiopeltis</u> <u>citri</u> Bitancourt was examined extremely closely as this is the only living species in which pycnidia (asexual spore-producing structures) have been described. Dilcher (1965) concluded that the fruiting bodies found in varying stages of development on the host cuticle should be interpreted as immature ascocarps rather than the more diminutive pycnidia. Alvin and Muir (1970) found very similar fructifications on conifer shoots resembling <u>Frenelopsis</u> from the English Wealden, however they queried the validity of including Dilcher's material in the living genus <u>Stomiopeltis</u> when no spores were present. Alvin and Muir (1970) were taxonomically more cautious and, as the material again had no associated spores, erected the form-genus <u>Stomiopeltites</u>, because Batista (1959) had distinguished living genera within the Micropeltidaceae largely on spore

characteristics. The diagnosis for the form-genus <u>Stomiopeltites</u> is as follows:

> "A reticulate mycelium present, lacking hyphopodia. Thyriothecia composed of a plectenchyma of irregularly arranged sinuous cells. Spores unknown." (Alvin and Muir, 1970).

Luttrell (1973) also based his key to the living genera of the family Micropeltidaceae to a large extent on spore characters. After careful comparison, again with <u>Stomiopeltis citri</u>, Alvin and Muir (1970) concluded that in spite of the striking similarity of the fossil material with <u>Stomiopeltis</u>, 'an equally good comparison could be made with a number of other genera of the Stomiopeltoideae'. This is despite Alvin and Muir (1970) having material which appeared to be more complete than that of Dilcher (1965). Alvin and Muir (1970) found structures which they interpreted as asexual pycnidia, as well as sexual fructifications (thyriothecia). Although no proof could be advanced to show that pycnidia and thyriothecia belonged to the same fungus, Alvin and Muir (1970) maintained that their occurrence and distribution provided some evidence that they probably were from the same fungus, and as a consequence included a description of the pycnidia in the diagnosis of <u>Stomiopeltites cretacea</u>. After a careful examination of the descriptions of <u>Stomiopeltis plectilis</u>, <u>Plochmopeltinites masonii</u> and <u>Stomiopeltites cretacea</u>, Pons and Boureau (1977) concluded that fructifications borne on cuticles of <u>Frenelopsis alata</u> from Cenomanian deposits of Anjou were conspecific with <u>Stomiopeltites cretacea</u>. Pons and Boureau (1977) admitted that the distinction between <u>Plochmopeltinites</u> and <u>Stomiopeltites</u> is not an easy one, especially if preservation of the fossils is not good.

PLATE 4   Fructifications (cf. _Plochmopeltinites_ _masonii_) from the
Newbury Deposit. Magnification X1,500.

Figure 1. Border of thyriothecium to show associated
vegetative mycelial hyphae.

Figure 2. Putative early stage in thyriothecial
development.

1
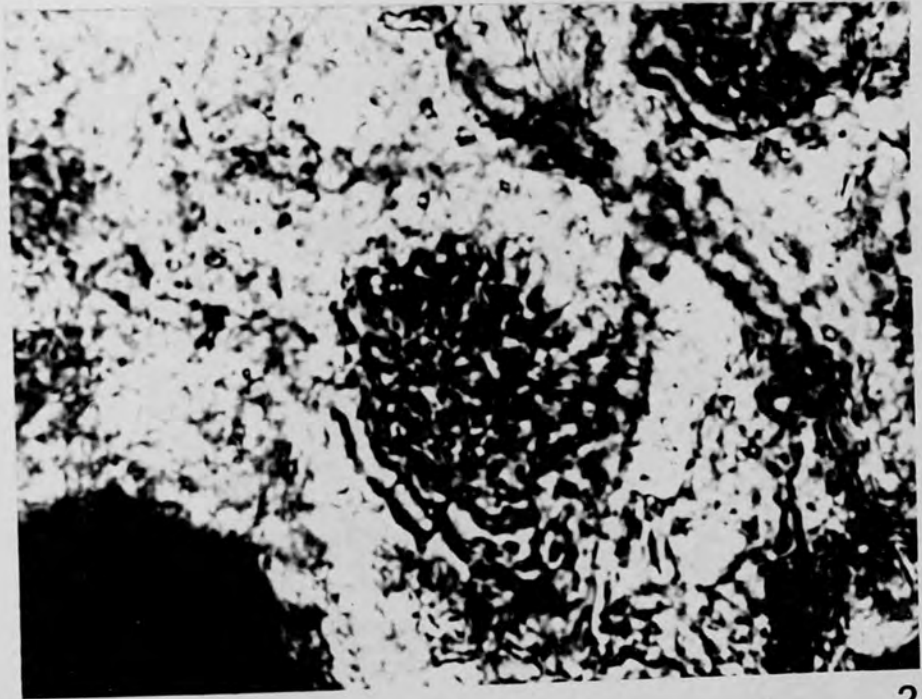
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However despite the absence of pycnidial stages, the overall similarity was, in their opinion, sufficient to include the Anjou material in S. cretacea.

MICROPELTIDOID FRUCTIFICATIONS FROM THE NEWBURY DEPOSIT

Modes of preservation also play a part when the specimens from Newbury and Hordle Cliff are considered. Material from Newbury has been found on the host leaf cuticle whilst that from Hordle Cliff is almost totally palynological. This could be explained by suggesting that the material from the Newbury deposit is more nearly autochthonous. With little, or minimal, transport prior to final deposition, there has been less mechanical fragmentation and, perhaps more relevant in this context, less likelihood for biologically-induced degredation. In contrast the Hordle Cliff material is more likely to have been allochthonous. Due to greater transport before final deposition, both mechanical abrasion, and especially as shown by the highly diverse flora of fossil fungal spores present, bio-degredation, have resulted in much smaller and more dispersed leaf and cuticle fragments. Both thyriothecia and vegetative mycelial hyphae are present on the host leaf cuticle from Newbury (see Plate 4, fig. 1) and thus all three genera, Stomiopeltis, Stomiopeltites and Plochmopeltinites must be considered as possibilities for their attribution. However, as some of the vegetative mycelia associated with the fructifications bear structures which could be interpreted as lateral hyphopodia (see Plate 4, fig. 2), the choice is potentially even wider. Hyphopodiate mycelia are characteristic of several microthyrialian families, but of these, only the families

Asterinaceae and Microthyriaceae warrant closer scrutiny. Pirozynski (1978) has stressed the parallel in fructification structure between Microthyriaceae and Asterinaceae but those of the Asterinaceae have no definite ostiole, but through crumbling, cracking or gelatinization of the central area form a large irregular or stellate crack. However as previously stated, Selkirk (1975) and Alvin and Muir (1970) came to markedly different conclusions to Pirozynski (1978) concerning the family to which Plochmopeltinites should be attributed, on the basis of the same evidence. Therefore despite the presence of structures that could be regarded as lateral hyphopodia on the vegetative hyphae, on the basis of lack of radiate construction, and no indication of an irregular or stellate opening the possibility that the Newbury material could belong to the Asterinaceae is discounted. The alternative interpretation is that the structures resembling hyphopodia are immature fructifications. Luttrell (1946) described the process of fructification formation in Stomiopeltis polyloculatis as follows:

'In the formation of an ascocarp, hyphae of the superficial mycelium produce branches which by twisting and branching and by irregular fusions and extensions of their cells fill the interstices of the mycelial net to form a continuous compact tissue'.

The configuration of the structures in question are such that this interpretation is plausible although they are too immature to determine whether they could alternatively be equated with the structures described as pycnidia by Alvin and Muir (1970). The young

thyriothecia illustrated by Dilcher(1965) for Stomiopeltis plectilis
show a more advanced organisation than the structures under
consideration from Newbury. The closest morphological agreement is
with the structures described as young thyriothecia of
Plochmopeltinites masonii illustrated by Selkirk (1975, fig. 7, Plate
9).

Although Alvin and Muir (1970) and Selkirk (1975) maintain that
P. masonii should be attributed to the Microthyriaceae this is solely
on their interpretation of the hyphae making up the thyriothecia
being radiate in arrangement. In this case the organisation is
regarded as sinuous and, following Cookson (1947a), Elsik (1978), and
Pirozynski (1978) the Newbury material is regarded as being more
closely allied to Micropeltidaceae than Microthyriaceae. The
material bears a close morphological similarity to the form-genus
Plochmopeltinites as diagnosed by Cookson (1947a):

"Fossil ascomata of dimidiate form with ascomal (sic) membranes
of sinuous plectenchyma. Ascospore characters unknown".

This diagnosis is far from exacting in the description of the
features characterising this form-genus. The more detailed diagnosis
of P. masonii as emended by Selkirk (1975) is:

"Fructifications superficial, scattered, occasionally crowded
and confluent, rounded, glabrous, ostiolate, up to 200 µm
diameter; margin entire-sinuate or irregularly lobed. Covering
membrane prosenchymatous, composed of slender wavy hyphae 2-5 µm
thick, those of the central area often thicker-walled than those

toward the periphery. Some hyphae may extend beyond the ascoma as free hyphae. Ostiole up to 25 μm in diameter, surrounded by slightly raised border of small thick-walled cells. Free hyphae, if present, indistinctly septate, sometimes forming a pellicle."

Apart from the interpretatin of the hyphal filaments making up the prosenchyma as being radiate the above diagnosis would easily accomodate the Newbury material. Especially as one of the Newbury thyriothecia shows a small central area of apparently thinner-walled cells as described and illustrated for P. masonii by Selkirk (1975, fig. 3, Plate 12). Thus the Newbury material can be regarded as congeneric with Plochmopeltinites and there is a very strong possibility of identity with P. masonii Cookson emend Selkirk.

MICROPELTIDOID FRUCTIFICATIONS FROM THE HORDLE CLIFF DEPOSIT

Very similar fructifications to those found attached to cuticles in the Newbury Palaeocene deposits are represented, predominantly as palynological forms, from the Eocene deposits at Hordle Cliff. Quite a high percentage of the Hordle Cliff specimens are still attached to cuticular fragments, but these fragments are too small to allow accurate determination of the host plant. As has been shown, the choice of form-genera appears to be between Stomiopeltites and Plochmopeltinites. The possibility of attributing dispersed fructifications to extant genera such as Stomiopeltis is not considered to be a valid one, on the basis that such dispersed forms

PLATE 5   Fructifications of <u>Stomiopelti~~tes~~</u> eocenica (nom. prov.)

from the Hordle Cliff Deposit. Magnification X1,500.

Figure 1. Detail of central region of fructification

to show cellular organisation.

Figure 2. Entire fructification on cuticular fragment

to show overall construction.
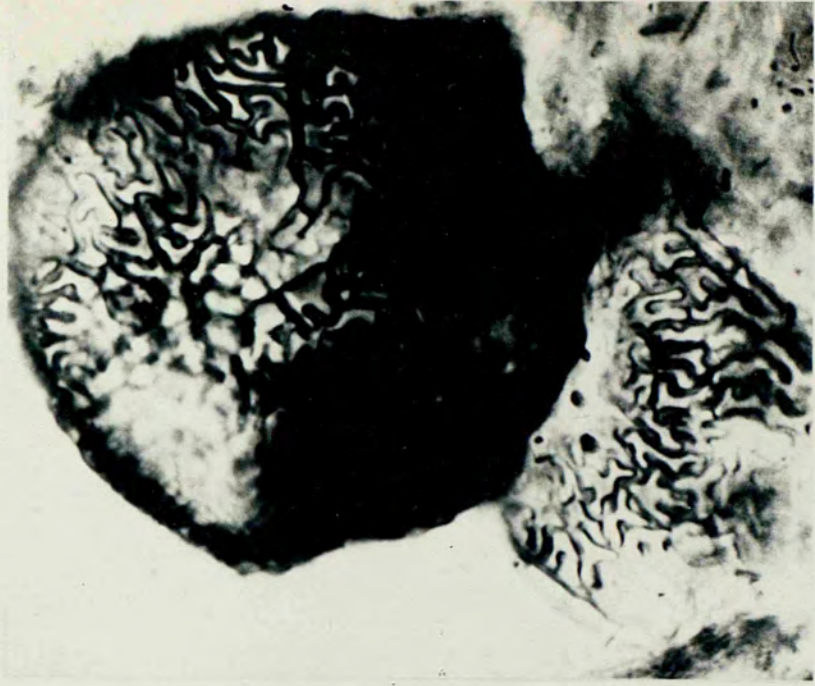
1

2

do not provide sufficient criteria to make such a procedure taxonomically sound.

Although Stomiopeltites has not been used for, and in fact has been regarded by Elsik (1978) as inapplicable to, palynological forms, some of the Hordle material, attached as they are, albeit to fragmentary cuticular remnants, could well be compared with those specimens previously included in this form-genus.

Although incomplete and apparently somewhat contorted, one Hordle Cliff specimen (see Plate 5, fig. 1) has the central portion extremely well preserved and there is sufficient clarity in parts of the more peripheral regions to determine the type of construction. The fossil specimen in question appears to be a plectenchymatous to pseudoparenchymatous construction, with the individual cells of the hyphae generally being highly sinuous rather than radiate in organisation. The disposition of these sinuous cells forming the fructification is such as to be compatible with the ontogenetic sequence for the formation of the ascocarps in Stomiopeltis polyloculatis described by Luttrell (1946) previously cited (p.166). Areas both of the central and peripheral regions can be seen to be made up of files of regular cells bearing short lateral branches which due to their tortuous shapes cannot be followed for any great distance over the surface of the fructification. These files of regular-shaped cells can be likened to the cells of the pre-existing superficial mycelial reticulum from which are produced short lateral branches 'which by twisting and branching and by irregular extensions

and fusion of their cells fill the interstices of the mycelial net to form a continuous, compact tissue' (Luttrell, 1946).

The overall morphological similarity between the fossil specimen and extant species of Stomiopeltis is, if the above interpretation is accepted, very close. There is no evidence of spores associated with the fossil specimen and thus, following Alvin and Muir (1970), attribution to Stomiopeltis would seem inadvisable. The appearance of the fossil specimen however makes the determination of whether this is a pycnidial stage or ascocarp stage difficult. As previously stated only Stomiopeltis citri has been shown to have pycnidial stages amongst the extant species although Luttrell (1946) commented upon the abundance of pycnidial material on the leaves of the type of Stomiopeltis cassiae Mendoza. These are similar to those of S. citri but Luttrell (1946) was non-committal concerning the linking of these pycnidia with S. cassiae. Pycnidia of S. citri are between 80 μm and 150 μm in diameter, both of which are in excess of the 60 μm diameter of the central portion of the fossil specimen. Comparison with extant species does not add any clarification as to the nature of the fossil structure. The pycnidia of S. citri are uniloculate but of the seven species of Stomiopeltis reviewed by Luttrell (1946), six also have uniloculate ascocarps. The fossil structure is, as far as can be ascertained uniloculate also. However due to its incompleteness, overall dimensions for the entire fossil structure cannot be given with any degree of precision although a diameter in excess of 150 μm is a conservative estimate, with the central part, as stated above, of the order of 60 μm. If this fossil structure is

taken to be an uniloculate ascocarp, comparison could be made with Stomiopeltis suttoniae (Mendoza) Luttrell. In this living species the ascocarp is differentiated into a central convex portion and a peripheral flat border. The measurements cited by Luttrell (1946) for S. suttoniae, 231-408 µm in overall diameter, 176-231 µm for the diameter of the darker, convex central region, and 27-95 µm for the lighter more parenchymatous border are far greater than those of the fossil material. Alvin and Muir (1970) made no reference in their diagnosis of Stomiopeltites cretacea to such a distinction between the central and outer parts of the fructification. Pons and Boureau (1977) in their description of the material they regarded as conspecific with S. cretacea state that the fructification is flat but slightly thicker toward the centre plus an external border formed of numerous septate branched, sinuous and irregularly lobed mycelial hyphae.

Although the Hordle Cliff material does not give any indication of what type of vegetative mycelial hyphae are associated with the fructification, the construction of the ascocarp is so similar to that which distinguishes and characterises the living genus Stomiopeltis, that attribution to the form-genus Stomiopeltites is, in my opinion, thoroughly justified. The Eocene Hordle Cliff material cannot be regarded as being conspecific with Stomiopeltites cretacea due to the absence of vegetative mycelial hyphae and the lack of presumed pycnidia as well as the difference in thyriothecial construction. It is proposed therefore to create a new species for this Eocene material, Stomiopeltites eocenica (nom. prov.).

PLATE 6   Fructification (cf. _Plochmopeltinites_) from the Hordle

Cliff Deposit.   Magnification X1,500.
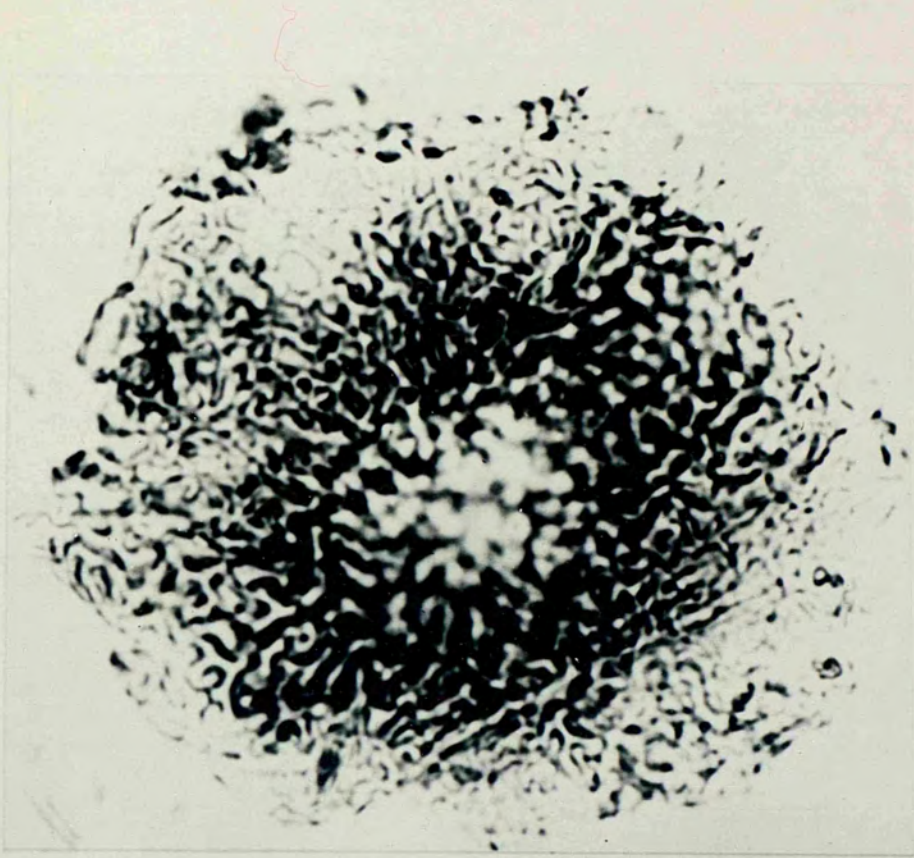
The Hordle Cliff deposit has also provided a suite of fructifications, both strictly palynological and attached to fragmentary cuticular remains which, by their sinuous non-radiate construction are best compared with Plochmopeltinites. Cookson (1947a) when erecting this form-genus and the species P. masonii, included strictly palynological forms and those on unidentifiable cuticular fragments together. Thus as Elsik (1978) has included Plochmopeltinites as a valid form-genus for palynological forms, here we have the happy circumstance of a form-genus able to encompass specimens presented in varying preservational forms. The organisation of the fructifications suggests that they are to be compared with Plochmopeltinites rather than with Stomiopeltites because there is little to no evidence of the incorporation of the more regular superficial mycelial hyphal cells which typify the Stomiopeltites mode of construction. The fructifications do tend to have a looser organisation toward their periphery (see Plate 6) suggesting that they are in accord with the description given by Luttrell (1973) to distinguish the Micropeltidaceae in his key to the families of the Hemisphaeriales:

'Shield composed of a hyphal reticulum, or of inordinately arranged, sinuous, irregularly lobed cells passing into a hyphal reticulum at the margins; mycelium superficial, brown or hyaline and inconspicuous'.

The central region of the fructifications exhibit a variety of degrees of opacity suggesting that these regions are composed of several layers of cells, again a feature of the mode of construction common to many extant genera of the Micropeltidaceae. In most cases however, there is no distinct ostiole present in these fossil forms

although in each case there seems to be a central area inside the putative thickened zone which is lighter in colour and is suggestive of a zone of weakness, or thinner walled cells, covering the eventual site of the circular ostiolar opening.. The overall similarity of these fructifications to those previously described within the Plochmopeltinites complex is here regarded as sufficient to include the Hordle Cliff specimens within this form-genus.

The present day Micropeltidaceae are almost exclusively tropical epiphytic or epiphyllous genera with a strong preference for evergreen plants with waxy leaves, however they show little evidence of host specificity (Pirozynski, 1978). The presence of this type of fructification in both the Newbury and Hordle Cliff deposits would appear to reinforce the conclusions drawn from the presence of the melioloid, callimothalloid, and cribritoid fossil fungal forms previously described. The totality of these fossil fungal forms strongly suggest that the host or source vegetation in each case occurred in climatic conditions analagous to those of present day tropical rain forest.

FIGURE 7.1
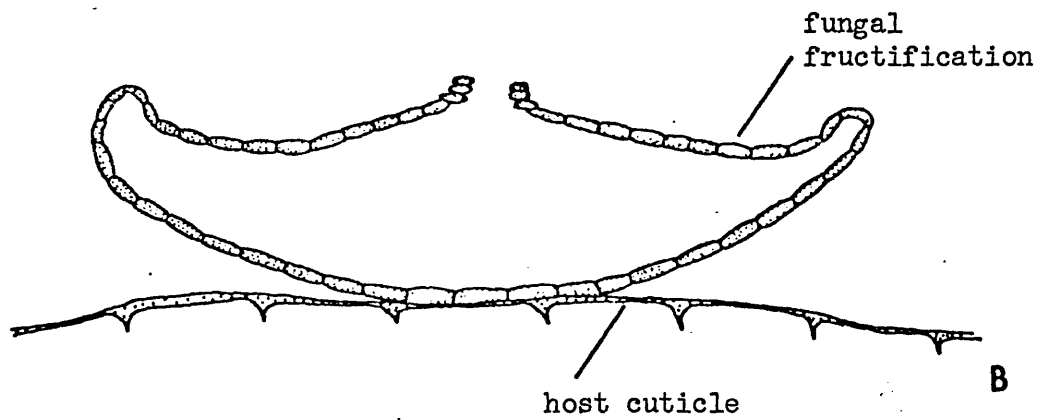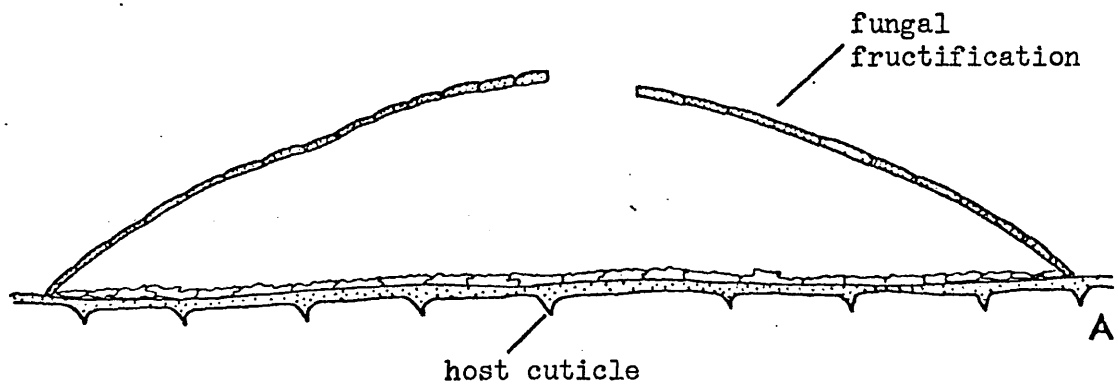
Diagrammatic representations of thyriothecia in vertical section.

(Magnification ca. X1,000)

A. Microthyrialian thyriothecium, modified from Talbot (1971).

B. Dothidealian thyriothecium, modified from Gaümann (1928).

7. FURTHER EPIPHYLLOUS FUNGI FROM THE LOWER HEADON BEDS

N.B.   Some of the material discussed in this chapter has been

published previously (see Smith, 1980 - Appendix III).

As well as the fossil fungal forms common to both deposits dealt

with in the preceding chapter, there is a wide and diverse range of

forms that occur only in the Hordle Cliff deposits from the Lower

Headon Beds.

TRICHOTHYRIACEOUS FRUCTIFICATIONS

Smith (1980) has shown that there has been some degree of

confusion in the literature on fossil fungi concerning the taxonomic

placement of some form-genera.   The uncertainty hinges upon the

interpretation placed upon the construction of the fructification

(thyriothecium).   Luttrell (1973) has catalogued the distinguishing

features of the various orders comprising the Loculoascomycetes (see

Table 4.3, p. 91 and Chapter 4, p. 92); and the main difference is

whether the fructification is dimidiate-scutate (that is, like an

up-turned saucer) characteristic of the order Microthyriales, or

perithecoid (that is, with a distinct cellular floor to the

fructification) characteristic of the order Dothidiales (see Fig.

7.1, p. 178).   The difference between the Dothidiales and

Microthyriales is summarised by J.P. Ellis (1976) as follows:

"Dothidiales are distinguished from the Microthyriales by having

lenticular (flattened turbinate) ascocarps. Both the upper and

lower walls are formed of brown, radially arranged plates of

quadrilateral cells joined at the rim ..... Microthyriales are characterised by having a convex hemispherical ascocarp, the upper wall of which is here referred to as a scutellum. The lower wall is formed of very thin-walled cells closely applied to the cuticle of the host."

This distinction between the presence and absence of a definite floor to the fructification is often extremely difficult to observe in living fungi and the distinction can be even more difficult when dealing with fossil forms. The distinction becomes even more difficult due to the ecological inter-relationship of the two families, the Trichothyriaceae (O. Dothidiales) and Microthyriaceae (O. Microthyriales). Trichothyriaceous fungi are specialised ectoparasitic genera, their hosts being the epiphyllous fungi of the families Microthyriaceae and Meliolinaceae. The work of Macko (1957) is an example of the confusion that exists in the literature, for he equated Phragmothyrites eocaenica (fossil form-species of Microthyriaceae) with the extant Trichothyrium fimbriatum, but from an examination of the illustrations (Macko, 1957; Plate LXXIII, numbers 3-8) it is obvious that there are two distinct thyriothecial forms some definitely attributable to Microthyriaceae (Macko, 1957; Plate LXXIII, numbers 3-5) and some that could possibly be compared with trichothyriaceous fructifications (Macko, 1957; LXIII, numbers 6-8) although no clear evidence of a persistent cellular floor can be drawn from Macko's (1957) illustrations. Pirozynski and Weresub (1979a) state that fructifications of fossil Trichothyriaceae (form-genus Trichothyrites) are often accompanied by the highly distinctive asexual spores (conidia) which have been attributed to the form-genus Spegazzinites. Neuy-Stolz (1958) illustrates such a

spore from the German brown coals and from this deduced the presence

of Trichothyrium-like fungi in that flora although none of the

fructifications illustrated (Taf. 2, figures 8-14) show

Trichothyrium-like construction. Rosendahl (1943) used the features

of a complete fructification, that is, possessing both upper and

lower walls, an erect ostiolar collar, the uppermost cells of which

bear setae to describe the form-species Trichothyrites pleistocaenica

The fructifications upon which the form-species was based were found

in association with both spruce needles and moss leaves from an early

Pleistocene deposit from Minnesota. Rosendahl (1943) commented on

the occurrence of vegetative mycelial hyphae and perithecia which he

tentatively identified as Herpotrichia a member of the Pleosporaceae

(sensu lato) associated with the fructifications on the spruce

needles. Close examination however failed to disclose any connection

between the fructifications and the Herpotrichia-type hyphae, and

Rosendahl (1943) concluded that the occurrence on both spruce needles

and two species of moss suggested a saprophytic existence for the

fungus. Rosendahl (1943) compared his material with fossil

fructifications described by Pampaloni (1902a), Engelhardt and

Kinkelin (1908), Nathorst (1915), Krausel (1920), and Edwards (1922)

and concluded that his Pleistocene material could perhaps be

congeneric with that described by Krausel (1920). This was on the

basis of a small line drawing (Krausel, 1920; figure 7, p. 353) which

is far from detailed, but which Rosendahl (1943) interpreted as

having 'a definite ostiole, an entire margin and composed of large

cells' plus the fact that Krausel's (1920) material was found on

leaves of Sequoia langsdorfii. However Rosendahl (1943) made the

important point that all the reports he cited were based upon the

surface view of the fossil fructification and therefore it is 'impossible to determine from the surface aspect alone whether the perithecia (sic) (ascomata) are dimidiate or complete .....' and consequently described the material from Minnesota as a fossil genus of the Trichothyriaceae, but made no attempt to relate this genus to any extant genus. Petrak (1950) elevated from sub-generic level to generic level the taxon Trichothyrina for predominantly saprophytic fungi as opposed to Trichothyrium which is characterised as being a genus parasitising other fungi. J.P. Ellis (1976) has constructed a key to the genus Trichothyrina and three other genera Microthyrium, Stomiopeltis, and Actinopeltis, based on characters that could be distinguished even in fossil fructifications. Both Trichothyrina and Actinopeltis are in the family Trichothyriaceae from the Order Dothidiales; Microthyrium from the Microthyriaceae, and Stomiopeltis from the Micropeltidaceae within the order Microthyriales. The first dichotomy of this key is the presence or absence of a conspicuous basal plate to the thyriothecium (see Fig. 7.1, p. 178). Selkirk (1975) has enumerated the difficulties involved in positive and definite identification of thyriothecia from fossil deposits as members of the Trichothyriaceae rather than the Microthyriaceae. The uncertainties centre upon determining the details of thyriothecial construction. These concern firstly the difficulty concerning the presence or absence of the basal plate of the thyriothecium stressed both by Rosendahl (1943) and J.P. Ellis (1976). The thyriothecia of the Trichothyriaceae open by means of a circular ostiole borne on a short papilla of thickened cells above the general level of the upper thyriothecial wall. This papilla may be difficult to observe in fossil specimens. Selkirk (1975) maintains that the presence of a

PLATE 7   Fructifications of <u>Trichothyrites</u> <u>hordlensis</u> Smith (1980)
           from the Hordle Cliff Deposit. Magnification X1,500.

           Figures 1. and 2. Specimens showing raised ostiolar
           neck and indications of lower wall of thyriothecium.
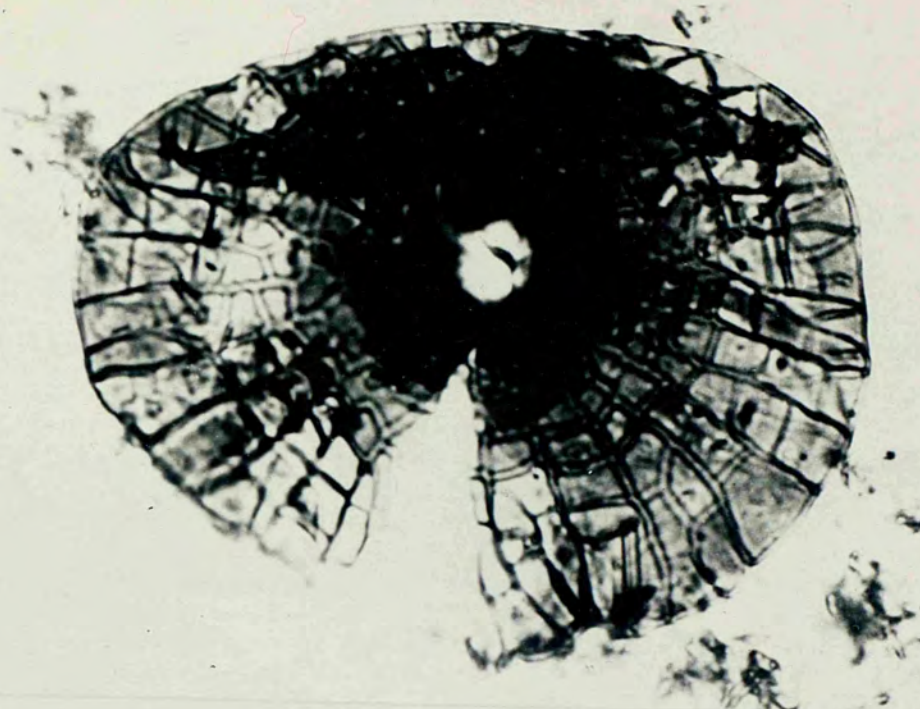
1
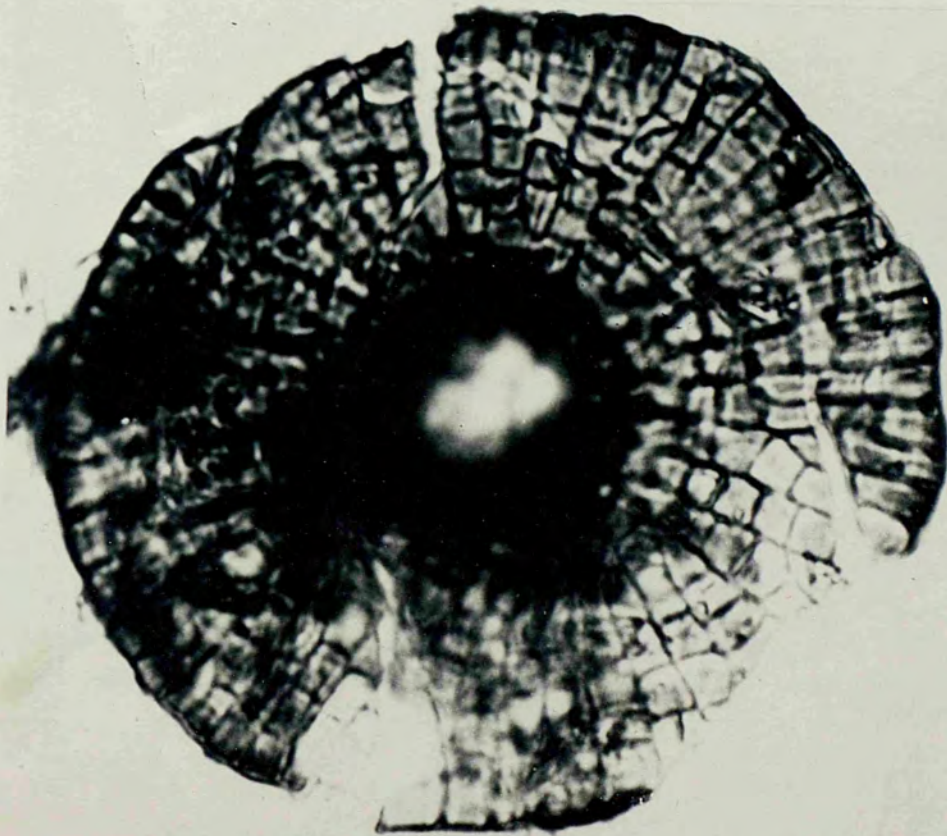
2

papilla can only be verified by sectioning the material; Smith (1980)
however maintained that the thickened cells of the ostiolar papilla
often retain sufficient height above the fructification, despite
dorsiventral compression of the entire fructification, to be readily
observable in a higher focal plane than the cells of the upper wall
of the fossil fructification (see Plate 7, fig. 2).

The Hordle Cliff material is strictly palynological and due to
the predominantly dorsiventral flattening, and perhaps the subsequent
preparative techniques employed, often leads to rupture of the upper
walls of the fructification allowing the presence of a well-defined
and complete lower wall to be seen (see Plate 7 , fig. 1). Although
size measurements given by Ellis (1977a) in defining living species
of Trichothyrina are close to those of Trichothyrites hordlensis
(Smith, 1980) and also Trichothyrites pleistocaenica (Rosendahl,
1943) these are insufficient to suggest a congeneric relationship.
The mode of nutrition for Trichothyrites pleistocaenica is uncertain
and, as the thyriothecia attributed to Trichothyrites hordlensis are
totally palynomorphic, there is no method or criterion for suggesting
any taxonomic relationship at less then the family level.

The taxonomic uncertainty of whether fossil fructifications can
be assigned to Trichothyriaceae is highlighted when the form-genus
Notothyrites is considered. Notothyrites was erected by Cookson
(1947a) with two species N. setiferus and N. airensis for fossil
specimens which were predominantly palynological. N. setiferus type
localities were given as Kerguelin Island and Kiandra (New South
Wales), N. airensis from Sentinel Rock Beds, Aire Coast (Victoria).

Cookson (1947a) made no reference to the previously published work of Rosendahl (1943), and, although several of the illustrations (Cookson 1947a; Plate XI, figures 1, 3, and 7) could be interpreted as indicating the presence of a definite lower wall to the thyriothecium, Notothyrites was assigned to the family Microthyriaceae. Selkirk (1975) described from the Kiandra deposits as 'fossil forms of doubtful affinity' specimens closely resembling Trichothyriaceae in association with hyphae attributable to fossil representatives of Asterina and Meliolinites from the upper cuticle of a fossil leaf tentatively assigned to the family Myrtaceae. Splits in the upper wall allowed the demonstration of a definite cellular floor to the thyriothecium. However Selkirk (1975) also described as N. kiandrensis specimens from the same deposits as Cookson (1947a) worked on, located on the lower cuticle of a putatively lauraceaous leaf, yet again was content to include this genus within the Microthyriaceae. Krassilov (1967) accepted Notothyrites as a fossil member of the Microthyriaceae and erected four species N. dictyozamiticola, N. cephalotaxi, N. podocarpi, and N. otozamiticola, isolated from lower Cretaceous gymnosperm hosts, however in each of the illustrations (Krassilov, 1967; Table 1, figures 1-9) it is clear that the thyriothecia are still attached to the host cuticles and there is very little chance of determining the presence of a distinct cellular floor to the thyriothecia in question.

Ramanujam (1963) described a species N. neyreli but the species was invalidly published as no text figure was given with the description (vide Kar, Singh and Sah, 1972). Jain and Gupta (1970)

described <u>N. padappakarensis</u> which they stated compared quite closely with <u>N. airensis</u> Cookson. Ramanujam and Rao (1973) similarly described <u>N. denticulatus</u> and Kar and Saxena (1976) described <u>N. amorphus</u>. All of these species were erected for palynomorphs and yet careful examination of the descriptions has shown no reference in any case to a possible cellular floor to the thyriothecia in question, suggesting perhaps an over-readiness to accept that the specimens are in fact con-taxic with the established form-genus. An excellent example of this is found in Eriksson (1978) in describing fossil fructifications of 'presumably either interglacial or Tertiary origin' from Northern Finland. The description of the fungi clearly stated:

> "Two layers can be distinguished in each ascoma, the upper one being darker and with thicker walled cells, the lower thin and transparent."

This clearly precludes the fungi in question from the Microthyriaceae, and yet two forms were distinguished as <u>Notothyrites</u> sp.1 and <u>Notothyrites</u> sp.2. Eriksson (1978) did however comment that the structure 'is also rather similar to the ascomata of trichothyriaceous fungi'. Eriksson (1978) also took an unfortunate typographic error in Cookson (1947a), where <u>Notothyrites setiferus</u> was abbreviated as <u>A. setiferus</u>, to mean that <u>Notothyrites</u> was to be regarded as a synonym for <u>Actinopeltis</u>, another genus of Trichothyriaceae. Eriksson's (1978) misinterpretation is quite understandable in that her <u>Notothyrites</u> sp.2 is morphologically identical with Holocene fructifications described by van Geel (1978) as <u>Actinopeltis</u> sp. Ellis (1977a) is of the opinion that the genera <u>Trichothyrina</u> and <u>Actinopeltis</u> are best separated on the orientation

FIGURE 7.2
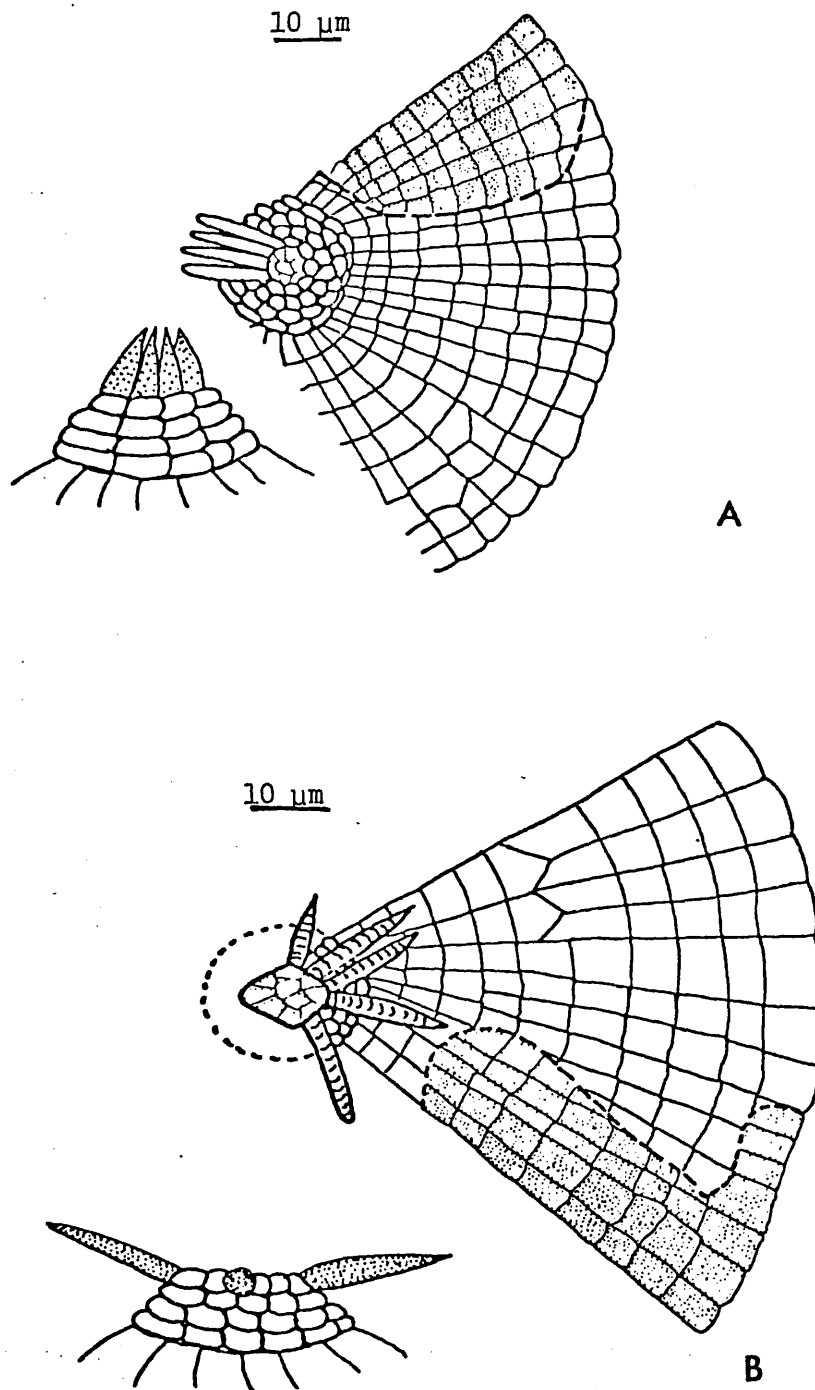
Diagrammatic representation of ostiolar organisation.

(Magnification ca. X1,000)

A. Trichothyrina alpestris (after Ellis, 1977a)

B. Actinopeltis palustris (after Ellis, 1977a)

of the setae on the ostiolar collar. Although Müller and von Arx (1962) separate these two genera on the presence or absence of setae on the ostiolar collar, Ellis (1977a) states that the type species _Trichothyrina_ _alpestris_ has ostiolar setae which converge above the ostiolar opening whilst all _Actinopeltis_ species have ostiolar setae which splay out horizontally from the ostiolar collar (see Fig. 7.2, p.188). Smith (1980) has already shown that fructifications reported from Quarternary deposits in England by Godwin and Andrew (1951) and by Vishnu-Mittre (1973) are best accomodated in the family Trichothyriaceae. Godwin and Andrew (1951) commented on the morphological similarity between their specimens and the extant genus _Loranthomyces_ and suggested a tentative affinity with this trichothyriaceous genus. Vishnu-Mittre (1973) attributed his specimens to two present day species of _Microthyrium_. Ellis (1977a) in her critical review of the extant British species of the Trichothyriaceae, however placed both the species in question, _M. culmigerum_ and _M. nigro-annulatum_ into synonymy with species of _Trichothyrina_, _T. alpestris_ (= _M. culmigerum_) and _T. nigro-annulata_ (= _M. nigro-annulatum_).

Elsik (1978) has made the bald statement that 'specimens assigned to _Notothyrites_ are synonymous to _Trichothyrites_ in all aspects including the occasional presence of setae around the ostiole'; and nominated _Trichothyrites_ _pleistocaenica_ Rosendahl as type species. Elsik (1978) however did not complete the nomenclatural exercise by fully citing the proposed synonymies or formally creating the new nomenclatural combinations necessary to transfer those previously described species of _Notothyrites_ to _Trichothyrites_.

An alternative procedure advocated here would be to isolate those fossil forms such as _Trichothyrites_ _pleistocaenica_ and _T._ _hordlensis_ in which the ostiolar collar shows no, or very little, evidence of large setal appendages. These forms can be compared either with _Trichothyrium_ (Pirozynski, 1978) or _Trichothyrina_ (Smith, 1980) as there is usually little or no way of determining exactly whether these fossil forms were myco-parasites or saprophytes. In these cases attribution to the form-genus _Trichothyrites,_ based as it is, more on family characters of the Trichothyriaceae than those of any particular genus, seems the most appropriate treatment. However, following Ellis (1977a), the two genera _Trichothyrina_ and _Actinopeltis_ can be distinguished on the basis of the presence and orientation of the ostiolar setae and Luttrell (1973) also distinguishes between the two genera on the presence or absence of ostiolar setae. It would therefore seem to be appropriate to separate those fossil specimens which clearly demonstrate the presence of large well-developed ostiolar setae, diverging from the ostiolar collar, as a distinct and new form-genus _Actinopeltites_ acknowledging the morphological similarity of the fossil fructifications with those of the living genus _Actinopeltis._ The diagnosis both of the proposed new form-genus and the type species would have to be based upon the description given by Eriksson (1978) for the material from Finland, described by her as _Notothyrites_ sp.2, as _Actinopeltites_ _tervolaensis_ (Eriksson) Smith (nom. prov.).

Although the family Trichothyriaceae is regarded as being 'predominantly tropical hyperparasites of other leaf-ascomycetes' (Pirozynski, 1978), Ellis (1977a) has recorded nine extant species of Trichothyrina and one extant species of Actinopeltis from British collections. The occurrence of fossil fructifications of this type could therefore be of a lesser value as palaeoclimatic indicators if taken in isolation from other epiphyllous fructifications and vegetative mycelial remains, such as those dealt with in the preceding chapter. Alternatively the demonstration of fossil fructifications of this type in upper Eocene deposits has been taken by Smith (1980) as possible evidence of a rapid diversification within the Ascomycotina during the Tertiary. The species of Notothyrites described by Krassilov (1967) from lower Cretaceous gymnosperm hosts could well push back the earliest fossil record of Trichothyriaceae-type fructifications to a geological age comparable to that given by Alvin and Muir (1970) for microthyrialian fructifications of the Stomiopeltis-type, and the microthyriaceous thyriothecium recorded by Singh (1971) from Albian deposits in Alberta, and referred by Elsik (1978) to Phragmothyrites.

Pirozynski and Weresub (1979a) (see Chapter 1, p.30) have briefly reviewed the record of presumed fossil ascomycetes in their postulates concerning the evolution of the Ascomycotina, especially the possession of anamorphic and teleomorphic stages. Pirozynski and Weresub (1979a) contended that the evolution of bitunicate ascomycetes, Loculoascomycetes, preceded that of unitunicate ascomycetes. Functionally bitunicate ascomycetes were postulated as widespread at the Jurassic/Cretaceous boundary when land-bridges or

island chains linked Laurasia with Gondwanaland. With the disruption of direct links between Laurasia and Gondwanaland in mid-Cretaceous times, a conspicuous dichotomy in the evolution of the Ascomycotina occurred. Bitunicates evolved, dispersed and speciated through isolation from parent taxa, predominantly in Gondwanaland and its fragments, while unitunicates evolved in Laurasia and its constituent land masses. This separate evolution, in relative isolation, was continued until the latter half of the Tertiary when connections between these two land masses and their derivatives were re-established. Thus the occurrence of possible trichothyriaceous fructifications in Lower Cretaceous deposits, as described by Krassilov (1967), would not be inconsistent with the postulates of Pirozynski and Weresub (1979a).

MICROTHYRIACEOUS FRUCTIFICATIONS

Another suite of fossil fungal fructifications from the Hordle Cliff deposits can best be compared with those previously described which have been attributed to the form-genus Phragmothyrites Edwards within the family Microthyriaceae. The involved and complex nomenclatural manoeuverings which have centred on this form-genus have already been outlined in Chapter 4 (p. 83 - 122 and Table 4.1, p. 88). Of the three recent treatments dealing with Phragmothyrites and its taxonomy and nomenclature, both Selkirk (1975) and Kar and Saxena (1976) have argued for the inclusion within Phragmothyrites of a greater or lesser number of other form-genera erected for fossil epiphyllous fungal fructifications. In contrast Elsik (1978) has maintained most of the form-genera which were submerged by both

SELKIRK (1975)	KAR and SAXENA (1976)
Phragmothyrites Edwards	Phragmothyrites Edwards
Microthyriacites Cookson	Phycopeltis microthyrioides Kirchheimer
Asterothyrites Cookson	Microthyriacites Cookson
Microthallites Dilcher	Callimothallus Dilcher
	Microthallites Dilcher
	Pseudosphaerialites Venkatachala and Kar

TABLE 7.1   Synonymies proposed for the form-genus

Phragmothyrites Edwards.

FIGURE 7.3
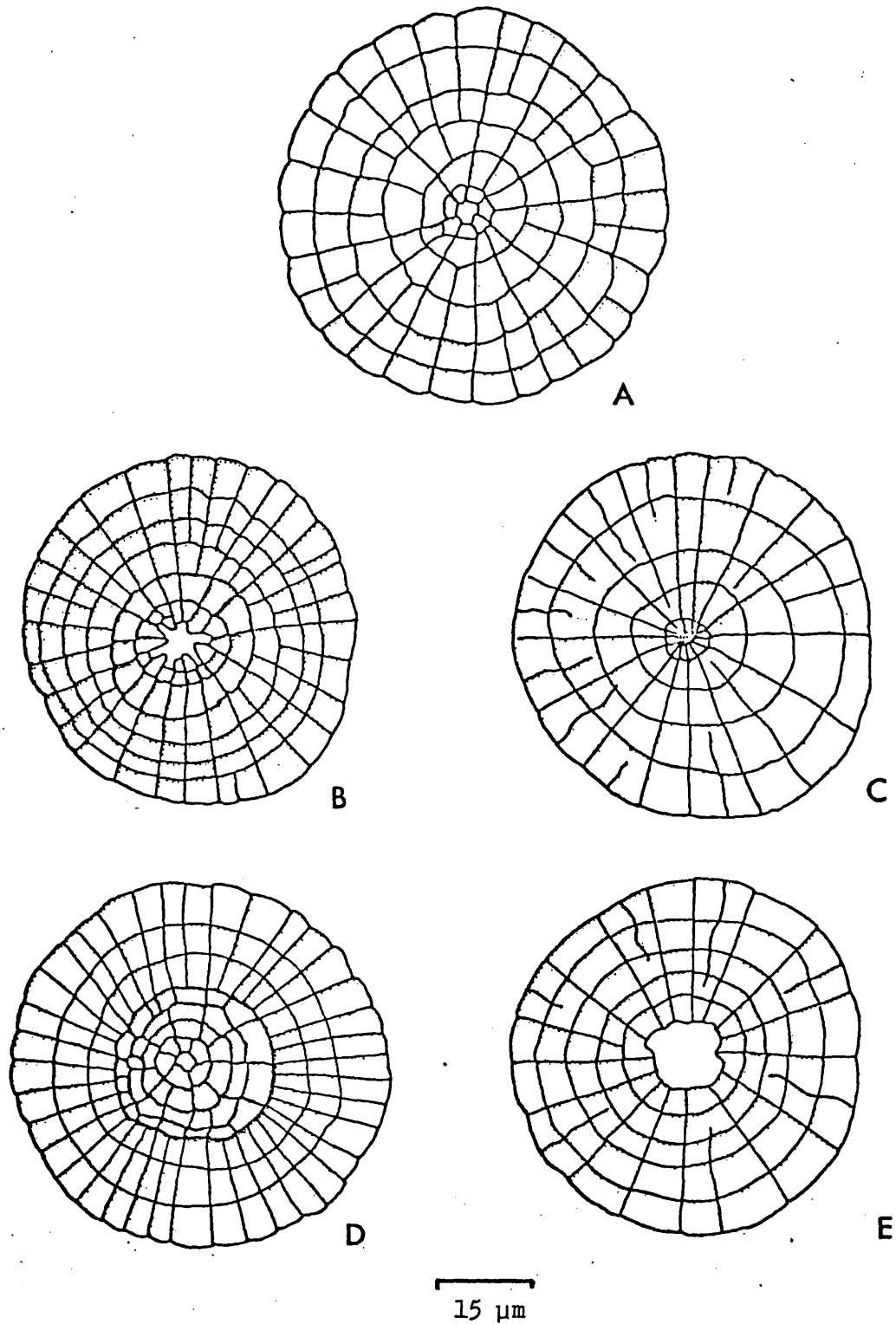
Diagrammatic representations of the <u>Phragmothyrites</u> complex of form-genera for epiphyllous fructifications.

A. <u>Phragmothyrites</u>   B. <u>Asterothyrites</u>   C. <u>Microthallites</u>

D. <u>Microthyriacites</u>   E. <u>Paramicrothallites</u>

Selkirk (1975) and Kar and Saxena (1976) as separate and discrete nomenclatural and taxonomic entities. The differences in end result as a consequence of these treatments of the same form-genera are largely due to the type of classification employed by the various authors and the eventual use to be made of the classification. Whilst Selkirk (1975) and Kar and Saxena (1976) tended toward a natural or phylogenetic approach, Elsik (1978) followed a more artificial classification. Elsik (1978) also has a more pragmatic or utilitarian outlook toward the use of classification systems, the intention being to use the palynomorphic fossil fructifications if possible, as stratigraphic markers and for stratigraphic correlations. With the more phylogenetic approach there is a danger that the creation of synonymies can lead to the circumscription of the form-genus being loosened to such an extent that the taxon becomes so lax as to be nothing more than a 'portmanteau' or 'pigeon-hole' rather than a well-knit taxonomic unit.

Both Selkirk (1975) and Kar and Saxena (1976) have broadened the generic concept of the form-genus _Phragmothyrites_ Edwards to include a varying number of other form-genera of fossil microthyriaceous fructifications (see Table 7.1, p. 193). In both cases however, their synonymies are incomplete as several other form-genera that have been erected need to be considered as well. But the arguments for the inclusion of those form-genera which both Selkirk (1975) and Kar and Saxena (1976) agree upon need to be considered in detail first (see Fig. 7.3, p. 194). Cookson (1947a) erected a number of form-genera for fossil microthyriaceous fructifications (see Table 4.4, p. 93) based largely upon those characters used by Stevens and

Ryan (1939) to distinguish two sub-families within the extant genera of Microthyriaceae. Cookson (1947a) followed Stevens and Ryan (1939) in placing great emphasis upon the presence or absence of free mycelial hyphae associated with the mature fructification (see Chapter 4, p. 95). Cookson (1947a) acknowledged that determining whether there are mycelial hyphae associated with the fossil fructification is difficult and thus also created 'Microthyriaceae Incertae Sedis' for fossil forms with no clear evidence of the presence or absence of mycelial hyphae. By implication, therefore, most palynomorphic forms which have been separated from the host cuticle would fall within the ambit of this latter grouping.

The form-genus _Asterothyrites_ was erected by Cookson (1947a) with the following extremely broad diagnosis:

"Mycelium superficial, persistent. Ascomata round, flat, radiate. Ascospores unknown."

No detailed statement of several other important diagnostic features was included. A careful reading of both the diagnosis of the form-genus and of the four species described by Cookson (1947a) reveals tacit assumption of the following features.

i) Attribution of _Asterothyrites_ to the sub-family Asterineae (_sensu_ Stevens and Ryan, (1939) due to the recognition of persistent mycelial hyphae means that _Asterothyrites_ cannot be applied to palynomorphic forms. All four of Cookson's (1947a) species are described from leaves of _Oleinites_.

ii) No mention is made of whether the fructifications are ostiolate or not, in the diagnosis of the genus. Of the four species

described by Cookson (1974a), three species are apparently non-ostiolate with only A. ostiolatus having '.... stoma round, 13 μm in diameter, formed by the breaking down of the central cells.' A. sinuatus however is stated to have 'dehiscence by a stellate fissure'.

iii) Cookson (1947a) did not designate any of the four species she described as the type species. Andrews (1955) listed A. sinuatus and Pirozynski (1978) apparently accepting this, removed the entire genus from the Microthyriaceae to the Asterinaceae due to the fructification opening by way of a stellate fissure or crack. Jansonius and Hills (1976) however, nominated A. minutus as the type species on the basis that the stellate dehiscence described for A. sinuatus is illustrated for A. minutus. Elsik (1978) maintains that all material of Asterothyrites can be transferred to Phragmothyrites 'except perhaps the specimens with a stellate dehiscence mark', but that 'This genus could be salvaged for forms with a stellate dehiscence mark if it could be shown that the illustrations for A. sinuatus and A. minutus were mislabeled, as the illustrations for Notothyrites and Plochmopeltinites were in Cookson (1947b)'.

The attribution of dispersed fossil fructifications to taxa is further clouded due to the presence within the literature of series of form-genera which have a greater or lesser degree of overlap in the concept of the form-genus coupled with the attribution of fossil material to extant genera. This problem has already been introduced in Chapter 4 (p.114) where one of the examples quoted is the Asterina/Asterinites/Asterothyrites sequence (see Table 4.2, p. 89 and Fig. 4.5, p. 116). In the present case however Asterinites

can be discounted as this form-genus erected by Doubinger and Pons (1973) is strictly for mycelial hyphae. Dilcher (1965) and Selkirk (1975) both attribute fossil fructifications to both the extant genus _Asterina_ and the form-genus _Asterothyrites_ acknowledging that these two genera occur in the sub-family Asterineae of the family Microthyriaceae, whereas Pirozynski (1978) placed these two genera within the family Asterinaceae. Edwards (1922) makes no direct statement as to which sub-family _Phragmothyrites_ belonged. However, by implication:

> "The form of the thyriothecia in this fossil is very similar to that of _Microthyrium_ itself, while in this and allied genera the mycelium is absent or evanescent."

It would appear that _Phragmothyrites_ is best placed within the sub-family Microthyreae (family Microthyriaceae _sensu_ Pirozynski, 1978). It would seem therefore, that _Asterothyrites_ can be regarded as belonging to either the family Asterinaceae or the family Microthyriaceae depending upon the taxonomic convictions of the individual worker. Also that the recognition of _Asterothyrites_ as a separate and distinct form-genus from _Phragmothyrites_ is to a large extent a matter of personal interpretation and conviction.

Cookson (1947a) also erected the form-genus _Microthyriacites_ for microthyriaceous fructifications present in Tertiary deposits from the southern hemisphere. The diagnosis of this form-genus was drawn extremely broadly:

> "Ascomata radiate and dimidiate. Information regarding the presence of a free mycelium either uncertain or wanting; ascospores unknown."

No reference was made by Cookson (1947a) in her diagnosis of the genus concerning the presence or absence of an ostiole; however the descriptions of the two species erected state them to be 'astomate'. Again Cookson (1947a) failed to designate either of the two species described as a type species. Venkatachala and Kar (1969) followed Sah (1967) in regarding Microthyriacites as being synonymous with Phragmothyrites yet maintained that the genus Microthyriacites can be retained to accomodate M. fimbriatus-type of perithecia by designating M. fimbriatus as the type species of the genus. Elsik (1978) followed Venkatachala and Kar (1969) and accepted M. fimbriatus as the type species 'characterised by thicker walled cells over the centre of the thyriothecium, on which Microthyriacites is differentiated from Phragmothyrites'. In contrast Jansonius and Hills (1976, 1977) designated the other species M. grandis as the type species and stating:

> "we consider that Venkatachala and Kar did not actually propose M. fimbriatus as lectotype species, but merely reflected on the merits of doing so."

A cogent observation in light of the fact that Venkatachala and Kar (1969) made no reference to the three species of Microthyriacites viz M. sahnii, M. edwardsi, and M. cooksonii previously described by Rao (1959) from Eocene and Miocene deposits in India and no synonymies were proposed to submerge these three Microthyriacites species into the form-genus Phragmothyrites. Both Selkirk (1975) and Kar and Saxena (1976) would submerge Microthyriacites (sensu Cookson, 1947a) into synonymy with Phragmothyrites whereas Elsik (1978) would retain Microthyriacites as a separate and distinct form-genus.

The form-genus _Microthallites_ Dilcher (1965) also has an equally

broad diagnosis:

> "Stroma radiate, more or less round, lacks free hyphae,
>
> ostiolate or non-ostiolate. Spores unknown."

The two species described by Dilcher (1965) were found on leaf

cuticles, _M. lutosus_ on _Sapindus_ leaves and _M. spinulatus_ on

Chrysobalanus leaves. The justification for the erection of this

form-genus hinged partly on the fact that Cookson's (1947a) genus

Microthyriacites was strictly for palynomorphs, but chiefly upon

Dilcher (1965) electing to interpret his material as not having free

mycelial hyphae associated with the mature fructification therefore

precluding the attribution of this form-genus to the sub-family

Asterineae of the Microthyriaceae (_sensu_ Stevens and Ryan, 1939) and

their automatic placement in the sub-family Microthyreae (_sensu_

Stevens and Ryan, 1939). The use of this particular criterion to

distinguish between different form-genera of fossil fungal

fructifications has already been discussed in Chapter 4 (p. 95).

But it is worth stressing again the cautionary approach advocated by

Selkirk (1975) concerning the two form-genera _Microthyriacites_ and

Microthallites:

> "If however the separation of _Microthyriacites_ and
>
> _Microthallites_ were retained, it would be possible for specimens
>
> of the same form to be placed in different genera depending on
>
> whether found isolated in palynological residues or on the
>
> surface of cuticles. The scattering of closely related and
>
> perhaps identical forms in a number of artificial genera appears
>
> to me to be undesirable."

Selkirk (1975) was referring to _Microthyriacites_ (_sensu_ Cookson,

1947a) and Microthallites (sensu Dilcher, 1965) but made no mention of Paramicrothallites, a form-genus separated from Microthallites Dilcher by Jain and Gupta (1970). Microthallites lutosus was described by Dilcher (1965) as follows:

".... a small thick-walled cell in the centre where an ostiole might be expected to develop ..."

In Microthallites spinulatus however, Dilcher (1965) stated:

".... simple ostiole appears to result from the dissolution of the cells of the stroma."

Jain and Gupta (1970) considered '... the presence or absence of an ostiole as a generic character to classify the dispersed microthyriaceous ascomata or thyriothecia' and transferred the ostiolate Microthallites spinulatus to the new form-genus Paramicrothallites as the type species P. spinulatus (Dilcher) Jain and Gupta and also described a new species Paramicrothallites menonii. This species appears from its description to be a palynomorph rather than a form attached to cuticle. Jain and Gupta (1970) commented upon the fact that P. menonii can easily be separated from P. spinulatus (sensu Jain and Gupta, 1970) because it lacks the highly characteristic two-layered stroma of both Microthallites species described by Dilcher (1965). As Jain and Gupta (1970) cite Microthallites spinulatus (sensu Dilcher, 1965) as the genotype for their new genus, the absence of a character specifically and explicitly in the original description of the proposed genotype:

"Stroma consists of two distinct layers, a bottom layer of dichotomizing radial hyphae ..... and a top layer of radiating rows of cells ....."

FIGURE 7.4
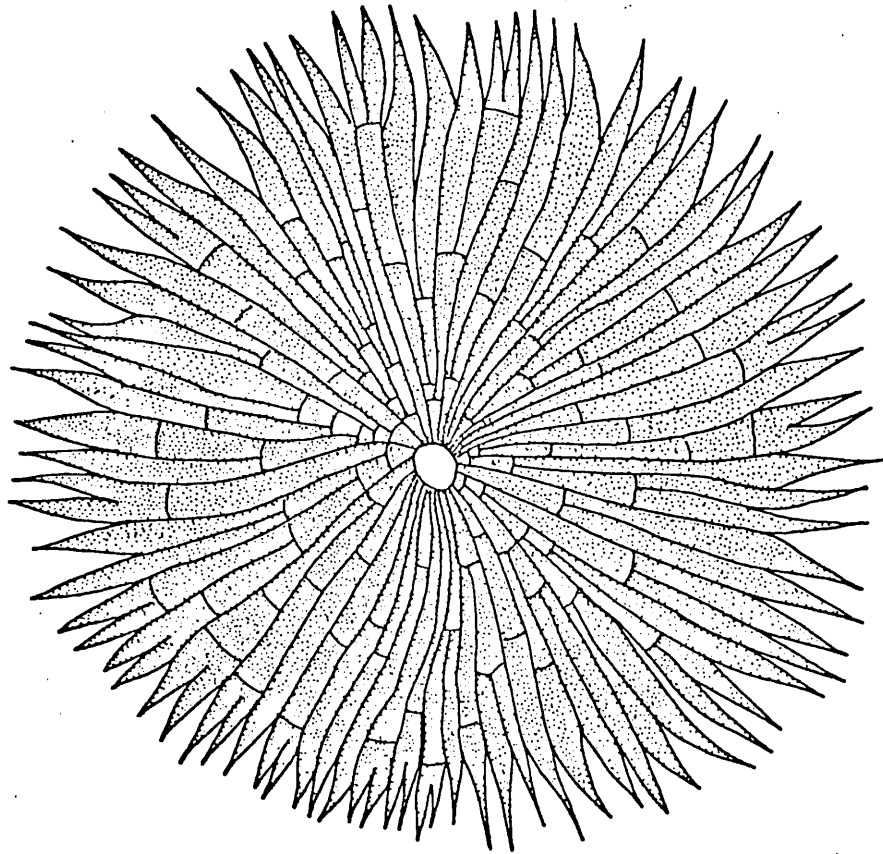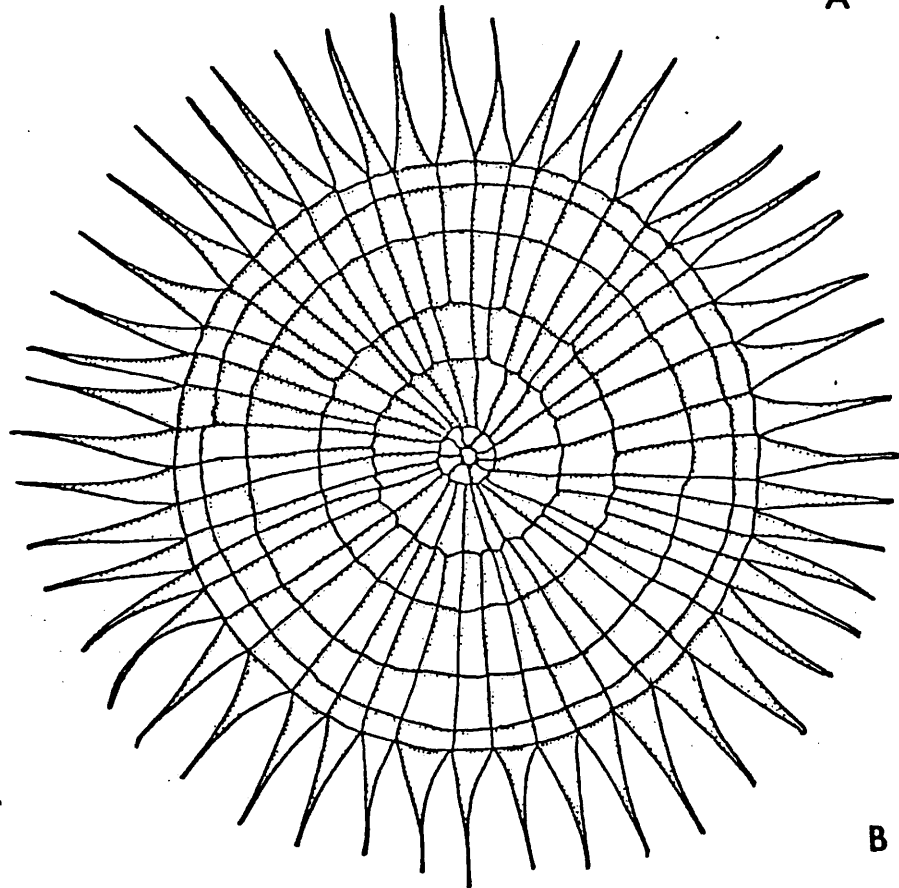
Diagram to show morphological similarity between A. _Actinopelte_ and B. _Parmathyrites_. (Magnification _ca_. X1,000)

would seem to make the attribution of P. menonii to this new genus questionable. The omission of this extremely characteristic feature of both Microthallites species from the diagnosis of the genus by Dilcher (1965) would seem to be highly unfortunate. Neither Selkirk (1975) nor Kar and Saxena (1976) make any mention of this criterion which seems to be of sufficient weight to question if the proposed inclusion by these authors, of this genus within Phragmothyrites is really warranted.

Jain and Gupta (1970) also created the form-genus Parmathyrites for fructifications found as palynomorphs from Miocene deposits from India. Parmathyrites was stated to be:

> "Comparable only with two genera, viz Phragmothyrites Edwards (1922) and Microthyriacites Cookson (1947a), in having non-ostiolate and non-porate nature of the pseudoparenchyma formed by radially arranged interconnected hyphae. But it differs mainly in having a peripheral sheath of spines around the fruit body."

The revisions of the genus Phragmothyrites, both by Selkirk (1975) and Kar and Saxena (1976), made no references to Parmathyrites in their proposed synonymies. Elsik (1978) questioned whether Parmathyrites is in fact microthyriaceous and suggested on the grounds of close morphological similarity, that Parmathyrites is in reality contaxic with the deuteromycete genus Actinopelte Saccardo (see Fig. 7.4, p. 202). If the attribution of the form-genus Parmathyrites to the Microthyriaceae is as dubious as Elsik (1978) maintained, the systematic position of the following four species: P. indicus Jain and Gupta (1970), P. cooksonii (Rao) Jain and Gupta

PLATE 8   Fructifications (cf. _Asterothyrites_) from the Hordle
           Cliff Deposit.   Magnification X1,500.
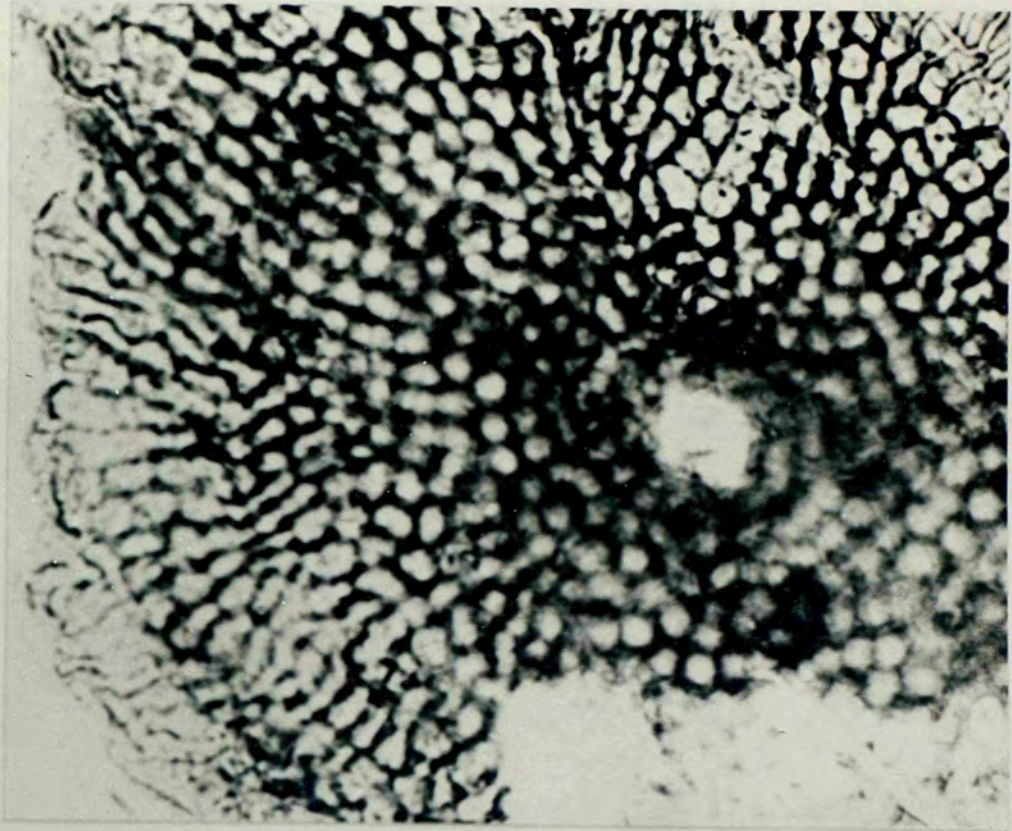
1
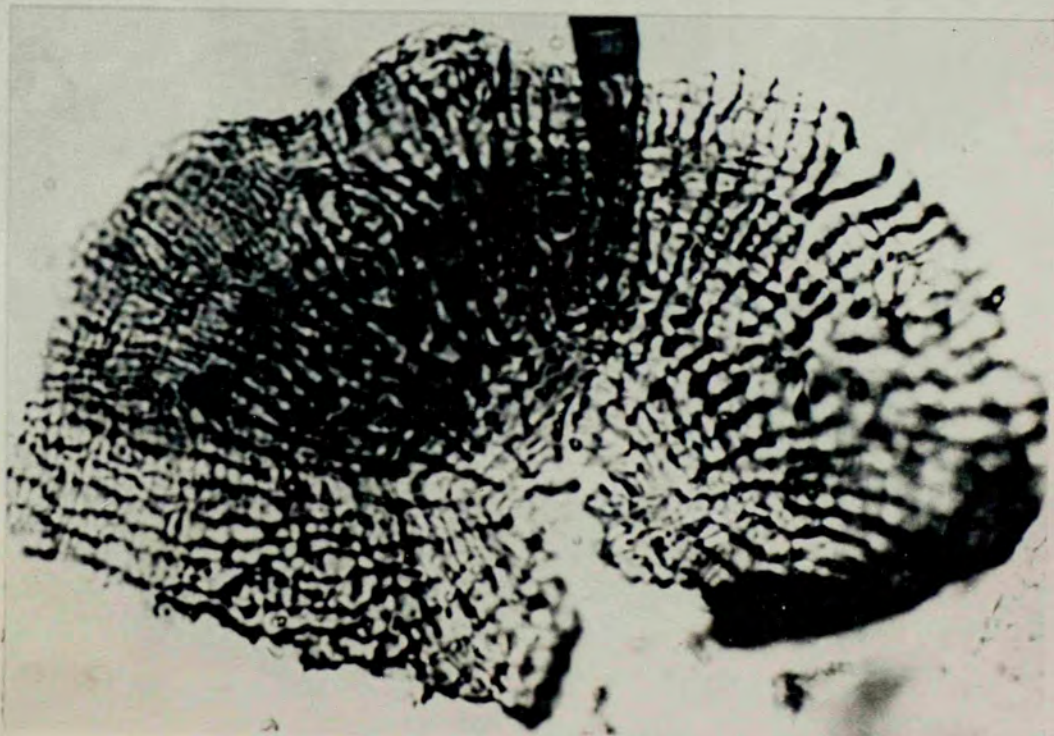
2

(1970) (= <u>Microthyriacites cooksonii</u> Rao, 1959), <u>P. robustus</u> Jain and

Kar (1979) and <u>P. turaensis</u> Kar, Singh and Sah (1972) requires a

careful re-examination.

As both the proposed revisions of the form-genus

<u>Phragmothyrites</u> seem to generate as many problems of nomenclature and

taxonomy as those which they attempt to solve, the Hordle Cliff

material will be described and attributed to pre-existing form-genera

irrespective of the synonymies advanced either by Selkirk (1975) or

Kar and Saxena (1976). However, due to the doubts concerning the

inter-relationships of the form-genera under consideration, it would

not be appropriate to do more than suggest affinities at the generic

level until these uncertainties have been further clarified.

The Hordle Cliff specimens are for the most part palynomorphic

and often incomplete making determination even to the form-generic

level difficult. The classification of dispersed fossil

Microthyriales given by Elsik (1978, Table 1, p. 337) is based on

quite readily discernible morphological features, demonstrable even

in partial fructifications. A series of fructifications both

complete and incomplete (see Plate 8 ,figs.1 and 2) isolated from

the Hordle Cliff deposit matrix can be grouped together on the basis

of the following morphological characters:

1) Multicellular fructifiations

2) Individual cells of fructifications non-porate

3) Fructifications show radiate construction

4) Margins of fructifications show no evidence of projecting

   spines

5) Presence or absence of an ostiole

Elsik (1978) did not define what he took to be an ostiolate fructification, however Elsik et al (1983) coupled with the illustrations in Elsik (1978) would place the Hordle Cliff material under consideration into the group of form-genera deemed by Elsik (1978) to be non-ostiolate viz Phragmothyrites, Asterothyrites and Microthallites.

6) Central cell modified

This feature is used to separate off Asterothyrites and Microthallites from Phragmothyrites with an unmodified central cell.

7) Star-shaped opening

This feature is used to separate Asterothyrites from Microthallites.

Using this set of criteria the Hordle Cliff specimens would therefore be closely comparable with species within the form-genus Asterothyrites (sensu Cookson, 1947a). However, as previously stated, the taxonomic position of this form-genus has been brought into question with the synonymies proposed by Selkirk (1975) and consequently, until such time as both the taxonomic and nomenclatural difficulties raised both by the proposed synonymies and the varied methods of classification are further clarified, I shall do no more than indicate the probable affinity of these specimens from Hordle Cliff as cf Asterothyrites Cookson (1947a).

PLATE 9 Fructifications (cf. <u>Asterina</u>/<u>Asterothyrites</u> and

     <u>Trichopeltina</u>/<u>Trichopeltinites</u>) from the Hordle

     Cliff Deposit. Magnification X1,500.

     Figure 1. <u>Asterothyrites</u>

     Figure 2. <u>Asterothyrites</u>/<u>Trichopeltinites</u>

     Figure 3. <u>Trichopeltina</u>
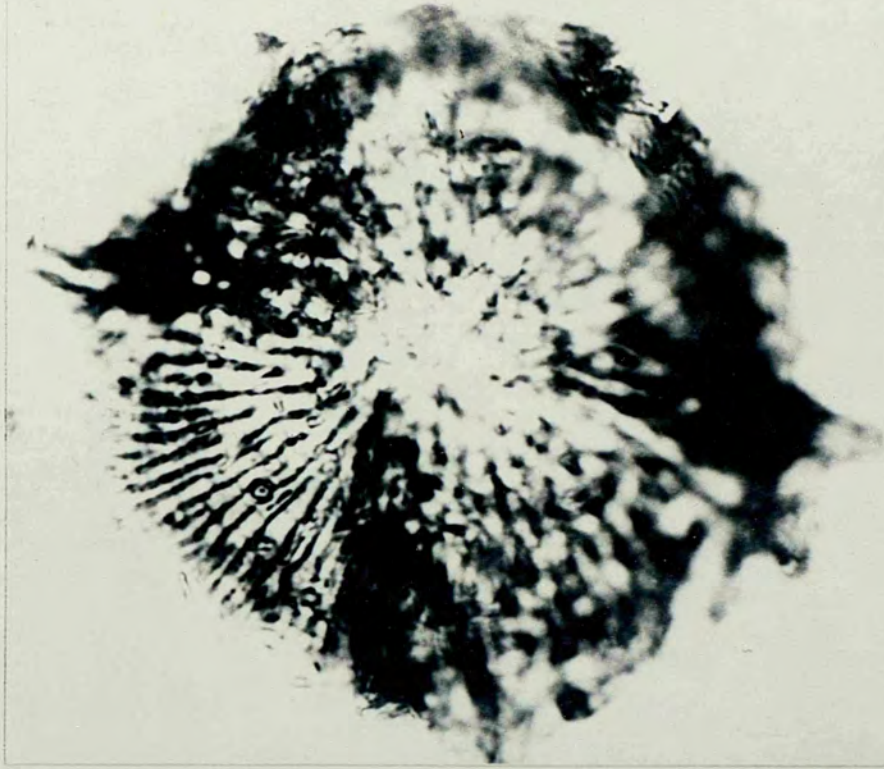
1
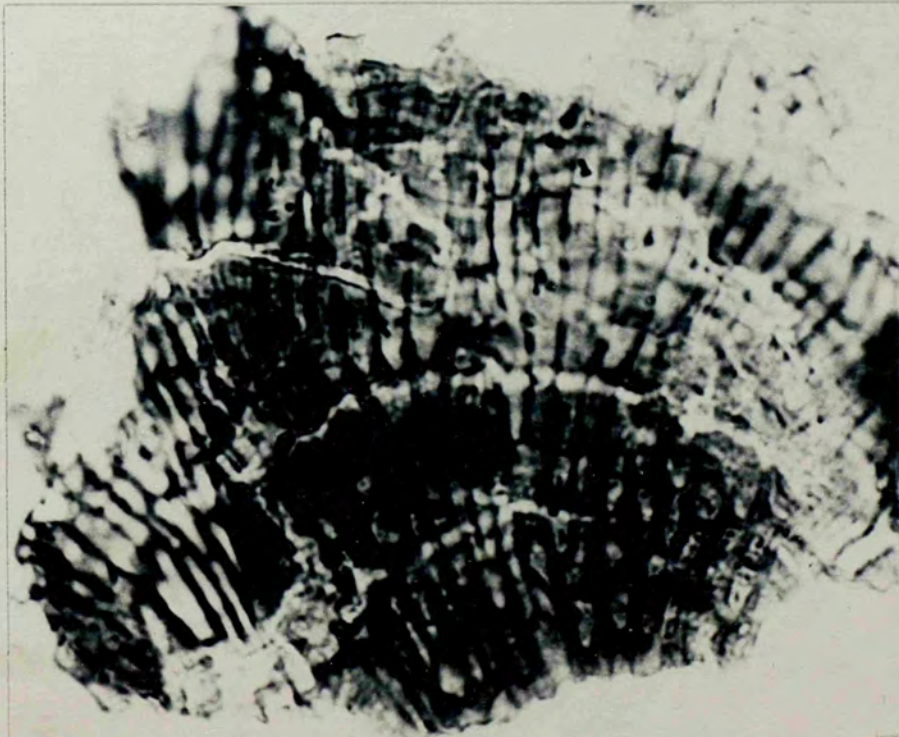
2
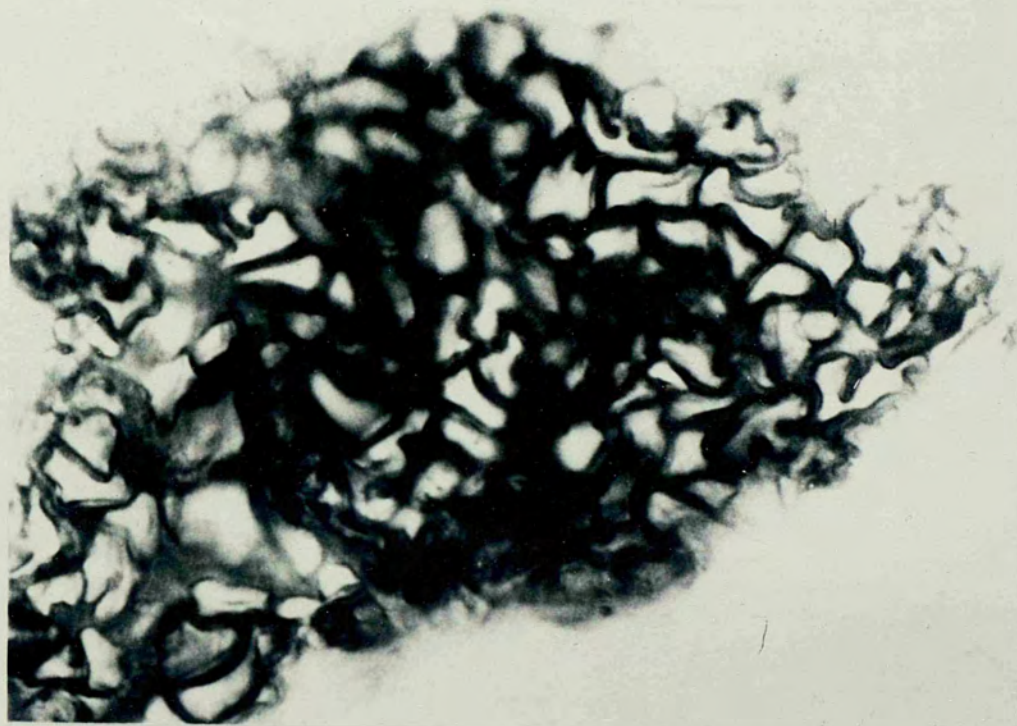
As previously stated <u>Asterothyrites</u> is one of a trio of genera with overlapping genera concepts. A further series of fructifications isolated from the Hordle Cliff deposit could equally well be attributed to the form genus <u>Asterothyrites</u> (see Plate 9, fig. 1). In fact, as they show evidence of hyphae attached to the fructification there is probably a greater justification for placing them in this genus than those already dealt with. An equally attractive alternative treatment for these fructifications on the other hand would be to emulate Dilcher (1965) and place them within the extant genus <u>Asterina</u>, parallel with <u>Asterina eocenica</u> Dilcher on the basis of the strong morphological resemblance between the fructifications figured by Dilcher (1965, Plate 8, figs. 62-65). In each case the fructification is composed of strongly radiate elongate cells which bifurcate strongly toward the margin of the fructification. Despite the close morphological resemblance in fructification construction this is not considered to be sufficient information to place the Hordle Cliff material in the extant genus <u>Asterina</u>. Dilcher (1965) was dealing with specimens still attached to the host leaf cuticle and consequently was able to adduce further characters to support his contention that the material he was investigating was sufficiently closely related to be regarded as contaxic with <u>Asterina</u>. These additional characters included the presence of vegetative mycelial hyphae bearing unicellular hyphopodia, bicellular echinate spores, some of which had germinated upon the cuticle of the host leaf to form the hyphopodiate mycelial hyphae. The Hordle Cliff specimens are only dispersed fructifications and present no evidence of these other highly characteristic diagnostic features enabling attribution to <u>Asterina</u>.

FIGURE 7.5
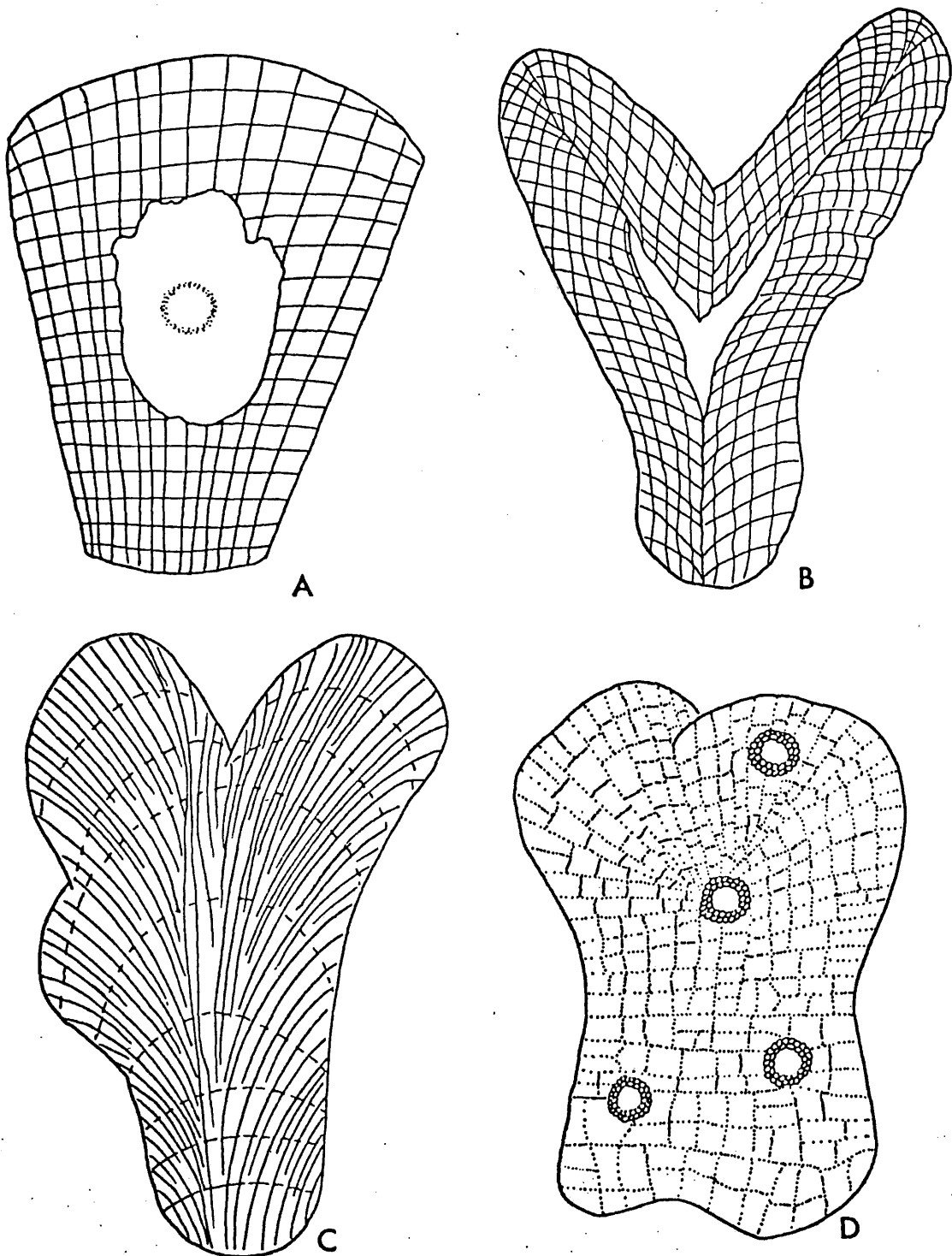
Diagrammatic representation of non-radiate epiphyllous fossil
fructifications. (Magnification ca. X1,000)

A. Brefeldiellites   B. Euthythyrites

C. Trichopeltinites   D. Dictyopileos

Therefore again, despite the close morphological resemblance to the fructifications of _Asterina_ _eocenica_ Dilcher (1965) this material will only be designated as cf _Asterothyrites_ Cookson (1947a).

The final set of dispersed fossil fructifications to be considered from the Hordle Cliff deposit are those which can best be accomodated within the group of families of epiphyllous fungi which do not have circular-radiate fructifications, but elongate or fan-shaped fructifications (see Fig. 7.5, p. 211). Two of the form-genera for this type of fossil fructification were erected by Cookson (1947a) viz _Euthythyrites_ and _Trichopeltinites_ (see Table 4.4, p. 93). Dilcher (1965) attributed several different fossil fructifications to extant genera and also erected the new form-genera _Pelicothallos_, _Brefeldiellites_, and _Dictyopileos_. Pirozynski (1976a) stated however that _Pelicothallos villosus_ Dilcher is the green alga _Cephaleuros_ _virescens_, which Round (1973) described as a a chaetophoralian alga,

> "an aerial epiphytic alga growing on many economic plants e.g. citrus fruits, avocado and tea bushes and is known in India as 'red rust'."

Euthythyrites was placed in the Asterineae and _Trichopeltinites_ and _Brefeldiellites_ in the Trichopeltinaceae by Pirozynski (1978) (see Table 4.2, p. 89), however _Dictyopileos_ was not linked with a recent family although Dilcher (1965) placed it tentatively within the family Micropeltidaceae. This highly distinctive form-genus with its multi-ostiolate fructification covered with a reticulum of interconnected hyphae is not represented within the Hordle Cliff material under consideration.

The attribution of one of the specimens to be dealt with from the Hordle Cliff material is highly problematical due to its fragmentary nature (see Plate 9, fig. 2). It could perhaps be interpreted as a fragment of a large _Asterothyrites_ type fructification; it could equally well be regarded as a fragment of a larger _Trichopeltinites_ type fructification. This alternative is tenable when the description given by Selkirk (1975) for the variability in colony shape for _Trichopeltinites_ _kiandrensis_ is taken into consideration.

"Colony shape in _Trichopeltinites_ _kiandrensis_ is very variable. All gradations from narrow linear thalli to almost circular colonies with tongue-like lobes occur."

The fragment under consideration could well be interpreted as representing a lobe of the fructification. This possibility is further reinforced by the construction of the upper wall of the fructification of radiate dichotomously branched hyphae, a feature that is clearly seen in _Trichopeltinites_ _pulcher_ Cookson, T. _fusilis_ Dilcher and T. _kiandrensis_ Selkirk. Thus this fragment is tentatively identified as cf _Trichopeltinites_ Cookson.

In contrast to the highly organised nature of fructification structure which has characterised the specimens and form-genera considered up to date, the remaining example is highly irregular in organisation (see Plate 9, fig. 3). No clear indication of an ostiole or other means of dehiscence is evident and there must be some doubt as to whether this specimen does represent a fructification or if it is no more than an aggregation of vegetative

mycelial hyphae forming some type of encrusting thalloid structure on the host leaf surface.

Structures with a very similar morphological appearance were described and figured by Dilcher (1965, Plate 12, figs. 98-99). His material was however still associated with the host leaf cuticle, in this case a leaf of _Sapindus_ sp. Two apparently dissimilar stromatic structures were grouped by Dilcher (1965); one a dichotomising linear stroma and the other a 'sheet of randomly orientated unequally shaped cells', as a fossil species of an extant genus _Trichopeltina exporrecta_. This diagnosis was based largely upon the discovery of germinated 2-cell hyaline spores which had produced free mycelial hyphae which in some cases had proliferated in an unorganised fashion to produce the randomly associated hyphal cells of the putative stromatal structures. In other instances the more strictly organised radiate prosenchymatous stroma had been formed. Dilcher (1965) also interpreted structures associated with the randomly associated cellular sheets as setal processes. An equally valid interpretation would be that these structures are vegetative mycelial hyphae. The Hordle Cliff material having been isolated from a palynological preparation, showed no evidence of such 'setal processes' and no bicellular hyaline spores could be demonstrated to be associated with the randomly organised cellular sheet. The taxonomic connection of this form must therefore be regarded as only a suggestion, and a highly tenuous one at that, to the material described by Dilcher (1965) as _Trichopeltina exporrecta_.

8. 'GERMLINGS' FROM THE HORDLE CLIFF DEPOSIT

AND THEIR USE AS PALAEOCLIMATE INDICATORS

The two conflicting theories advanced to explain the nature and taxonomic position of these highly distinctive structures have already been introduced and discussed in Chapter 4 (p. 100). In summary the major disagreement is whether to regard these structures as algal (Kock, 1939; Kirschheimer, 1942; Hansen, 1980) or fungal. The second uncertainty concerns their affinity within the fungi, either as relatives of the parasitic unicellular chytrids (Bradley, 1967) or the more generally accepted interpretation that they are related to the microthyriaceous fungi (Edwards, 1922; Dilcher, 1965; Lange, 1976). On the basis of comparative morphology and "'picture book mycology' - a time-honoured and fruitful pastime" (Kendrick and Carmichael, 1973) it could equally well be argued that at least some of the 'germlings' could be related to the dematiaceous deuteromycete Desmidiospora myrmecophila Thaxter (1891), except that this living genus is one of a very small group of entomogenous hyphomycetes (Subramanian, 1983). This species D. myrmecophila appears to be a rare parasitic fungus and may be specific to queens of the tropical ant genus Camponotus. Evans and Samson (1984) stated that the two known records of this fungus are from queen ants hidden in logs; an extremely highly specialised ecological niche far removed from the far more catholic epiphyllous occurrence of the Tertiary 'germlings' under consideration. The conidiospores of D. myrmecophila were described by Evans and Samson (1984) from their Ghanaian material:

"...reddish-brown, successively dichotomously lobed (up to 6) with irregular chambers, 45-65 μm X 20-50 μm."

FIGURE 8.1
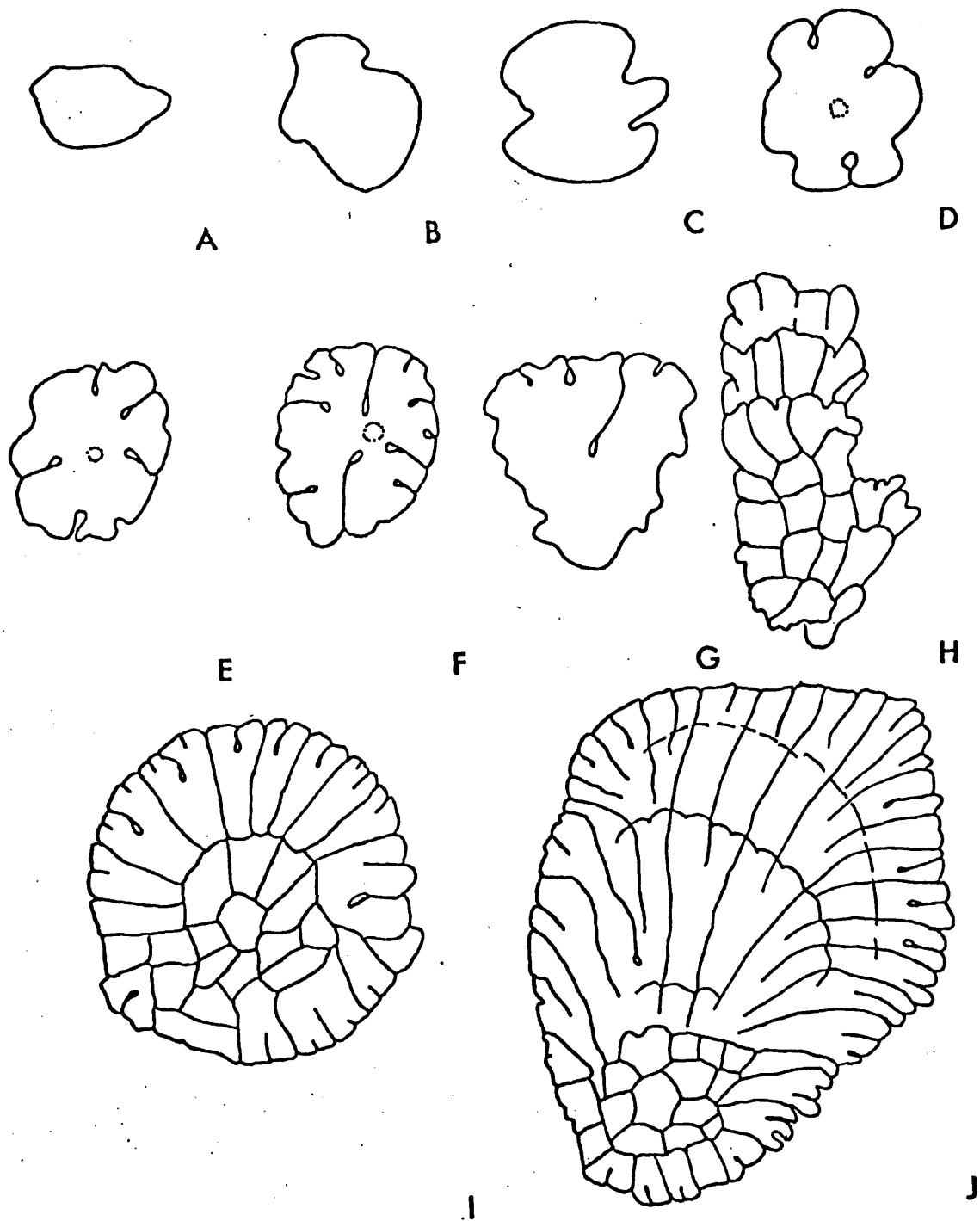
Diagrammatic sequence showing increasing morphological complexity in 'germlings' (after Köck, 1939). (Magnification ca. X1,000)

Thaxter (1891) gave the following measurements: 80-100 µm X 68-90 µm

for conidiospores from his North American material. Although Evans

and Samson (1984) suggest that the characteristic spores of $\underline{D}$.

myrmecophila could function as chlamydospores of long-term survival

value, the large disparity in size, the diameters cited being in the

order of 5 - 6 times as great as those of the most complex

'germlings' cited by Lange (1976), would seem to be sufficient to

separate these two similar structures.

'Germlings' show a great variety of morphological form. These

forms are readily arranged into a series based on increasing

complexity which can be interpreted as showing stages in development

from a unicellular spore-like structure to a multi-cellular stromatic

structure (see Fig. 8.1, p. 216). This purported developmental

sequence has been advanced by proponents of the 'algal' school (Köck,

1939; Kirschheimer, 1942) and 'fungal' school (Edwards, 1922;

Dilcher, 1965) as prima facie evidence to support their hypotheses.

The arguments advanced by Lange (1976) tend to support the

fungal nature of the 'germlings' although he is far more circumspect

in restricting their affinity solely to microthyriaceous fungi. The

arguments and reasoning by Lange (1976) concerned with using Tertiary

fossil 'germlings' as palaeohabitat, and ergo palaeoclimatic

indicators have already been reported and discussed in Chapter 4 (p.

104). Before attempting to apply this technique to dispersed

fossil 'germlings' from the Northern Hemisphere deposits from Hordle

Cliff, a more detailed examination of the criteria used by Lange

(1976) to order his modern equivalents found in leaf litter into the

FIGURE 8.2

A

10 μm

B

C

D

E

10 μm
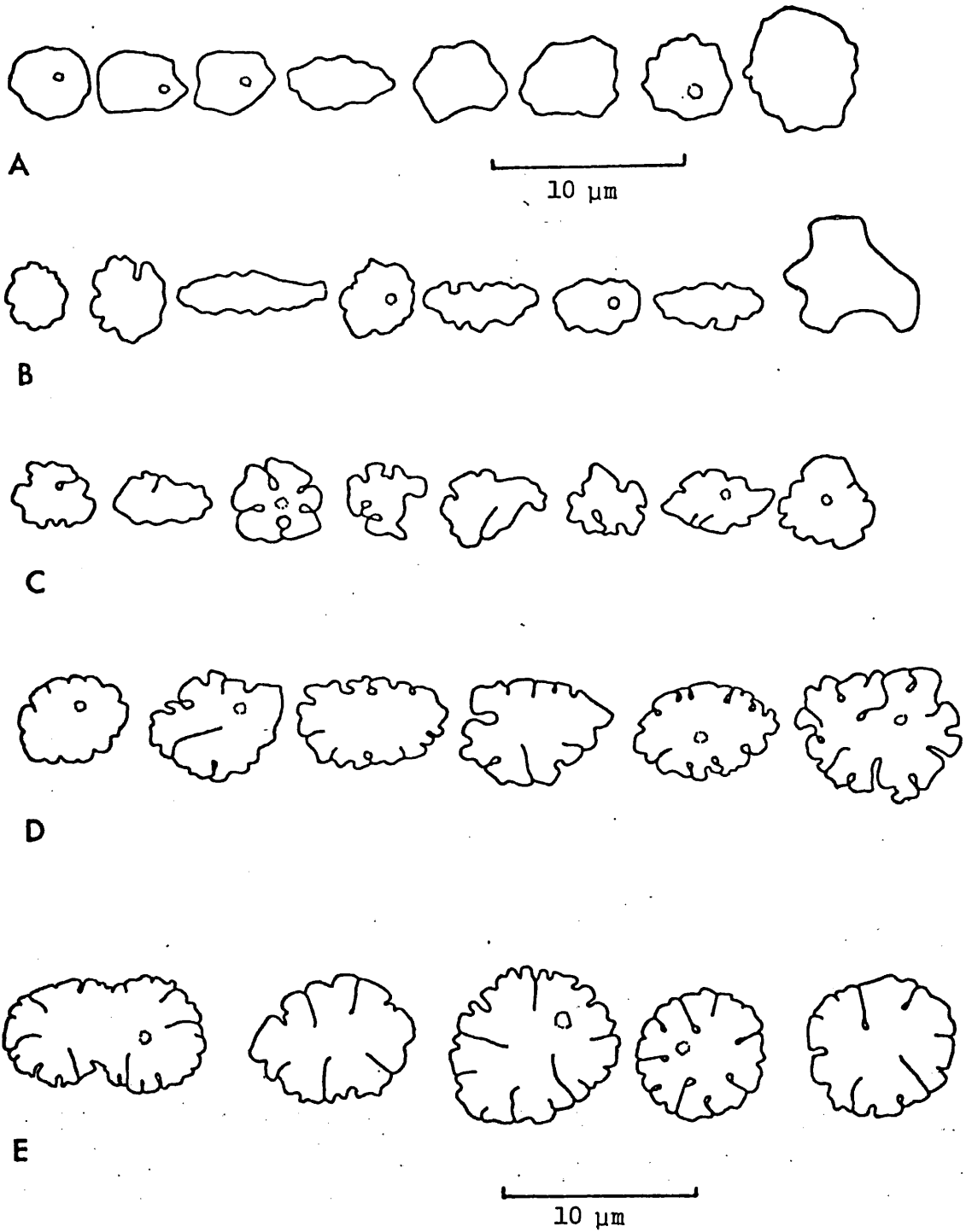
Grade of 'germling' complexity from modern
equivalents, after Lange (1976).

various 'grades of complexity' is needed. It is important to remember that Lange's (1976) ad hoc classification of morphological forms, and hence the 'grades of complexity' was formulated on the basis of the comparison of present day epicuticular structures isolated from samples from 72 sites within the Australasian plant geographic region (see Chapter 4, p. 104). The classification was then applied to fossil 'germlings' with corresponding morphologies.

GRADE I   (See Fig. 8.2A, p. 218). Simple outlines, usually distorted but recognisable as circular, ovoid, reniform or angular; the perimeter may be wavy but not so as to obscure the basic shape; there are no notches, grooves, lobes or internal structures; maximum breadths range from 5 μm to 10 μm.

[This grade would correspond with the earliest stage in the developmental series proposed by Köck (1939), see Fig. 8.1A, p. 216 .]

GRADE II   (See Fig. 8.2B, p. 218). More complicated outlines, shapes not recognisably circular, ovoid etc., but irregular; in particular they tend to have small lobes and wide shallow bays in the outline; never closed to suggest in optical section the development of dorsal grooving or centripetal wall formation. Size range as for Grade I.

GRADE III   (See Fig. 8.2C, p. 218, and cf Fig. 8.1B and 8.1C.)
In optical section these forms have the initial
appearance of centripetal grooves, knobs or walls
restricted to part of the outline; or shapes that
depart greatly from simple ovoid outlines or both;
maximum breadth 13 µm.

GRADE IV   (See Fig. 8.2D, p. 218, and cf Fig. 8.1D and 8.1E.)
Outlines tend to approximate regular oblongs, ovoids,
ellipses or circles; around most of the outline they
have a sequence of lobes and 'invaginations' which
lack regularity or , if regular lack depth of
penetration. Maximum breadth 13 µm.

GRADE V   (See Fig. 8.2E, p. 218, and cf Fig. 8.1F and 8.1G.)
These have regular outlines overall, either
elliptical, circular or fanned; perimeters regularly
'invaginated' in sequences either of irregular
notching separated regularly by long centripetal
grooves, or definite long-short alternation. (Maximum
diameter 13 µm, from illustrations of Lange, 1976.)

On the evidence of the comparative morphology of the living
equivalents to the fossil 'germlings', Lange (1976) concluded that
there was no justification in extrapolating the 'germling' continuum
to the septate stromatic discs (cf Fig. 8.1H, I, J, see p. 216) as
both Köck (1939) and Dilcher (1965) had done. Lange (1976)
maintained that these latter structures, at least on the evidence of

FIGURE 8.3
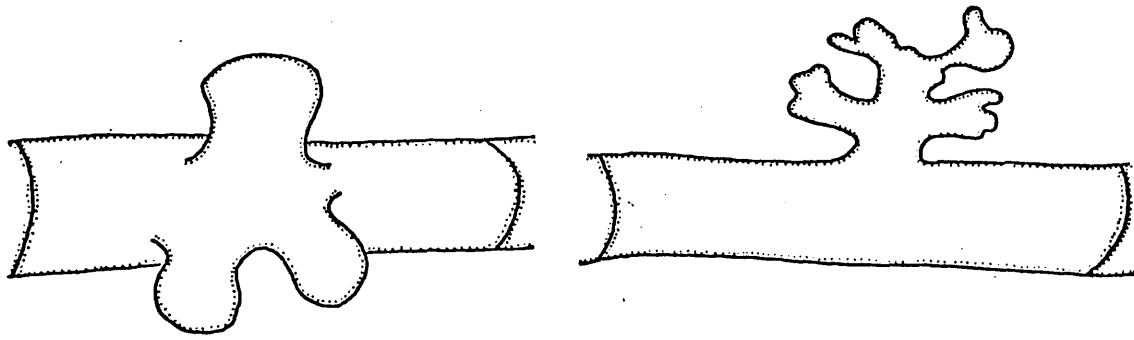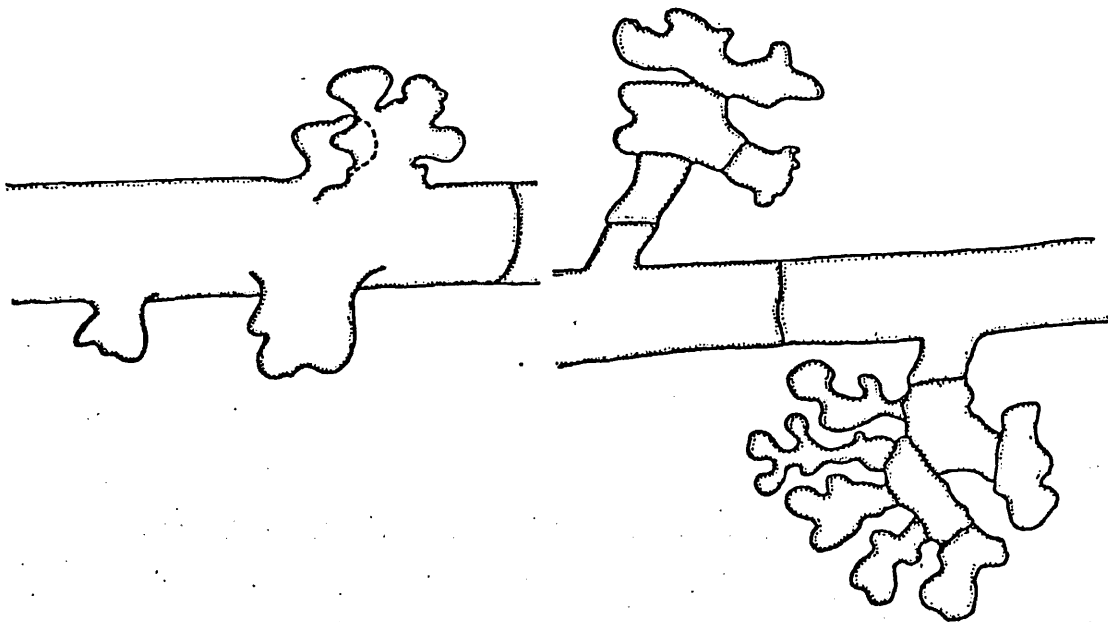
Types of appresorial hyphae:

A. **Erisyphe graminis**   B. **Microsphaera alphetoides**

C. **Microsphaera polonica**   D. **Rhizoctonia solani**

A - C after Talbot (1971), D after Flentje (1957)

the recent material, often could be shown to have a separate and distinct set of initials from the recent 'germling' structures. A number of morphological features were given that set these initials apart from the 'germlings':

(1) Coarser more dematiaceous structure.

(2) Simultaneous rather than centripetal development of internal multicellularity.

(3) Deeper optical sections.

(4) Less discrete lateral perimeters.

(5) Close association with vegetative mycelium.

(6) Stomiocentric origin.

However the application of some of these criteria to separate fossil material into 'germlings' and 'stromatal initials' would be more difficult.

Similarly Lange (1976) was confidant that other structures that could possibly be confused with 'germlings', or at least the modern equivalents of these structures, were quite easily distinguishable. In this category he included amerospores, i.e. single celled spores, and appressorial and hyphopodial outgrowths from hyphae. Talbot (1971) defined an appressorium (see Fig. 8.3, p. 221) as

"a simple or lobed swelling, often mucilaginous, on a germ tube or hypha attaching these to the surface of the host or other substratum. Appressoria are formed by some types of parasitic fungi usually at an early stage of infection of the host, but are also formed by some other types of fungi whose germ tubes or

hyphae are in contact with a hard surface. Besides attaching the hypha, the appressorium of a parasitic fungus assists the fine infection pegs, or penetrative branches, to pierce the host cuticle by providing a firm hold which counteracts the force of penetration."

A hyphopodium (see Fig. 8.3, p. 221) was defined by Talbot (1971) as: "a short branch, one or two cells in length, of an external hypha in certain leaf-inhabiting parasitic Ascomycotina. The terminal cell of a hyphopodium may be expanded and rounded or lobate, or pointed;sometimes it may produce a haustorium. Hansford (1946) regards hyphopodia as special absorbing structures in fungi whose mycelia are mainly external to the host."

The major feature used by Lange (1976) to separate 'germlings' from appressorial and hyphopodial structures was the observation that in the modern leaf litter equivalents of the fossil 'germlings' no attachment to hyphal material could be demonstrated. This is in complete contrast to the appressorial and hyphopodial structures found in the modern leaf litter. Lange (1976) suggested that this would be a distinguishing characteristic tenable in the separation of fossil forms also. This would appear to be the case as, from observation in fossil fungi such as Meliolinites the capitate hyphopodia do not as a general rule, fragment in such a fashion as to leave the capitate head cell as an unicellular entity. Usually the mycelium breaks up leaving the characteristic short lateral hyphopodial branches intact (cf Fig. 4.3, p. 107 and Plate 1). Conversely, in the unlikely event of the head cell separating from

the remainder of the vegetative hypha, the configuration of the head-cell would set them apart from the 'germlings'. Even in those living species of <u>Meliola</u> which have lobate head cells, these would be a smooth region on the periphery corresponding to the septal attachment of the head cell to the mycelium rather than the regular alternating pattern of long and short invaginations around the entire periphery which characterise the 'germlings'. Similar arguments can be advanced to justify the separation of 'germlings' from appressoria. Lange (1976) figures (fig. 2 nos. 7, 8 and 24) several forms which, due to their continued attachment to hyphae are set apart from the totally isolated 'germlings'.

Lange (1976) concluded that the distribution of the modern equivalents of 'germlings' from the Australasian region, on the basis of 'highest morphological grade detected' gave at least a partial index of annual average rainfall but not of latitudinal patterning. Lange (1978b) therefore extended his analysis of the modern leaf-litter samples to include other epiphyllous structures (see Chapter 4, p. 105). For this expanded analysis (including grade 5 'germlings', marginuloid hyphae, rangiferoid setae, germinated melioloid spores, callimothalloid and cribritoid shields) the inferred palaeohabitats, equivalent to those of the modern vegetational types, would become more restricted toward conditions similar to those that prevail in wet tropical vegetation.

Lange (1976) based his original attempt at correlating 'germlings' with palaeohabitat upon quantitative analyses of modern-day equivalents of 'germlings' in leaf litter. The analyses

FIGURE 8.4

'Germling' grade of complexity
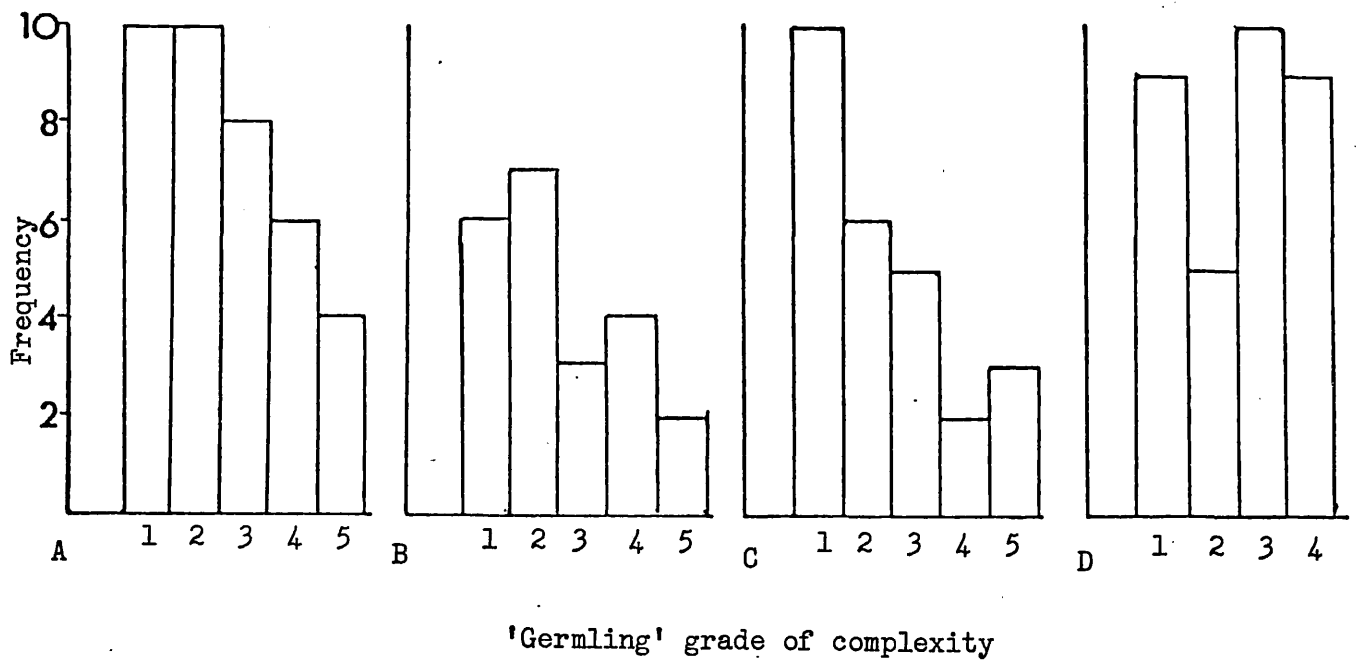
Frequency distribution of 'germling' grades at:

A. Fullerborn Harbour   B. Cascade

C. Orbost   D. Smoko Creek

after Lange (1976)

FIGURE 8.5
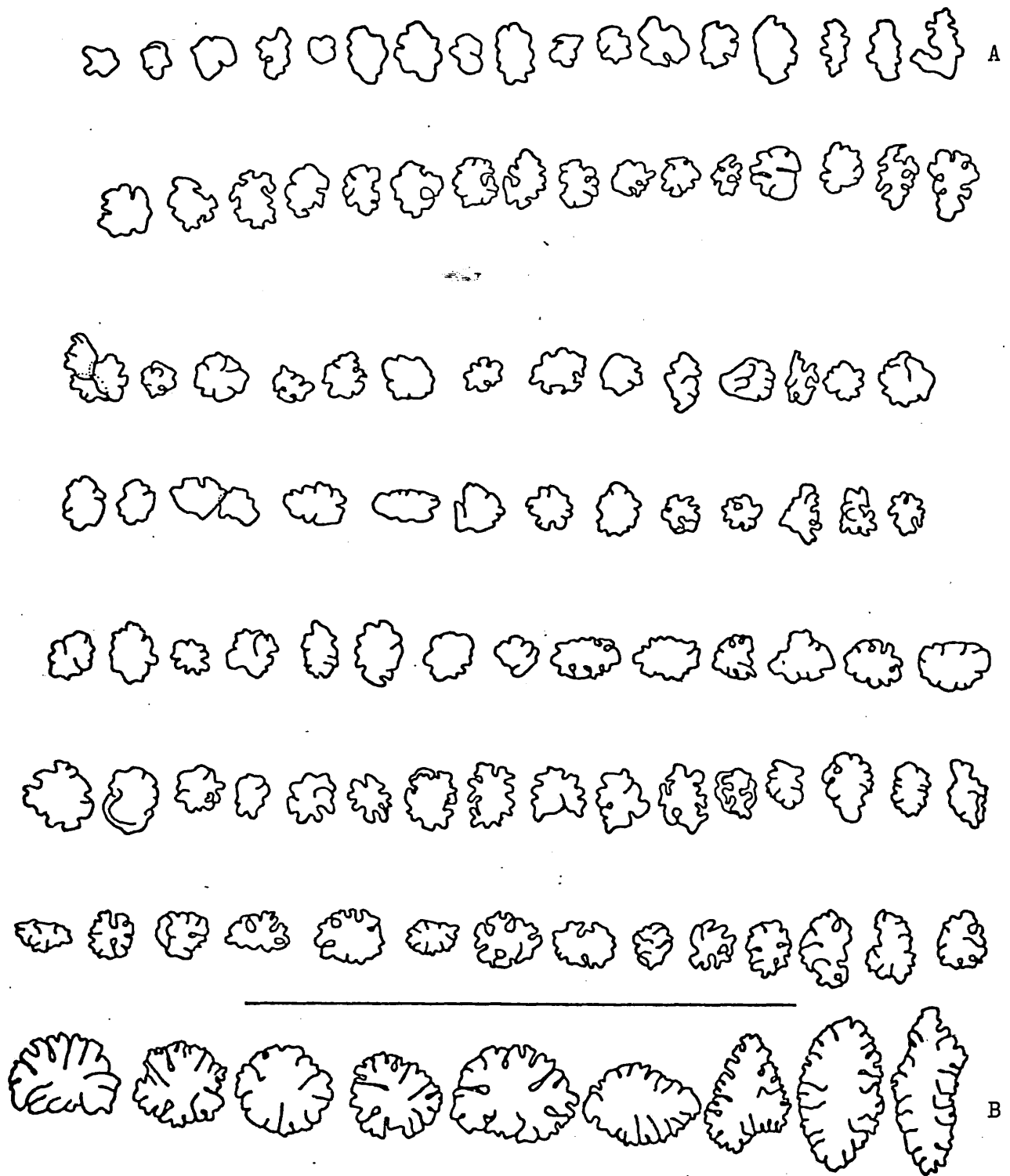
Outline morphologies of 'germlings' from the Hordle Cliff
Deposit.   Magnification A. X1,000   B. X1,500

were based upon two criteria, the fraction of leaf cuticles which bore 'germling' equivalents of any particular grade; and the average density per square centimetre of cuticle of the particular grade of 'germling'. Lange (1976) concluded that this type of analysis was prohibitively time consuming and based all his further analyses upon the single criterion - 'highest grade of 'germling' detected'. Lange (1976) was able to demonstrate a highly significant statistical association between this criterion and the source vegetation type. The four samples of leaf litter fully analysed for frequency and density data had a wide latitude distribution. Fullerborn, Harborn, New Britain (circa 6° S), Cascade, New South Wales (circa 32° S), Orbost, Victoria (circa 38° S) and Smoko Creek, Tasmania (circa 42° S). This latitudinal spread means that the four source vegetations were of completely different types and floristically extremely diverse. The frequency data collected by Lange (1976) from these sites is represented graphically in Fig. 8.4 (p. 225).

The Hordle Cliff material yielded a wide range of morphological forms of 'germlings' (see Fig. 8.5, p. 226). These however were predominantly specimens which had been separated from their host cuticle and therefore direct comparisons with the frequencies recorded by Lange (1976) are not totally valid. If Lange's (1976) 'highest grade of 'germling' detected' is applied as the sole criterion, the occurrence of grade 5 'germlings' (see Fig. 8.2, p. 218) as 6% of the Hordle Cliff population would by analogy suggest that the host vegetation of these 'germlings' grew in conditions where annual rainfall exceeded 20 dm. Being dispersed (i.e. palynological) there is not strong evidence that these grade 5

'germlings' are autochthonous, they could well have been transported for some distance prior to their final deposition. However, Fowler et al (1973) have suggested that the palaeoenvironment of this area was at the time coastal alluvial flood plain, with open marshes, and swamp forests. Chandler (1961) on the basis of the fruit and seed flora concluded that the source vegetation of the Lower Headon Beds was tropical and commented that associated animal remains including Crocodilus hastingsiae are also indicative of a warm climate. Machin (1971) after studying the Lower-Upper Headon Beds of the Isle of Wight concluded from the palynological forms present that the flora represented a sub-tropical swamp vegetation comparable to those of present day Florida and with a strong affinity to the modern swamp and more dry ground flora of subtropical/warm temperate south-east Asia. Machin (1971) followed Chandler (1961) in regarding this flora as another aspect of the London Clay Flora but one less rich in species.

Collinson et al (1981) having examined fossil floras of fruit, seeds, pollen and spores from Palaeogene deposits of both the London and Hampshire Basins could find no evidence for a sudden climatic change at the end of the Eocene (cf Wolfe, 1978). Rather they found two major periods of floristic change. These two changes are interpreted as possibly indicating a progressive lowering of land surface temperature during the Middle Eocene in southern England. The second of these changes, which occurs within the Headon Beds is suggested by Collinson et al (1981) as being more rapid than the first. Daley (1972) has placed the latitude of Southern England during the Eocene as $40^{\circ}N$, and it would therefore be tempting to

FIGURE 8.6
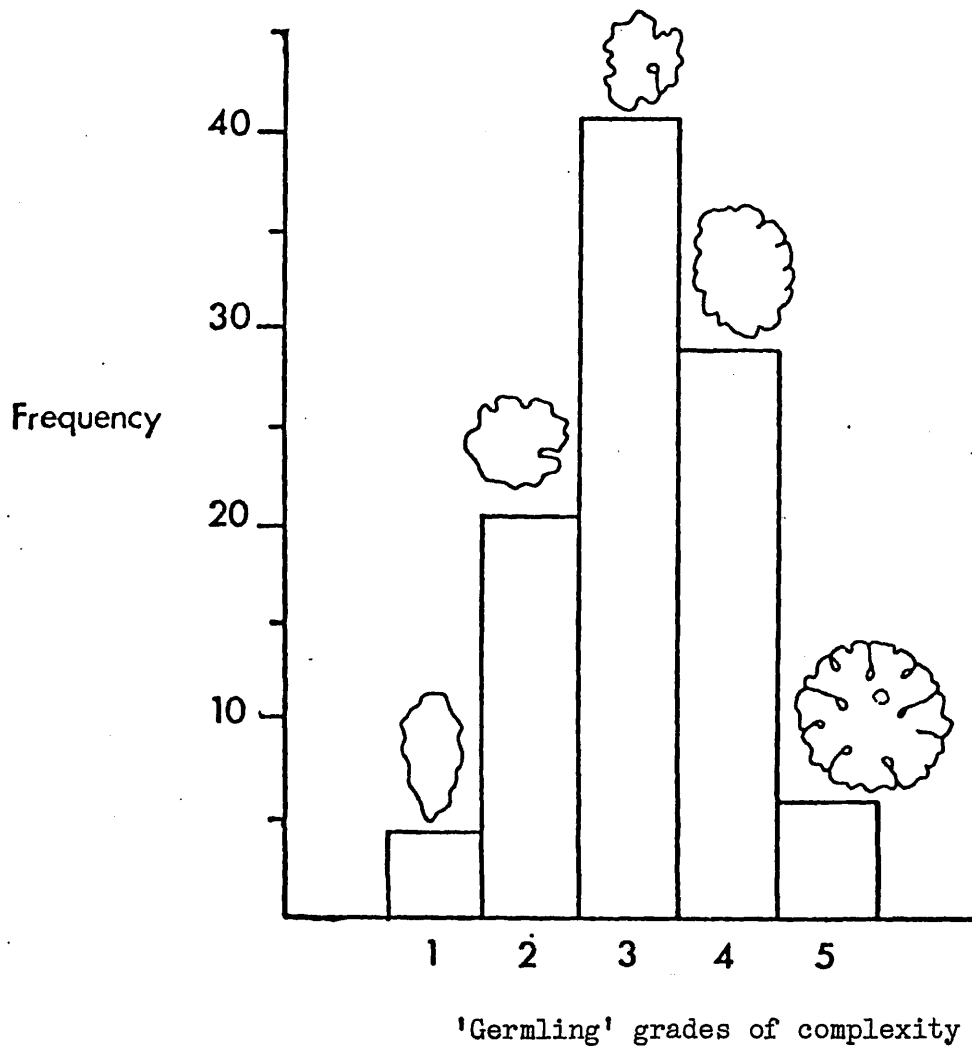
Histogram to show frequency of occurrence of
'germling' grades in the Hordle Cliff preparations.

compare the frequency count of the Hordle Cliff material (see Fig. 8.6, p. 229) with those of similar latitude from the Southern Hemisphere (see Fig. 8.4C and D, p. 225). Although floristic comparisons of the Northern and Southern hemisphere sites would be of little or no scientific value, there has not been any evidence advanced within the literature that 'germlings' are restricted in their host range. In fact the data from Lange (1976) would tend to indicate the opposite. If conditions are suitable, these conditions at present being undefined, 'germlings' will be established regardless of the floristics of the host vegetation.

The frequency counts cannot be compared directly as the Hordle Cliff material is solely palynological and thus the lower grades (grades 1 and 2) could well be under-represented due to the difficulty in separating palynomorphic 'germlings' of simpler morphology from amerospores. Grades 3-5 are readily recognisable. The frequencies (40: 29: 6) of these grades in the Hordle Cliff material cannot be equated directly with any of the Southern Hemisphere sites. The closest resemblance would be with that of Cascade, New South Wales (circa 32°S) a warm temperate rainforest.

It must be concluded then, that although dispersed palynological 'germlings' can be used to give a first approximation of palaeohabitat, especially the higher grades, this indication can only be an adjunct to other climatic indications. The characteristic morphology of the higher grades is easily recognised even in palynological preparations and observation of these forms should be regarded as evidence of wet conditions associated with the host vegetation.

FIGURE 9.1

A

B
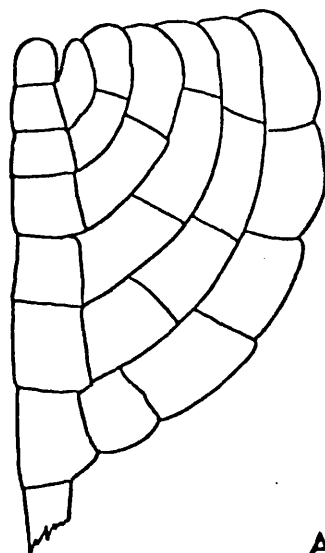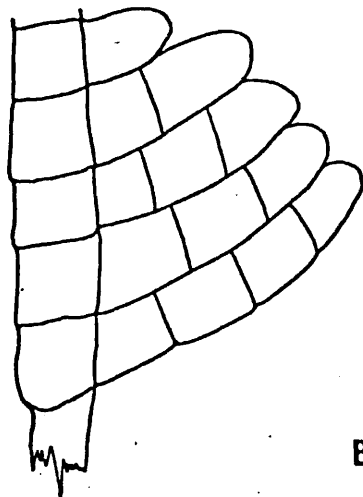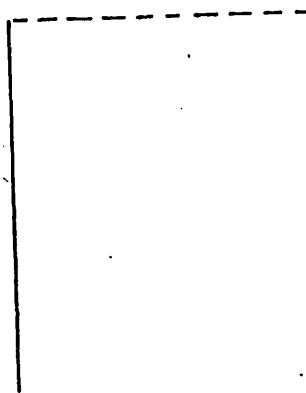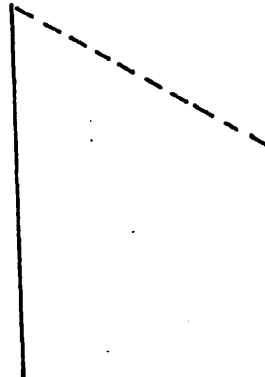
Diagrammatic representation of branch

orientation in Ctenosporites

A. C. eskerensis (sensu Elsik and Jansonius, 1974)

B. C. wolfei (sensu Elsik and Jansonius, 1974)

9. DISPERSED SPORES OF THE FORM-GENERA CTENOSPORITES AND PESAVIS

N.B. Some of the contents of this chapter have been published previously (see Smith, 1978; and Smith and Crane, 1979).

These two highly distinctive fossil fungal spore genera were erected by Elsik and Jansonius (1974) based upon material isolated from Palaeocene and Eocene deposits from the Canadian northwest Pacific and Arctic regions. Both form-genera were at first thought to be geographically restricted to the Canadian deposits, however Lange and Smith (1975a, 1975b) and Lange (1978c) have located both form-genera in the Eocene, Maslin Bay flora of South Australia. Smith (1978) and Smith and Crane (1979) have demonstrated the presence of Ctenosporites in Eocene and Pesavis in Palaeocene deposits from southern England.

CTENOSPORITES

Elsik and Jansonius (1974) recognised two species within the genus, C. eskerensis isolated from a late Eocene deposit near Esker Creek, Alaska and C. wolfei from middle to late Eocene deposits of the Kulthieth Formation, Samovar Hills, Alaska. The two species were distinguished on the basis of two morphological characters. Ctenosporites is characterised as a cheiroid structure, a main axis with a series of multicellular lateral branches along one side of the main axis. C. eskerensis was typified by the presence of a rounded apical cell at the tip of the main axis and the tendency of all the lateral branch tips to reach an imaginary plane through the stem apex, perpendicular to the long axis of the main axis (see Fig. 9.1A,

FIGURE 9.2
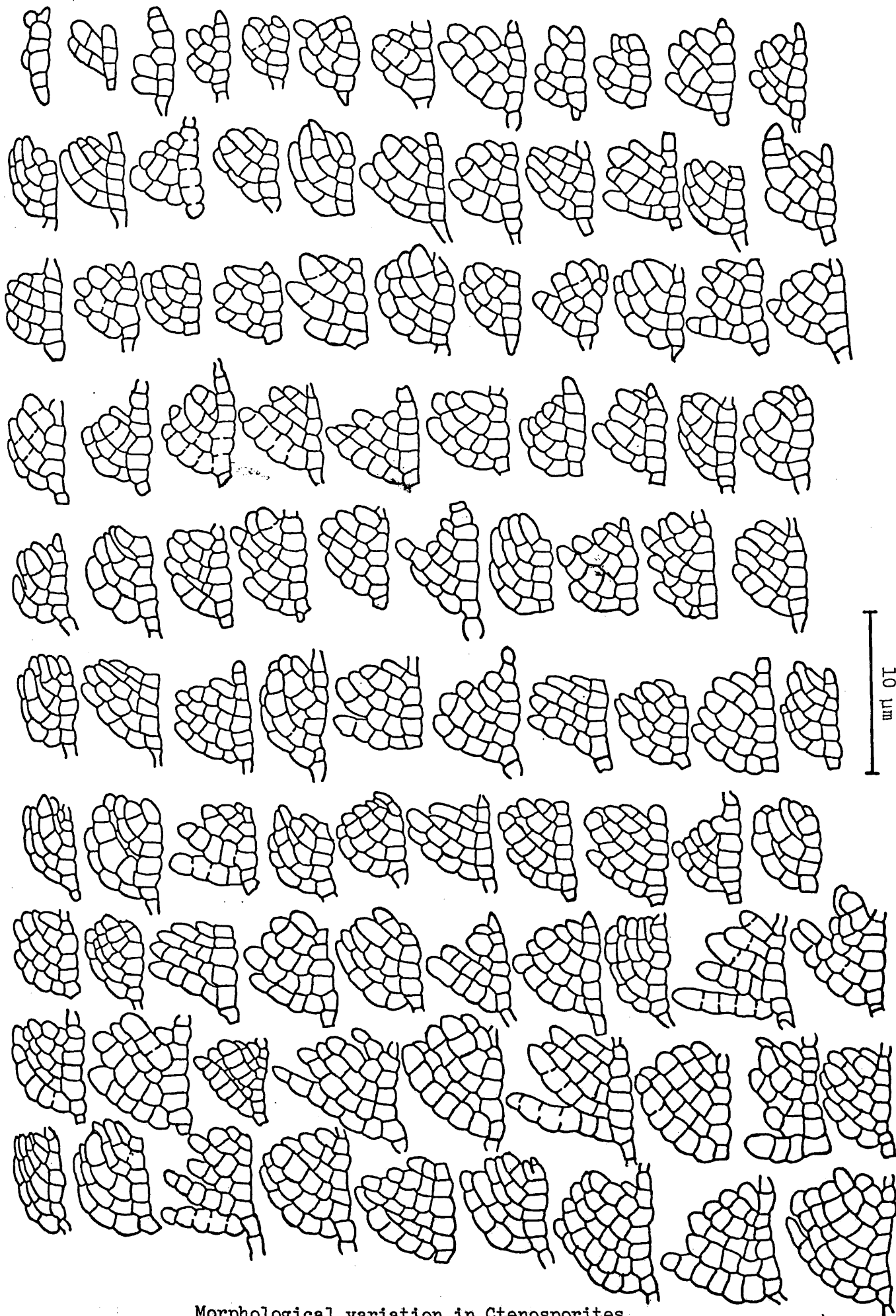
Morphological variation in _Ctenosporites_.

p. 231). C. wolfei lacks a complete rounded apical cell at the tip of the main axis and the lateral branches, relatively shorter than those of C. eskerensis, have tips which make an acute angle to the long axis of the stem (see Fig. 9.1B, p. 231).

Lange and Smith (1975b) reported the presence of Ctenosporites material associated with a fossil angiosperm anther containing pollen grains of proteaceous affinity. More significantly Lange and Smith (1975b) were able to demonstrate organic connection of the Ctenosporites type spores to mycelial hyphae and thus remove the South Australian examples from Sporae Dispersae. The spore morphologies of the Ctenosporites showed a high degree of variability including forms attributable to both C. eskerensis and C. wolfei. Lange and Smith (1975b) concluded that all the variable forms were in fact one biological species although they would undoubtedly be described as more then one form-species if found as Sporae Dispersae. Lange and Smith (1975b) made no formal description of the South Australian material either as one of the two previously described species or as a new form-species preferring instead to re-emphasise their contention (Lange and Smith, 1971) that taxonomic treatments of dispersed fossil fungal spores must of necessity be based upon population studies to ensure that all possible morphological variability is recorded prior to establishing specific limits (see also Smith, 1981). Smith (1978) analysed a large population of Ctenosporites found as Sporae Dispersae in the late Eocene deposits from Hordle Cliff and found a large range of morphological variation (see Fig. 9.2, p. 233) which called into question the morphological criteria used by Elsik and Jansonius (1974) to establish the two

form-species C. eskerensis and C. wolfei. The combination of apical cell presence or absence and angle of lateral branches to the main axis, plus the number of thick-walled cells in the main axis (7 in C. eskerensis sensu Elsik and Jansonius, 1974; 4-5 in C. wolfei sensu Elsik and Jansonius, 1974) were not found to be sufficient to make a clear distinction of the population under consideration. An analysis of three parameters; the number of thick-walled cells in the main axis, the number of lateral branches, and the number of cells in the basal branch on 500 specimens of the Hordle Cliff populations was performed. The results of this analysis are represented graphically in Text-fig. 2 Smith (1978) showing that each of the parameters gave results approximating a normal distribution. These were interpreted as indicating that species delineation within this form-genus as proposed by Elsik and Jansonius (1974) was based upon two extreme conditions within a continuum of variability and as a consequence C. wolfei (sensu Elsik and Jansonius, 1974) was submerged into synonymy with the type species C. eskerensis with an emended diagnosis to allow for the wider range of variability.

Despite the characteristic morphology of the Ctenosporites material there has been no exact matching with an extant fungus. As Lange and Smith (1975b) and Smith (1978) have already pointed out some superficial morphological similarity exists between Ctenosporites and the dematiaceous hyphomycete genus Dictyosporium. Ellis (1971) illustrates four species of Dictyosporium and in his key separates three species, D. elegans, D. toruloides and D. oblongum as having conidia flattened in one plane. Of these three species it is only D. toruloides in which the conidia are clearly cheiroid (i.e.

FIGURE 9.3

20 μm

20 μm

A

B

20 μm

50 μm

C

D
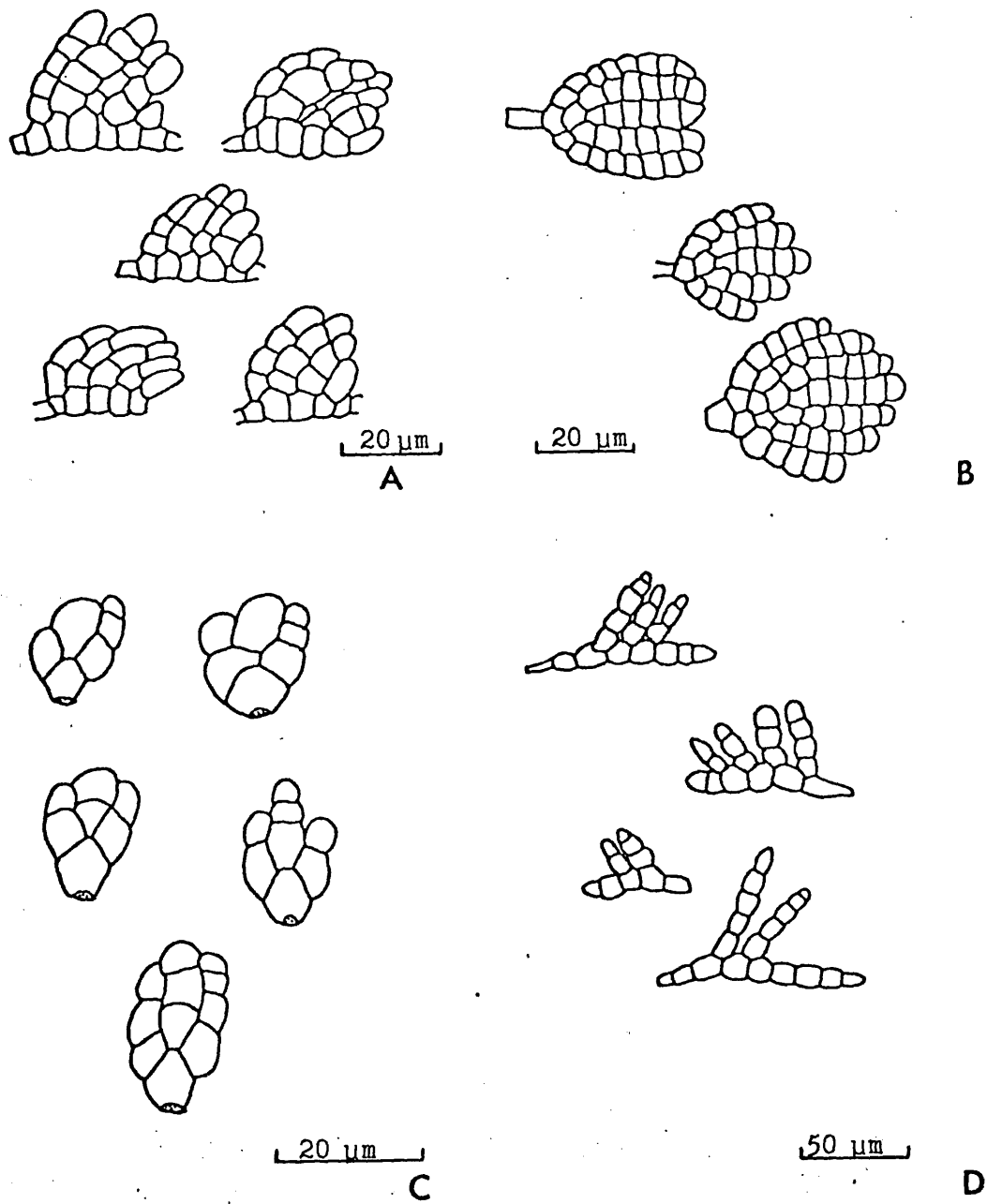
Morphology of Ctenosporites and its possible extant
affinities:

A. Ctenosporites   B. Dictyosporium

C. Kamatia   D. Dendrospora

hand-shaped) with branches of different lengths (see Fig. 9.3, p. 236). The overall branching pattern is not that of Ctenosporites, as the branches in Dictyosporium toruloides are arranged on either side of the central axis, rather than unilaterally, as in Ctenosporites. A similar superficial morphological similarity could be suggested to the dematiaceous hyphomycete genus Kamatia indica described by Rao and Subhedar (1976). Here the conidiospores again are cheiroid in organisation and although the branching pattern tends to be oriented more toward the unilateral as in Ctenosporites, Rao and Subhedar (1976) place great importance on the fact that the conidiospores are tretic. This means that unlike both Ctenosporites and Dictyosporium there is no evidence of an attachment cell in the conidiospore but rather a well-defined hilum on the basal cell of the conidiospore (see Fig. 9.3, p. 236). A third possible genus with which affinity to Ctenosporites could be suggested is the aquatic hyphomycete genus Dendrospora moniliformis described by Descals and Webster (1983), based upon conidiospores produced in pure culture from a conidiospore isolated from freshwater foam from the Scottish highlands. Descals and Webster (1983) make the point that conidial (conidiospore) branching tends to be more profuse and irregular; nevertheless several of the morphologies they illustrate for D. moniliformis are remarkably similar to those exhibited by Ctenosporites (see Fig. 9.3, p. 236). Two orders of branching have been observed in D. moniliformis, the branching although lateral may be only in one plane, but more often the laterals are in more than one plane. Ingold (1943) erected the genus Dendrospora and designated the conidiospores as aleuriospores, i.e. hyaline spores, an observation reiterated by Descals and Webster (1980) in their

taxonomic review of Dendrospora species. The cell walls of the spores of Ctenosporites are for the most part thick and tend to suggest a closer relationship to the dark-coloured dematiaceous forms rather than the hyaline forms of hyphomycetes. Habitat requirements of the three recent genera under consideration as possible affinities for Ctenosporites do not help to clarify matters to any great extent.

Dictyosporium toruloides is reported by Ellis (1971) as 'common on wood and dead herbaceous stems', however Ellis et al (1951) in their descriptions of fungi found in British marshes and fens commented that D. toruloides (described as Speira toruloides) occurs occasionally on leaves. Ellis et al (1951) list Angelica sylvestris, Cladium mariscus, Epilobium hirsutum, Filipendula ulmaria and Juncus effusus as hosts, or at least, source vegetation for D. toruloides.

Rao and Subhedar (1976) collected their material of Kamatia indica from living leaves of the South Indian genus Schleichera trijuga, a tree of the family Sapindaceae. The natural substrate of Dendrospora moniliformis is still unknown, having been cultured from a conidiospore isolated from stream foam. Descals and Webster (1980) characterised the genus Dendrospora as "saprophytic hyphomycetes from moist or submerged freshwater habitats".

All three of these substrates could plausibly be regarded as contributing to a deposition site; Elsik and Jansonius (1974) and Smith (1978) have recorded Ctenosporites only as isolated spores and although Lange and Smith (1975b) have recorded Ctenosporites apparently growing on an angiosperm anther this cannot rule out at

least two of the modern genera advanced for comparison _viz_ the two
saprophytes <u>Dictyosporium</u> and <u>Dendrospora</u>. Spores of both these
genera, one terrestrial and one aquatic could easily be transported
to the deposition site, or if the deposition site was subjected to
periodic flooding; the spores, if related to <u>Dendrospora</u> could be
developed more or less _in situ_. A similar line of argument could be
proposed for <u>Kamatia</u> although the morphological similarity between
this epiphyllous genus and the fossil <u>Ctenosporites</u> is rather more
tenuous, nevertheless the nature of the host substrate for the fungus
is such that dispersed spores could easily be transported to
deposition sites. The observation by Lange and Smith (1975b) that
the South Australian material did not have a narrow host specificity,
occurring on non-proteaceous leaf material as well as the anther,
also has a bearing in these considerations. Smith (1978) compared
the apparent lack of host-specificity of <u>Ctenosporites</u> with the
similar host range of <u>Dictyosporium toruloides</u> and suggested this as
a possible contributing factor to the wide range of morphological
forms within the Hordle Cliff population. This suggestion was based
upon the known effects of nutrient levels upon extant spore
morphology as previously discussed in Chapter 3 (p. 68) in
relation to classification of dispersed fossil fungal spores.

PESAVIS

Elsik and Jansonius (1974) erected this form-genus with two species from material isolated from Palaeocene and Eocene deposits within the same geographical area as those from which Ctenosporites was isolated. Smith and Crane (1979) described similar material from the Palaeocene deposits from Cold Ash Quarry near Newbury and Lange (1978c) has recorded a single specimen from the Eocene Maslin Bay deposits of South Australia. A single incomplete specimen attributable to this genus has also been observed from the Eocene Hordle Cliff deposit. Wilkinson and Boulter (1980) recorded the presence of ten specimens of Pesavis from the Bellbrook borehole from the east of Lough Neagh, Ireland. The Lough Neagh clays are considered by Wilkinson and Boulter (1980) to be of Late Oligocene age.

Elsik and Jansonius (1974) erected the form-genus Pesavis with two species P. tagluensis and P. simplex. However the differences in morphologies exhibited by these two species far outweigh their similarities and Pirozynski (1976a) has already commented upon the fact that P. simplex is virtually indistinguishable in construction from the spores of the dematiaceous hyphomycete Ceratosporella bicornis; an extant species of a genus that occurs on dead or dying plant material (S.J. Hughes, 1951; Ellis, 1971). Thus there is the strong suggestion that P. tagluensis and P. simplex are not closely related and it would seem highly questionable to retain such disparate entities within the same form-genus. Despite his observations on the relationships of P. simplex Pirozynski (1976a) made no formal moves to clarify the nomenclatural and taxonomic

position of this material. Similarly Jansonius (1976) figures a form

which he termed 'P. parva (prelim. name)'. Elsik (1976b) in a table

showing the stratigraphic occurrence of fungal spores within the

Cenozoic distinguished between P. tagluensis and Pesavis spp.; the

implication of this being that species such as P. simplex (sensu

Elsik and Jansonius, 1974) and others such as 'P. parva' (sensu

Jansonius, 1976) are in fact valid species. After applying the

population analysis advocated by Lange and Smith (1971), Smith and

Crane (1979) demonstrated that the population of Pesavis spores

isolated from the Cold Ash Quarry Newbury exhibited a wide range of

morphological variation. The range of variation did however fall

within the ambit of Pesavis tagluensis in that the basic construction

of the spore is as follows:

A central basal cell bearing two septate incurving arms which

can be of equal or unequal cell number, the tip cells of the

primary branches may either touch or overlap. Cells of the

primary arms bear a single or more usually a pair of inwardly

directed short straight septate arms.

The Newbury material corresponds in size to that given by Elsik and

Jansonius (1974) for their holotype 32 X 38 μm and paratype 40 X 35

μm. Disregarding Pesavis simplex as a species of Pesavis the

proposed 'P. parva' which corresponds remarkably closely in

morphology with a specimen figured by Elsik and Jansonius (1974) as

"a small probably immature specimen (of P. tagluensis) lacking

secondary hyphae". Secondary hyphae are the inwardly directed short

arms and the specimen in question (Elsik and Jansonius, 1974; Plate

1, fig. 10) clearly shows evidence of at least two such inwardly

directed lateral branches, one from a cell of each of the incurved

FIGURE 9.4
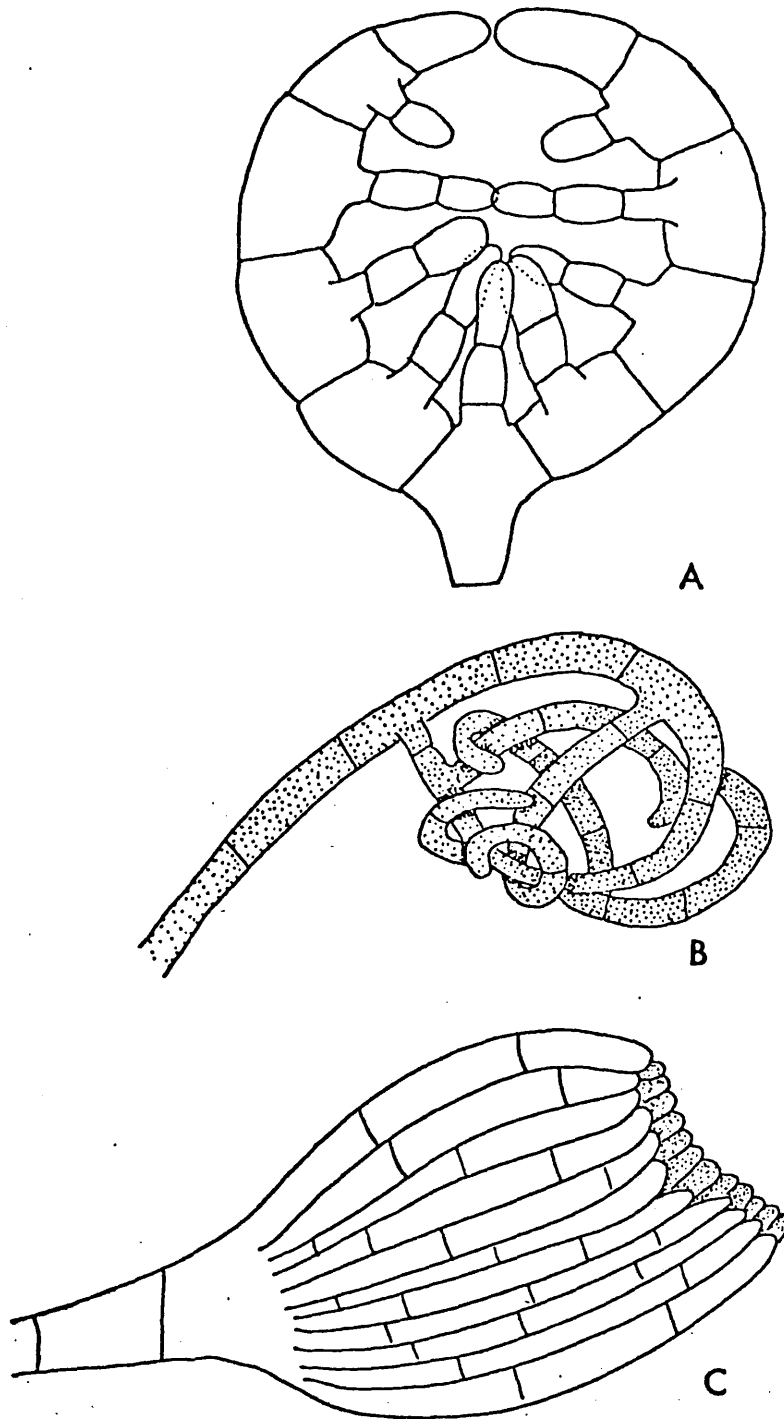
Diagrammatic comparison of the structure of

A. <u>Pesavis</u> B. <u>Spirosphaera</u> C. <u>Cancellidium</u> spores.

B. after Kendrick and Carmichael (1973)

C. after Webster and Descals (1981)

primary arms. Smith and Crane (1979) did not formally submerge 'P. parva' (sensu Jansonius, 1976) into synonymy with P. tagluensis as there was no formal taxonomic description accompanying the original proposal. No subsequent validation of Jansonius's proposed binomial has been encountered and thus 'P. parva' is to be regarded as a nomen nudum. The morphological variant which the Jansonius (1976) proposal was meant to accomodate is best treated as a small, perhaps immature, form of P. tagluensis.

Despite the strikingly characteristic structure of P. tagluensis (see Fig. 9.4A, p. 242) there does not appear to be any living fungus which produces a spore of similar construction. Elsik and Jansonius (1974) stated that they were uncertain as to whether Pesavis (more especially P. tagluensis) "represent spores, fruiting bodies or snaring mechanisms of predatory parasitic fungi". Several types of soil-inhabiting fungi have been found to capture nematodes by means of various kinds of snares. Subramanian (1983) detailed the various types of snares found in the hyphomycete fungi specialised in this way:

1) capture by adhesion to a simple erect branch coated with adhesive all over its surface

2) capture by adhesion to stalked or sessile knobs, the knobs above being coated with adhesive

3) capture by adhesion to two-or three-dimensional nets or loops coated with adhesive all over the surface

4) capture by non-constricting rings that are passive in their action; nematodes being trapped when they glide into the rings that wedge around their body

Beverwijkella pulmonaria | DICTYOSPORE?

Cancellidium applanatum | STAUROSPORE (?)

Candelabrum brocchiatum | STAUROSPORE

    C. spinulosum

Clathrosphaerina zalewski | CLATHROSPORE (=DICTYOSPORE)

Fusticeps bullatus | PHRAGMOSPORE

Helicodendron articulatum | HELICOSPORE
    H. congolomeratum
    H. fractum
    H. giganteum
    H. intestinale
    H. luteo-album
    H. multicatenulatum
    H. paradoxum
    H. triglitziensis
    H. tubulosum
    H. westerdijkae

Helicoon fuscosporum | HELICOSPORE

    H. pluriseptum

Peyronelina glomerulata | DICTYOSPORE/STAUROSPORE?

Spirosphaera beverwijkiana | HELICOSPORE
    S. floriforme
    S. minuta

TABLE 9.1   Genera and species of aero-aquatic hyphomycetes. Compiled from data from Subramanian (1983), Kendrick and Carmichael (1973) and Webster and Descals (1981).

5) capture within constricting rings; cells expanding rapidly
in an inward direction following entry of a nematode,
resulting in tightening of the ring around the nematode.

The configuration and construction of P. tagluensis is such that
several of these mechanisms (1 to 3) can be discounted immediately
and the remaining two mechanisms do not seem very plausible.

Smith and Crane (1979) advanced an alternative hypothesis as to
the nature of P. tagluensis. The architecture of the spore could
be an adaption to an aero-aquatic mode of existence. In contrast to
the aquatic hyphomycetes which grow, develop and liberate their
characteristically hyaline tetraradiate spores (Ingold, 1975) under
water, aero-aquatic hyphomycetes produce mycelial hyphae under water
but produce conidia when the leaf-litter substrate is exposed above
the surface of the water. Subramanian (1983) stated that many of the
aero-aquatic fungi are known to be abundant in shallow water-filled
ditches subject to intermittent flooding where the leaf litter layer
is just a few centimetres below the water surface. Exposure of the
leaf litter to the air during dry periods induces these fungi to
sporulate vigourously producing conidiospores with special flotation
devices. Subramanian (1983) lists 25 species from 7 genera (see
Table 9.1, p. 244) which have been found to occur in this type of
habitat. The morphological structure of the conidiospores of the
genera concerned are taken from Kendrick and Carmichael (1973) and
Webster and Descals (1981). Three dimensional barrel-shaped spores
formed by the tight winding of spiral hypha characterise the genera
Helicoon and Helicodendron, the conidia so formed enclose air as they
develop at the air/water interface at the surface of the moist

substrate and are extremely buoyant. In <u>Clathrosphaeria</u> the propagule is a hollow clathrate sphere formed by repeated dichotomous branchings and incurving of the branches. <u>Candelabrum</u> has a more flattened arrangement of dichotomous branchings each ending in vertical spiny lobes which touch one another. <u>Peyronelina</u> has a series of incurved spiny arms containing a cluster of globose cells, which are the fertile cells. Air is trapped between the spiny arms and also between the globose cells, a similar situation being found in <u>Beverwijkella</u> <u>pulmonaria</u>. <u>Fusticeps</u> <u>bullatus</u> produces a club shaped transversely septate spore bearing studs derived from the outer spore wall. These studs trap air between them to allow the spores to float when flooded. Although <u>Peyronelina</u> has a certain morphological similarity, although not close, with <u>Pesavis</u>, there is a high degree of functional similarity. This paralleling of morphology and function is however considerably closer when the genera <u>Spirosphaera</u> and <u>Cancellidium</u> are examined (see Fig. 9.4B & C, p. 242). <u>Spirosphaera</u> produces a buoyant propagule by trapping air between a large number of short incurved branches whilst <u>Cancellidium</u> develops a series of finger-like septate hyphae in the shape of a wine glass; air becomes trapped in the bowl thus formed and the propagule breaks from its uniseriate stalk and floats when flooded.

It is interesting to note Lange's (1978c) observations on the occurrence of <u>Pesavis</u> in the Maslin Bay flora, that nine other South Australian fossil fungal assemblages have failed to reveal either <u>Pesavis</u> or <u>Ctenosporites</u> and that none of the present day litter samples used for present day equivalents to 'germlings' and microthyrioid and callimothalloid shields have either. Lange (1978c)

illustrates a single specimen from the Maslin Bay flora, in contact with but not connected to a leaf fragment, the specimen is broken and lacks the basal cell subtending the two incurving arms. The absence of Pesavis-like structures from present day leaf litter samples is more readily explained if the proposed aero-aquatic nature of Pesavis is considered. Fisher (1978) has studied the survival of aero-aquatic fungi in the field and under dessication in the laboratory. Mycelial material of Helicodendron triglitziensis was recoverable from dried leaf powder kept in a dessicator for over a year. Webster is reported as having stated in a discussion following Webster and Descals (1979)

"... Indeed, the dried leaves containing viable mycelium may be an important means of dispersal: when the pond dries up these leaves can be blown considerable distances by the wind."

This hypothesis could also explain the extremely disjunct occurrence of fossils of this type (Arctic Canada, Southern Britain, Lough Neagh Ireland, and Maslin Bay South Australia) from deposits ranging from Palaeocene to Oligocene in age. The governing feature for their presence could well be the occurrence of temporary pools or streams of fluctuating depth to provide the specialised conditions required for sporulation, rather than other climatic or floristic features.

FIGURE 10.1
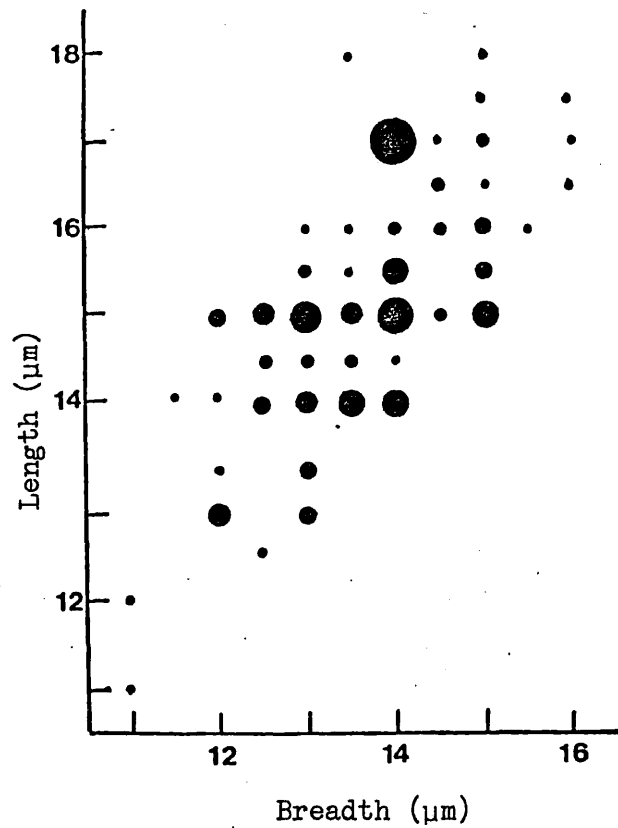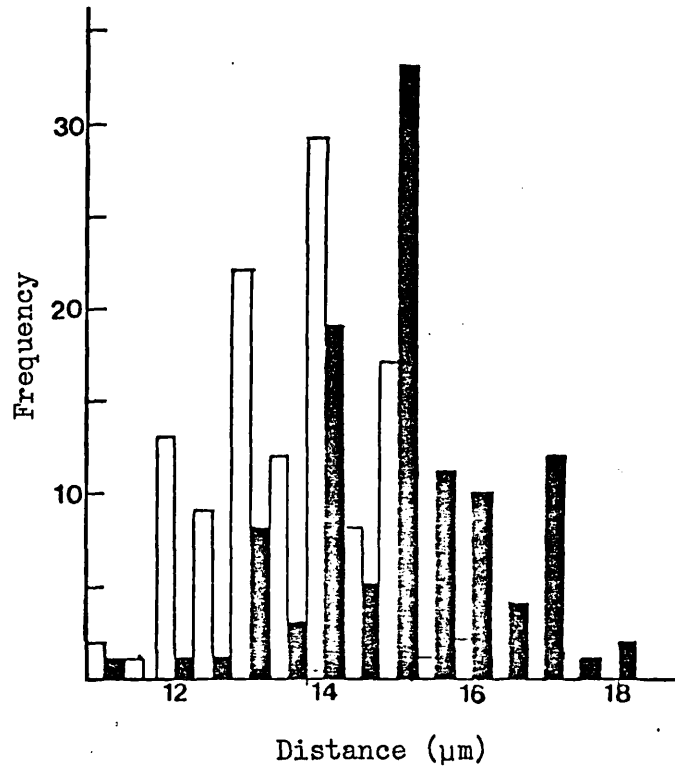
A. Length and breadth measurements of T. sp. A, solid bar - length, open bar - breadth.

B. Dimensions of individual T. sp. A spores; size of circle indicates frequency of occurrence.

10   SELECTED DISPERSED FUNGAL SPORES FROM THE HORDLE CLIFF DEPOSIT

The intention in this chapter is to illustrate the population analysis method as advocated by Lange and Smith (1971) as it is applied to sets of fossil fungal spores of very different morphologies, and to show that in some cases specific boundaries are readily distinguished but that the species concept in some other cases is difficult to establish.

TROCHOPHORISPORITES SP. A

Dispersed helicoid spore, constructed of a single gyre, subdivided into four cells by three thick dark transverse septa. Outer spore wall may be constricted at the septa. Terminal (apical?) cell usually shorter and more hyaline than remaining cells, with a bluntly rounded appearance, sometimes touching or overlapping the opposite (basal?) cell, which tapers to a truncate base. This basal cell bears a submedian lateral process which protrudes into and overlaps the centre of the gyre, giving the inner wall of the entire spore a thicker and darker character. Overall length of spore 11-18 μm, diameter 11-16 μm.

The proposed generic name is based upon that of the living deuteromycete genus Trochophora due to the close morphological similarity of the fossil spore with those of Trochophora simplex (see Fig. 10.2, p. 248). Whilst no mention is made of the presence of a submedian lateral process in the diagnosis of the spores of the extant species Trochophora simplex, the extent of the morphological similarity plus the overlapping size ranges of the

fossil spores (11-18 µm X 11-16 µm) with those of the extant fungus (10-20 µm X 9-12 µm) seem to be a sufficient concensus to allow the basing of the new generic name upon that of Trochophora. Conidiospores of Trochophora are described as strongly curved or helicoid, pale to mid-brown, psilate with three thick transverse septal bands (Ellis, 1971). In the fossil spores, although inaperturate, the distinction between the two terminal cells can be made quite readily. The truncate tapering cell is interpreted as the basal cell, the truncate region being regarded as the attachment of the spore to the conidiophore. This interpretation is strengthened by the observation that within the population of the fungal spores under consideration there are a small number of spores in which development had apparently been arrested. These aberrant forms contain only two septa (i.e. three cells) however the tapering cell bearing the submedian protuberance and with the truncate attachment area was found as in the usual four-celled spores. In both the three-celled and four-celled forms the most distal cell from the basal cell was more rounded and more hyaline in appearance.

Admittedly the interpretation of which of the terminal cells of the fossil spore should be regarded as the attachment cell is a personal interpretation. The truncate cell bearing the submedian lateral process could equally well be interpreted as apical with the more haline rounded cell as the basal cell. This alternate interpretation is perhaps strengthened by the occurrence in some of the fossil specimens of a thinner region in the wall of the rounded tip of the hyaline cell which could be regarded as a hilum. If this interpretation is accepted the fossil fungal spore could well be

compared with the deuteromycete genus <u>Diplorhyncus</u> <u>biloba</u> Arnaud (1952). <u>D. biloba</u> (see Fig. 10.1, p. 248) has a flat tightly spiral spore in which the apical cell is divided into two lobes. These terminal lobes are oriented one on either side of the preceding coil of the gyre. The spore is described as tightly coiled hyaline with few septa; Arnaud (1952, figs. 7v and 7x) shows only two septa and the size of the spore of <u>D. biloba</u>, with a diameter of 35-45 µm, is much greater than that of the fossil spores under consideration. Furthermore it is difficult to envisage a method of compression which would result in the described configuration of the majority of the fossil spores found from a spore with the tightly coiled construction and bilobed terminal cell of <u>D. biloba</u>. In <u>Trochophorisporites</u> sp. A recognition of the lateral lobe produced in a submedian position from the truncate attachment cell, depends to a large extent upon the orientation of the spore. Figure 10.1 (p. 248) shows a diagrammatic representation of the spore oriented such that the presence of the lobe can only be inferred from the apparent greater thickness of the inner spore wall and the slight colouration of the central region of the gyre. If on the other hand, the spore is oriented with the 'obverse face' uppermost as in Figure 10.1 (p. 248) the lateral lobe can be seen to emerge from the inner wall of the truncate basal cell and expand to overlap the central portion of the gyre and the inner walls of the other two or three cells of the spore.

The presence of both three-celled and four-celled forms of this spore within the population may well be regarded by some workers as sufficient evidence to separate them as two separate and distinct form-genera. However the very low frequency of three-celled types

FIGURE 10.2
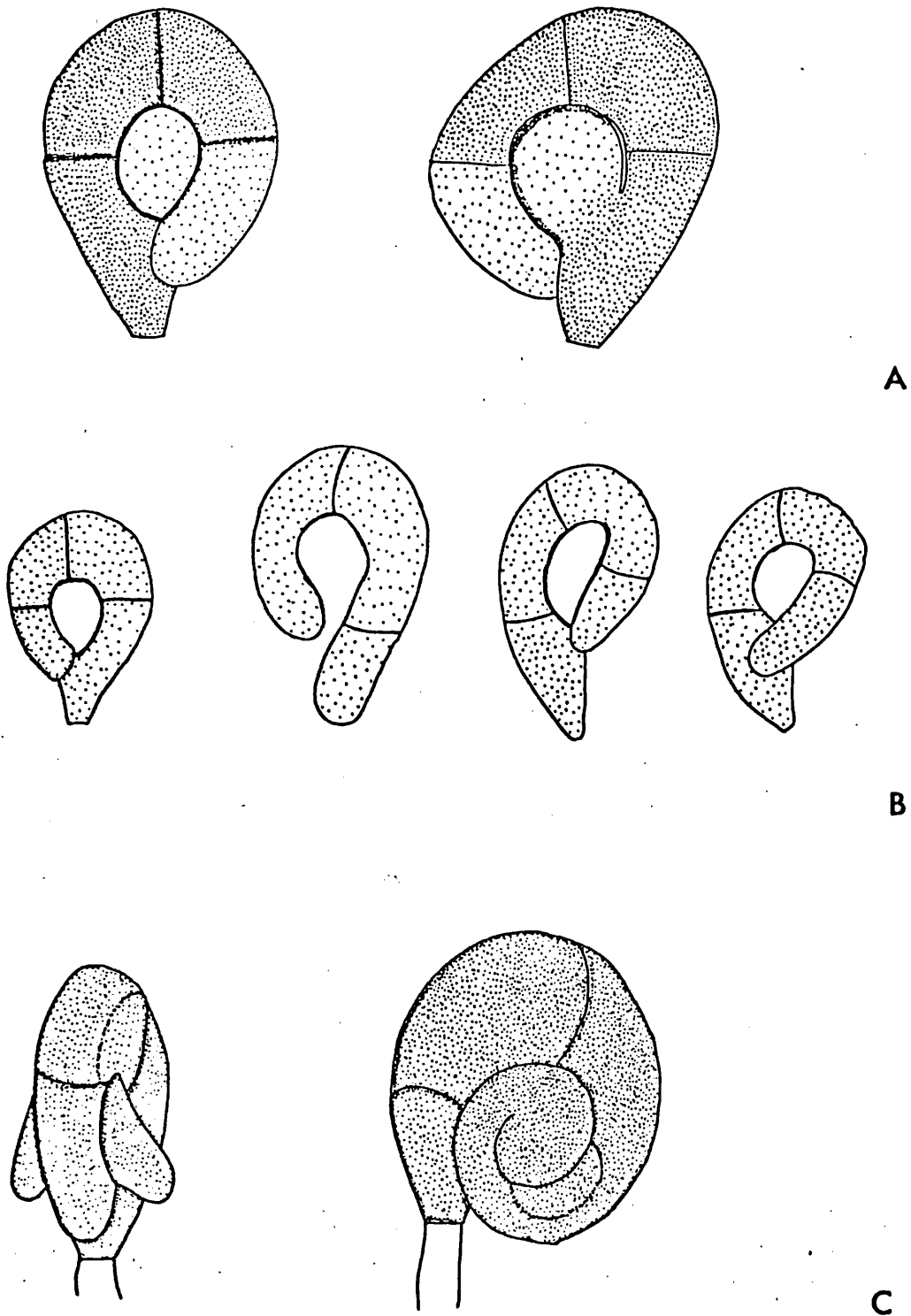

Diagrammatic comparison of spore morphology of:

A. <u>Trochophorisporites</u>

B. <u>Trochophora</u>

C. <u>Diplorhynchus</u>

(17 in 400 spores, i.e. approximately 4%) within the population does not, in my opinion, warrant such a separation. Within the population of four-celled spores a fair degree of morphological variation can be observed. Figure 10.2A (p. 252) shows in graphical form the distribution of both length and breadth (diameter) measurements found within the sample population. The extremely high frequency of breadth (diameter) values of 14 µm and length values of 15 µm shown by this method of data presentation would tend to suggest these as 'typical' measurements for a spore from this population. If however the same data is presented as in Figure 10.2B (p. 252) where length and breadth measurements of individual spores are plotted, it can be seen that spores of breadth 14 µm and length 17 µm occur at a very similar frequency to those of breadth 14 µm and length 15 µm. In fact these are two of the most frequent foci within the wide range of length and breadth combinations found within the sample population. There is no evidence of a natural hiatus in this continuum of variation that would suggest subdivision of the population into more than one species.

Trochophora simplex, upon which this form-genus is based, is recorded both by Linder (1929) and Ellis (1971) as occurring only on living leaves of the angiosperm genus Daphniphyllum. The monotypic family Daphniphyllaceae is geographically restricted to Eastern Asia and Malaya. Linder (1929) recorded T. simplex from the lower leaf epidermis of a species of Daphniphyllum from Ceylon; Ellis (1971) extended the occurrence of T. simplex to include both Hong Kong and Taiwan; whilst Subramanian (1971) has extended the occurrence of T. simplex to an Indian species of Daphniphyllum. Host specificity is a

FIGURE 10.3
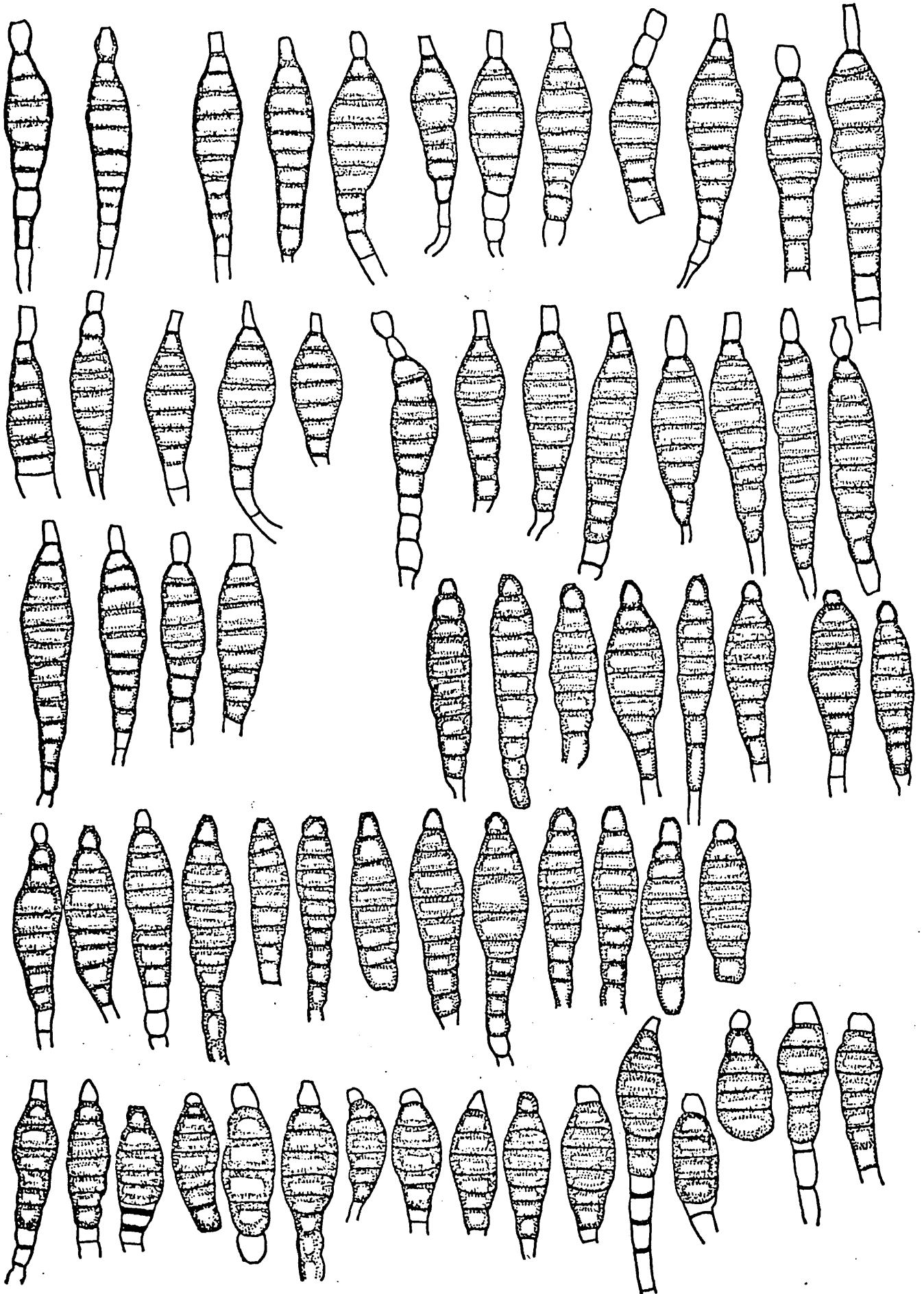
Outline drawings of selected Sporidesmium-like phragmoconidia
from the Hordle Cliff Deposit. Magnification X1,250

well documented phenomenon in many groups of living epiphyllous fungi. Therefore if a close relationship between Trochophora simplex and Trochophorisporites sp. A can be inferred from the morphological similarity between the two spore types; occurrence in the Hordle Cliff deposits of T. sp. A lends mycological support to the Indo-Malaysian affinity of the flora of the British early Tertiary.

SPORIDESMIUM-LIKE PHRAGMOCONIDIA

The following suite of dispersed fossil fungal spores (see Fig. 10.3, p.254) has been selected to illustrate some of the problems encountered when attempts are made to incorporate such fossil material into the existing classification of fungi, especially within the 'form-taxa' or 'anamorph-taxa', as the neo-mycologists prefer to call them, which constitute the Deuteromycotina. Kendrick (1981) made some extremely pertinent comments concerning some of these 'anamorph-genera':

"..... M.B. Ellis described no fewer than 64 species in this 'anamorph-genus' Sporidesmium. The breadth of his interpretation of this genus can be appreciated by browsing through these papers (Ellis 1958, 1959, 1961, 1963a & b, 1965) ..... He describes the conidiophores as discrete mononematous, unbranched and brown, conidiogenous cells as integrated, terminal, determinate or percurrent: and conidia as solitary, dry, borne apically, unbranched and of various shapes (straight, curved, sigmoid, cylindrical, fusiform, obclavate, obpyriform, obturbinate and sometimes beaked) ..... This is obviously a broad circumscription. In fact in some senses the limits of this anamorph-genus can be best expressed in terms of the

features that currently separate other, similar dematiaceous hyphomycetes from it. Clasterosporium and Ceratophorum both produce hyphopodia and in Annellophora the conidia often proliferate at the apex to form secondary conidiophores and conidia, becoming annellate in the process. Sporidesmium then, lacks hyphopodia and its conidia do not proliferate."

Kendrick (1981) stated that the generic concept of Sporidesmium as established is so broad that it makes the visualization of the 'ideal Sporidesmium' virtually impossible. The extremely broad limits of this genus concept, and the plasticity of morphological forms it encompasses, although making the genus a difficult one to identify for the non-specialist, is regarded by Kendrick (1981) as probably advantageous for the delimitation of species within the genus. Ellis (1971) illustrated and described 12 species within the genus Sporidesmium. A further 60 species were illustrated and described, and a key to their identification provided in M.B. Ellis (1976). Of these further 60 species, 11 were separated from the remainder on the basis that their conidiospores (conidia) are pseudoseptate, i.e. the transverse septa give the appearance of not reaching from wall to wall. The intensity of septal pigmentation makes this a difficult to impossible criterion to apply to fossil spores under consideration. The second series of septate Sporidesmium species were separated into 6 groups by M.B. Ellis (1976) on the basis of the substrate on which they occur:

1) overgrowing Microthyriaceae

2) on palms

3) on leaves other then palms

FIGURE 10.4
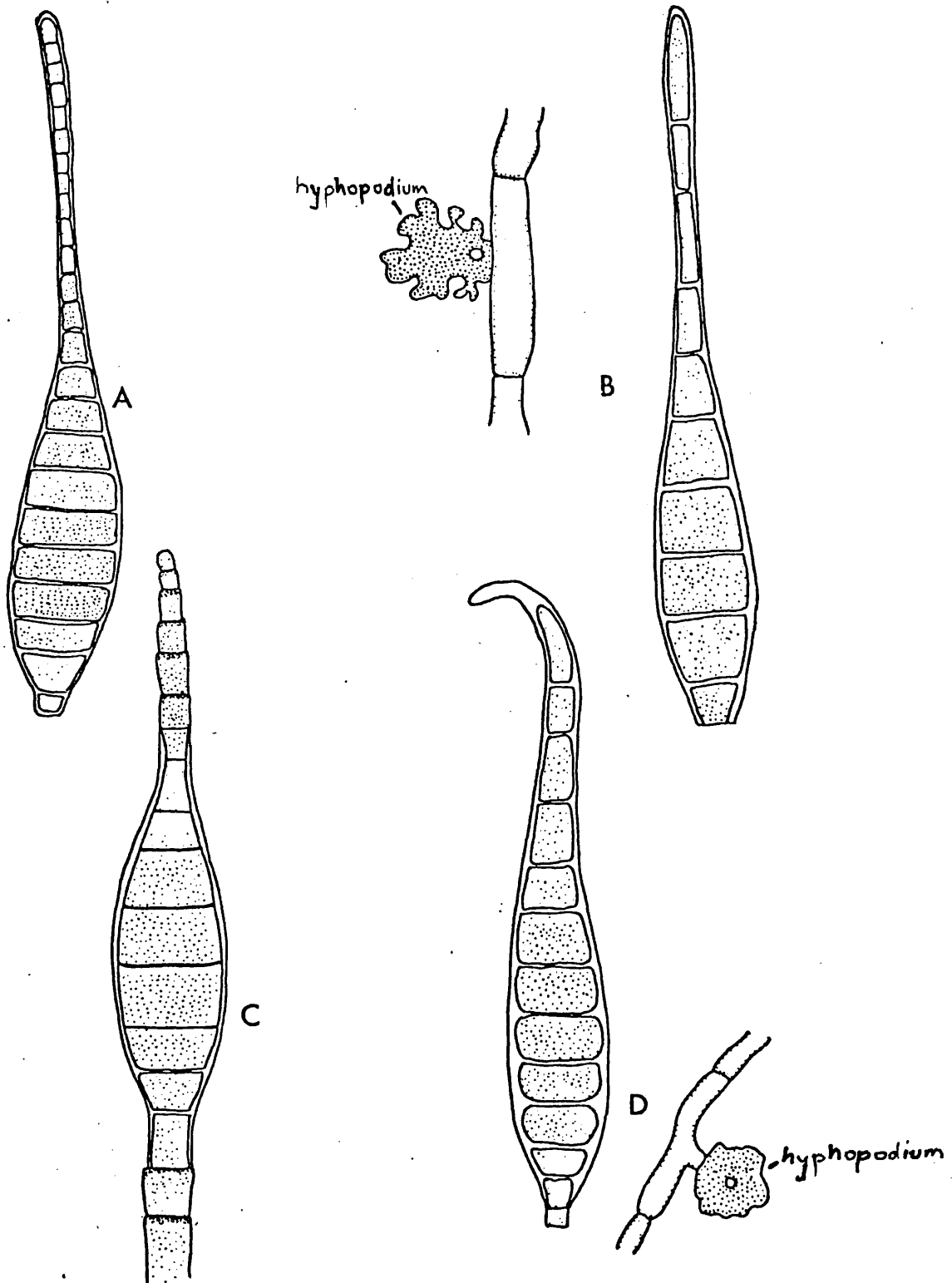
Diagrammatic comparison of spore morphology of

Sporidesmium and associated genera, after Ellis (1971).

A. Sporidesmium   B. Clasterosporium

C. Annellophora   D. Ceratophorum

4) on wood and bark of conifers

5) on wood and bark of other trees and herbs

6) in seawater on test blocks.

Thus, even if choice 6 of the above is disregarded, containing as it does a single species, as the suite of fossil fungal spores are generally found as totally dispersed entities there is no indication of their original substrate. Thus there is little chance of a more exact comparison than with Sporidesmium at the generic level. However, if this is the case then the other 'anamorph-genera' mentioned by Kendrick (1981) as being closely similar need to be re-examined for similarity to the fossil spores. Annellophora can be discounted in this context as it is set apart from the remaining genera by the production of secondary conidiophores and conidia from the apical cell of the primary conidia. Production of these secondary conidia is highly characteristic in that these conidia are annellospores (see Fig. 10.4, p. 257), a feature that would be readily recognised in the fossil spores. Ellis (1971) describes the spore features of the three other living genera in question as follows:

"Sporidesmium: Conidia solitary, dry, acrogenous, simple, straight, curved or occassionally sigmoid, cylindrical, fusiform, obclavate, obpyriform or obturbinate, sometimes rostrate, subhyaline, straw coloured or pale to dark brown, olivaceous brown or reddish brown, smooth or verruculose, transversely septate or pseudoseptate.

Clasterosporium: Conidia solitary, acrogenous, simple, straight or curved, cylindrical or obclavate, sometimes rostrate,

FIGURE 10.5

Conidiospore length (μm)
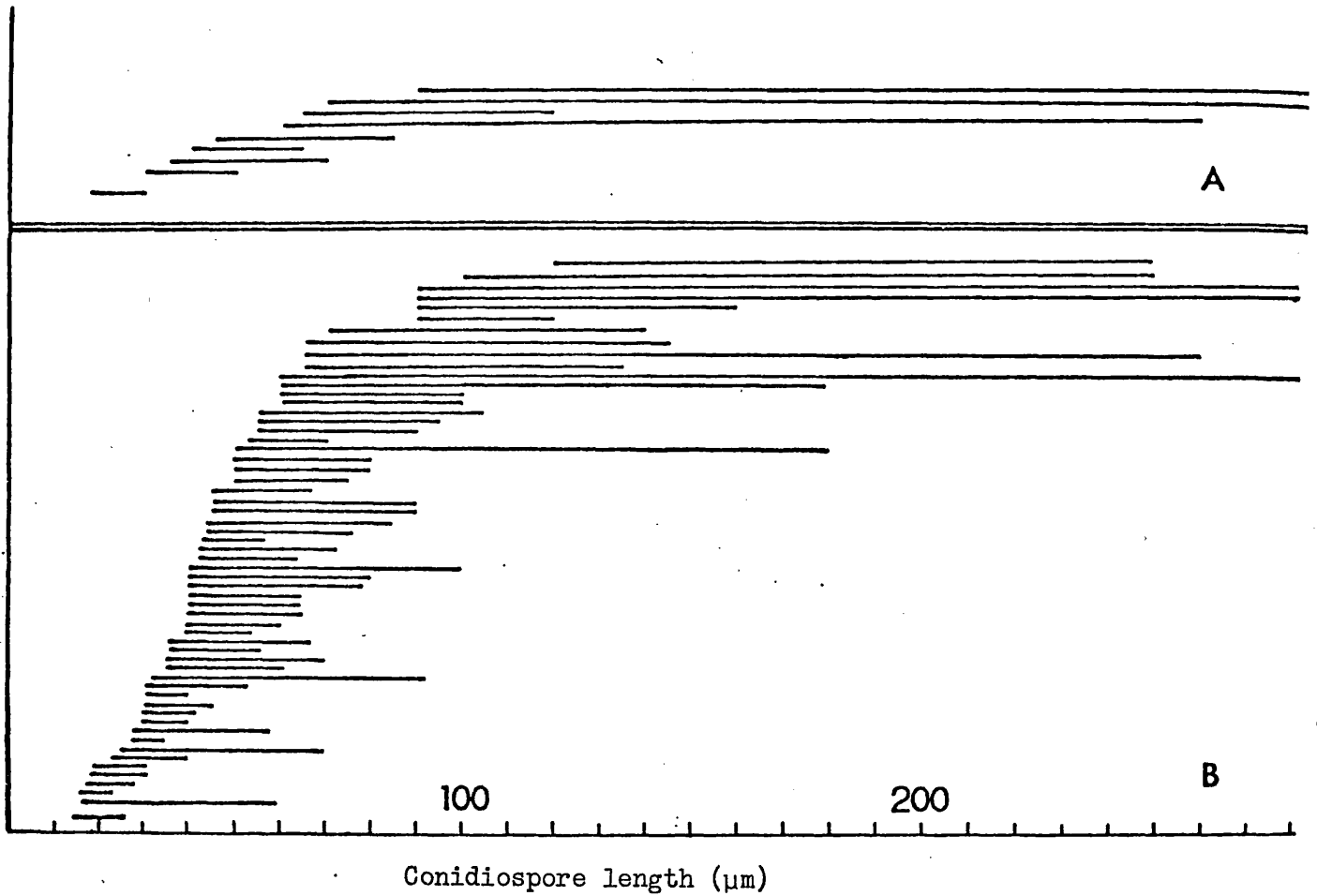
Extent of conidiospore length variability for living
species of: A. <u>Clasterosporium</u>   B. <u>Sporidesmium</u>.
Data from M.B. Ellis (1971, 1976). Each line represents
the range in conidiospore length for an individual species.

transversely septate, mid to dark brown, smooth, rugose or verrucose.

Ceratophorum: Conidia solitary, pleurogenous, simple, obclavate, rostrate, often coiled at the apex, truncate at the base, dark reddish-brown, basal cell and beak pale, smooth, pseudoseptate."

Ceratophorum thus can be disregarded on the basis of the coiled or hooked nature of the rostrate portion of the spore; a feature not evident in any of the fossil spore suite. The pseudo-septate nature of the spore of Ceratophorum is an important feature which is difficult to discern in the fossil material. On the whole the two other diagnoses are remarkably similar. That for Sporidesmium allows for a much greater diversity in spore morphology than in the case for Clasterosporium, yet the range of morphological variation exhibited by the spores of these genera overlaps quite considerably.

M.B. Ellis (1971, 1976) appear to be the most thorough recent taxonomic treatments of these two genera and, using data from these, lengths of conidiospores of species of Sporidesmium and Clasterosporium have been plotted in Figure 10.5 (p. 259). It can be seen that one possible morphological criterion for genus separation in the fossil material must be discarded because of the broad overlap, there being no clear break between lengths of Sporidesmium conidiospores and those of Clasterosporium.

Reference to previously published work on fossil Sporidesmium-like spores does not lend any clarification. Dilcher (1965) described as Sporidesmium henryense a fossil fungus with

hyphopodiate mycelial hyphae producing conidiophores bearing two to three septate conidiospores. Dilcher (1965) was following Moore (1958) in regard to the genus concept of Sporidesmium. Moore (1958) had submerged the genus Clasterosporium into synonymy with Sporidesmium in contrast to Ellis (1958) who maintained both Clasterosporium and Sporidesmium as separate and distinct genera primarily on the lack of hyphopodial mycelial hyphae in Sporidesmium. M.B. Ellis (1976) in his descriptions of the 60 Sporidesmium species shows in his synonymies at least 8 which have been transferred from the genus Clasterosporium. It would however seem that Dilcher (1965) was incorrect in attributing this fossil material to either of the genera in question. Pirozynski (1976a) has 'matched' S. henryense with the extant dematiaceous fungus Hansfordiella asterinum; a species parasitic on the epiphyllous fungus Asterina.

Fritel and Viguier (1909) created the genus Clasterosporites eocenicum for a fossil fungus found in the cortical spaces of a fossil Equisetum rhizome. Largely on the basis of the similarity of the fossil spores 3 - 11 cells long and their dark colour plus their interpretation of hyphal similarities the fossil fungus was thought to be a saprophyte related to the living genus Clasterosporium although they were not aware of any living Clasterosporium species that had been found associated with extant Equisetum species.

Stockmans (1936) described two further species within Clasterosporites : C. variabilis for dispersed spores one group of which were 2 -3 celled, the other 2 - 6 celled, and C. inflatus for 2, 3 or 4 celled ovoid conidiospores. Stockmans (1936) in his search for

other fossil fungal spores to compare his material with noted the work of Renault and Roche (1898) in which fossil spores of broadly similar morphology were attributed to the extant genus Helminthosporium but commented that the species cited H. hirudo Saccardo and H. obovatum Oudemans had since been transferred to the genus Clasterosporium. M.B. Ellis (1976) shows both these species in his synonymies for Sporidesmium. The problem therefore, Sporidesmium or Clasterosporium? still stands, and is not made easier if the alternative procedure of allocating the fossil spores to purely morphographic form-taxa is examined.

The form-genus to which this suite of fossil spores could most readily be assigned would be Pluricellaesporites (sensu lato). This form-genus was erected by van der Hammen (1954a, 1954b) with an extremely broad diagnosis:

> "Fungal spores composed of several grains or cells aligned along a single axis."

Since its inception Pluricellaesporites has had an extremely chequered nomenclatural existence having undergone several revisions of its original diagnosis. Clarke (1965) restated the diagnosis as:

> "Fungal spores, uniseriate, individuals consisting of five to numerous cells; cells flattened at common boundary, convex on sides, each cell connected by a slit-like opening through the septa."

Elsik (1968) provided the following emended diagnosis:

> "Monoporate, psilate fungal or algal spores of three or more cells; two or more septa, cells linear along one long axis."

This in turn was emended by Sheffy and Dilcher (1971) to:

"Monoporate, psilate to scabrate fungal or algal spores of three

or more cells; two or more septa, cells linear along one long

axis."

Finally, Elsik and Jansonius (1974) emended this to:

"Fungal spores of three or more cells, two or more septa,

symmetrical or very nearly so around the long axis. There is a

single aperture, pore, hilum, or exitus, at one end. Septa may

be entire, perforate or split. Cells are short to long in

relation to overall spore length. Spore outline is lenticular,

oval, or cylindrical. One or two cells at the aporate end never

constitute the bulk of the spore. Exine is psilate to variously

ornamented; if ornament is present it is subdued, i.e. of low

relief."

Little need be said of this 'developmental series' of diagnoses

except that there still is an extremely ill-defined circumscription

to this form-taxon.   Each restatement or emendation was due to the

author or authors extracting from the Pluricellaesporites complex

(sensu van der Hammen, 1954a and 1954b) a sub-set of similar

morphological forms and elevating them to form-genus level. By

restricting Pluricellaesporites to 'monoporate, multiseptate fungal

spores', Elsik (1968) erected the new form-genus Multicellaesporites;

his diagnosis was emended by Sheffy and Dilcher (1971) to include a

wider range of spore ornamentation:

"Inaperturate, psilate to scabrate fungal spores or algal bodies
of three or more cells; two or more septae. Shape variable
around a long axis."

Several of the species of Multicellaesporites created by Sheffy
and Dilcher (1971) especially M. irregularis (see Sheffy and Dilcher,
1971, Plate 16, fig. 43) and M. attentuatus (see Sheffy and Dilcher,
1971, Plate 16, fig. 48) have exact homologues within the Hordle
material. Equally close morphological homologies from within the
Hordle suite could be drawn with species of Pluricellaesporites
(sensu Elsik and Jansonius, 1974), Diporicellaesporites Elsik (1968)
and Fractisporites Clarke (1965). The diagnoses of these latter two
form-genera also having such broad circumscriptions to be applicable
to at least some of the spores of the Hordle suite.

Fractisporites: "Fungal spores, uniseriate; fragments consist of
four to many rectangular to square cells, sides generally
parallel." Clarke (1965)

Diporicellaesporites: "Elongate, diporate, multicellate fungal
or algal spores; one pore at each end of the spore; shape and
ornamentation variable except never coiled; two or more septae."
Elsik (1968)

The major diagnostic distinction between these form-genera is
the presence or absence, and number or pores, this feature being of
paramount importance in any palynological diagnosis. But as
Pirozynski and Weresub (1979b) point out:

"Fungal spores have germ pores and slits that may be called pores or apertures ..... But in many descriptions of fossil spores, there is no knowing what those terms may be referring to, for they are applied indiscriminantly to germ pores and slits, to marks on conidia which are scars of attachment to a conidiophore or to other conidia in a chain, to openings that result from the disintegration of delicate end-cells or appendages, even to broken ends of propagules or hyphae."

Elsik et al (1983) has, with the 'Annotated Glossary of Fungal Palynomorphs', attempted to clarify the confusions in terminological usage. Fungal structures are defined wherever possible in neo-mycological terms, for example the palynological term 'aperture' being separated into pore, germ pore, germ slit and furrow. However, these distinctions, although extremely necessary, are not retro-active and have not, as yet, been incorporated into the diagnoses of the form-genera under consideration. The confusion as to the nature, in the mycological sense, of the pores or apertures in the form-genera still exists, and because of this, the preservational state of the individual fossil spore could be the major factor determining which of the four form-genera the spore would be attributed to.

On balance therefore, both the attribution of the fossil spores to an extant genus and the alternative of attribution to a morphographic form-taxon, seem to be far from clear cut procedures. Lange (1978a) reiterated the contentions first made by Lange and Smith (1971), having made the observation

".... that fungal spores are unattractive taxonomically when dissociated from their source mycelia and, palynologically, relatively unworthy of research effort..... The state of taxonomy of fossil fungal spores is under-developed relative to the diversity of spores encountered and the literature displays tendencies of authors to force spores into the published genera, or to publish fresh genera on an ad hoc basis without supporting population studies! (the emphasis is mine, P.H. Smith) ..... For progress with the systematics of dispersed fossil fungal spores, some compromise between cataloguing and taxonomy seems necessary. Cataloguing, using the mycological terminology has much to commend it for broad systematic distinctions; but taxonomic studies are essential within the end groups of the catalogue, particularly for the purpose of distinguishing and circumscribing form-genera."

Lange (1978a) has extended the morphological categories used by Lange and Smith (1971) to 9 major groupings:

1. Helicospores and circinate-complicate spores

2. Staurospores

3. Dictyospores, excluding muriform-circinate spores

4. Phragmospores of many scalariform cells

5. Phragmospores of many catenulate spores

6. Phragmospores of four to five cells

7. Phragmospores of three cells

8. Didymospores

9. Amerospores

Each of these 9 major groups are further sub-divided. As the Hordle

A. SCOLECOSPORES

    1. Broken; some septa with triangular flaps; dematiaceous, minutely granular.

    2. Broken; pallid with straight thick perforate septa; width and septal spacing irregular; attachment cell tapered elongate.

B. HELMINTHOID DEMATIACEOUS SPORES

    1. Cylindrical-aduncate; septa very dark; thick; attachment cell pallid to hyaline.

    2. Fusoid bulges in the length of spore; cells very much broader than long; truncate-conical end cell.

    3. Verruculose, narrow-fusoid, hyaline end cells.

C. FUSOID TO TRUNCATE DEMATIACEOUS SPORES WITH ROBUST WALLS

    1. Septal flaps or distortions, hyaline end cell.

    2. No hyaline end cell or septal distortion.

D. ELONGATE THIN-WALLED PALLID SPORES WITH LONGITUDINAL FRACTURES

E. HYALINE BROADLY ELLIPTICAL SPORES (i.e. symmetrical about a median transverse septum, with cell size diminishing toward the poles.)

F. MISCELLANEOUS HYPHOID LENGTHS

TABLE 10.1   Morphological categories of phragmospores, after Lange (1978b).

suite would generally find accomodation in group 4, the subdivisions within this grouping as proposed by Lange (1978a) are detailed in Table 10.1 (p. 267). Pirozynski and Weresub (1979a) combined the approach of Lange (1978a) with the contention of Pirozynski (1976a, 1976b) that most fossil fungal spores can be attributed to living genera. Fossil spores, very similar to those of the Hordle suite, were identified as 'Sporidesmium-like phragmoconidia'.

The central dilemma has not then been resolved, whether to attribute the material to an existing morphological form-taxon such as the Pluricellaesporites-complex; or as Pirozynski (1976a, 1976b) would advocate, indicating possible relationships with extant fungal taxa. This second alternative is the more attractive procedure provided that the new form-taxon is erected only after exhaustive population studies as advocated by Lange and Smith (1971) have been undertaken.

The problem of the possible delimitation of distinct species sub-groupings within this fossil spore population is quite daunting. Some of the criteria used by M.B. Ellis (1976) in his key to the 60 extant species of Sporidesmium have already been discussed, and these must unfortunately be discarded as being inapplicable to the population of dispersed fossil spores. Ellis (1958), in his earlier key to a smaller number (50) of extant species of Sporidesmium did not use the host-plant criteria and based the key on the more detailed characters of spore morphology such as:

1) length of conidiospore

2) maximum breadth of conidiospore

3) number of septa

4) conidiospores smooth or rough walled

5) shape of conidiospore.

These are criteria that can be distinguished readily in the fossil spores and therefore could be the basis for species delimitation.

As can be seen from Figure 10.3 (p. 254) there are several distinct morphologies encompassed within this suite of fossil spores. Several major variations can be distinguished:

1) Multicellular, elongate-obclavate spores.

Bulk of spore with a varying number of thick dark transverse septa; tapering at base to a truncate attachment cell, with lighter cell walls than bulk of spore. Spore rostrate with a varying number of more elongate cells with lighter cell walls than bulk of the spore.

2) Multicellular, elongate obovate to obclavate spores.

Bulk of spore wall with a varying number of thick dark transverse septa, tapering at base to a truncate attachment cell with lighter cell walls than bulk of the spore. Spore not rostrate but with one or two cells with thinner and lighter coloured transverse septa and the end opposite to that bearing the tapering truncate attachment cell.

There is little difficulty, in the course of a detailed population study of realising that there is an easily-made connection between these two morphological groups which have been described. The most simplistic possibility is that the difference between form 1 and 2 is due to the breakage, the elongate cells of the rostrate form

FIGURE 10.6
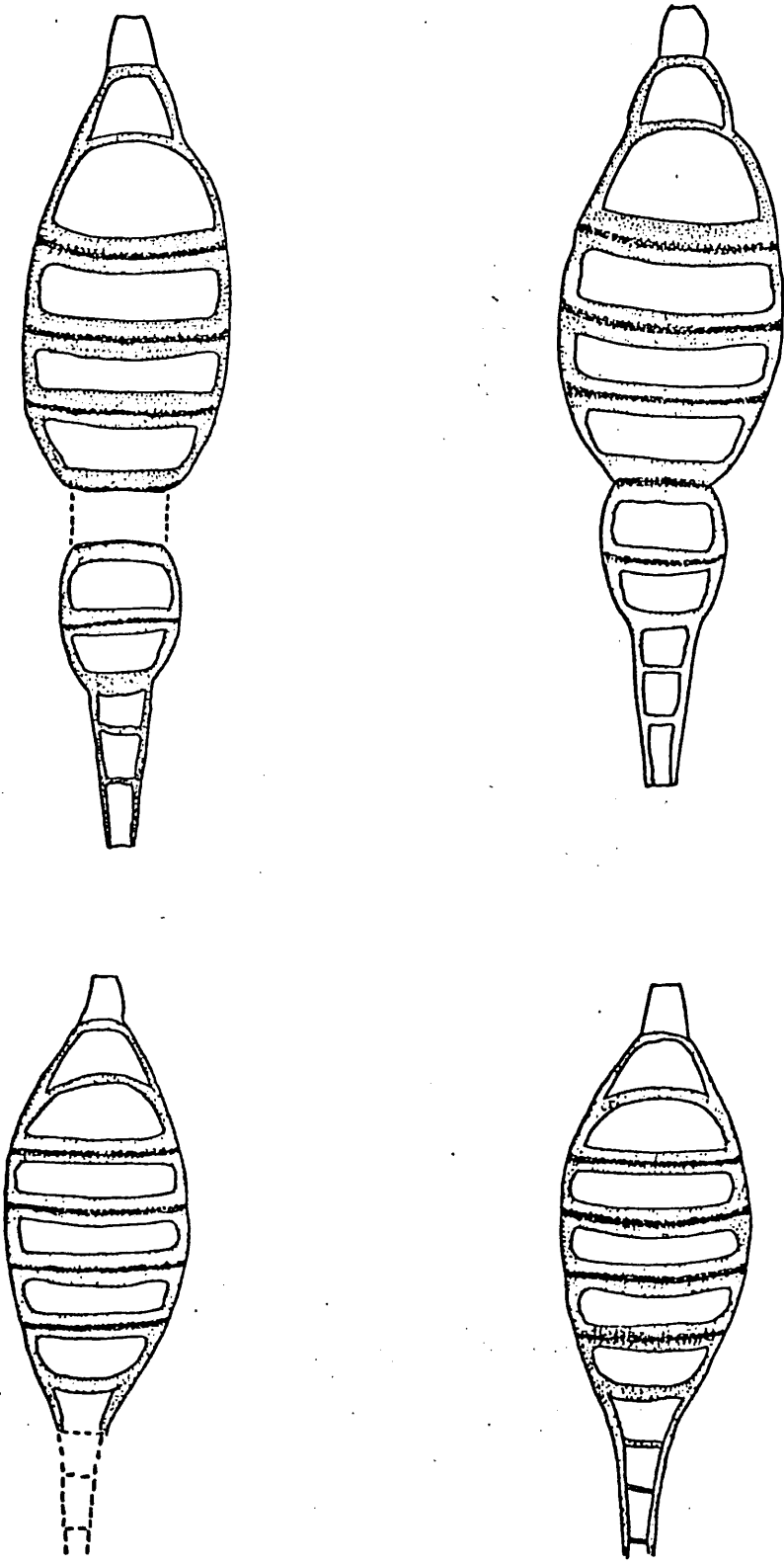
Diagrammatic representation to show possible
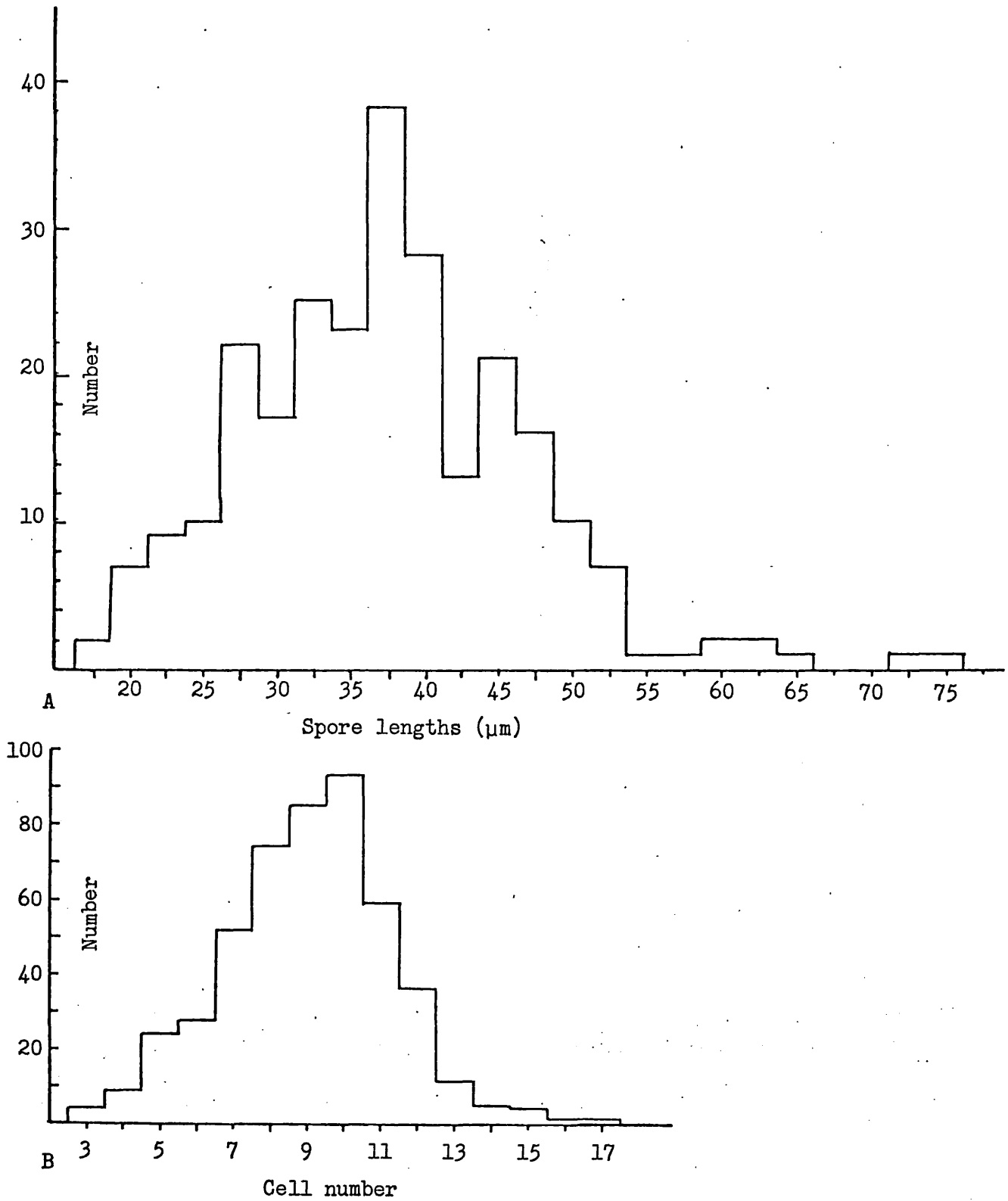sources of variability in fossil phragmoconidia.

FIGURE 10.7

Population parameters of Sporidesmium-like

phragmoconidia from the Hordle Cliff Deposit.

being lost, either prior to or during deposition and preservation of the spores (see Fig. 10.6, p. 270). An equally plausible connection between the two forms follows from the observation that a percentage, small but appreciable, of the rostrate forms do not have a regular outline but exhibit a distinct 'waisting' (see Fig. 10.6, p. 270). Any breakage and separation of the segments of the elongate rostrate spore at this 'waist' could cause the formation of at least one segment with the morphological character of the second of the two spore forms decribed above.

If these two distinct morphological forms are in actuality two aspects of a larger single population, measurements of population parameters should show this. Figure 10.7A (p. 271) shows the distribution of one of the most obvious of the parameters available namely the overall length of the conidiospore. A sample of 250 spores was measured and the sizes ranged from 17.5 μm to 75.0 μm. The recorded distribution and frequency of fossil spore lengths gives no clear evidence of any marked subdivisions within the proposed uniform population, as the shape of the histogram approximates that of a normal distribution. The size range of the fossil spores measured is easily accomodated within those recorded for the living genera Sporidesmium and Clasterosporium (see Fig. 10.5, p. 259).

Another easily recorded morphological parameter of the fossil spore population is total cell number. Data from a larger sample (upward of 500 spores) is recorded as a histogram in Figure 10.7B (p. 271). Again the distribution and frequency of total cell number approximates to a normal distribution with no indication of any

FIGURE 10.8
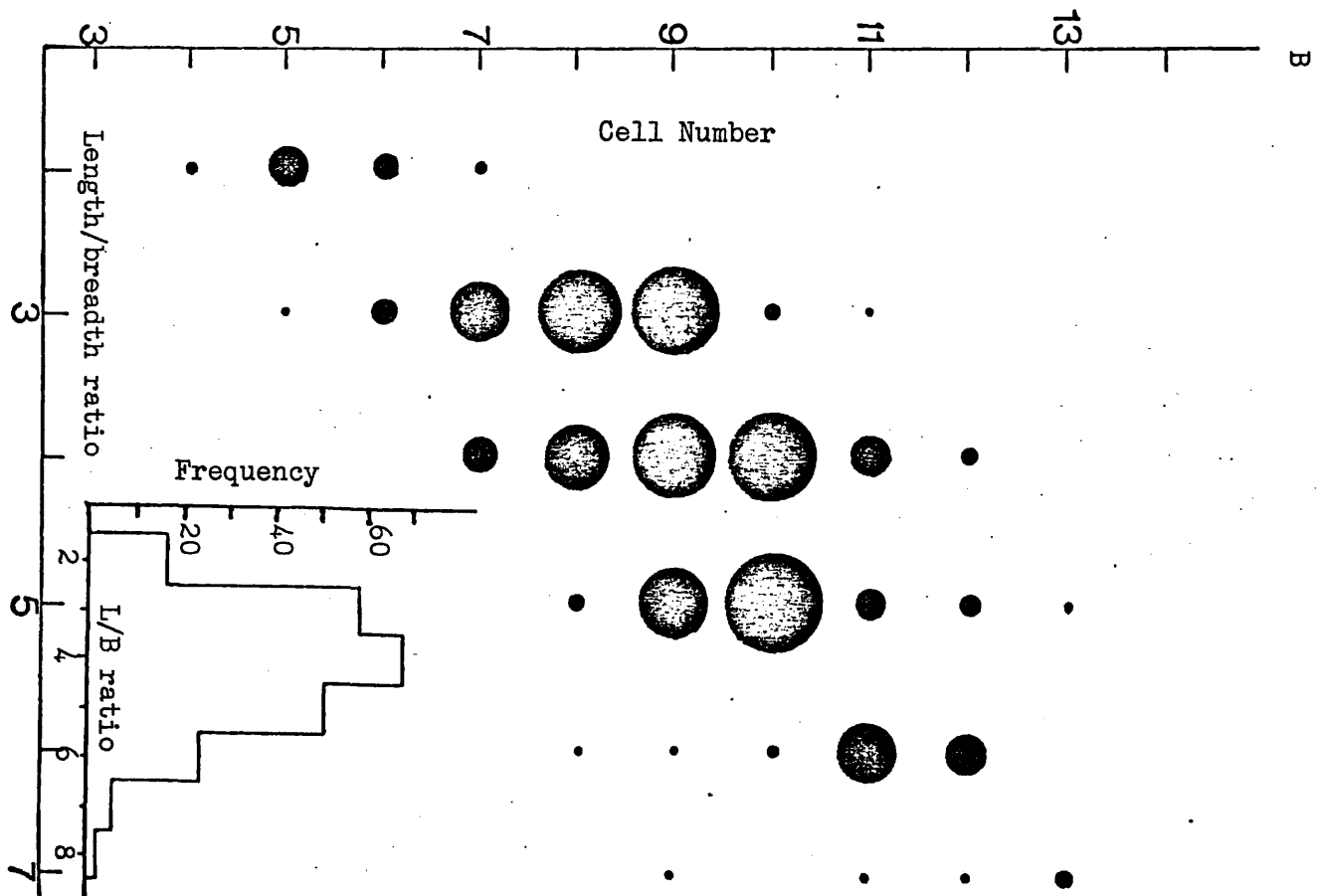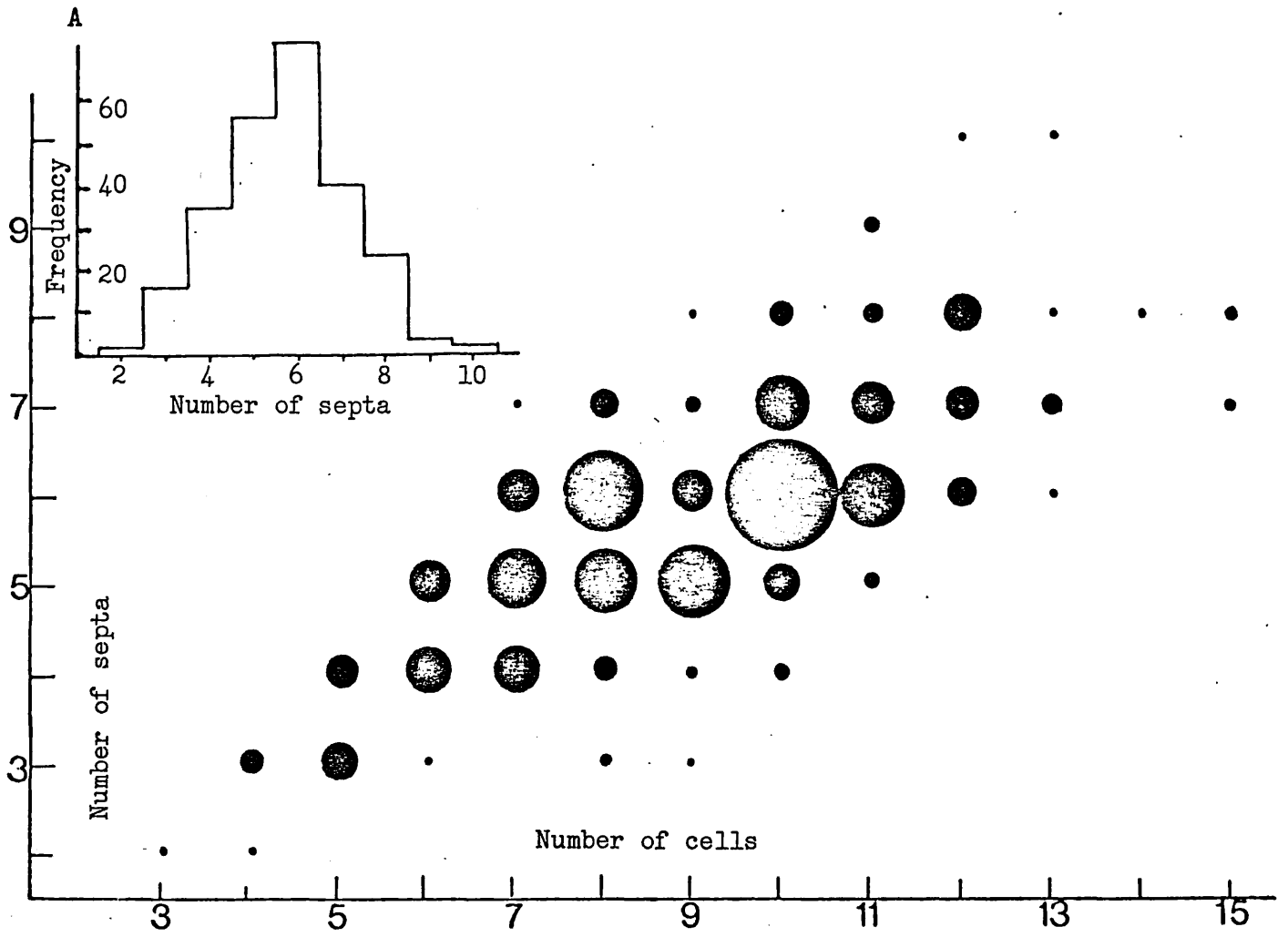
natural break or hiatus to allow any definite sub-grouping of the population on the basis of this character.

M.B. Ellis (1958, 1976) in his keys to the extant species of Sporidesmium often used the maximum breadth of the conidiospore as a criterion to separate species. However this is a character that is of very little value in subdividing the population of fossil spores under consideration as the range of breadth is only between 7.5 μm and 10 μm. If the length to breadth ratios are calculated for a sample of the fossil spores, the results grouped into value classes and recorded as a histogram (see inset to Fig. 10.8B, p. 274), the frequencies again suggest a normal distribution without any natural breaks to indicate anything other than a single population. This supposition is borne out when the length/breadth ratios are plotted against the total cell number of the individual conidiospores within the population sample (see Fig. 10.8B, p. 274). The frequencies of the ratios of length/breadth of conidiospores plotted against total cell number reflect the range of total cell number found within the fossil spores sampled (see Fig. 10.8B, p. 274) however the distribution of the values obtained suggest a single population rather than a series of clearly defined subgroupings. This contention is further borne out if another character used by M.B. Ellis (1958, 1976) to separate species of Sporidesmium is examined. This is the number of very thick dark transverse septa so characteristic of this spore type. The range of thick septa occurring within the population (see inset to Fig. 10.8A, p. 274) and if septal number is plotted against total cell number (see Fig. 10.8A, p. 274) the distribution appears to be another example of

continuous variation with no indication of subdivisions within the population sample.

Thus, apart from the feature of the presence or absence of the narrow rostrate extention to the conidiospore, a character of highly dubious validity, there would not seem to be any morphological feature or combination of morphological features that could be used with any great facility to subdivide this highly variable population.

Because of the high degree of morphological variation exhibited by the fossil population it is highly questionable whether there is sufficient justification to create another form-genus to accomodate spores of this type. Until comparable population studies are undertaken on conidiospores of living Sporidesmium species to ascertain whether similar broad ranges of morphological characters occur, this population is best described as 'Sporidesmium-type phragmoconidia'.

11 FURTHER FOSSIL FUNGAL SPORE FORMS FROM THE HORDLE CLIFF DEPOSIT

The conclusions drawn from the examination of the Sporidesmium-type phragmoconidia in the preceding chapter suggest the Pirozynski (1976a) contention, that Tertiary fossil fungal spores are readily attributed to living fungal genera, is not without its difficulties. This is not, of course, a new observation. Lange (1978a) had stressed that assignation of a fossil spore directly to a genus of living fungi is possible. However for this to be possible there must be an exclusive match between the fossil spore and that of the living species.

".... Unfortunately this approach breaks down because it is easy in most cases to find general resemblances such as might relate a Tertiary spore with its modern descendant but these matches are rarely unequivocal or exclusive to a particular genus. Even with spores as charcteristic as Beltrania, for example, there would still be the genera Beltraniopsis, Beltraniella, Ellisiopsis and Pseudobeltrania to consider, with corresponding difficulties for determining the true affinities of the fossil fungal spore." (The emphases are mine, P.H. Smith).

The group of genera used by Lange (1978a) to illustrate his comments all possess, with certain variation, an extremely characteristic turbinate/biconic spore with a transverse hyaline band. Ellis (1971) describes the conidia of the genera in question thus:

Beltrania: Conidia solitary, acropleurogenous, biconic, appendiculate, the free end being usually spicate or apiculate, 0-septate, smooth, pale olive to dark reddish brown with a distinct hyaline transverse band immediately above the widest part of the conidium.

Beltraniopsis: Conidia solitary, acropleurogenous, simple, biconic, rostrate (beak short), 0-septate, pale olivaceous brown, smooth with a hyaline transverse band.

Beltraniella: Conidia solitary, acropleurogenous, simple, turbinate or biconic, often caudate, 0-septate, smooth, pale olivaceous to brown with a distinct hyaline transverse band.

Ellisiopsis: Conidia solitary, acropleurogenous, simple, straight, turbinate, the base drawn out to a fine point, pale olivaceous with a hyaline transverse band just above the centre, smooth, 0-septate.

Pseudobeltrania: Conidia solitary, dry, acropleurogenous or acrogenous, simple, biconic, apiculate, olivaceous brown, smooth, 0-septate but with a median transverse hyaline band.

The features used by Ellis (1971) to separate these four genera with very similar spores being those of the presence or absence of mycelial setae; the form and construction of the conidiospores and whether the conidiospores are apiculate/spicate or caudate. The first two of the characters are totally inapplicable to a population

of dispersed spores. The third character could be used provided that the fossil spores clearly exhibited an attachment scar or hilum. However, for absolute clarity of this character, the way the conidiospore is attached to the conidiophore needs to be clearly demonstrated; and would reduce the choice of possible living comparisons from 5 to 3 genera, viz Beltrania, Beltraniopsis and Pseudobeltrania.

The procedure adopted for the spore populations to be described in this chapter will be to

1) allocate the individual populations to the appropriate Saccardoan spore category

2) illustrate and describe the population variability

3) suggest affinities with extant genera where possible.

AMEROSPORAE

"Not much is achieved by calling featureless amerospores anything different" Lange and Smith (1971).

This group of fossil fungal spores is without question the least amenable to the proposed treatment especially the attribution, or even the suggestion of affinity, to extant genera and species. This is due in no small part to the fact that the amerosporous type of spore is virtually ubiquitous and ranges through all the major fungal groups and can be the end product of both sexual (ascospores and basidiospores) and asexual (conidiospore) reproductive processes. Thus for the most part the subdivisions of this extremely large and diverse group have been made on what must be regarded as

BASIDIOSPORITES	Elsik (1968)
DIPORISPORITES	van der Hammen (1954b)
EXESISPORITES	Elsik (1969)
HAPLOGRAPHITES	Felix (1894)
INAPERTISPORITES	van der Hammen (1954b)
INAPERTISPORITES	van der Hammen ex Rouse (1959)
LACRIMASPORONITES	Clarke (1965)
MICROCOCCITES	Meschinelli (1898)
MICROSPORONITES	Jain (1968)
MONOPORISPORITES	van der Hammen (1954b)
POLYPORISPORITES	van der Hammen (1954b)
RETICULATISPORONITES	Elsik (1968)
RETIDIPORITES	Varma and Rawat (1963)
STRIADIPORITES	Varma and Rawat (1963)
TRICHOSPORITES	Felix (1894)
TRIPORISPORITES	van der Hammen (1954b)
TRIPORISPORONITES	Sheffy and Dilcher (1971)

TABLE 11.1   Amerosporous genera of fossil fungal spores with authors.

'palynological' features; shape, size, colouration, ornamentation and presence or absence and number of pores and thus the genera are for the most part form-genera. Table 11.1 (p. 280) lists 17 form-genera which could be used to segregate any suite of amerospores. The most commonly cited genera however exclude the early genera of Felix (1894) and Meschinelli (1898) in which there is a tacit implication of botanical affinity, the present preference being toward those more 'modern' genera based on the purely morphological characters of the spores. The difficulties arising from the use of strictly morphological criteria have been dealt with at some length in Chapter 3 and will only be briefly alluded to here. Virtually every worker who decides to allocate fossil amerospores to one of these existing form-taxa has been dissatisfied with the generic diagnoses and has emended it. Inapertisporites van der Hammen is an object lesson in this 'polishing'. The original diagnosis from van der Hammen (1954b) was:

"Fungal spores without preformed aperture"

and Inapertisporites variabilis was later nominated as the type species. Rouse (1959) however deemed Inapertisporites van der Hammen not to be validly published (cf Jansonius and Hills, 1976) and thus redescribed the genus:

"Spores free or grouped, anisopolar, and inaperturate. Shape circular, oval or elliptical; outline often uneven because of wrinkles or folds. Ornamentation variable ranging from laevigate to pseudoreticulate. Size range 5 - 100 μm"

with I. pseudoreticulatus Rouse as the genotype. Thus there has been a dichotomy as to which diagnosis was followed by other workers. Elsik (1968) emended the brief van der Hammen diagnosis to:

"Inaperturate, psilate fungal spores. One cell no septae (sic).

Shape variable."

but made no mention of which species he regarded as the genotype.
Sheffy and Dilcher (1971) followed Rouse (1959) and regarded I.
pseudoreticulatus as the type species but emended the generic
diagnosis to:

"Fungal or algal. Spores unicellate, non-septate, and

inaperturate. Shape globular or sub-globular; outline smooth or

often uneven because of wrinkles or folds. Ornamentation

variable. Size range 5 - 11 µm."

And finally Ediger (1981) further emended the diagnosis as follows:

"Unicellular fungal spores without preformed aperture; shape

variable, mostly irregularly rounded; one or more cells usually

randomly clustered; exine not too thick, folded or cracked,

scabrate or usually pitted."

Despite this diagnosis being extremely broad Ediger (1981) regards I.
variabilis van der Hammen as the type species and has by listing the
full synonymy reconstituted Inapertisporites as a single entity
without the internal schism of van der Hammen versus Rouse, with the
added bonus that another of the 17 form-genera, Microsporonites Jain
(1968) is also submerged into synonymy with Inapertisporites.
However, notwithstanding this act of nomenclatural clarification the
problem is far from settled. Rouse (1962) described a further 3
species: I. globulosus, I. elongatus and I. tetradus. Of these I.
elongatus is the only amerosporous form, I. globulosus appears to be
a total confusion between a single celled spore and a multicelled
toruloid mycelial hypha and I. tetradus is a four celled
dictyosporous form. The generic diagnosis as emended by Rouse (1959)

allows for 'grouped' spores but interpreting a multicellular structure as a set of grouped spores is totally incorrect. Ediger (1981) accepted uncritically this interpretation of 'grouped' as meaning associated and figured examples of I. globulosus and I. tetradus (both sensu Rouse, 1962) plus erecting I. rotundus a species encompassing single cells, two- and four-celled 'clusters'. From the illustrations given, it is difficult to determine whether these latter forms are aggregations of 2 or 4 amerospores or multicellular spores viz didymospores and dictyospores. Neither Elsik (1968) nor Sheffy and Dilcher (1971) made any comment concerning I. globulus or I. tetradus, however the generic diagnoses formulated in both papers state unequivocally that Inapertisporites is unicellular. The diagnosis as emended by Ediger (1981), in following Rouse (1959), although reuniting the two schools of thought at least nomenclaturally, does not do so conceptually where the majority opinion would restrict Inapertisporites to single celled spores. Therefore a further emendation will be needed to redefine Ediger's (1981) phrase "one or more cells usually clustered" to incorporate a requirement that such randomly clustered or aggregated cells are demonstrably single cells lacking shared faces or septa with other cells in the cluster or aggregation. As the matter stands at present 30 species of Inapertisporites have been described in the six papers mentioned above:

Van der Hammen (1954b) 3 species, Rouse (1959) 3 species, Rouse (1962) 3 species, Elsik (1968) 2 species, Sheffy and Dilcher (1971) 16 species, and Ediger (1981) 3 species.

Even with the removal of I. globulosus (Rouse, 1962), I. tetradus (Rouse, 1962) and I. rotundus (Ediger, 1981), as spore forms

PLATE 10   Amerospores and mycelial remnants (cf. <u>Nigrospora</u>)

from the Hordle Cliff Deposit.
Magnification × 1,500
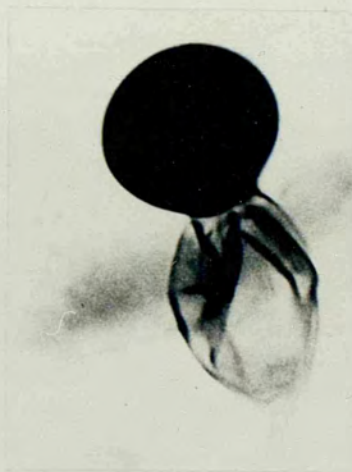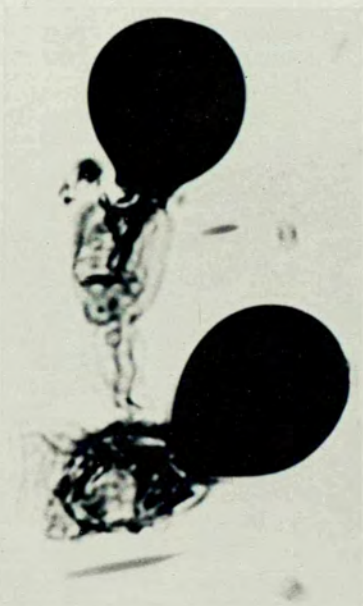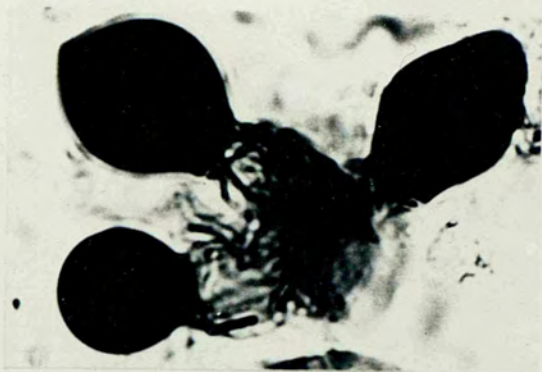
incorrectly allocated to <u>Inapertisporites</u>, 27 validly described species remain in these papers alone. As stated in Chapter 3, Lange (1978a) has questioned the validity of the status of many of the <u>Inapertisporites</u> species erected by Sheffy and Dilcher (1971), and that nothing is to be gained at present by adding to the species list within this genus without extensive revision of the previously published species. Examples of this form from the Hordle Cliff deposit will therefore only be catalogued as inaperturate amerospores cf <u>Inapertisporites</u> (van der Hammen) emend Sheffy and Dilcher (1971).

Similar nomenclatural modifications could be cited for most of the other form-genera of amerospores erected, especially those of van der Hammen (1954a, 1954b), many of which fall into the category of form-genera criticised by Stafleu (1967):

"Some of the form-genera are so extremely artificial that in my opinion they entirely lose the character of a taxonomic concept and become a terminological concept instead."

A similar procedure to that adopted for inaperturate amerospores will be used for other amerospores with apertures.

As well as the attribution of amerosporous fungal spores to the purely morphological form-genera (see Table 11.1, p. 280), several types have been directly attributed to extant genera. Rouse (1962) erected the fossil species of <u>Scleroderma echinosporites.</u> These spores are ornamented with radiating spines and Rouse (1962) commented that the fossil spores are identical with spores of the modern puffball (Basidiomycotina) genus <u>Scleroderma,</u> many species of

which have the same order of magnitude as those of S. echinosporites.

Elsik in several publications (1969, 1976b) has referred to Hypoxylon (Ascomycotina Xylariaceae) type spores with their characteristic elongate furrow and deep melanic colour. Elsik (1977) acknowledged that this morphology also occurs in other groups (cf Arthrinium, Cordella, Pteroconium, Wardomyces - Deuteromycotina) but has consistently referred to spores of this morphology as Hypoxylon spp (Elsik, 1969) or Hypoxylon type spores (Elsik, 1976b). 'Hypoxylonites' (nom. prov.) has been quoted in several publications but to my knowledge Elsik has not as yet published a formal diagnosis to validate this provisional name. The highly characteristic morphology of this spore form is sufficiently distinct to suggest that its separation and segregation from the great variety of other amerosporous types is warranted. The separation must be only of the form-taxon type as there is insufficient evidence to allow an exact attribution to an extant genus.

The Hordle Cliff material also contains a set of dark melanic amerospores which are attached to mycelial remnants (see Plate 10). These remnants are best interpreted as conidiophores, and generally give the appearance of being thin walled and swollen. In many cases the spores still have these conidiogenous cells still attached but a small percentage of the population exhibit a small coronal attachment that could be interpreted as the remnants of the conidiogenous cells. If this interpretation of the nature of this coronal attachment is the correct one then this could be an important pointer toward the botanical affinity of this particular spore type. Webster (1952) has

described   the   violent   discharge   mechanism   of   <u>Nigrospora</u> (Deuteromycotina):

> "Spore liberation in <u>N. sphaerica</u> is by a syringe mechanism in which the development of a high hydrostatic pressure within the penultimate cell of the conidiophore leads to the release of its contents as a jet, and the conidium is shot off with a jet following bursting of the terminal cell on which the conidium is perched" (Subramanian, 1983).

Ellis (1971) cites <u>N. sphaerica</u> as a cosmopolitan species especially widespread in tropical countries on many different kinds of plants. Subramanian (1983) commented that <u>N. sphaerica</u> could be parasitic in its colonising stages but that this initial stage was followed by a:

> "clearly marked phase of vigorous saprophytic spread and survival as evidenced from its ability to sporulate on senescent tissues."

The sizes quoted by Ellis (1971) for the:

> "simple   spherical   or   broadly   ellipsoidal,   compressed dorsiventrally, black, shining smooth non-septate"

conidia of <u>N. sphaerica</u>, i.e. 14 - 20 μm but mostly 16 - 18 μm diameter, are similar to those of the fossils in question. However several other genera have very similar conidia and are separated largely upon their mode of nutrition. There is a group of genera including <u>Acremoniula</u>, <u>Humicola</u> and <u>Allescheriella</u> which are characteristically isolated from woods of present day subtropical to tropical areas which also deserve careful consideration. All of these genera plus <u>Nigrospora</u> are placed in the hyphomycete grouping of the Deuteromycotina.

FOSSIL TAXON	AUTHOR	LIVING TAXON
Allepeysporonites (scabratus)	Ramanujam and Rao (1978)	Grallomyces (portoricensis)
Ctenosporites	Elsik and Jansonius (1974)	Dictyosporium
Dicellaesporites (in part)	Sheffy and Dilcher (1971)	Balanium
Brachysporites	Lange and Smith (1971)	Brachysporium
Granatisporites	Elsik and Jansonius (1974)	Endophragmia-Bactrodesmium complex
Involutisporonites	Clarke (1965)	Cirrenalia/Zalerion
Lacrimasporonites (in part)	Sheffy and Dilcher (1971)	Acrogenospora
Multicellaesporites	Sheffy and Dilcher (1971)	Bispora
Pesavis (simplex)	Elsik and Jansonius (1974)	Ceratosporella (bicornis)
Pluricellaesporites	Sheffy and Dilcher (1971)	Endophragmia
Pluricellaesporites	Elsik and Dilcher (1974)	Drechslera
Pluricellaesporites	Singh (1971)	Sporidesmium
Pluricellaesporites (glomeratus)	Srivastava (1968)	Pithomyces (pulvinatus)
Retihelicosporonites (elsikii)	Ramanujam and Rao (1978)	Hiospira (hendrickxii)
Spegazzinites	Felix (1898)	Spegazzinia
Sporidesmium (henryense)	Dilcher (1965)	Hansfordiella (asterinarum)
Staphlosporonites	Sheffy and Dilcher (1971)	Altenaria
Transeptaesporites	Ediger (1981)	Altenaria

TABLE 11.2   Fossil taxa and their corresponding extant

hyphomycete taxa, after Pirozynski (1978) and

Subramanian (1983).

FIGURE 11.1
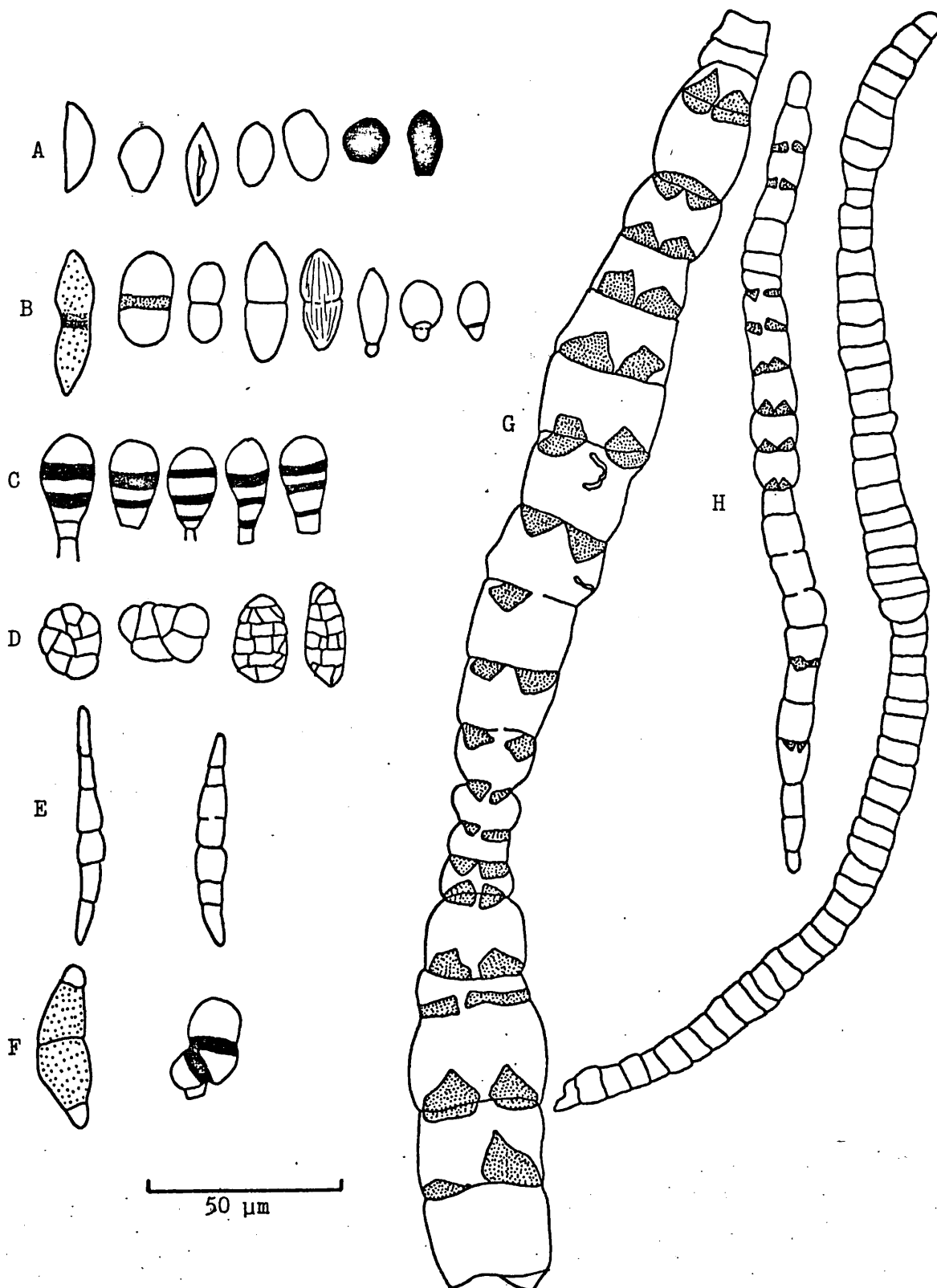
Other dispersed fossil fungal spores from the Hordle Cliff Deposit.

A. amerospores   B. didymospores   C.   cf. Brachysporisporites

Lange and Smith   D. dictyospores   E. cf. Multicellaesporites

F. cf. living Curvularia   G. Pluricellaesporites (sensu lato)

H. Scolecosporites Lange and Smith

Subramanian (1983) has reviewed the extremely important role that fungi of this type play as constituents of the mycoflora of living senescent leaves, leaf litter, wood, bark and soils. It would therefore seem reasonable to search for possible extant relatives of the fossil spores from within the often highly distinctive conidial morphologies of this now well documented group of fungi. In Figure 11.1 (p. 290) as well as the amerosporous forms, other dispersed fosil spores from the Hordle Cliff population are illustrated. Again these are, at present, only catalogued to their Saccardoan spore morphology group. This is because each individual morphological form must be subjected to close and detailed population studies in order to establish taxonomic boundaries (see Smith, 1981). Only after these exercises have been completed can the second exercise, the comparison with and hopefully the attribution to modern genera be undertaken. Subramanian (1983) in his chapter on Fossil Hyphomycetes has stated the problems involved in this exercise:

"The majority of hyphomycetes occur as dispersed spores. The identification of a great many of these is not easy and requires expertise in fungal taxonomy. Fungal propagules have different ontogenies, functions, and adaptations, and familiarity of the structures and reproduction of living forms is needed for recognition and identification of fossil forms. With such expertise it is possible to identify dispersed conidia. Preliminary identification of conidia could well be on Saccardoan lines, but more critical study should lead to comparison with, and assignment to, extant forms."

Table 11.2 (p. 289) is compiled from Subramanian (1983) based largely upon Pirozynski (1976b); plus further linkages between extant and

fossil forms suggested by Pirozynski (1978), and shows that at least in some cases direct attribution of fossil material to extant genera is possible. It is to be hoped that this list will be further extended to include many of the Hordle Cliff forms when these preliminary investigations are transformed into detailed studies of variability within the individual populations of dispersed forms only catalogued here.

CONCLUSIONS

The problems of the overall evolution of fungi within the fossil record are not greatly clarified in this study; however it has been clearly established that the highly specialised loculoascomycete family, Trichothyriaceae, which has modern genera specialised as leaf parasites and saprophytes had epiphyllous representatives in the British Eocene flora. The isolation of dispersed fossil fungal fructifications which can be attributed to the form-genus Trichothyrites, extends the geological range of this form-genus from the Pleistocene into the Palaeogene. Whether Trichothyrites eocenica Smith (1980) should be regarded as the earliest occurrence of this family in the geological record is still debatable. This is due to the uncertainty of the taxonomic relationship of Trichothyrites Rosendahl with other form-genera especially Notothyrites Cookson. Krassilov (1967) described lower Cretaceous fossil fungal fructifications from a variety of gymnosperm source plants as species of Notothyrites Cookson within the family Microthyriaceae. Elsik (1978), on the grounds of overall similarity of appearance, was happy to regard Trichothyrites and Notothyrites as synonymous. However the exact inter-relationship of these two form-genera will not be resolved easily as both form-genera have specimens isolated from palynological residues and specimens from leaf cuticle preparations attributed to them. In the latter case it is extremely difficult to establish the presence or absence of a clearly discernible lower floor of cells in the fructification; in my opinion the decisive criterion for separating Trichothyriaceae from Microthyriaceae.

The occurrence of form-genera of fossil epiphyllous fungi that have links of varying strength with the living ascomycete families Asterinaceae, Meliolaceae, Micropeltidaceae, Microthyriaceae, Trichothyriaceae, and Parmulariaceae, gives evidence of an extremely diverse epiphyllous fungal flora in the British Palaeogene. This broad spectrum of form-genera from both the Newbury (Palaeocene) and Hordle Cliff (Eocene) deposits can best be taken as some evidence that, parallelling the rapid evolutionary diversification of the angiosperms during the Cretaceous and lower Tertiary and the provision of an abundance of leaf surface, the ascomycete families represented as fossils must have undergone a similar rapid radiation to capitalise on the various new ecological niches provided.

The presence of such a variety of fossil epiphyllous forms can also be used to deduce information concerning the palaeoclimatological regimes of the host or source vegetation. Palynological fossil fungal fructifications loosely identified as 'microthyriaceous' have generally been accepted as indicative of a tropical vegetation as their source. The use of these fossil fructifications as indicators of tropical conditions has been based upon the predominantly tropical distribution of presentday Microthyriaceae. Used in isolation this group of fossils is assumed to give a fair approximation of the palaeohabitat of the source vegetation, but if they are used in conjunction with 'germlings' the predictive value will be much stronger. Lange (1976) has demonstrated the value of 'germlings' as palaeohabitat indicators and how, using 'germlings' in conjunction with other fossil fungal structures (Lange, 1978b) the combined characters can be compared

with similar fungal structures derived from extant leaf litter samples from different habitats.

In the case of the Hordle Cliff deposit of Eocene age, the combination of a diverse group of epiphyllous fungal form-genera and 'germlings' which, using Lange's (1976) ad hoc scale, are of the highest grade of morphological complexity, reinforces the hypothesis that the source vegetation for this deposit was tropical or subtropical. However, as the 'germlings' are for the most part palynological, rather than still being attached to cuticles of leaves, this can not be regarded as an absolute correlation as the 'germlings' may have been transported from an extremely different vegetation type than that, or those, from which the epiphyllous fructifications were derived.

When the dispersed fossil fungal spores present in these Palaeogene deposits are investigated, several different aspects need comment. Firstly, the type of classification to be used, either purely morphographic and hence artificial, or whether the spores are to be incorporated if at all possible into the pre-existing classification of living fungi as advocated by, amongst others, Pirozynski and Weresub (1979b). From the examples of the very varied types of fossil fungal spores present in the deposits, which were selected for more intensive study it is clear that both types of treatment have their merits. If the purely morphographic classification is based upon the well established spore morphology categories established by Saccardo (1882) for living fungal spores there is opportunity for accurate and acceptable descriptions of the

various types of spores. Any taxonomic exercises resulting in the erection of new form-genera and species must however be based upon full and exhaustive population studies. Delineation of population variability in the very few morphological features available upon which separation of species can be based is essential. If no modern fungal spore of equivalent morphology is known with which comparison can be made, the form-genus is the end point of the exercise. If however an affinity with a Recent genus can be established, despite the suggestions of Pirozynski and Weresub (1979b), the nomenclature of the fossil spore should, I feel, reflect that this affinity is based solely upon spore characters, and hence advocate the retention of the suffix -sporites in any fossil fungal spore genus.

Of the spore genera treated in this study two genera, Ctenosporites and Pesavis fall into the category of morphological form-genera, Trochophorisporites (nom. prov.) is based upon the recent genus Trochophora and the Sporidesmium-like phragmoconidia are placed in the Saccardoan grouping of phragmoconidia due to the lack of sufficient diagnostic characters to make a definite match with the spores of a living genus.

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Fungal spores of the genus *Ctenosporites* from the early Tertiary of southern England

BY

P. H. SMITH

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FUNGAL SPORES OF THE GENUS
CTENOSPORITES FROM THE EARLY
TERTIARY OF SOUTHERN ENGLAND

by P. H. SMITH

ABSTRACT. Dispersed fungal spores from Late Eocene deposits from the Hampshire Basin are placed in the genus *Ctenosporites* Elsik and Jansonius. The population studied shows continuous morphological variation between individuals conforming with *C. eskerensis* Elsik and Jansonius and with *C. wolfei* Elsik and Jansonius. *C. wolfei* is therefore placed in synonymy with *C. eskerensis*. Although previously described from Canadian and South Australian Tertiary assemblages, this is the first European Tertiary record of this highly distinctive genus.

THE genus *Ctenosporites* Elsik and Jansonius (1974) has been erected for certain highly distinctive fossil structures of fungal origin. Although first thought to be restricted to the Canadian north-west Pacific and Arctic regions, it has since been shown to occur in an early Middle Eocene deposit from Maslin Bay, South Australia (Lange and Smith 1975*a*, 1975*b*). *Ctenosporites* has now been observed in the course of an examination of dispersed fungal spores from the Leaf Bed, Bed X (Tawney and Keeping 1883) of the Lower Headon deposits (uppermost Eocene or basal Oligocene) from Hordle Cliff (Grid reference SZ 262923), Hampshire.

A sufficiently high frequency of occurrence (more than one per thousand fungal spores counted) has enabled comparative studies based upon a large population sample to be made. Description of the morphological variation found, and some comments upon the delimitation of species as described by Elsik and Jansonius (1974) are presented.

MATERIALS AND METHODS

Small samples of matrix were pared to remove the outer surface exposed at the time of collection and thus to expose new faces and minimize the risk of contamination with recent fungal spores. The matrix was treated with concentrated hydrofluoric acid followed by concentrated hydrochloric acid. The dissociated matrix was washed with distilled water and centrifuged several times. The organic material was concentrated by centrifugation in zinc bromide (S.G. 2·2). After further washing, the organic material was mounted in glycerine jelly for microscopical examination.

TAXONOMY

Lange and Smith (1971) have stressed the inherent difficulties in the nomenclature and taxonomy of dispersed fossil fungal spores and have urged that taxonomic distinctions and limits be drawn only on the basis of large-scale population studies. Adequate species circumscription depends upon the availability for comparative study of the

entire continuum of variability. Elsik and Jansonius (1974), in erecting the genus *Ctenosporites*, recognized two species distinguished largely upon the pattern of lateral branching and the shape, if present, of the apical cell of the basal filament. Using the population-study method, the morphological variation present in the Hordle Cliff material appears to have at least three major foci when the pattern of lateral branching is considered. Two of these correspond to those branching patterns already designated by Elsik and Jansonius as separating *C. eskerensis* from *C. wolfei*. The major specific difference, as published, is the tendency of the lateral branches to curve and reach a common level parallel to the apical cell of the basal filament in *C. eskerensis* (text-fig. 4*f*, *h*) whilst the lateral branches of *C. wolfei* (text-fig. 4*c*, *e*, *g*) do not exhibit the same degree of curvature. The tips of the lateral branches therefore do not reach a common level parallel with the apical cell. These two conditions are shown diagrammatically in text-fig. 1*a*, *b*; text-figs. 1*c*, and 4*d*, *j* show the form of branching characterizing the third focus, found in the Hordle Cliff material. Here the lateral branches tend to be more nearly perpendicular to the basal filament than in the first two forms.
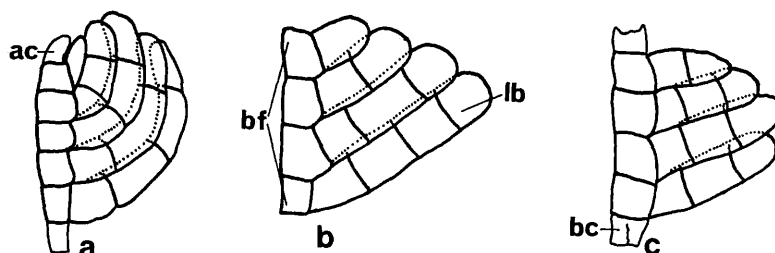
TEXT-FIG. 1. Diagrammatic representations of the branching pattern in *a*, *Ctenosporites eskerensis*, *sensu* Elsik and Jansonius; *b*, *Ctenosporites wolfei*, *sensu* Elsik and Jansonius; *c*, Hordle Cliff form. ac, hyaline apical cell; bf, thickened cells of basal filament; lb, lateral branch; bc, hyaline basal cell.

Whether this variant of branching pattern is sufficient basis to create a third species is highly questionable. Elsik and Jansonius (1974) also place great weight upon the presence or absence of an entire (intact?) hyaline apical cell of the basal filament as a character separating the two species described. In both the Australian material (*see* Lange and Smith, 1975*a*, fig. 1; 1975*b*, fig. 29) and the English material, spores have been found showing the branching pattern of *C. wolfei* but with intact apical cells, calling into question the presence or absence of the apical cell as a sound diagnostic character. The number of non-hyaline, thick-walled cells of the basal filament has also been used to separate the two species, *C. eskerensis* (7 cells) and *C. wolfei* (4–5 cells).

The Hordle Cliff material showed such a wide spectrum of forms, that in order to ascertain whether this could be accommodated in the two described species, measurements of three parameters were made on a sample of 500 spores. The parameters used were the number of thick-walled basal filament cells, the number of lateral branches, and the number of cells in the longest lateral branch. The results of these counts are represented graphically in text-fig. 2.
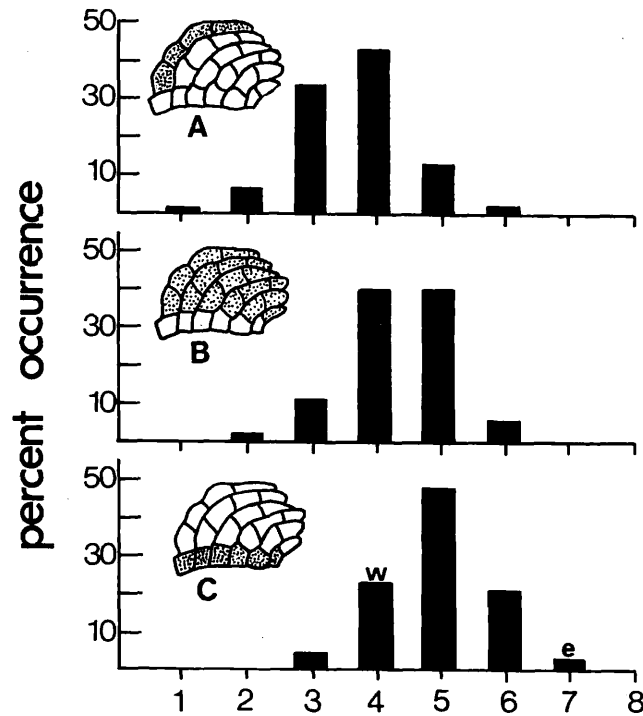
TEXT-FIG. 2. Graphic representation of the distribution of three parameters measured in the Hordle Cliff population: A, number of cells in longest lateral branch; B, number of lateral branches; C, number of thick-walled cells in basal filament. w, *C. wolfei* sensu Elsik and Jansonius; e, *C. eskerensis* sensu Elsik and Jansonius.

The wide morphological variation observed might be accommodated by two alternative taxonomic procedures. One extreme course would be to recognize fifty or so new species, to cover the number of morphological forms observed. Alternatively (and more practically), the generic concept of Elsik and Jansonius (1974) could be accepted, recognizing a single species with wide and continuous variation. The variants within this highly distinctive taxon, although not warranting elevation to specific or subspecific level, are significant enough to warrant cataloguing and illustrating as comprehensively as possible (Lange and Smith 1971, 1975b).

Ctenosporites eskerensis (Elsik and Jansonius, 1974) emend.

Type species. C. eskerensis Elsik and Jansonius (1974) (p. 957, pl. 1, fig. 1).

Synonymy.

  C. wolfei Elsik and Jansonius (1974) figs. 2–4.

  C. cf. *wolfei* Lange and Smith (1975a) fig. 1.

  Ctenosporites sp. Lange and Smith (1975b).

  'Unidentified fungi', Hills (1965) plate 15, fig. 16.

Emended diagnosis. Multicellular structure of fungal origin; basal (main) filament consisting of a variable number (3–9) of thickened cells; with or without a more hyaline basal (attachment?) cell; apical hyaline

cell may be present; lateral filaments, although always more or less parallel to one another, showing varying degrees of curvature towards apex of basal filament; lateral filaments usually decreasing in septation from base to apex of basal filament.

Discussion of Hordle Cliff material. The specimens figured as text-figs. 3*a–e* and 4*a* are interpreted as immature forms, due to the relative lack of thickening of the basal filament cells. Corresponding forms from the South Australian material are illustrated by Lange and Smith (1975*b*, figs. 1 and 21).
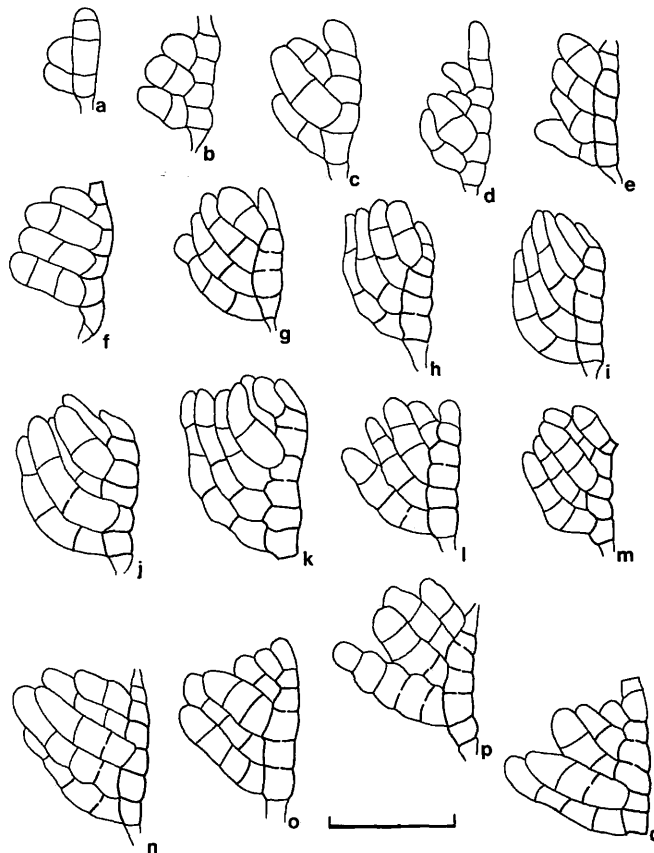
TEXT-FIG. 3. Camera lucida drawings of variation in spore morphology shown in Hordle Cliff population. Scale bar, 25 μm.

The specimens shown in text-figs. 3*h, k* and 4*f, h* correspond to the species *C. eskerensis (senso strictu)* as originally described by Elsik and Jansonius (1974). That shown in text-fig. 3*l* would have been placed in *C. eskerensis*, due to the presence of an intact apical cell, whilst that shown in text-fig. 3*m* would have been designated *C. wolfei* due to the lack of an intact apical cell. Text-fig. 3*o, p* shows forms which have lateral filaments almost perpendicular to the basal filament but differ in the presence of an intact, or broken apical cell, whilst text-fig. 3*q* differs only in the absence of an apical cell and in possessing a thin-walled penultimate basal filament cell.
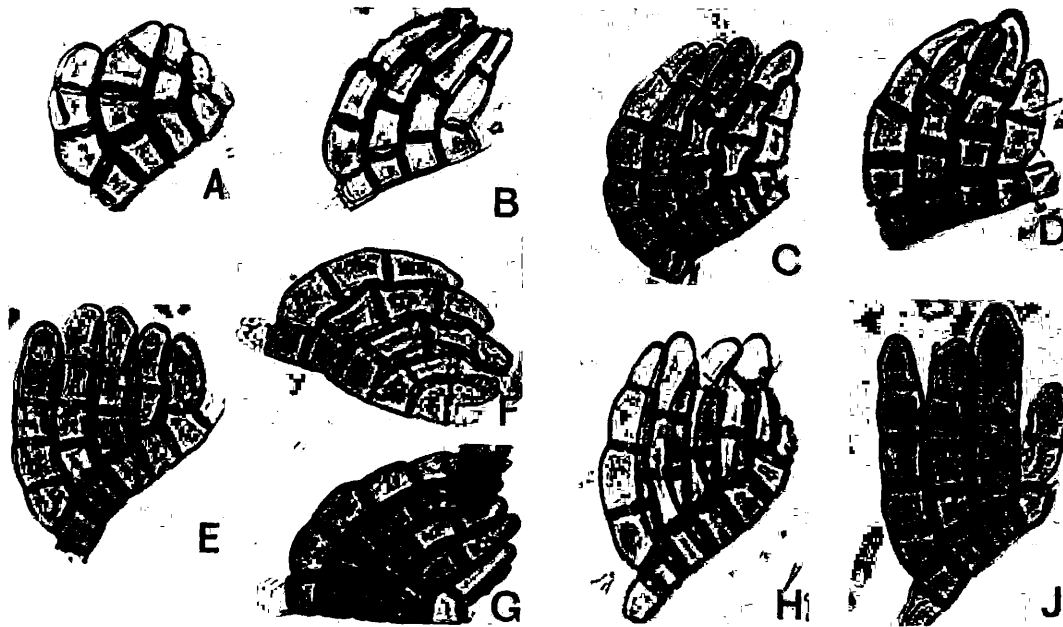
TEXT-FIG. 4. Photomicrographs of some morphological variations found in Hordle Cliff material. Magnification × 1000. Specimens illustrated in text-figs. 3 and 4 are from slides V58924–V58926, deposited in the British Museum (Natural History).

Although the majority of the forms observed in the Hordle Cliff material are characterized by the unilateral branching pattern, several structures were found which correspond to the form illustrated by Lange and Smith (1975b, fig. 10). This particular form, or a closely similar structure, has also been catalogued and illustrated as 'Fungal Spore A' by Clarke (1965) from Upper Cretaceous deposits from Colorado. As stated by Lange and Smith (1975b) this form is probably a member of the genus *Ctenosporites* but, due to the possession of a branching pattern which is not unilateral, it cannot be assigned to the genus as it is presently delimited.

CONCLUSION

The occurrence of *Ctenosporites* in deposits from the Hampshire Basin widens the recorded distribution of the taxon within early Tertiary floras whilst still maintaining a stratigraphic restriction to the Eocene and Oligocene Periods. Although no modern fungal genus has been shown to have spores with the characteristic unilateral branching of *Ctenosporites*, it is thought to have affinities with the conidia of the saprophytic dematiaceous hyphomycete *Dictyosporium*, which are branched, cheiroid spores usually flattened in one plane (Ellis 1971, fig. 25, p. 56). Conidial stages of *D. toruloides*, figured as *Speira toruloides*, from dead wood, herbaceous stems, and occasionally leaves, in marsh and fen conditions (Ellis *et al.* 1951), show a certain degree of similarity with the branching pattern of *Ctenosporites*. The lack of host-specificity

in *Dictyosporium* (Ellis 1974) corresponds with the apparent lack of host specificity already noted for *Ctenosporites* (Lange and Smith 1975*b*).

The inclusion of such a wide variation of spore morphology within a single species is justified by an examination of extant species of Fungi Imperfecti. A similar range of variation is often found within the spores of a single species. Underlying causes of this variation have been shown to include such environmental factors as the nutritional status of the substrate. Brown and Horne (1926) demonstrated that in *Fusarium* species a low carbon/nitrogen ratio led to the production of short spores with few septa; and conversely that long spores with increased septation resulted from a high carbon/nitrogen ratio in the substrate. Although the mode of nutrition, either parasitic or saprophytic, cannot be inferred from dispersed spores, the apparent lack of host-specificity in *Ctenosporites* could well be a contributing factor in the wide range of spore morphology observed. If *Ctenosporites* was an element of a floristically diverse community, this would present a large number of alternative substrates with correspondingly variable nutrient levels available for utilization. Substrate variability could be a contributing factor in the morphological variation of the mature spore of *Ctenosporites*.

This first European record for *C. eskerensis* broadens the known distribution of this taxon and, as with the previous records, other fungal remains found in association with this spore type are indicative of moist, warm, climatic conditions. The fungal remains thus bear out the earlier conclusions of Reid and Chandler (1933) and Daley (1972) that higher rainfall and elevated temperature characterized the Palaeogene climate of southern Britain.

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Fungal spores of the genus *Pesavis* from the Lower Tertiary of Britain

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Dispersed fungal spores from the Reading Beds (Palaeocene) near Newbury, Berkshire are referred to the genus *Pesavis* Elsik & Jansonius, and a possible affinity with aero-aquatic fungi is suggested. This highly distinctive Palaeogene sporomorph has not previously been described from the European Tertiary.

CONTENTS

INTRODUCTION

The Reading Beds (Upper Palaeocene) near Newbury, Berkshire have recently yielded well-preserved angiosperm plant remains from several isolated clay and silt lenses occurring amongst unconsolidated cross-bedded sands (Crane, 1978). An examination of dispersed fossil fungal spores from the argillaceous deposits has resulted in the recognition of the distinctive genus *Pesavis* Elsik & Jansonius, which has previously been recorded only from Palaeocene and Eocene deposits in Washington, British Columbia, Alaska, the Mackenzie Delta and Northwest Territories of Arctic Canada (Elsik & Jansonius 1974; Jansonius, 1976), and from deposits of Middle Eocene age in South Australia, Maslin Bay (Lange, 1978). At all these localities *Pesavis* has been found associated with another Tertiary fossil

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fungal spore *Ctenosporites*, but this has not yet been recorded from the Newbury site. However, the locality has provided a sufficiently large sample of *Pesavis* to permit comparisons with the species described by Elsik & Jansonius, description of morphological variation, and comments on the delimitation of species. The methods employed in the preparation of samples are those given by Smith (1978). Slides with representative specimens have been deposited in the Department of Palaeontology, British Museum (Natural History): registration numbers V. 59790 and V. 59791.

SYSTEMATICS

The genus *Pesavis* was erected by Elsik & Jansonius (1974) to include two species, *P. tagluensis* and *P. simplex*. The type species *P. tagluensis* (Fig. 1A, B) has a remarkable construction consisting of a central basal cell bearing two incurving septate primary arms. The central cell and the majority of the primary arm cells each bear a pair of inwardly directed, septate, secondary arms (Fig. 1C, D), which Elsik & Jansonius term secondary hyphae: these are absent from the terminal cells of the primary arms. The terminal cells may overlap (Figs 1A, 7) or meet (Figs 1B, 6), the number of cells in the primary arms varies from five to rarely eight in the published data. *P. simplex* consists of a central cell bearing two straight widely divergent lateral arms lacking secondary appendages. All the Newbury material resembles *P. tagluensis*, both in qualitative characters and overall diameter (30–40 µm). *P. simplex* has not been isolated from the Newbury matrix.

The specimens designated as the holotype and paratype of *P. tagluensis* both have an equal number of cells in each of the primary arms. The majority of the Newbury specimens are of this equal-armed construction, but 30% of the population is unequal-armed having a considerable degree of overlap in the terminal cell region (Figs 1A, 5, 7). Figure 8 illustrates graphically the percentage
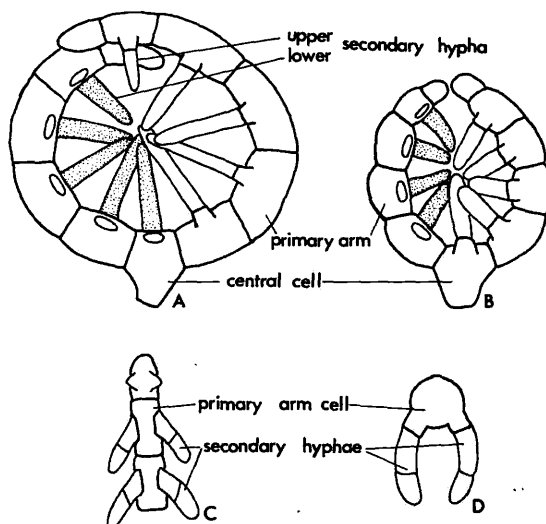
Figure 1. Diagrams to show the construction of *P. tagluensis*: A, unequal-armed form showing overlap of primary arm terminal cells; B, equal-armed form (A and B only one of the pair of secondary hyphae illustrated); C, vertical section showing paired arrangement of secondary hyphae on primary arm; D, transverse section of primary arm showing secondary hyphae.
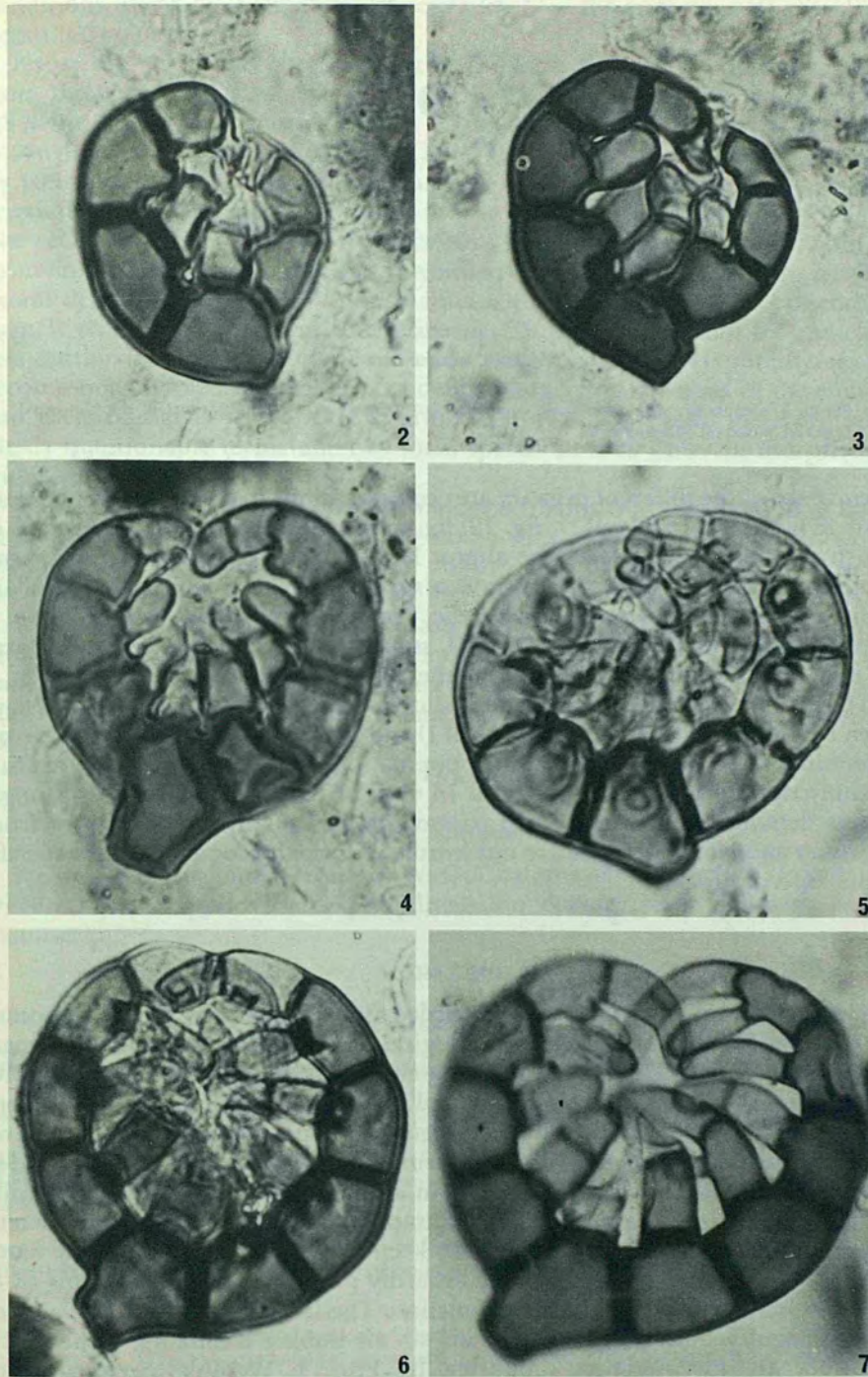
Figures 2 to 7. Photomicrographs of *P. tagluensis* specimens from Newbury. Figs 2, 3. Small forms resembling '*P. parva*' Jasonius. Fig. 4. Form with terminal cells overlapping. Fig. 6. Form with terminal cells meeting. Figs 5, 7. Forms showing large overlap of terminal cells. All × 1500.
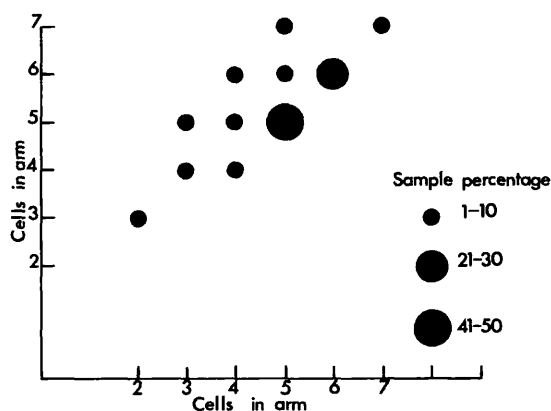
Figure 8. Graph showing percentage occurrence of primary arm configurations in the Newbury material (based on 50 specimens).

occurrence of the different primary arm configurations in the Newbury material. Elsik & Jansonius (1974: pl. 1, fig. 10) figure a small specimen of *P. tagluensis* in which secondary appendages are almost lacking, as a possible immature form. Jansonius (1976: pl. 1, fig. 2) illustrates a small specimen in which the secondary arms are poorly developed, under the "preliminary name, *Pesavis 'parva'* ". Similar small, poorly-developed forms, some bearing only one secondary arm on each primary arm cell, also occur in the Newbury material.

The problems involved in the systematics of dispersed fossil fungal spores have been emphasised by Lange & Smith (1971) and Smith (1978), who urged the consideration of a large sporomorph population as essential to the realistic circumscription of fossil fungal taxa. In view of the variability of fossil fungal spores demonstrated in these two papers the variants mentioned above from Newbury and North America are not worthy of formal recognition at the specific or sub-specific level.

DISCUSSION

The affinities of *P. tagluensis* were regarded as problematic by Elsik & Jansonius (1974) who made tentative morphological comparisons with living fungal structures. Lange (1978) found no living equivalent to *P. tagluensis* in extensive studies of leaf litter from a wide range of present day habitats in the Southern Hemisphere, but concluded that *P. tagluensis* appeared to be epiphyllic on terrestrial plants. Glenn-Bott (1951) describes in detail the spores and method of sporulation in *Helicodendron giganteum*, an aero-aquatic fungus (Van Beverwijk, 1951). These spores have a bubble of air trapped in their tightly coiled structure which contributes to effective dispersal by keeping the spore floating on the water surface. We suggest that the paired, inwardly projecting secondary arms of *P. tagluensis* may have served a similar function. The large, internal surface area of the propagule could trap and maintain an air bubble facilitating dispersal by flotation, an interpretation supported by Prof. J. Webster (personal communication). If it is accepted that *Pesavis* was an aero-aquatic fungus then it is clear that *P. tagluensis* would only be found in those sediments deposited under

conditions involving fluctuations in water level, or the reworking of previously deposited plant detritus.

Pirozynski (1976) has observed that *P. simplex* is practically indistinguishable from the conidia of *Ceratosporella bicornis*, a living dematiaceous hyphomycete. All living species of *Ceratosporella* occur on dead or dying plant material and none is truly aquatic (Hughes, 1951, 1952; Ellis, 1971). *Arachnospora fagicola* described by Hennebert (1963) from decaying cupules of *Fagus sylvatica* bears a superficial resemblance to *P. tagluensis*; however, the globose or ovoid conidia, with one or two central body cells, of this dematiaceous fungus contrast markedly with the incurving primary arms and bilateral symmetry of *P. tagluensis*. There are very few extant dematiaceous aquatic or aero-aquatic fungi and there is no evidence to suggest that *P. tagluensis* was dematiaceous. Thus there may not be any close relationship between *Pesavis tagluensis* and *P. simplex*. All living Hyphomycetes are accommodated in form genera, now defined largely on the basis of the conidia and their ontogeny (Kendrick & Carmichael, 1973). It would therefore seem highly questionable to include two fossil species of such different morphology within the same genus.

The occurrence of *P. tagluensis* in Palaeocene deposits from the London Basin extends the known distribution of the taxon within early Tertiary floras, whilst retaining its stratigraphic restriction to the Palaeocene and Lower Eocene. Jansonius (1976) has demonstrated that *P. tagluensis* is a sporomorph of considerable stratigraphic value and Lange (1978) has stressed the importance of *Pesavis* and *Ctenosporites* as links between the Palaeogene floras of the Northern and Southern Hemispheres. The present study supports the view that fossil fungal spores must come to play a much more important role in stratigraphic palynology.

ACKNOWLEDGEMENTS

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Trichothyriaceous fungi from the early Tertiary of southern England

BY
A.H. SMITH

THE PALAEONTOLOGICAL ASSOCIATION

TRICHOTHYRIACEOUS FUNGI FROM THE EARLY TERTIARY OF SOUTHERN ENGLAND

by PETER H. SMITH

ABSTRACT. Isolated ascocarps (thyriothecia) from Upper Eocene deposits of the Hampshire Basin are described as a new species of the genus *Trichothyrites* Rosendahl within the Trichothyriaceae, a family of epiphyllous fungi not previously recorded from English Tertiary deposits. Comparisons are made between the fossil material and the extant genus *Trichothyrina* Petrak to establish their affinity. Earlier records of epiphyllous fossil fungi from British deposits are reconsidered in view of recent taxonomic changes in living taxa.

IN the course of an examination of fungal material from the Leaf Bed (Bed X of Tawney and Keeping 1883), of the Lower Headon deposits (Upper Eocene/Lower Oligocene) from Hordle Cliff, Hampshire, thyriothecia ascribable to the Trichothyriaceae have been recognized (see Smith 1978 for grid reference and methods of isolation). Examples of this type of fructification have not previously been described from deposits earlier than Quaternary in Britain.

Although ascomycetous fungi have been shown to be present in fossil deposits of Upper Carboniferous age (Batra *et al.* 1964) it is interesting to note that the majority of fossil epiphyllous ascomycete forms are reported only from Tertiary deposits. As shown by Tiffney and Barghoorn (1974) the bulk of Tertiary ascomycetes are epiphyllous forms occurring in association with leaf cuticles. Graham (1962) attributes this to rapid adaptive radiation of the ascomycetes to capitalize on the vast expansion of potential habitats within the phyllosphere following the appearance of the angiosperms. However, as Tiffney and Barghoorn caution, this apparent rapid diversification and numerical increase in fossil forms may in part be due to the large number of palaeobotanical investigations made upon leaf bed deposits from the Tertiary. Apart from the epiphyllous fungi from the Lower Cretaceous flora described by Krassilov (1967), there is little published evidence to suggest that a diverse epiphyllous fungal flora existed prior to the Tertiary. This could well be due to the fungal element being overlooked or disregarded as not worthy of further investigation by workers concentrating on the leaves themselves.

The presence of fructifications of epiphyllous fungi in Tertiary fossil deposits has generally been accepted as indicating warm sub-tropical to tropical climatic conditions, in light of the predominantly tropical distribution of extant taxa of the Microthyriales. This contention is reinforced by the comparative work on fossil and extant forms of epiphyllous fungi of Lange (1976, 1978) from the Southern Hemisphere.

TAXONOMIC CONSIDERATIONS

Considerable recent advances have been made in the understanding of the taxonomic relationships of extant taxa (Müller and von Arx 1962; Luttrell 1973). Few workers interested in fossil forms have had these modern treatments available for consultation, and have often tended to use 'microthyriaceous' in an all-embracing term. Records of British fossil epiphyllous fungi can now be ordered as follows (see Table 1) using the classification of Luttrell (1973). Godwin and Andrew (1951) reported the common occurrence of *Microthyrium*-like thyriothecia (with a tentative affinity with *Loranthomyces* von Höhnel of the Trichothyriaceae) in Post-Glacial peat deposits ranging from the Pennines to Somerset. Vishnu-Mittre (1973) attributed thyriothecia from Flandrian peat deposits at Whittlesey Mere to two extant species, *M. culmigenum* Sydow and *M. nigro-annulatum*

TABLE 1

CLASS LOCULOASCOMYCETES

ORDER: MICROTHYRIALES	ORDER: DOTHIDEALES
FAMILY: MICROTHYRIACEAE	FAMILY: TRICHOTHYRIACEAE
	Microthyrium-like cf. *Loranthomyces* von Höhnel, 1917 (Godwin and Andrew 1951)
Microthyrium culmigenum Sydow, 1921 ──────→ (From Vishnu-Mittre 1973)	*Trichothyrina alpestris* (Sacc.) Petrak, 1950 (From Ellis 1977)
Microthyrium nigro-annulatum Webster, 1952 ──────→ (From Vishnu-Mittre 1973)	*Trichothyrina nigro-annulata* (Webst.) Ellis, 1977 (From Ellis 1977)
*Phragmothyrites** *eocenica* Edwards, 1927	
*Phragmothyrites** *hibernica* Johnson, 1949	
FAMILY: MICROPELTIDACEAE	
*Stomiopeltites** *cretacea* Alvin and Muir, 1970	

* Denotes fossil genus.

Webster, and commented upon the similarity of the material to that described by Godwin and Andrew. Ellis (1977), however, in her critical taxonomic review of extant British Microthyriaceae, has removed the species cited by Vishnu-Mittre both from the genus *Microthyrium* and the family Microthyriaceae (see Table 1). Based largely upon differences in thyriothecial construction, both species have been placed in the genus *Trichothyrina* Petrak in the family Trichothyriaceae. These are the only Dothidealian fungi in the fossil record from Britain. Microthyrialian fungi are only slightly better documented. Alvin and Muir (1970) erected the genus *Stomiopeltites* for fructifications resembling those of *Stomiopeltis* Theissen from the family Micropeltidaceae. These fossil forms were borne on leafy conifer shoots from the Lower Cretaceous deposits of the English Wealden. Edwards (1922) described *Phragmothrites eocenica* based on fructifications borne on conifer leaves of Eocene age from Mull, Scotland, whilst Johnson (1949) described *P. hibernica* on cuticles attributed to *Fagus* from an Eocene deposit of Ireland.

Selkirk (1975) has enumerated the difficulties involved in positive identification of thyriothecia from fossil deposits as members of the Trichothyriaceae, rather than Microthyriaceae the uncertainties involved being centred upon details of thyriothecial construction. These concern the ostiole borne on a short papilla of thickened cells often, but not always, bearing setae on the uppermost ring of ostiolar collar cells (see text-fig. 1A and B), and the cellular pattern and construction of the thyriothecium. In contrast to the dimidiate construction of fructifications of Microthyriaceae where the lower wall is extremely thin and delicate, those of Trichothyriaceae are complete with well-developed upper and lower walls, each composed of radiate files of cells which appear almost isodiametric in surface view (see text-fig. 1c). This pattern of cellular arrangement of quadrilateral cells is also present in the upper wall of the thyriothecia of Microthyriaceae close to the ostiole, but cells generally become more elongate towards the margins.
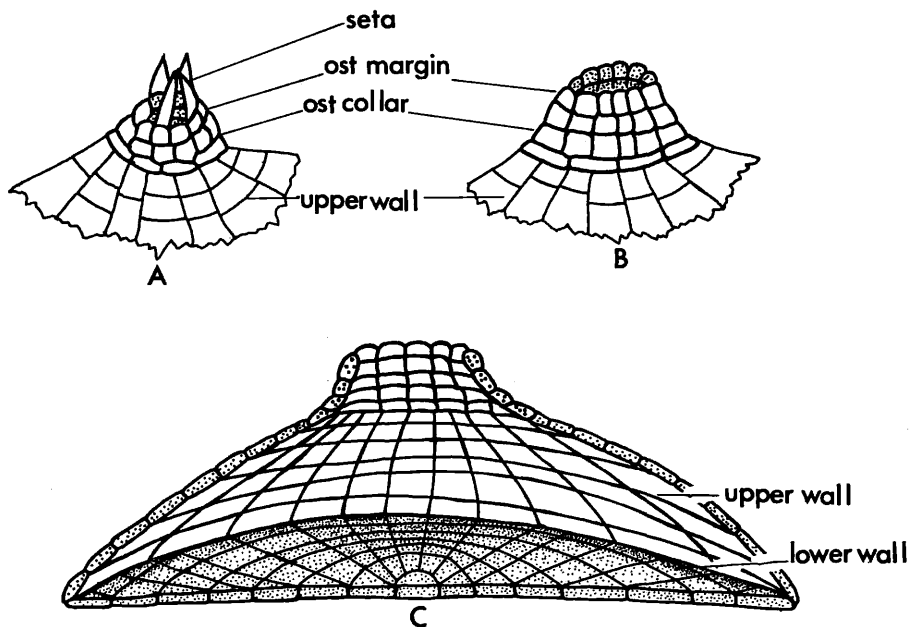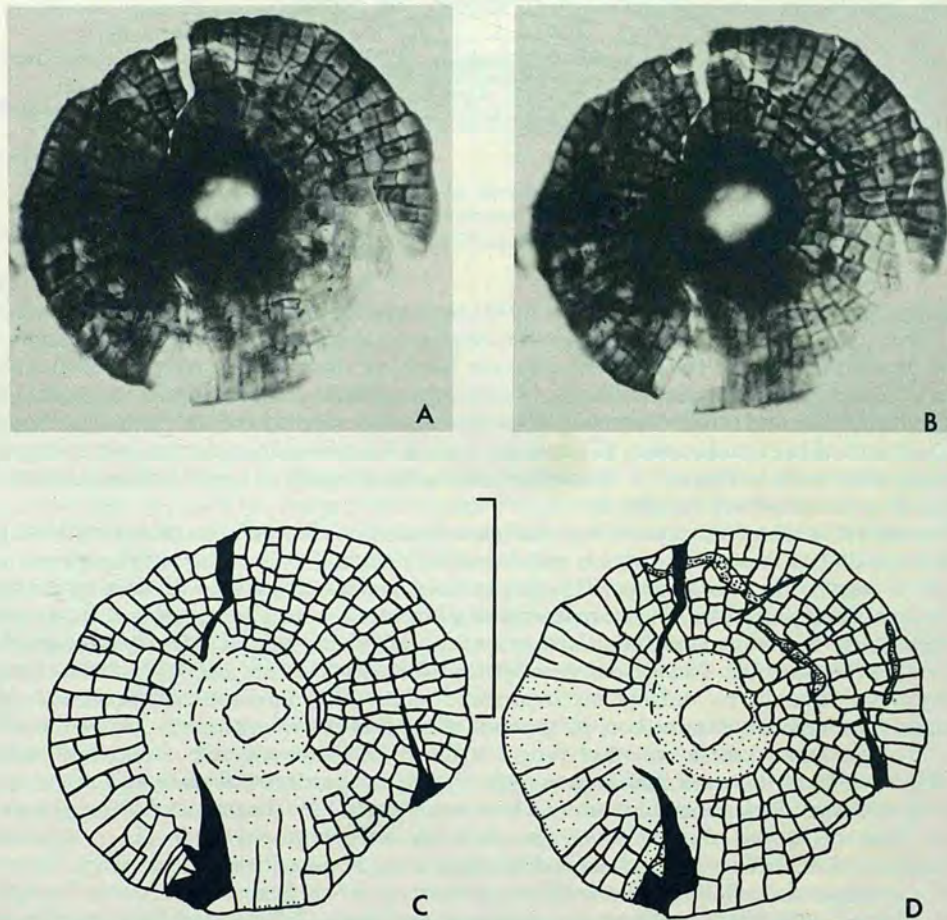
TEXT-FIG. 1. Diagrammatic representations of thyriothecium constructions in Trichothyriaceae. A, ostiole bearing setae on ostiolar margin. B, ostiole with smooth ostiolar margin. C, vertical section of the thyriothecium showing 3D structure. ost = ostiolar.

Microscopic examination of the Hordle Cliff thyriothecia has resulted in the recognition of several criteria that it is felt allow accurate assignment of the fructifications as those of Trichothyriaceae. The papilla bearing the ostiole has retained sufficient height in the fossils to remain a distinguishing feature. Despite dorsiventral compression of the entire fructification the thickened cells of the papilla usually remain erect and thus the terminal ostiole is observable in a higher focal plane than the cells of the upper wall of the fructification. Compression of the fructification and subsequent preparation treatment often leads to rupture of the walls enabling the presence of a well-defined and complete lower wall to be seen (seen text-fig. 2).

Rosendahl (1943) used the features of a complete fossil thyriothecium (i.e. possessing both upper and lower walls), with an erect ostiolar collar and the marginal cells of the pore bearing setae, to describe *Trichothyrites pleistocaenica*. This species was found in association with both spruce needles and moss leaves from an early Pleistocene deposit from Minnesota. Those found on spruce needles were reported to be in close association with other fungal hyphae which were tentatively identified as a species of *Herpotrichia*. The relationship between these hyphae and the thyriothecia, however, remained problematic; no definite myco-parasitic relationship could be demonstrated. Myco-parasitism was further questioned on the grounds of the presence of apparently identical fructifications on moss leaves where no other fungal hyphae were demonstrable. Rosendahl therefore concluded that *T. pleistocaenica* was saprophytic, but no comparison was made with extant species. Since publication of Rosendahl's description, however, Petrak (1950) has elevated from subgeneric to generic level the taxon *Trichothyrina* for predominantly saprophytic fungi, as opposed to *Trichothyrium* Sacc. which is characterized as being a genus parasitizing other fungi. This would suggest that the closest affinity for *Trichothyrites* Rosendahl, would be this extant genus *Trichothyrina* Petrak. This is further borne out by an examination of the Hordle Cliff material. Here the thyriothecia are not associated with host material in most instances, but those that have been observed attached to cuticle are not in association with any other fungal hyphae, which would appear to preclude any suggested myco-parasitic relationship.

Size measurements used by Ellis (1977) in defining living species of *Trichothyrina*, would also suggest close affinity of the Hordle Cliff material with extant species. However, one of the major diagnostic features for separation of living species remains their mode of nutrition, a character impossible to ascertain with certainty in fossil material.

A number of fructifications of epiphyllous fungi from the Tertiary of the Southern Hemisphere and Lower Cretaceous of Siberia have been assigned to the genus *Notothyrites* (Cookson 1947; Selkirk 1975; Kemp 1978; Krassilov 1967). This genus bears a close resemblance to the material described here with the exceptions that no mention of a lower thyriothecial wall has been made in the descriptions nor shown in any of the specimens that have been figured. On these grounds *Notothyrites* has hitherto been considered as a genus of the Microthyriaceae. As no detailed comparison with the Southern Hemisphere material has yet been made it seems appropriate, at present, to retain *Trichothyrites* Rosendahl with an emended diagnosis allowing the incorporation of the Hordle Cliff material.

TEXT-FIG. 2. Construction of fossil thyriothecium. A and C, photographic and diagrammatic representation of upper thyriothecial wall. B and D, the same specimen at a lower depth of focus showing splits in upper wall and presence of lower wall. Scale bar = 50 μm.

SYSTEMATIC PALAEONTOLOGY

Genus TRICHOTHYRITES Rosendahl, 1943 emend.

Emended diagnosis. Thyriothecia appearing disc or saucer-shaped due to compression; possessing definite upper and lower walls of radiate rows of almost square cells (3–8 μm × 3–8 μm). Cell walls of upper layer of thyriothecium generally more strongly thickened than those of the lower layer. Thyriothecia ranging from 70 μm to 200 μm in diameter and bearing on upper wall an erect ostiolar collar (papilla) made up of from two to six tiers of small (2 μm × 2 μm) extremely thick-walled quadilateral cells. Uppermost tier (ostiolar margin) of cells may have short prolongations (setae) in some cases. Thyriothecial outline usually smooth but may appear lobate.

Type species. *Trichothyrites pleistocaenica* Rosendahl (1943), figs. 8–10, p. 132; figs. 18–20, p. 135.

Trichothyrites hordlensis sp. nov.

Text-fig. 3A–F

Holotype. Text-fig. 3A, B, and C, British Museum (Natural History), Department of Palaeontology slide no. V60215.

Type locality. Hordle Cliff, Hampshire (Grid ref. SZ262923).

Horizon. Hordle Leaf Bed (Upper Eocene/Lower Oligocene).

Diagnosis. Maximum diameter of thyriothecia 75 μm. Erect ostiolar collar of 3–4 tiers of small (2 μm × 2 μm) thick-walled quadrilateral cells, diameter of collar 20 μm; ostiolar marginal cells not produced into setae,
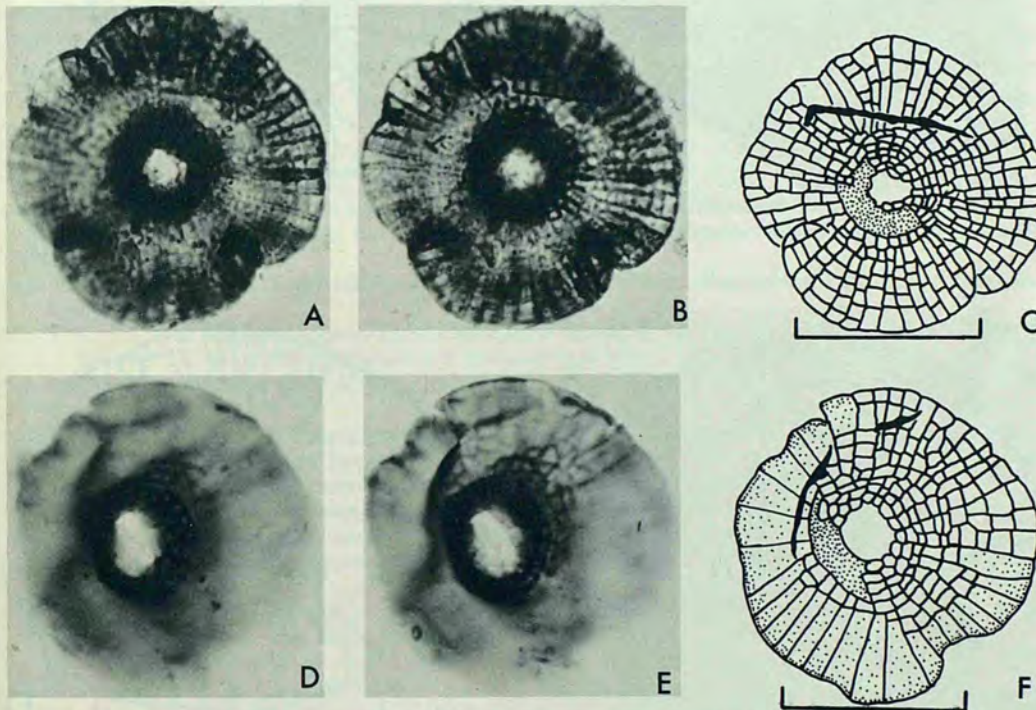
TEXT-FIG. 3. *Trichothyrites hordlensis.* A and B, fructifications at two focal planes showing thyriothecial construction especially upper wall. D and E, details of ostiolar region of *T. hordlensis.* C and F, interpretative drawings of specimens. Scale bar = 50 μm.

ostiolar pore diameter 10–15 μm. Upper wall of thyriothecium consisting of quadilateral cells arranged in rows radiating from ostiolar collar, cell size ranging from 3 μm × 3 μm near collar to 6 μm × 8 μm at margin. Cells of lower wall similar but with more delicate cell walls. Thyriothecia usually found as isolated structures not in association with cuticle or other fungal hyphae. Spores absent.

Discussion. The affinity of these fossil thyriothecia cannot be stated exactly as the final diagnostic character used for species determination by Ellis (1977) is the nature of the host substrate coupled with the shape of the ascopores. Although the large cells at the base of the ostiolar collar (see text-fig. 3A, B) may tend to suggest an affinity with *Trichothyrina alpestris* (Sacc.) Petrak, 1950, there is no clear indication that these cells are perforate in the fossil material. Similarly, although setal processes from the cells of the ostiolar may or may not be present in *T. alpestris*, their absence from the fossil material, coupled with the small over-all size of the fructification (75 μm v. 200 μm), small ostiolar collar diameter (20 μm v. 25–40 μm), all combine to suggest a closer affinity with *T. ammophilae* Ellis, 1977.
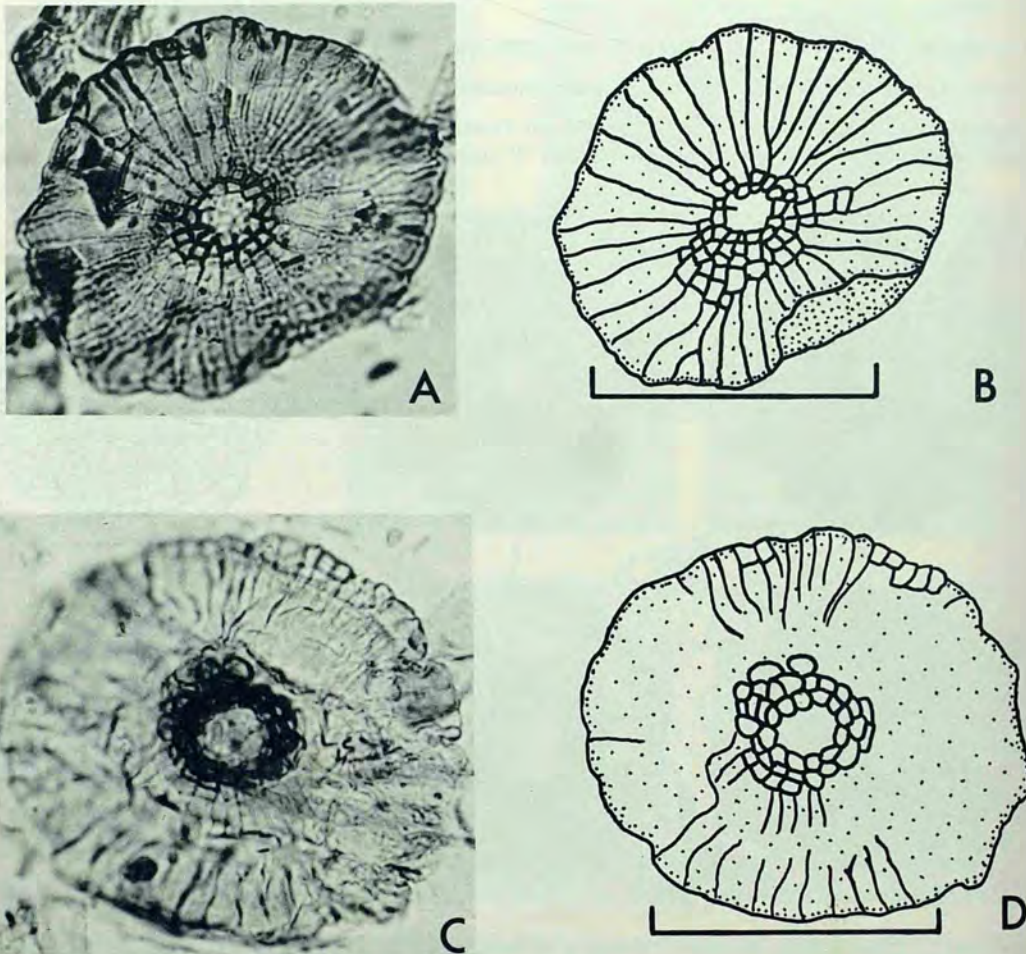
TEXT-FIG. 4. A, *Trichothyrites* sp. A. C, *Trichothyrites* sp. B. B and D, interpretative drawings. Scale bar = 50 μm.

Trichothyrites sp. A

Text-fig. 4A, B

Fructifications of this type are present in the Hordle Cliff material at a much lower frequency than those of *Trichothyrites hordlensis*. Insufficient numbers have been isolated so far to erect a detailed specific diagnosis but a tentative affinity with *Trichothyrina pinophylla* (von Hohn.) Petrak, 1950 is suggested due to the smaller number of tiers in the ostiolar collar and the much smaller (60 μm) overall diameter of the fructification.

Trichothyrites sp. B

Text-fig. 4C, D

Again, insufficient material precludes a formal specific diagnosis for this type of fructification; however, the characteristic appearance of the ostiolar collar due to the outward curvature of the cells of the ostiolar margin allows easy separation from the two preceding forms. Affinity with *Trichothyrina nigro-annulata* (Webster) Ellis, 1977 is suggested.

CONCLUSIONS

Previous records have concentrated upon Microthyriaceous forms within the Tertiary. The demonstration of Trichothyriaceous forms from the Upper Eocene is indicative that these fungi also were involved in the apparently rapid diversification of ascomycete groups during the Tertiary. Careful re-examination of material from pre-Tertiary deposits to establish the presence or absence of epiphyllous fungi, similar to the Trichothyriaceae would be of great interest. This might establish whether, with the advent of the angiosperms, the Trichothyriaceae arose as epiphyllous forms and only later attained their present far more specialized myco-parasitic nature.

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SYMPOSIUM

CHITINOZOAIRES (NATURE ET SYSTÉMATIQUE) – PALÉOMYCOLOGIE

SOME PROBLEMS IN DEFINING TAXONOMIC LIMITS
IN FOSSIL FUNGAL SPORE POPULATIONS

by Peter H. SMITH*

Résumé. — Indépendamment du fait que les spores fossiles soient classées en utilisant une classification morphographique strictement utilitaire, ou incorporées dans la classification des champignons actuels, la définition des genres et plus particulièrement des espèces peut se révéler difficile. Les caractères diagnostiques utilisables sont avant tout morphologiques et les descriptions devraient donc prendre en compte toutes les variations possibles de la morphologie des spores. Il apparaît que la morphologie sporale de beaucoup de champignons actuels peut être modifiée par un large éventail de facteurs externes. La variabilité de la morphologie sporale qui en découle sera illustrée à partir des données concernant plusieurs espèces vivantes. Trois populations très distinctes de sporomorphes fongiques du Paléogène seront également examinées quant à leur variabilité et les conséquences de cette variabilité seront discutées en termes de descriptions taxinomiques.

Abstract. — Irrespective of wether fossil fungal spores are ordered using a strictly utilitarian morphographic classification, or incorporated into the classification of living fungi, circumscription of genera and especially species can be difficult. Diagnostic features available are predominantly morphological and descriptions should therefore take into account any possible variation in spore morphology. The spore morphology of many extant fungi has been shown to be markedly altered by a wide range of external factors. The ensuing variability in spore morphology will be illustrated using data from several living species. Three highly distinctive Palaeogene fungal sporomorph populations will also be examined for variability and the consequences of this variability discussed in terms of taxonomic descriptions.

Although I wish to concentrate upon the problems that the palaeomycologist encounters at the generic and specific level, it is as well to introduce these in the context of the overall approach to the classification of fossil fungal remains. The various systems that are used can be divided into the morphographic; where although being recognised as fungal in origin, little or no information is given or postulated concerning their inter-relationship with living fungi. This method is in direct contradistinction with the treatment advocated by some workers where the maximum correlation possible between living and fossil forms is aimed for, fossil forms being incorporated wherever possible into the taxonomic and nomenclatural framework of the living fungi. Both approaches have their advocates, e.g. ELSIK (1976) and PIROZYNCKI & WERESUB (1979), but despite the philosophical arguments that can be advanced to favour either of these two methods, both have features in common. The material must be described in terms of their physical appearance, size and shape, and finally regardless of the approach, described and typified using the binomial system of nomenclature. It is axiomatic that any structures such as a population of fungal spores will exhibit a certain degree of inherent variability and there is no reason to suggest that this inherent variability is not present in fossil fungal spores. The problem for the palaeomycologist is, however, compounded by the fact that the very structure under investigation, has been shown in

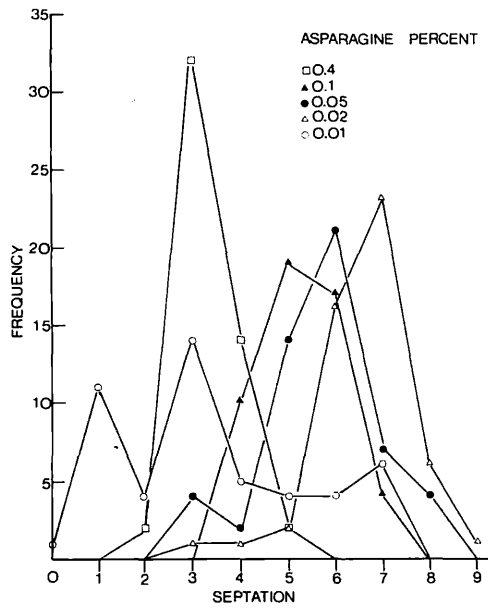* Department of Botany, Birkbeck College, University of London, Malet Street, London, WC1E 7HX (England).

ASPARAGINE PERCENT

□ 0.4
▲ 0.1
● 0.05
△ 0.02
○ 0.01

Fig. 1. — Variation in degree of septation in spores of *Fusarium* caused by differing levels of asparagine in the culture medium.
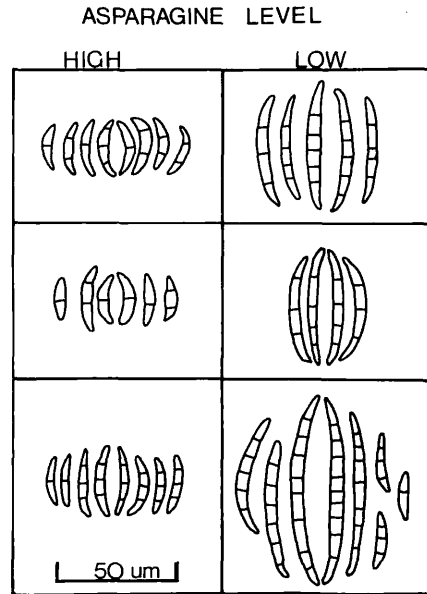

ASPARAGINE LEVEL

HIGH   LOW

50 um

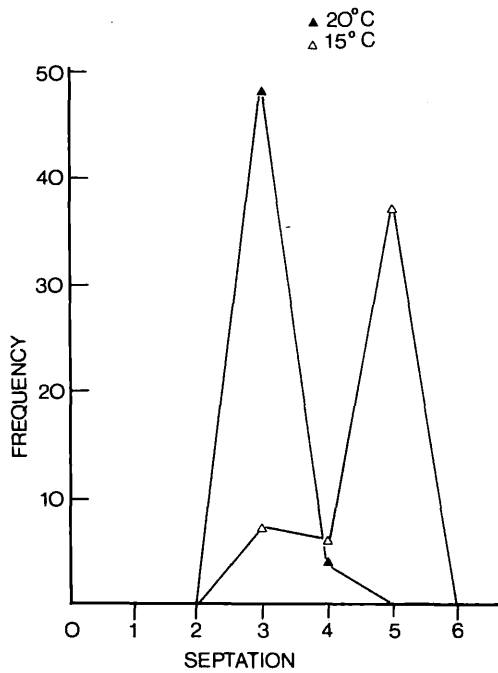Fig. 2. — Variation in spore morphology in *Fusarium* caused by different levels of asparagine in the culture medium.

▲ 20°C
△ 15°C

Fig. 3. — Effect of temperature on degree of septation of *Fusarium* spores.
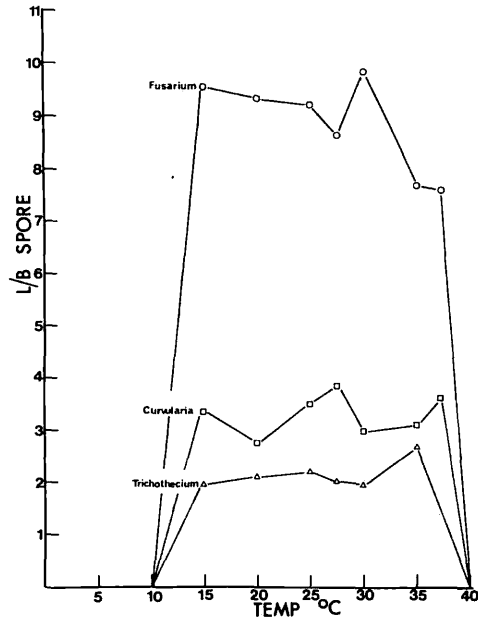

Fusarium

Curvularia

Trichothecium

Fig. 4. — Variation in Length/Breadth ratio of spores of *Fusarium semitectum*, *Curvularia lycopersi* and *Trichothecium roseum*, cultured under different temperature regimes.
(Calculated from KAKKAR & MEHROTRA, 1971b).

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living fungi to be extremely susceptable to changes in external factors. The influence of these factors usually being expressed in the very features of the spore that the palaeomycologist must depend upon as the basis for species distinction in fossil spore genera.

BROWNE & HORNE (1926) working with strains of a single species of *Fusarium*, were able to show that the length of the spore, and the degree of septation could be altered by a large number of factors including :

(1) the concentration of nitrogenous material in the culture medium - especially asparagine; (2) high acidity or high alkalinity ; (3) increased temperature.

The variation in septation that occurred with changes to the carbon/nitrogen ratio of the medium, caused by altering the asparagine content of the substrate is shown in Figure 1. The significance and implications of this sort of variation to any palaeomycological investigation is emphasised more fully if the appearance of the spores produced in conditions of extreme asparagine supply are represented as in Figure 2. All the spore forms illustrated could be incorporated into existing genera for fossil fungal spores. The extreme morphological diversity between the spores would mean, however, that due to differences in size, shape and amount of septation that at least three existing form genera could be considered as appropriate repositories for these specimens. The effects of one external factor would therefore cause the separation of one highly variable genus into three genera, viz. *Dicellaesporites, Pluricellaesporites* and *Multicellaesporites*. A very similar situation is encountered if the effect of temperature on septation in *Fusarium* is considered. As can be seen in Figure 3, temperature changes that could not be regarded as extreme fluctuations can also have marked effects on spore morphology.

HORNE & MITTLER (1927) have demonstrated that large changes in spore morphology due to external factors are to be found in many species of *Fusarium*, and KAKKAR & MEHROTRA (1971 a et b) have shown similar effects in genera other than *Fusarium*. As a measure of the variability of morphology, I have calculated the length/breadth ratios from their data and present this figure as a measure of the variation encountered. Fig. 4 shows the fluctuations in length/breadth ratio of the spores over a
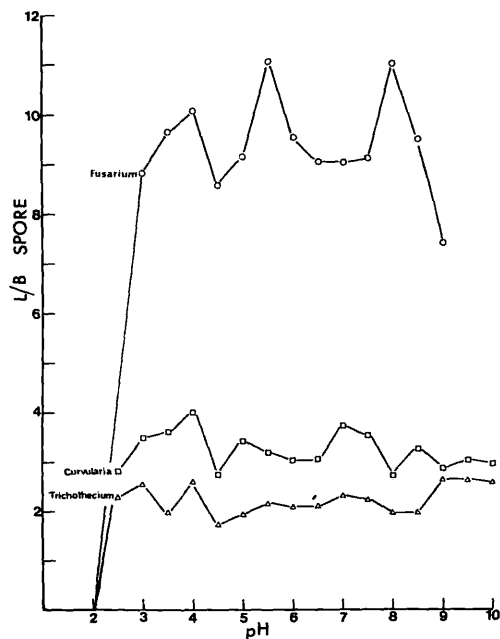

Fig. 5. — Variation in Length/Breadth ratio in spores of *F. semitectum, C. lycopersi* and *T. roseum* cultured in media of different initial pH.
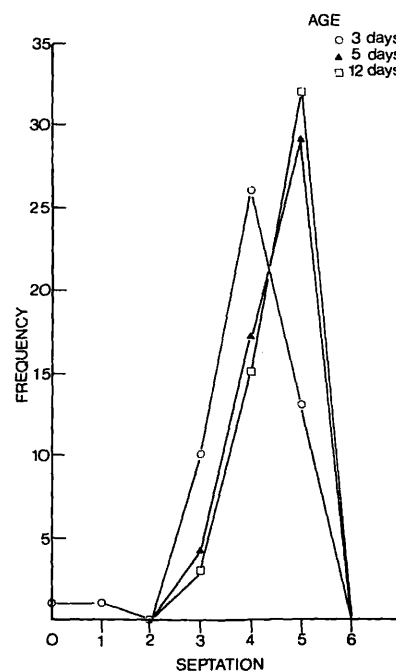(Calculated from KAKKAR & MEHROTRA, 1971a).

Fig. 6. — Variation in septation in *Fusarium* spores from sample of different ages.

wider range of temperature than that of BROWNE & HORNE. Again the *Fusarium* species used shows the greatest changes but both the other genera show considerable fluctuation in this ratio over the range of temperatures at which sporulation could take place. The effects of the initial acidity or alkalinity of the medium upon the length/breadth ratio of the same three genera are shown in Figure 5, and again the fluctuations are most pronounced in *Fusarium* but the figures do indicate a range in spore morphology in the other two genera also.

Although in studying dispersed fossil fungal spores it is virtually impossible to make any meaningful conclusions concerning the maturity of the fungal mycelium that was their source, Figure 6 shows that spore morphology in *Fusarium* can be influenced by the age of the culture at the time of sporulation. Work by FISCHER (1957) on spores from a mildew on *Laburnum* leaves shows that spore morphology also shows considerable variation depending upon the time of the year when spores are produced. Figure 7 illustrates the variation in length and breadth measurements found by FISCHER during the life cycle of the fungus. The variability need not be attributed solely to the age of the fungus, however, both temperature and the nutritional status of the host leaf material could also play a contributory role in producing this variation. The spores in this case are amerospores, which in a palaeomycological context constitute a morphological group containing several genera which have been shown by LANGE (1978a) to need revision and clarification. Due to the lack of other constant distinguishing features dimensions of individual spores have been accorded undue emphasis as the basis for characterising genera and species.

Il must also be remembered that fungal spores are readily transported in the atmosphere (GREGORY, 1973). Thus in any population of fossil fungal spores one cannot be totally sure of their source. CORNER (1947) has shown (Figure 8) that the spore morphology of the same basidiomycete species can be extremely different if populations from different geographic localities are compared.

It is with this background of the sources of possible variation that we turn to the difficulties encountered in drawing meaningful specific circumscriptions in some selected genera of Palaeogene fungal spores. In each case a large number of individual spores has been examined in the hope that the size of the sample will enable variability in spore morphology to be adequately represented (LANGE & SMITH, 1971). Two of the genera, *Ctenosporites* and *Pesavis* are extremely interesting in that despite their remarkably distinctive morphologies they have only been reported from three extremely widely separated geographic regions, Arctic North West Canada (ELSIK & JANSONIUS, 1974), South Australia
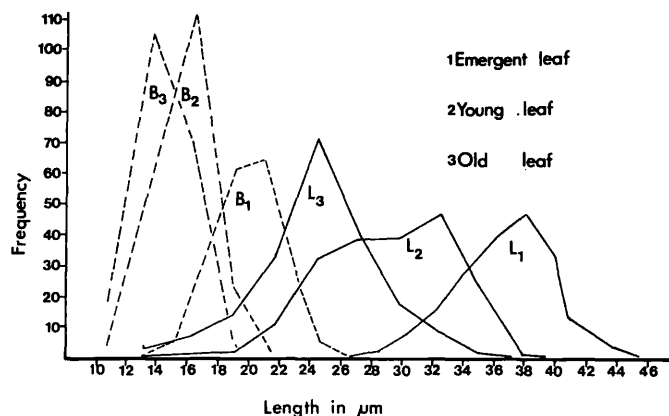

Fig. 7. — Variation of length & breadth dimensions of spores of
Oidium from *Laburnum* leaves of different age.
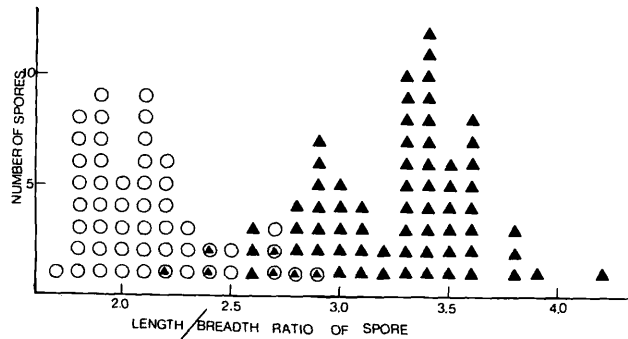Ex. FISCHER (1957).

Fig. 8. – Variation of length/breadth ratio of spores of *Clavaria formosa* from two sites.
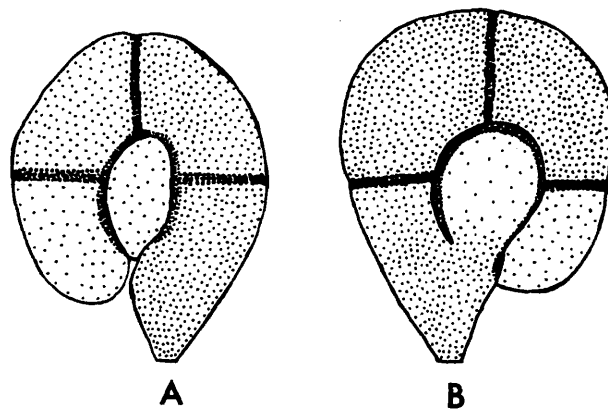○ - Austria   ▲ - England   (After CORNER, 1947)

Fig. 9. – Diagrammatic representation of *Trochophorisporites* (nom. prov.) to show morphology.
A. Appearance of helical spore with cells overlapping central lobe.
B. Opposite orientation of spore to show relationship of lateral lobe to basal cell.

(LANGE & SMITH, 1975 ; LANGE, 1978b) and southern England (SMITH, 1978 ; SMITH & CRANE, 1979). The third, *Trochophorisporites* (nom. prov.) is at present represented only from deposits in southern England.

This is the name I propose for a distinctive helicoid spore type which bears a close morphological similarity to the spores of the living dematiaceous fungus *Trochophora simplex*. Figure 9 shows the appearance of the spore ; a basal attachment cell with a lateral lobe, and three further cells which encircle and to some extent overlap this lobe. In analysing any possible variation in morphology, apart from the number of septa and number of cells which are remarkably constant, the most obvious parameters are spore length and breadth. The data from such an investigation is represented graphically in Figure 10, with two curves of such a shape as to suggest normal distribution curves for both length and breadth. Thus one could be excused in citing a spore of length 15 μm and breadth 14 μm as the holotype and recording maximum and minimum dimensions for length and breadth in the diagnosis. But if the same information is represented as in Figure 11 with individual diameters plotted against length it is clearly evident that this pair of measurements is only one of the most frequent combinations. Both 15 x 13 μm
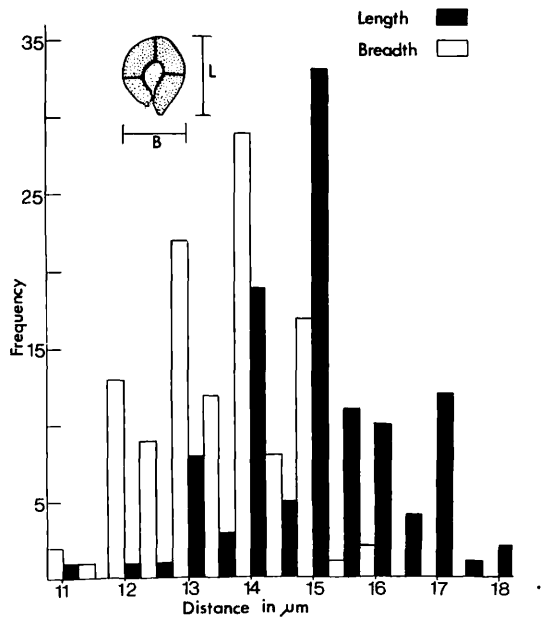
Fig. 10. – Distribution and frequency of length and breadth measurements in a population of *Trochophorisporites* (nom. prov.).
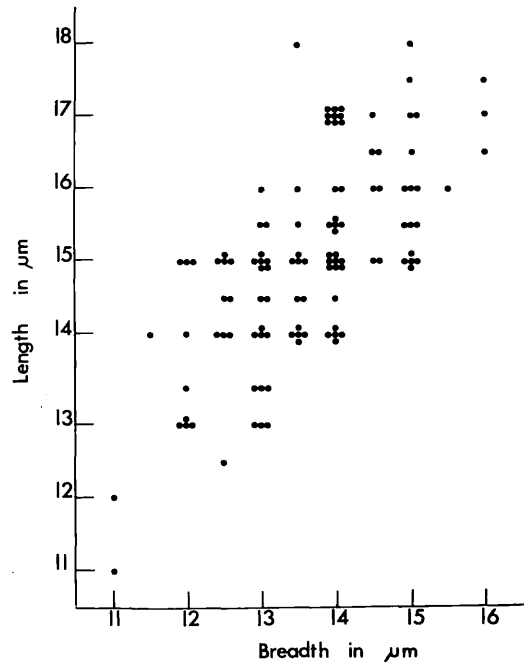

Fig. 11. – Occurrence and frequency of individual length/breadth combinations in a population of *Trochophorisporites* (nom. prov.).
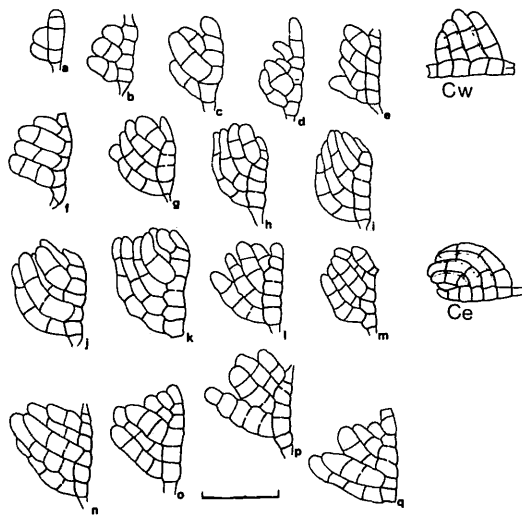

Fig. 12. – a-q. Morphological variation from a population of *Ctenosporites*.
C.w. *Ctenosporites wolfei*
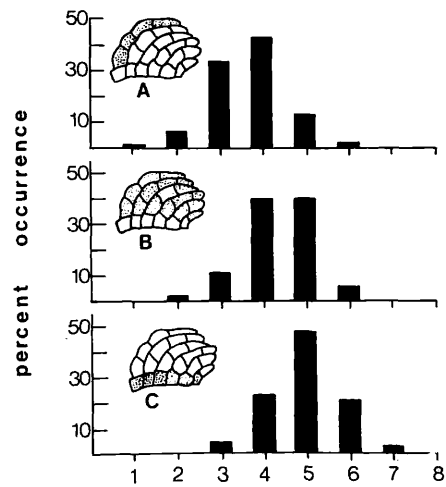C.e *Ctenosporites eskerensis*.
Scale bar 25 μm.

Fig. 13. – Distribution of variation in spores of *Ctenosporites* for 3 parameters.
A. Number of cells in basal lateral arm.
B. Number of lateral arms.
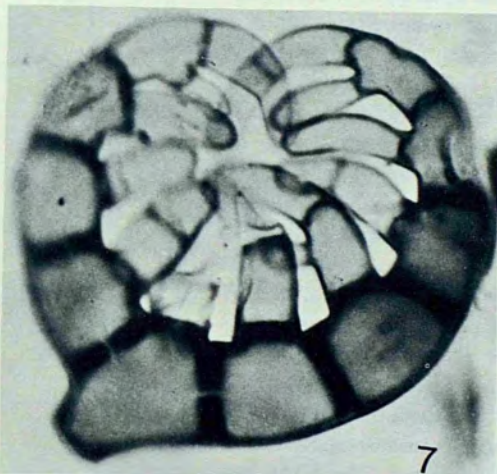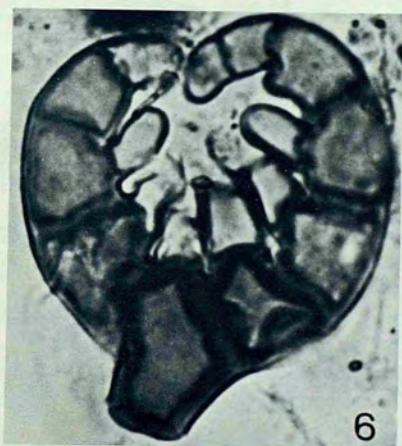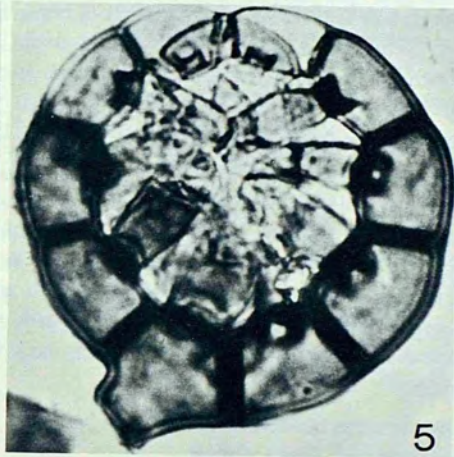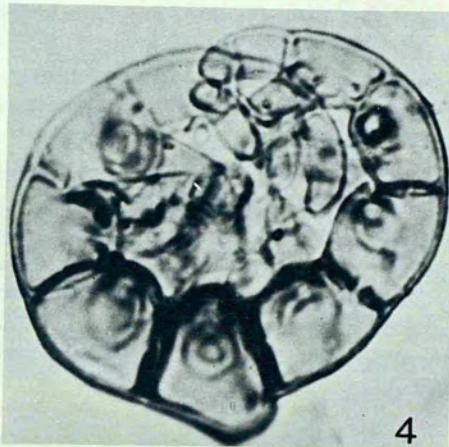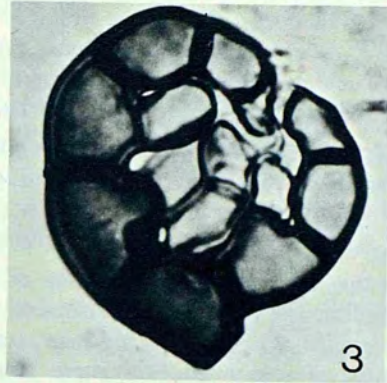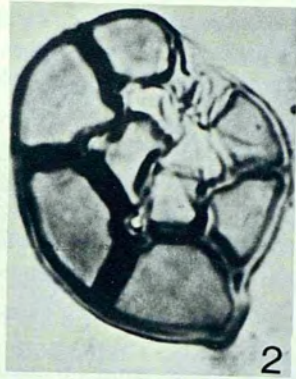C. Number of thick walled cells in basal filament.

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Fig. 14. – Variation in spore morphology in a population of *Pesavis tagluensis* from the Palaeocene of Southern England.

and 17 x 14 μm combinations occur at very similar frequencies. Should one or other of these be treated as the holotype? or should all three be treated as syntypes? These would appear to be the only two alternatives that deserve consideration. Having established the possibility of the number of external factors which could influence spore morphology, I can see no possible justification in trying to create more than a single variable species from this material.

ELSIK & JANSONIUS (1974) erected the genus *Ctenosporites* and recognised two species, *C. eske-rensis* and *C. wolfei*, the distinction between these species being made upon three morphological criteria:
(1) Pattern of branching of the lateral arms; (2) Presence or absence of an intact hyaline cell at the apex of the basal filament; (3) Number of thick-walled non-hyaline cells in the basal filament.

The variation that was found in a population of *Ctenosporites* from an Eocene deposit in Southern England is illustrated in Figure 12 and compared with the morphologies of the two described species. Results of an analysis of a population for three paramaters:
(a) number of cells in the basal lateral arm; (b) number of lateral arms; (c) number of thick-walled non-hyaline cells in the basal filament

are represented in Fig. 13. The parameter is of importance as it formed part of the original basis for separating *C. eskerensis* and *C. wolfei* but again it would appear that these are but two points within a continuum of variation. The distribution of the other two parameters also led me to reinterpret the material as a single highly variable species. Therefore I felt justified in reducing *C. wolfei* to synonomy with *C. eskerensis* on the basis of this investigation (SMITH, 1978).

The Palaeocene genus *Pesavis* has also been shown to be highly variable in morphology. ELSIK & JANSONIUS (1974) described two species *P. tagluensis* and *P. simplex* but this latter species has since been linked with the living genus *Ceratosporella bicornis* by PIROZYNSKI (1976). Due to its bizarre shape (Fig. 14) *P. tagluensis* has been suggested as being related to the aero-aquatic fungi (SMITH & CRANE, 1979) although no definite affinity with any living fungus has been established. The Newbury deposits in Southern England have yielded a wide range of configurations (Figure 15) suggesting that once more the effects of external factors may be influencing the final morphology of the spores under consideration.

It would seem therefore that circumscription of fossil fungal spore material at generic level, due in no small part to the highly distinctive morphologies of the sporomorphs, can be relatively straight forward. However, the limited number of features possessed by any given assemblage of spores which are available for comparison plus the possibility of wide variations in their expression due to the effects of external factors make distinctions at species level much more difficult. I have tried to show the application of a method whereby these problems are, if not surmounted, at least taken into consideration and allowances made for them when any forms of taxonomic treatment of fossil fungal spores in undertaken.
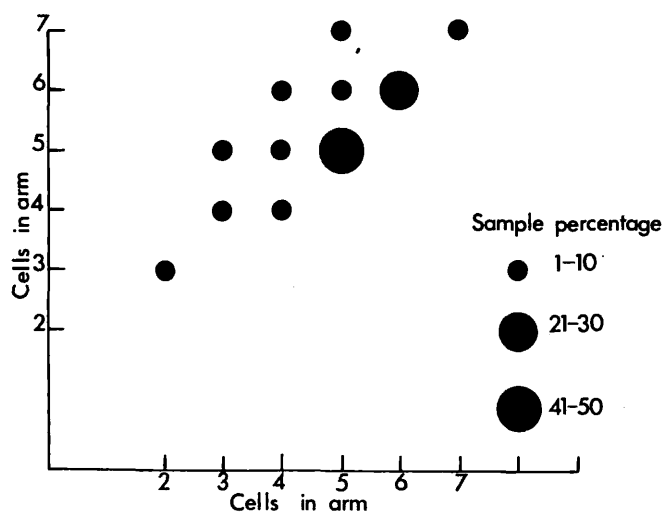

Fig. 15. — Frequency of occurrence of spore morphology configurations in a population of *P. tagluensis* from Southern England.

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APPENDIX B.

1.   Raw data for length/breadth measurements of 112 spores

      of _Trochophorisporites_ (nom. prov.).

BREADTH (μm)	LENGTH (μm)	FREQUENCY
11	11	1
11	12	1
11.5	14	1
12	13	3
12	13.5	1
12	14	1
12	15	1
12.5	12.5	1
12.5	14	3
12.5	14.5	2
12.5	15	4
13	13	3
13	13.5	3
13	14	4
13	14.5	2
13	15	6
13	15.5	2
13	16	1
13.5	14	5
13.5	14.5	2
13.5	15	4
13.5	15.5	1
13.5	16	1
13.5	18	1
14	14	5
14	14.5	1
14	15	8
14	15.5	5
14	16	2
14	17	9
14.5	15	2
14.5	16	2
14.5	16.5	2
14.5	17	1

BREADTH (μm)	LENGTH (μm)	FREQUENCY
15	15	5
15	15.5	3
15	16	3
15	16.5	1
15	17	2
15	17.5	1
15	18	1
15.5	16	1
16	16.5	1
16	17	1
16	17.5	1

APPENDIX B.

2. (a)   Cell number for 484 _Sporidesmium_-like phragmoconidia.

   (b)   Thickened septa/total cell number for 276 _Sporidesmium_-
like phragmoconidia.

   (c)   Length and breadth measurements of 246 _Sporidesmium_-
like phragmoconidia.

   (d)   Length/breadth measurements of _Sporidesmium_-like
phragmoconidia.

(a)

NUMBER OF CELLS	FREQUENCY
3	4
4	9
5	24
6	28
7	52
8	74
9	85
10	93
11	59
12	36
13	11
14	5
15	4
16	1
17	1

(b)

SEPTA/CELL	FREQUENCY
2/3	1
2/4	1
3/4	6
3/5	8
4/5	8
3/6	1
4/6	10
5/6	9
4/7	10
5/7	13
6/7	9
7/7	1
3/8	2
4/8	5
5/8	13
6/8	18
7/8	6
3/9	1
4/9	2
5/9	16
6/9	9
7/9	3
8/9	1
4/10	3
5/10	8
6/10	25
7/10	12
8/10	5
5/11	3
6/11	14
7/11	9
8/11	4
9/11	3

SEPTA/CELL	FREQUENCY
6/12	6
7/12	7
8/12	8
10/12	1
6/13	1
7/13	4
8/13	1
10/13	1
8/14	1
7/15	2
8/15	2

	LENGTH (μm)	BREADTH (μm)	FREQUENCY
(c)	17.5	7.5	1
	17.5	10	1
	20	7.5	7
	22.5	5	2
	22.5	7.5	4
	25	7.5	8
	25	10	1
	27.5	7.5	14
	27.5	10	8
	30	7.5	11
	30	10	6
	32.5	7.5	11
	32.5	10	8
	35	5	1
	35	7.5	12
	35	10	10
	37.5	7.5	23
	37.5	10	15
	40	7.5	19
	40	10	9
	42.5	7.5	7
	42.5	10	6
	45	7.5	10
	45	10	11
	47.5	7.5	10
	47.5	10	6
	50	7.5	5
	50	10	5
	52.5	7.5	3
	52.5	10	4
	55	7.5	1
	57.5	10	1
	60	10	1
	65	10	1
	72.5	7.5	1
	75	10	1

(d)

RATIO	FREQUENCY
1.75	1
2.25	5
2.3	1
2.5	1
2.6	7
2.75	8
3.0	33
3.25	8
3.3	8
3.5	10
3.75	29
4.0	20
4.25	6
4.3	17
4.5	13
4.6	12
4.75	6
5.0	5
5.25	4
5.3	19
5.6	7
5.75	1
6.0	13
6.3	10
6.6	5
7.0	4
7.3	1
7.5	1
7.6	1
8.3	1
8.6	1

RATIO	FREQUENCY