

MICROBIOLOGICAL COLONIZATION AND ATTACK ON SOME CARBONIFEROUS MIOSPORES

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ABSTRACT. The paper describes *Palynomorphites diversiformis* gen. et sp. nov., a saprophytic organism thought to be related to the Fungi, and which is responsible for some part of the microbiological attack on Carboniferous miospores. The different organization of this attack on several groups of miospores of widely varied structural characteristics is described. The miospores were preserved in a chert band within the Upper Oil Shale Group of the Calcareous Sandstone Series of Scotland at a horizon considered on the evidence of goniatites to be of Upper Viséan age.

DURING studies of the micropalaeontology and constitution of the Scottish Carboniferous Oil Shales, problems of the recognition and possible interrelationships of the organic contents of the Oil Shale were encountered. The presence of a relatively opaque organic groundmass in close association with inorganic material led to difficulties in the resolution of the finer organic material as seen in normally prepared thin-sections. This was also true of larger organic entities such as wood cells, spores, or algae embedded in the groundmass. To some extent these difficulties were overcome by the production of microtomed sections and by the application of peel techniques to polished and etched surfaces. On the other hand, the improved techniques indicated the presence of a considerable content of fine cellular material within the groundmass and upon the surface of many larger remains such as fragments of wood and spores. The application of maceration techniques resulted in the isolation of some ingredients e.g. spores and algae, and provided substantiation of the presence of microbiological remains upon their surface or within their body. These studies also indicated the possibility of selective, partial, or complete destruction of the various organic constituents during the varied maceration processes. However, in favourable preparations considerable quantities of fine thread-like filaments, or small rounded cells often in groups or chains, were present within the groundmass and upon subjects embedded within it. This material, present to some extent in all the oil shales studied, appeared to play a significant part in the constitution of certain types of oil shales.

In order to investigate what appeared to be evidence of microbiological attack, possibly of a saprophytic character, upon the organic material, other rocks within the Oil Shale succession were studied. These included calcareous shales, limestones, ironstone nodules, and chert nodules and bands. This account describes the evidence provided by one chert band, and from the sum total of the microbiological attack on a wide variety of organic remains presents that evidence concerned with the attack on miospores. Subsequent papers will be concerned with the attack on other plant remains by a variety of microbiological agents.

Brief summary of previous work. There is considerable literature concerned with the presence of microbiological remains of a type resembling in morphological details those [Palaeontology, Vol. 6, Part 2, 1963, pp. 349-72, pl. 54-56.]

herein described. The occurrences relate to most geological systems from the Precambrian (Tyler and Barghoorn 1954) to the present day, with particular abundance within the Tertiary (Meschinelli 1902). The remains have been recorded from a wide diversity of rock types in association with fossil plant and animal remains, or as isolated entities. The ubiquitous distribution is striking and references to either Fungi, Algae, or Bacteria are equally varied and controversial. In many cases the association of microbiological remains with recognizable fossil plants or animals led to a direct comparison with existing organisms and their known methods of attack, and resulted in identification of genera and species which imply genetic affinity with members of these three main classes.

Bacteria have long been regarded as the main instruments of organic decay and an early record of their fossil occurrence was due to Van Tieghem (1879), who recorded *Bacillus amylobacter* from silicified Coal Measures rocks of St. Etienne. This work was followed by Renault (1896, 1900), who described and named a great variety of bacteria, both micrococci and bacilli. On the basis of their morphology and association with particular organic material, a number of genera and species were erected principally for Carboniferous and Permian forms.

A further group of organisms consisting of fine filaments from 0.7μ to 2.0μ in diameter have received consistent reference in literature. Thus Wedl (1858) described remains from animal shells of various geological ages as due to the 'alga' *Saprolegnia ferox* (Kützing), while other authors, e.g. Kolliker (1859), referred similar organisms to the Fungi. Renault (1900) referred to fine aseptate filaments of the saprophytic fungus *Phellomyces* in the bark cells of Carboniferous plants; similar remains from carbonaceous shales, oil shales, and cannel coals were referred to the saprophyte *Anthracomyces cannellensis*.

Kidston and Lang (1921) described forms of somewhat greater geological age consisting of a felt of aseptate unbranched tubular filaments 2μ in diameter from the Rhynie chert. The organisms, designated Schizophyta No. 2 and No. 3, were compared with *Archaeothrix contexta* and *A. oscillatoriformis*, and, while they were regarded as possible fungal hyphae, they were believed to be suggestive of the Trichobacteria, *Beggiatoa* or *Oscillatoria*.

In recent years organisms with affinities between Fungi and Bacteria have received considerable attention as the Actinomycetes. Although some indecision is evident regarding the systematic position of these organisms from the works of Drechsler (1919), Henrici (1947), Waksman (1950), and Bergey (1948), there is a clear understanding of their morphological characteristics. Thus according to Waksman, the Actinomycetes are organisms forming elongated, usually filamentous, cells; the filaments are usually 1μ or less and do not exceed 1.5μ in diameter. They multiply by special spores (oidiospores) or by conidia; the oidiospores are formed by segmentation or simple division of the filaments, whilst conidia are formed singly at the ends of simple conidiophores. The genus *Actinoplanes*, a fungus allied to the Actinomycetes, was responsible for the attack on certain modern pollen described by Goldstein (1960).

There have been few references to the attack of micro-organisms on fossil spores; this is particularly true for those of Carboniferous age. Reinsch (1884) figured and described what he believed to be fungi on spore coats, and Renault (1900, p. 204) described the presence of the saprophytic fungus *Anthracomyces cannellensis* on the surfaces of micro- and megaspores, and from within the latter.

The attack of modern aquatic and soil-inhabiting fungi on pollen has long been known to botanists. Goldstein (1960) gave a summary account of some of this work and described the attack by Phycomycetes, both filamentous forms and Chytrids. He draws attention to the importance and interest of the degradation and destruction of pollen grains in pollen analysis studies, and amongst other conclusions refers to the different modes of attack of the various fungi on pollen, and to the greater susceptibility to attack of some types of pollen grains.

Sangster and Dale (1961) carried out controlled experiments on three genera of pollen, *Populus*, *Pinus*, and *Typha*, placed in four different habitats: pond, lake, swamp, and bog. Their work indicated considerable variability in preservation and fossilization of these genera under identical conditions. They concluded also that the decomposition of a given pollen is dependent on the environment which affects not only the rate of decomposition, but the nature of the processes involved. The processes were in part microbiological, and, particularly in the cases of *Populus* and *Typha*, were due to bacteria, although these organisms were not described nor the nature of the decomposition discussed. Other experimental evidence indicated oxidation to be an important factor in disintegration for certain environments and suggested that the resistance of the exine to an oxidizing agent favours fossilization. The *Pinus* pollen was very resistant to disintegration and was well preserved in all four sites; *Typha* pollen was preserved only in the bog; *Populus* disintegrated at all four sites. The authors concluded that the exines possess in varying proportions the material 'sporopollenin', a substance of extraordinary chemical resistance; they drew attention to differences in the percentage frequency of species in the pollen rain spectrum and the fossil spectrum. These differences follow from the differential preservation of the exine, and also from the fact that bog environments or stagnant water will not necessarily 'fossilize' pollen grains.

Studies on the degradation of modern and near-recent plant tissues have focused attention upon the importance of the microbiological action of fungi and bacteria as the most effective agents of degradation. Many authors, including Barghoorn (1952), Siu and Reese (1953), Savory (1954), and Reese (1959), have described these processes and the factors which affect susceptibility to microbial attack. Of considerable relevance to the present study is the readiness with which cellulose is attacked and the effect of the amount and nature of the non-cellulosic components. Where the latter are resistant, e.g. lignin and waxes, the more resistant is the structure to microbiological decomposition. Barghoorn (1952) drew attention to the pronounced differences in the rates of degradation of various cellulosic layers of a single cell wall. This differential degradation of cellulosic lamellae is stated to be a consistent feature of anaerobic decomposition. It is thought to be due to chemical differences in the more resistant lamellae of the cellulosic framework and to the presence of substances, notably lignin, which retard the hydrolysis of cellulose. Lignin is stated to be a primary factor in retarding the action of many fungi and most bacteria.

The mechanism of microbiological attack upon cellulose described by Siu and Reese (1953) and Reese (1955, 1959) is dependent upon physico-chemical action. The active hyphal tip of the fungus produces hydrolytic enzymes which diffuse into the substrate and digest it, the hypha growing into the digested region and maintaining contact with the substrate. The growing fungus appears to follow the cellulose distribution and in certain cases seems to have followed the orientation of the cellulose fibrils (Bailey and Vestal 1937, Savory 1954, Reese 1959).

The possibility of an interrelationship between the presence and activity of the attacking organism and the distribution of materials of varied constitution over the spore body cannot be overlooked. This may be brought about by distribution of material resulting from major differences in the structure of the spore, or may be due to differential changes in composition in a given layer or in different layers of the exine. For this reason the microbiological attack on miospores is presented in a systematic manner in the following pages.

THE CHERT BAND

Locality and horizon. The chert band occurs within the Midhope Burn of Midlothian, where it outcrops on the south bank of the stream at the locality described by Kennedy (1943, p. 12) and within the following section:

	<i>ft.</i>	<i>in.</i>	
Dark shales with ironstones bands and nodules	30	0	
Hard, bedded ashy limestone	4	0	
Dark shale with plant remains (<i>Lepidostrobus</i>)		6	
Dark shale with entomostraca and fish remains		6	
Grey micaceous shale	1	6	
Entomostracan limestone		2	
Shale with plant detritus		6	
Black coaly shale, irregular distribution in small pockets		0-2	} Horizon of Two Foot Coal
Chert brown or grey in nodules, mammillated upper surface—plant remains		0-3	
Calcareous and ferruginous siltstone, containing chert nodules and banded black chert		0-1	
Thin coaly shale		1	
Impure ferruginous sandstone		2-6	
Black, sulphurous carbonaceous shale with entomostraca		6	
Oil shale of inferior quality		6	

This section occurs within the Upper Oil Shale Group of the Calciferous Sandstone Series, and towards the top of that Group. Kennedy (1943, p. 12) observed the chert band to contain petrified plant remains and considered that it replaced the normal position of the Two Foot Coal. The band occurs below the Raeburn Shell Bed which is exposed within the Midhope Burn and nearer Dovecotes Farm. Stratigraphically the horizon appears to lie within the Bollandian Stage of the Lower Carboniferous and possibly within the lower part of that stage, namely P_1 . Such a reading of horizon follows Currie (1954, p. 531) and depends upon the correlation of the goniatite-rich Fordell Marine Band of Fife, with a horizon near to that of the Raeburn Shell Bed. Currie (1954, p. 533) also pointed out that corroboration of such correlation follows from the occurrence and range of *Posidonia becheri*, which reaches a maximum in the higher Basket Shell Bed. The latter horizon by analogy with the local maximum in the north of England would indicate Zone P_{1b} . The chert band probably occurs within P_1 , possibly near the base of that zone, and is thus of Upper Viséan age.

Mode of occurrence of the chert. The upper layer of the chert has a nodular or mamillated surface, the hollows of which are filled by a black laminated coaly shale of very irregular distribution. The higher or brown chert is remarkably pure and contains well-preserved macroscopic plant remains; it is principally from this part of the chert that the organic remains have been obtained. The lower black and banded chert is organic rich but impure, and evidence of replacement of the original sediment by chert is seen in thin-section and will be described elsewhere. The combined evidence supports Kennedy's opinion (p. 12) that the horizon marks the position of the Two Foot Coal Seam. It points to penecontemporaneous inundation of a peat or soil by siliceous waters prior to diagenesis of the underlying sediment. Whether the upper band of the chert contains precisely autochthonous plant material, or whether that material was introduced by the invading solutions cannot be ascertained. However, much of the plant material could not have been transported far in view of the delicate structures preserved. The material represents the decayed remnants of a terrestrial flora in which the processes of decay were arrested by saturation in the siliceous water and subsequently preserved in the chert. The methods of disintegration, the various stages reached, and the selective action of parasitic or saprophytic attack upon a variety of organic ingredients provides important evidence of the microbiological agents concerned with the eventual disintegration of organic material. At the same time, some appreciation of the intermediate and final products of decay is of inestimable value in a consideration of the organic detritus which would be swept from a soil or peat into the depositional areas of the oil shale accumulation.

The mode of occurrence of the chert and state of preservation of the organic material is reminiscent of the remarkable Rhynie chert of Aberdeenshire described by Kidston and Lang (1921); there is, however, no detailed evidence of peat succession and inundation such as occurred at Rhynie. The wide range of microfossils, including spores and pollen, wood cells, algae, fungi, and presumed bacteria, together with fragments of insect remains and possible protozoa, suggests the presence of a very shallow water cover such as a pool or pond at the time of inundation.

Preservation of plant material. The organic material is preserved within the chert with no sign of appreciable chemical alteration of the spore coat substances. Such a conclusion is suggested by examination of thin-sections, and demonstrated by the ease with which the organic matter can be chemically released by hydrofluoric acid. There is little or no subsequent alteration of the material by bituminization or coalification processes, such as would lead to darkening of colour or disruption of structures. Consequently it has been unnecessary to subject the material to maceration techniques other than that involving hydrofluoric acid digestion; therefore the difficulties of partial or selective destruction of some material in attempts to clear the remainder have been avoided.

Chert provides the best possible medium for the preservation and study of microbiological remains. It is homogeneous and its hardness prevents compression. The relative insolubility, and the unjointed and non-porous character of the rock, preclude the introduction of a microbiological population by groundwater or surface solutions. Likewise, it is resistant to weathering and erosion and prevents the subsequent introduction of those microbiological remains associated with rock weathering and disintegration.

Techniques of study. The upper brown or grey chert was cut into a rectangular block and thus freed from the possibility of surface contamination. Smaller slices from this block

were placed in polythene containers to which 40 per cent Analar hydrofluoric acid was added. A light-brown sludge settled on to the base of the container from which the hydrofluoric acid was removed by repeated dilution with distilled water. This was carried out manually at high acid concentration, and later by means of a suction pump using an inverted micro-porcelain filter until acid reaction was negligible. The filter was attached to a suitable cover and set at a constant level within the container, thereby causing a minimum amount of mechanical movement in the organic material and preserving detailed structures. The organic material, taken direct from the polythene container, was mounted in glycerine jelly while still moist. Since the difference of refractive indices between the material and mounting medium was sufficient to provide good resolution of detail at high magnifications, the majority of the slides were thus prepared. Some of the organic material was stained with safranin or Cotton Blue with the original objective of improving resolution of detail. However, the material proved to be selective in its absorption of stain and particularly so with safranin, and this selectivity provided an initial basis for the recognition of related but scattered organic components; some remains in the slides were avid in their absorption of Cotton Blue. Concurrently with examination of these mounts, the study of thin-sections served to demonstrate the presence of similar material within the chert, but the mounted isolated organic material possessed considerable advantages for study of detail. The mounts have been prepared for a number of years and in some instances a series of photographs taken of the same object. In no single case have there been any changes in the nature or distribution of the microbiological remains associated with the spores and pollen described in this paper. Under these circumstances the author is confident that an indigenous microflora was responsible for the saprophytic attack, and that such studies can be conducted with advantage, particularly when chert is the parent rock.

THE MICROBIOLOGICAL ATTACK

The various forms described are all characterized by a prominent, dark, and relatively thick cell wall which encloses colourless or pale-yellow contents of high refractivity. The commonest forms are spherical cells of the coccoid type which range in size from 0.75μ to 1.5μ , but a frequent modification provides larger ovoid cells which reach $1-2\mu$ on the longer axis.

The cells may occur singly or in pairs of either rounded or ovoid forms, and this arrangement is usually in the 'end-on' position when the appearance resembles the diplococcoid organization. Occasionally a T-shaped grouping of three cells is observed, but more commonly an irregular grouping of the cells results. Increase in the number of spherical individuals in the 'end-on' position forms a chain which resembles the streptococcal organization. The presence of predominantly ovoid or elongate cells in a linear arrangement forms a beaded filament. The latter may be short ($2-3\mu$) or much longer ($10-20\mu$) and occasionally show lateral bifurcation; the termination of such a filament is marked by a highly refractive and larger spherical cell, but there is no clear evidence of septation. Rod-shaped forms ($2-3\mu$) resembling bacilli in appearance are present; these do not show a beaded structure and may possess either bluntly rounded ends or swollen terminations. While straight forms are more common, simply curved examples have been observed.

Filaments with well-defined parallel walls and resembling hyphae in appearance vary from 0.75μ to 1.5μ in thickness and may be straight, flexuous, or with polygonal, curved, or concentric arrangement, and vary considerably in length. Branching of the filaments is a common feature and the angle of bifurcation most variable from acute to right-angled and obtuse. At the point of bifurcation there is usually some swelling and the point is generally marked by the appearance of a spherical cell. Occasionally single swollen vesicles may occur along the length of a filament, and many filaments end in a beaded structure or are represented by a beaded filament at certain points. No evidence of septation has been observed in any of the filaments examined.

Organization of attack. The small spherical cells are commonly randomly distributed, but they may show some orientation which follows the structure of the host material. When this occurs their form becomes ovoid and the long axis of the cell lies in the orientated direction. Under these circumstances pairs of cells in the 'end-on' position result, and the eventual linear arrangement of elongate cells gives rise to a beaded filament which possesses a prominent orientation. The filaments commonly show a similar orientated relationship, particularly when they are in part beaded or are in close association with beaded filaments. However, when the filaments are particularly well developed they may indicate an independence of structural orientation.

The considerable diversity of elements may suggest more than one kind of organism to be concerned with the attack. However, the similarity in size and appearance, and the continued association of all these elements, point to a single organism exhibiting various stages of vegetative development and which may be observed on the several regions of the same spore. Modification of the host material following upon changes in the degree of attack may lead to changes in the vegetative form of the attacking organism at a given point. In this manner the incidence of attack by coccoid or ovoid cells may lead to the presence of beaded filaments and finally give rise to filaments. The latter in turn may produce beaded filaments or fragment into cocci when absorption is completed. Some supporting evidence occurs in cases where well-defined filaments cross areas of totally destroyed exine, they become beaded in part and possess large terminal spherical cells.

The biological affinity of the attacking organism is in doubt; morphologically it might be similar to certain bacteria, actinomycetales, or fungi. The filaments respond only faintly to staining and are merely tinted with Cotton Blue. From the evidence presented in this paper it is impossible to decide on the parasitic or saprophytic nature of the attack. Nevertheless, the presence of this or a similar organism on a wide variety of organic material, such as could only be brought together as a result of continued processes of decomposition, suggests the action to have been saprophytic.

This saprophytic attack upon various groups of miospores is described below. In some instances it has been possible to follow the attack from its incidence to its completion by selecting spores (of the same genus) which clearly show a progression of events. In this manner some degree of selectivity of the saprophyte upon the host is demonstrated, and the structural features of the various spores are shown to exert considerable control over the distribution and manner of attack; the organism follows these features to a great extent. In spores where there is no marked structural differentiation the ornament of the exine, particularly in thick-walled forms such as *Convolutispora* (p.364), plays an important part in controlling the distribution of the attack and the manner in which it is carried out.

SYSTEMATIC DESCRIPTIONS

Fungi incertae sedis

The organism in some of its characteristics bears resemblances to the small saprophytic fungus referred to by Renault (1900, p. 334) as *Anthracomyces cannellensis* and recorded from a variety of Carboniferous and Permian rocks. Renault considered this fungus to be closely related to the groundmass of the carbonaceous rocks and to be generated within this medium, spreading on to the other recognizable organic fragments contained within it. His insistence upon the rôle of this fungus as a means of producing organic detritus under certain conditions is reflected in the specific name *A. cannellensis*. The fungus was described as forming a small plant 5–6 μ in height, with straight sinuous or branching filaments 2–2.9 μ long and 0.85 μ wide. Short branches were noted to end in a spherical conidium. The propagation of individual plants was believed to form a felt which spread over the organism attacked.

Renault did not provide a systematic diagnosis of generic characters or give a specific definition, and no reference was made to the method or organization of the attack by the fungus. Considerable difficulties are involved in interpreting the very general and much-restricted account of the organism as given by Renault, especially since the present work has shown a very much wider range of variation on both sides of what might be considered the mean characteristics referred to by Renault. As a result it is proposed, at a later stage in these studies, to emend the genus *Anthracomyces* and to restrict its use for the reference of similar saprophytic fungi present in the disorganized organic matter of carbonaceous rocks. The present organism, in view of its considerable morphological variation and the close relationship of its organization with the structural features of the spores, is referred to a new genus *Palynomorphites*. There may well be overlap between the new genus *Palynomorphites* and the forms to be included in the emended genus *Anthracomyces*, but at the present stage of the investigations it is necessary to refer to form genera.

Genus PALYNOMORPHYTES gen. nov.

Type species. *P. diversiformis* sp. nov.

Diagnosis. Single coccoid, ovoid, or bacilli-like cells, or aggregates of such cells; beaded or non-beaded filaments, aseptate. 0.75 μ to 1.5 μ in cross-section and occurring on or within fossil spores.

Palynomorphites diversiformis sp. nov.

Holotype. Plate 54, fig. 13; fungal elements investing a specimen of *Densosporites*.

Type locality. Slide Mb/Ch/3/4/907260. Chert Band, Midhope Burn, Upper Oil Shale Group of Calciferous Sandstone Series (Scotland), Upper Viséan, P₁ subzone.

Diagnosis. Coccoid or ovoid cells 0.75 μ to 1.5 μ arranged in a linear 'end-on' position, and associated aseptate filaments 0.75 μ to 1.5 μ in width.

Description. Cell walls dark and well defined; cell contents highly refractive, colourless or pale yellow. The filaments may be straight, flexuous, or curved, or exhibit simple bifurcation to produce a rounded or reticulate pattern. At the point of bifurcation a rounded cell is present and filaments may terminate in a swollen rounded cell.

ERRATUM

Palaeontology, Volume 6, part 2, page 356, line 27:

For 'Genus PALYNOMORPHYTES gen. nov.'
read 'Genus PALYNOMORPHITES gen. nov.'

Coccoid cells may occur alone as on *Punctatisporites*, Plate 55, fig. 10, or be associated with beaded filaments only as on *Punctatisporites*, Plate 56, fig. 2c. Filaments both beaded and non-beaded may occur in close association and of very variable length. They may occur together or singly without the normal association of coccoid cells. These features are exemplified by *Lycospora*, Plate 54, fig. 11.

Comparison. *P. diversiformis* sp. nov. in certain characteristics bears resemblance to *A. cannellensis* Renault (1900, pl. 22, figs. 4-10; text-fig. 24) but *A. cannellensis* Renault (1900, p. 334) was defined as 'a plant 5-6 μ high, with straight branching or sinuous filaments 2-2.9 μ long and 0.85 μ wide'.

DESCRIPTION OF MICROBIOLOGICAL ATTACK ON VARIOUS MIOSPORES

Schulzospora (Pl. 54, figs. 1, 2, 3).

The grain of *Schulzospora* consists of a circular central body, with an enveloping saccus which may be attached to the proximal polar region of the central area.

The three grains illustrated represent the varying degrees of saprophytic investment observed for this genus. Thus Plate 54, fig. 1 indicates incipient attack by isolated irregularly distributed coccoid cells, while in Plate 54, fig. 2, with a greater intensity of action, some pattern of distribution becomes apparent. With the heavier concentrations near the equatorial margins of the saccus, and in a region near the junction of the saccus with the central area, there is a tendency to the formation of chains of cells and beaded filaments. On the saccus alone there is little definite arrangement but many filaments cross on to the region underlain by the central area where a distinct radial arrangement is followed. Many of the filaments branch or coalesce to enclose irregularly shaped polygonal or rectangular areas of pitted or thin exine. In some cases the proximal exine has been removed from the polar region of the central area as at Plate 54, fig. 2. A high concentration of saprophytic material around the junction of the saccus and central area and over the surface of the latter is demonstrated by Plate 54, fig. 3. The concentric organization of the disturbed wall substance appears to have resulted from attack in depth which has totally disorganized the saccus covering and the exine of the central area. Some part of the disorganized infected exine was partly moved from the body of the spore during mounting and is seen (Pl. 54, fig. 3) to consist of coccoid cells and beaded filaments.

Other examples of this type of spore were noted in which the central area was either partly destroyed or even absent. These may indicate the ultimate effects of the form of attack upon the saccus and central area, or alternatively the partial destruction of the enveloping saccus may lead to release of the central body. There appears to be some relationship between the form of the spore and the resulting organization of attack. Thus the polygonal or rectangular habit of the filaments enclosing the pits on the flatter polar region of the central area gives place to a radial orientation of elongate cells and beaded filaments on the sloping sides of that area. The fringes of the saccus show a less definite arrangement over their flattened surface, but the concentric orientation of elongate cells followed in Plate 54, fig. 3 appears to be directly related to the presence and influence of the central body. The dark region on the central area of Plate 54, fig. 1

consists of a dense mass of very thick-walled dark-brown cells of a type differing from those under present description.

Lycospora (Pl. 54, figs. 4–12)

The illustrated spores represent common forms in the preparations and they have been selected to show the varying degree of saprophytic attack and its manifestations on the various structural units of the spore. There is a close correlation between areas of microbiological action, the nature and orientation of the attacking cells, and the structure of the spore. Demonstration of this relationship follows from a study of proximal and distal surfaces, and as a result of separate consideration of the central area and cingulum. The latter is further subdivided into the thickened inner region (crassitudo) and the outer equatorial flange.

Plate 54, fig. 4 depicts in proximal view a typical *Lycospora* with granular ornament and carrying incipient attack over its surface by isolated or small groups of coccooid cells. A concentration of elongate cells and beaded filaments with a linear orientation occurs along the dehiscence slits of the central area. The crassitudo carries a similar concentration of cells orientated in a concentric manner.

The central area. On the proximal surface along the margins of the triradiate marks, the concentration of linearly orientated cells, and the subsequent development of beaded filaments are characteristic but variable features. Plate 54, fig. 4 depicts the earlier stages of this development, which is continued in Plate 54, figs. 5 and 6. The spores of Plate 54, fig. 10, and particularly Plate 54, fig. 11, illustrate the eventual production of relatively thick-walled filaments. Each proximal intertectal segment carries independently orientated elongate cells or beaded filaments traversing the exine between the triradiate marks in broken or continuous lines, as illustrated by Plate 54, figs. 5, 6, 8. Some of the filaments either branch or coalesce to enclose rounded, rectangular, or polygonal areas of altered exine, as shown by the circular pale areas of Plate 54, fig. 5a.

The absence of haptotypic features on the distal surface of the spore leads to a different organization of attack. In the initial stages this consists of rounded coccooid cells which

EXPLANATION OF PLATE 54

All figures are of specimens from the Chert Band, Midhope Burn, Upper Oil Shale Group of the Calciferous Sandstone Series (Scotland). Upper Viséan, P₁ subzone. Magnification $\times 750$ unless otherwise stated. Slides all labelled M.B.Ch.

Figs. 1–3. *Schulzospora* sp. 1, 3/5/726.334, proximal surface. 2, 3/7/793.200, proximal surface. 3, 3/3/776.341, distal surface.

Figs. 4–12. *Lycospora* sp. 4, 3/7/712.260, proximal surface. 5, 3/6/779.403, proximal surface; a, rounded and polygonal areas of altered exine on central body. 6, 3/6/803.360, proximal surface. 7, 3/6/810.247, distal surface with reticulum of filaments. 8, 3/6/776.295, distal surface; a, single large lumen; b, concentrically orientated elongate cells and radial filaments on the equatorial flange. 9, 3/6/730.256, distal surface, $\times 1500$. 10, 3/6/766.290, proximal surface. 11, 3/6/811.230, proximal view of 'Palynomorphites pseudomorph', $\times 1500$; a, fragments of the equatorial flange with filaments spreading from the annular zone. 12, 3/7/690.322, distal view, $\times 1500$.

Figs. 13–17. *Densosporites* sp. 13, 3/4/907.260, distal surface. Type of *Palynomorphites diversiformis* gen. et sp. nov. investing distal surface of *Densosporites* sp., $\times 1500$. 14, 3/8/805.188, distal surface, $\times 1000$. 15, 1/4/798.140, distal surface. 16, 3/5/750.197, presumed distal view, concentric arrangements of filaments within annular region, $\times 1500$. 17, 3/5/782.166, presumed proximal view.

are either randomly distributed or show a very general concentric organization, e.g. Plate 54, fig. 8. The development of elongate cells, beaded filaments, and short true filaments (Pl. 54, fig. 9) results in the formation of irregular areas from which the exine has been destroyed; a single lumen is shown in Plate 54, figs. 8*a* and 9. The eventual pattern of attack for the distal surface is represented by Plate 54, fig. 7, in which the surface of the central area is represented by a reticulum of filaments.

The Cingulum, thickened inner zone (crassitudo). One of the most remarkable areas of investment is the thickened annular ring of exine concentric to and bordering the central area of the spore. Incipient action on this region (Pl. 54, fig. 4) is represented by rounded or elongate coccoid cells orientated longitudinally in a concentric manner. With more severe attack prominent filaments lie within the structure, and their strong concentric orientation is particularly well illustrated by Plate 54, figs. 5, 7, 11. Prominent vesicle-like swellings give rise to filaments which branch on to or into the central area of the spore, particularly with respect to the distal surface (Pl. 54, figs. 7, 12), but also at some points on the proximal surface (Pl. 54, fig. 11). Other filaments radiate from this region into the flange area towards the equatorial margin of the spore, and are seen in Plate 54, figs. 11*a*, 8*b*.

The Cingulum, equatorial flange. This region extends from the outer area of the thickened zone to the equatorial margin of the spore and consists of a double layer of thin colourless exine. The radiating filaments referred to above cross the flange and either end in a spherical vesicle at the equator of the spore or are connected with beaded filaments developed there. The equatorial margin is often markedly indented and carries concentrically orientated elongate cells and filaments, e.g. Plate 54, figs. 4, 8*b* and the lower equatorial margins of Plate 54, figs. 5, 6, 7. The flange is often much reduced in width and may be absent.

Plate 54, fig. 4 illustrates incipient attack on the equatorial flange by isolated coccoid cells with some radial and concentric filaments. The area of the flange is often reduced by increased microbiological activity upon its equatorial margin, e.g. Plate 54, figs. 5, 7, 8, but equally severe action also takes place from the inner margin of the flange at a stage when the attack on the thickened inner zone (*crassitudo*) is well defined. Thus Plate 54, figs. 5–8 show a colourless and irregularly patterned area from which the exine of the inner margin of the flange has been removed, due either to the concentration of radial filaments or, more likely, to the absorptive effect of the concentric filaments in the neighbouring annular zone. This destruction of the inner flange exine is due to microbiological action, and not to mechanical effects since the remaining flange exine is entirely isolated from the central body of the spore, except at those points where the radial filaments which cross this area act as connecting links. In Plate 54, figs. 5, 6, 8 the filaments alone hold the remainder of the flange to the body of the spore. Such a fragile connexion serves to emphasize the importance of microbiological destruction of the external border of the flange, for it is most unlikely that the apparently eroded configuration of the external margin would result from mechanical disintegration without disrupting the entire flange structure. The absence of a flange from parts of Plate 54, fig. 6, its almost total absence from Plate 54, figs. 10–12, the presence of delicate filaments at the present flange margins of Plate 54, figs. 6, 10, 11, indicate disintegration of the flange to be principally due to microbiological action, and not to mechanical deformation.

The remarkable specimen illustrated by Plate 54, fig. 11 indicates the essential unity of the microbiological attack in its later organization, to produce a 'Palynomorphites pseudomorph' of *Lycospora*, represented by the filaments developed in the thickened inner cingulum region and along the triradiate marks. The exine from the central area has been almost completely removed, while mere fragments of the equatorial flange remain (Pl. 54, fig. 11a). The severity of this attack is remarkable, and the preservation of such a delicate structure indicates the action to have taken place after settlement and with little or no subsequent mechanical transport. The most frequently occurring forms exhibiting advanced stages of attack are shown (Pl. 54, figs. 10, 12); where the equatorial flange has been removed and a well-defined triradiate attack has developed, the remainder of the spore breaks up into three triangular segments. These isolated segments, bounded on one side by concentric filaments and with linear filaments along two other tapering margins, are common ingredients of the preparations; they may contain remnants of partially altered original exine.

The attack on *Lycospora* is very clearly controlled by the structural features of the spore. The order of this attack is less clearly defined; it is somewhat variable in the relative time of onset and in the degree of severity on or within the various areas of the spore. The effect of the microbiological action is to reduce partially or completely the equatorial flange, to destroy the exine of the central body, and to cause break-up of the spore into segments. Where the development of filaments has been particularly strong a 'pseudomorph' of the spore results.

Densosporites (Pl. 54, figs. 13-17)

The illustrated spores represent common forms of this genus in the preparations and are selected to indicate both the methods of microbiological attack and its organization and relationship to the structure of the spore. The method of attack is very similar to that described for *Lycospora*, and since the structure of the two spores is essentially similar this is to be expected. The weaker development of haplotypic features in *Densosporites* as compared with *Lycospora* does not lead to such well-differentiated features of attack on the proximal surface of the former. In many cases the action was so severe that recognition of the two surfaces of the spore was a matter of considerable difficulty. For descriptive purposes the following regions of the spore are considered: central area and cingulum, (a) inner thickened zone, (b) outer equatorial flange.

Central area. Plate 54, fig. 13 indicates the elements which constitute the basis of the investment. They consist of coccoid cells and elongate bacilli-like fragments in association with beaded filaments and short thick-walled branching filaments often carrying spherical terminal vesicles. The filaments may be straight or curved and towards the margin of the central area are somewhat radially directed from the inner thickened zone of the cingulum; they appear to originate from dense filaments within this zone. The result is a loose reticulum of filaments which produces an overall concentric pattern of pentagonal to polygonal lumina. Within each lumen the exine has been either partially or totally absorbed or destroyed. Plate 54, fig. 14 indicates a completely reticulate distal surface with partially absorbed exine, while in Plate 54, fig. 15 fragments of exine are only present around the margins. Some filaments still retain the elements of reticulate patterning and preserve filamentous connexions across the destroyed middle portion of the

central area. The eventual result of microbiological action on the central area is to destroy it completely, as shown by Plate 54, fig. 16.

Cingulum, inner thickened zone. The dense brown region which represents an inner thickened and annular zone of the cingulum is the most heavily invested part of *Densosporites*. Upon and within this structure the elements of microbiological attack form an anastomosing and interweaving bundle of concentric cellular 'tissue' which completely fills this annulus. This organization is particularly well seen in the spores (Pl. 54, figs. 13, 14, 16). At certain points, beaded filaments proliferate into thicker masses from whence arise other filaments which either pass into and over the central area of the spore or extend into the equatorial flange as far as the present equatorial margin.

Many spores which show an advanced stage of attack upon this feature (Pl. 54, figs. 15, 17) exhibit some degree of disorganization within the concentric structure at certain points. There is a tendency for the filaments to be replaced by swollen masses of coccoid or elongate cells, which occur in dense groups without any particular orientation. The break in outline shown by Plate 54, fig. 17 coincides with such an area and is likely to coincide with the position of a trilete ray affecting the structure of the inner zone. The eventual result of the attack is to break the thickened annular zone into fragments which, by the concentric organization of filaments, can still be recognized in the preparation as fragments of *Densosporites*.

Cingulum, outer equatorial flange. Where the flange is reasonably complete there is little significant orientation of the attacking cells. Thus Plate 54, fig. 13 carries coccoid cells and occasional beaded filaments occur at various points upon the flange. With a greater degree of investment filaments spread from the annulus in a general radial direction towards the equator of the flange; these are well seen in Plate 54, figs. 13, 15-17. The fretted nature of the equatorial margins (Pl. 54, 15-17) is governed in part by the position of filaments emanating from the inner thickened zone. At the same time the existing margin of the spore is marked by elongate cells and beaded filaments which are not continuous, but which show a concentric orientation (Pl. 54, fig. 13). Thus in part, the attack on the equatorial flange also takes place from its outer margin; its absence at some points and partial representation at other points in Plate 54, figs. 15-17 is principally the result of biological absorption rather than mechanical disintegration.

While the attack on *Densosporites* is mainly controlled by the structural features of the spore body, the order of this attack on the various features is less clearly known. The inner thickened zone of the cingulum may be preferentially selected and rapidly invested with either concomitant or subsequent spreading of filaments into neighbouring regions of the spore. Alternatively, the attack may be more widespread initially, but, due to the rapidity of growth within the annulus, the organization there outstrips that at other places on the spore. The central area is severely affected at an early stage and its entire removal may be brought about before major changes are effected in the equatorial flange. The latter may be partly or entirely removed, and when this coincides with the removal of the central area a 'Palynomorphites pseudomorph' of *Densosporites* remains, which consists of a brown mass of concentric filaments representing the inner thickened zone or annulus of the cingulum as shown in Plate 54, fig. 16. A comparison of the 'pseudomorphs' of *Densosporites* and *Lycospora* emphasizes the difference in structure between

the two spores, and illustrates the part played in structural control by the trilete rays. The eventual break up of the 'pseudomorph' after *Densosporites* into fragments completes the biological disintegration of this type of spore.

Leiotriletes (Pl. 55, fig. 1)

Plate 55, fig. 1 illustrates the proximal surface of a thick-walled yellow resinous spore with broadly rounded apices and slightly concave sides. While the exine on the proximal surface is present and reasonably complete, that of the distal surface has been partially destroyed. The microbiological attack on this spore appears to be located in two main regions, (a) near the equatorial margin, (b) along the triradiate structure.

Near the equatorial margin. The body cavity near the equatorial margin carries beaded filaments which anastomose but in general follow the spore outline; their beaded character is visible at several points near the right-hand margin of Plate 55, fig. 1. That this feature is not to be confused with an optical effect is demonstrated at Plate 55, fig. 2, where, after following the equatorial outline, a prominent filament curves into the centre of the spore. There, in conjunction with a filament which has followed a triradiate ray, it encloses an elliptical area of pale-yellow partially absorbed exine.

Along the triradiate structure. The broken wall of exine following this structure is accompanied along part of its course by isolated coccoid and elongate cells, and beaded and non-beaded filaments. Occasionally, beaded filaments with swollen terminal vesicles branch on to the triradiate segments and enclose the elliptical areas of pale partially absorbed exine referred to above. The characteristic form of the beaded filament and terminal vesicle is well seen at Plate 55, fig. 1b.

Leiotriletes (Pl. 55, figs. 2-5)

The illustrations (Pl. 55, figs. 2-4) represent an advanced stage of investment upon a thick-walled resinous triangular spore possessing blunt or flattened apices and concave

EXPLANATION OF PLATE 55

All figures are of specimens from the Chert Band, Midhope Burn, Upper Oil Shale Group of the Calciferous Sandstone Series (Scotland), Upper Viséan, P₁ subzone. Magnification $\times 750$ unless otherwise stated. Slides all labelled M.B.Ch.

- Figs. 1-5. *Leiotriletes* sp. 1, 3/6/731.245, proximal surface; a, curved filament partly enclosing elliptical area of partially absorbed exine; b, beaded filament with swollen terminal vesicle. 2, 3/7/665.289, distal surface taken with ground-glass filter. 3, Same spore, proximal surface taken with ground-glass filter. 4, Same spore, distal surface in ordinary light illustrating details of attack. 5, 3/6/728.245, distal surface, $\times 1500$.
- Fig. 6. *Granulatisporites* sp., 3/7/677.312, distal surface with view of underlying triradiate mark, $\times 1500$; a, beaded filaments surrounding an area from which the exine has been partially removed; b, curved filaments enclosing areas of thin or totally absorbed exine.
- Figs. 7-9. *Convolutispora* sp. 7, 3/6/765.248, proximal surface, $\times 1500$. 8, 3/5/826.250, presumed distal surface, focal plane slightly below equator of spore to show surface detail, $\times 1500$. 9, 3/10/731.170, surface unknown, advanced stage of attack with well-defined and branching filaments.
- Figs. 10-12. *Punctatisporites* sp. 10, 3/11/790.179, proximal surface, $\times 1500$. 11, 3/7/784.169, proximal surface, partial investment of the surface of the spore by coccoid cells and marginal filaments, $\times 1500$. 12, 3/10/768.192, distal surface, coccoid, paired cells, chains of cells, beaded filaments on the surface.

inter-radial margins. The distal and proximal surfaces, taken with a ground-glass filter in order to illustrate major features, are represented by Plate 55, figs. 2, 3 respectively; Plate 55, fig. 4 represents the distal surface of the same spore in ordinary light.

Distal surface. The surface is marked by coccoid and orientated elongate cells, beaded and non-beaded filaments, all arranged in a general concentric manner around areas where the exine is absent. These areas are illustrated by Plate 55, figs. 2, 4 and although the distal exine has been entirely removed from most of them, thin fragments remain nearer the margins of the spores. The attack appears to result from the establishment of isolated centres and to spread outwards, eventually producing a reticulate pattern. The margins of the lumina in Plate 55, figs. 2, 4 are formed partly by filaments, but also in part by ridges of incompletely destroyed or unattacked exine. The remaining exine may represent a thicker part of the spore wall such as would be the case if the original spore exine was differentially ornamented; strong features at the equatorial margin of the spore suggest this possibility. It is evident that the microbiological action has destroyed well-defined areas of exine so that either an original structure has been emphasized by partial destruction of the exine, or a reticulate pattern has been created by the attack and is now represented on the distal surface.

Proximal surface. The method of degradation on this surface is essentially similar but for the presence of haptotypic features. Between the thickened exine associated with a triradiate mark and lip and the equatorial margin along the left-hand side of the spore the exine has been removed from one continuous vacuity; a similar feature also marks the right-hand side of the spore. However, in the upper segment the exine between the triradiate structure and the equatorial margin is more complete and contains smaller well-defined vacuities which produce a reticulate pattern. The indented marginal form of the larger vacuoles indicates a more advanced stage of destruction, whereby the intervening exine which formed the margins of the smaller lumina has been destroyed, leading to coalescence into one larger vacuity.

The evidence provided by this thick-walled resinous spore is of particular interest since microbiological action on both surfaces of the same specimen is represented. It is principally superficial with independent action on the two surfaces and which initially leads to destruction of exine from circular or polygonal areas, with the eventual formation of large, elongate vacuoles. The thickened exine along the triradiate mark is effective in restricting the organization of the attack on the proximal surface, but that on the distal surface is not so restricted. It may to some extent be controlled by other factors such as an original thickness differentiation or material differentiation of the exine. A further and similar spore (Pl. 55, fig. 5) emphasizes the features of the attack described, and depicts clearly the nature of the organism responsible. Very little of the original exine remains on the body of this spore. The spores described represent to a great extent 'skeletons' of microbiological decay, and differ in important respects from the 'pseudomorphs' of *Lycospora* and *Densosporites*. Principally they differ in the facts that no major structural elements of the spore are missing, and that some part of the skeleton consists of original exine which preserves the spore form. The 'skeleton' may break down further into fragmentary remains; the thick rounded radial extremities of these spores are preserved in the preparations.

Granulatisporites (Pl. 55, fig. 6)

The distal surface is represented in the focal plane of the illustration, and the triradiate mark of the proximal surface is visible beneath it. The spore is much compressed, has broadly rounded extremities with deeply concave sides, and a thin yellow exine ornamented with granules. There is little structural differentiation of the spore body, and consequently a less well-defined distribution and organization of microbiological attack. The latter is carried out by elongate orientated cells and beaded filaments, but thick-walled filaments are present and these in particular occur within the spore body. The equatorial outline is followed, along most of its length, by prominent filaments which are particularly well developed and proliferate in the neighbourhood of the radial extremities. The upper extremity is most severely affected; there, beaded filaments arising from a marginal filament enclose a region from which the exine has been partially removed. This lighter-coloured area and its surrounding filaments are shown in Plate 55, fig. 6a. At the concave lateral margin, beaded and non-beaded filaments follow a modified course. They swing in towards the centre of the spore by means of prominent curved but irregular loops and thereby enclose areas of thin or totally absorbed exine (Pl. 55, fig. 6b) so inaugurating a coarse reticulate pattern.

Convolutispora (Pl. 55, figs. 7-9)

The spores illustrated are characterized by a very thick resinous exine, and rugulate ornament. The rugulae may either consist of irregular ridges with a rounded cross-section and protruberances (Pl. 55, fig. 8) or of flattened ridges (Pl. 55, fig. 7), and are separated by lower-lying areas. The three spores illustrated indicate the method of microbiological attack. In Plate 55, figs. 7, 8 this organization is well seen upon spores which retain sufficient original structure to warrant recognition of the genus. The spore in Plate 55, fig. 9 represents a much more advanced stage of destruction, and although the thicker irregularly distributed exine is still partially visible, reference to the spore genus is more doubtful.

The proximal surface of a spore with incipient attack is represented by Plate 55, fig. 7, where elongate cells and beaded filaments predominate but occasional thick-walled filaments occur. The distribution is very localized and follows a linear organization in the neighbourhood of two rays of the triradiate mark and a concentric direction at several points near the equator of the spore. In places the exine has been destroyed and circular or irregular perforations are surrounded by elongate cells flanking the thicker exine of the marginal wall.

Plate 55, fig. 8 represents the distal surface of a spore upon which the attack is very diversified and locally intense. The lower part of the spore is reasonably unaffected; the prominent rugulae are devoid of attached cells, but the inter-spaces between the rugulae carry coccoid cells and short beaded filaments. The right-hand margin of the spore illustrates a progressively greater intensity of investment in which beaded filaments, occurring in the hollows of the surface, produce a concentric pattern. At the upper margin of the spore, coalescence of the beaded filaments surrounding the rugulae has resulted in a linear organization of beaded filaments. The region of greatest investment is the dark area along the left-hand side of the spore, where the entire surface is covered by a fine cellular mat of elongate cells and beaded filaments which fan out in a 'ray-like' manner from darker centres. The most severe attack is located on the upper central portion of

the spore, where a red highly refractive spherical body is seen as a sphere on the plate. This appears to be a reproductive body caused by fusion of the filaments, or it is the focal point from which filaments radiate in several directions. Around this body the exine has been totally destroyed, for the light-coloured areas hereabouts are circular or polygonal vacuities, many of which have coalesced. The method of destruction of the exine is further emphasized by Plate 55, fig. 9, in which severe action has culminated in the complete removal of exine from areas in the central regions of the spore and from deep embayments into its equatorial margin. These areas are surrounded by the thicker remaining exine which carries filaments, some of which extend into and across the vacuities. With this more advanced stage significant changes are notable in the nature of the attacking organism. Thus beaded filaments give way to well-defined thick-walled and larger filaments which are straight or curved and commonly branched. Several branches may arise from or fuse in a common centre which then carries one or more small spherical vesicles or radiating groups of beaded filaments. The action is also in depth, for the bundles of filaments cross one another at lower focal planes. The overall organization produces a reticulate pattern, and at this more advanced stage of destruction the investing organism may be less seriously controlled by the structure of the remaining exine. Thus a broadly concentric organization develops in which filaments follow the spore contour and are interconnected by other radial filaments.

In thick-walled ornamented spores of the *Convolutispora* type there are no outstanding differential structural units of the spore body, and the haplotypic features are of minor importance in controlling the attack. However, the strong ornamentation produces hollows of relative protection from which centres of microbiological action could be generated; the same regions contain thinner and possibly more favourable exine for organic assimilation. The exine is therefore more rapidly absorbed with the formation of vacuities, and the rugulae isolated by this means. The resulting configuration passes from one in which the exine has been removed from smaller circular polygonal or irregular vacuities, to one of larger irregular but rounded vacuities. A 'skeleton' spore results in which both the remaining exine and the attacking organism play a part. The breakdown of the spore into a number of isolated, irregularly shaped, and thickened fragments is envisaged as the final stages in its destruction.

Punctatisporites (Pl. 55, figs. 10–12; Pl. 56, figs. 1–3)

The spores included in this genus are characterized by a circular outline, with little structural differentiation of the body except in the presence of a frequently well-marked triradiate feature. They are characterized by an infra-punctate or infra-granular exine. There is consequently little selectivity of this uniform surface for microbiological activity and a degree of uniformity pertains in distribution and organization of attack. Thus Plate 55, fig. 10 illustrates a spore generally free of saprophytic cells and which therefore exhibits the typical infra-granular exine structure over most of its surface. At one point a colony of saprophytic cells is clearly visible, which at a higher focal plane consists of orientated beaded filaments and elongate cells with a radial symmetry. The only other attack on this spore is associated with the triradiate mark, where the dark areas consist of linear chains of cells and beaded filaments. A greater concentration of saprophytic material is illustrated for the proximal surface of the spore (Pl. 55, fig. 11), where half of the surface is covered by coccoid cells often paired in the streptococcal manner. They

possess little definite or regular orientation, for while some occur as radial clusters, others towards the margin show a general orientation following the spore contour. The dark marginal area on the upper border represents a region of concentrically orientated filaments.

The complete investment of a distal surface is illustrated in Plate 55, fig. 12, where the principal elements are coccoid cells. Groups of cells with radial arrangements are found in association with cells containing two or more individuals in streptococcal arrangement, or with short beaded filaments $2-3\mu$ in length. Over the greater part of the spore the distribution presents an impression of minute reticulation. The dense marginal distribution produces a concentric pattern which eventually results in a curvilinear distribution of beaded filaments. The spore exine is severely attacked and the isolated mass of cells lying off the margin of the spore (Pl. 55, fig. 13) illustrates the elements responsible for the investment. A possible further stage of this attack is represented by Plate 56, fig. 1, in which a change in the form of the saprophytic elements is notable. While the streptococcal-like cells are still common there is a preponderance of beaded filaments and of short branching filaments $2-5\mu$ long. This development has resulted in an irregular but distinct reticulate appearance particularly evident in the central regions of the spore. This figure (Pl. 56, fig. 1) is taken at a slightly higher than median focus to accentuate the affected and partially destroyed exine, which therefore appears as white lines or areas. An overall concentric reticulate pattern for most of the spore suggests a contour control, but this is lost towards the margins. There a distinct radial distribution may indicate a change in the underlying spore exine or merely a region of originally modified spore contour.

The four spores described illustrate the increased areal degradation upon a surface which shows little differentiation. It is questionable whether the infra-granular structure of the exine exercises much control upon the organization of attack, and yet it is significant that the earliest stages of investment are by minute coccoid cells and beaded filaments only. The spores also indicate the degrees of intensity or stages of the attack, for, as the microbiological action becomes well established and the exine is made viable, there are significant changes. These result in the development of branching filaments with the establishment of a reticulate pattern and the final breakdown of the spore wall.

The spore in Plate 56, fig. 2 is referred to the genus *Punctatisporites* with some doubt, in view of the general lack of original exine visible. The investment is predominantly by elongate cells, beaded and non-beaded filaments. The latter are $0.75-1.5\mu$ wide and may be short branched forms of $2-3\mu$, or long unbranched forms $10-15\mu$ long. There is a very general concentric orientation of the saprophytic remains, particularly near the margin of the spore, where the darker regions consist of both types of filaments. Several of the filaments curve inwards towards the centre and are seen in connexion with other concentrations of filaments near the centre of the spore. There is a secondary concentric arrangement illustrated by the pale patches of Plate 56, fig. 2, and which exhibits some diversity and may represent progressive stages in the attack. Thus Plate 56, fig. 2a represents some areas of thin and altered exine upon which occasional coccoid cells and filaments remain; they are surrounded by a diffuse boundary along which occurs a concentration of orientated cells and filaments which form an incomplete concentric boundary. At Plate 56, fig. 2b the structure is larger and the exine from the upper surface of the spore has been removed. The boundary is formed by concentrically-arranged beaded

filaments and by filaments which are in connexion with well-defined thick-walled filaments traversing other areas of the spore. The structure at Plate 56, fig. 2c is surrounded for the most part by a concentric bundle of beaded filaments, the left-hand margin has suffered mechanically, and the exine is folded upon itself. The exine from the upper surface of the spore has been removed, but a part of that of the lower surface is still represented.

This organization appears to be significantly different from that described for other members of this group and appears to commence with an original cover of saprophytic material distributed in a broadly concentric pattern. Within this general pattern, localized areas have been affected more seriously than others, and the spread of the attack outwards results in a concentration of filaments around the margins. Similar features are shown around the marginal region of the spore (Pl. 56, fig. 3).

Microreticulatisporites (Pl. 56, fig. 4)

The surface of this spore carries a great number of coccoid- and streptococcal-type cells of two or three units, dispersed over the surface in irregular groups. There are, however, two regions of the spore where some organization is noticeable. Firstly, the equatorial margin is densely covered and the cells are orientated in a concentric manner and may pass into beaded filaments as near the lower border: the broken left-hand margin indicates the cellular nature hereabouts and gives little evidence of the presence of exine. Secondly, the most remarkable organization is that based on the irregularly shaped reddish-brown and resinous mass in the centre of the spore. Leading to it or from it, according to its function, is a complicated irregular system of anastomosing lines of saprophytic cells which are organized, and orientated in the direction of the main structure. The resulting pattern is the encirclement either completely or partially of areas of the surface; nearer the centre of the structure the enclosed areas are irregular but they tend to become hexagonal or polygonal in shape at some distance away. It is significant that many of the pale areas from which the exine of the upper surface has been removed are bounded by cells and filaments marking the furthestmost extensions of the structure.

The 'focus' of the system appears to be a vesicle or vegetative reproductive centre from which the attack commenced. The organization of the ensuing attack possibly bears some resemblance to that already described (Pl. 56, fig. 2), but comparison is not obvious. The meandering nature and quasi-reticulate pattern of this particular organization is symptomatic of microbiological action upon a uniform structure lacking surface ornamentation.

Knoxisporites (Pl. 56, figs. 5, 6)

The spores included in this genus and represented by the above figures have a very different appearance. The spore in Plate 56, fig. 5 is red-brown with a thick resinous exine, while Plate 56, fig. 6 represents a pale-yellow central region with a thin colourless outer zone, the exine being considerably thinner for the spore as a whole. Despite these differences, there is a similarity of structure, in that both spores consist of a central body bearing haptotypic features and surrounded by a cingulum. The latter structure is subdivided into an inner thickened annulus concentric with the central body and a thinner outer flange. This differentiation is most marked in Plate 56, fig. 6.

The attack on the heavier spore (Pl. 56, fig. 5) is restricted and simple, consisting of

coccoid cells and beaded filaments irregularly scattered over the outer flange, but with a tendency to overall concentric distribution. Locally, the coccoid cells occur in small concentric groups enclosing small circular areas from which the exine has been partially removed to provide a pitted surface, illustrated at Plate 56, fig. 5*a*. Filaments follow a discontinuous but concentric path nearer the margin of the flange and are best seen where the exine has been partially destroyed, as at Plate 56, fig. 5*b*. A much greater degree of attack is shown by the thinner-walled spore (Pl. 56, fig. 6, distal surface), and the organization follows closely upon the structural elements of the spore in a manner previously described for spores of a similar structural type, e.g. *Lycospora* and *Densosporites*.

Central body. A dense infestation of coccoid cells and filaments characterize this region; the filaments are curved or branched and, while they produce no distinctive pattern, they tend to surround circular regions from which the exine is either partially destroyed or absent as in the light areas (Pl. 56, fig. 6).

Cingulum, inner thickened zone. The darker-brown thickened zone forming an annulus around the central body is heavily attacked and both types of filaments are present as bundles with an entirely concentric orientation which follows this structural feature of the spore. At various points branching filaments spread both on to the central body and outwards over the outer flange. At two points on the lower part of the structure (shown as dark areas on Pl. 56, fig. 6) a dense mass of filaments containing swollen vesicles results in unusual expansion of the concentric structure, and a similar but smaller aggregate occurs in the opposed segment of the annulus. These masses represent a concentration of saprophytic activity at points along the prolongation of the triradiate rays and where these cross the annulus.

Cingulum, outer equatorial flange. Very little of the original exine remains and even where the equatorial margin is complete the exine is much altered. The presumed outer margin is marked by highly refractive beaded filaments (Pl. 56, fig. 6) which are often present

EXPLANATION OF PLATE 56

All figures are of specimens from the Chert Band, Midhope Burn, Upper Oil Shale Group of the Calciferous Sandstone Series (Scotland). Upper Viséan P₁ subzone. Magnification $\times 750$ unless otherwise stated. Slides all labelled M.B.Ch.

Figs. 1-3. *Punctatisporites* sp. 1, 3/11/820.315, presumed distal surface, figure at slightly higher than median focus to illustrate reticula. 2, 3/11/782.177, presumed distal surface; *a*, areas of thin and altered exine with coccoid cells and filaments; *b*, area bounded by concentric filaments, exine removed from the upper surface of the spore; *c*, area bounded by concentric filaments, exine removed from upper surface over whole area and from lower surface over part of the area (white), $\times 1500$. 3, 3/5/796.186, proximal surface.

Fig. 4. *Microreticulatisporites* sp., 3/6/710.213, presumed proximal surface.

Figs. 5-6. *Knoxisporites* sp. 5, 3/13/802.334, proximal surface; *a*, small circular pits in the exine; *b*, filaments with concentric organization. 6, 1/1/784.190, distal surface.

Fig. 7. *Auroraspora* sp., 1/4/680.161, proximal surface; *a*, alignment of attacking cells on the saccus and near the position of the triradiate mark; *b*, dark line marking present line of saccus margin.

Fig. 8. *Diatomozonotriletes* sp., 4/6/737.142, proximal surface; *a*, circular area surrounded by a filament, exine destroyed.

Figs. 9-10. *Incertae sedis*, presumed 'Palynomorphites pseudomorph', 9, 3/4/850.183, $\times 1500$. 10, 3/4/850.184, $\times 1500$.

even where the remainder of the flange has been destroyed. Other filaments arise from the region of the annulus, cross the equatorial flange radially, and are connected or fused with the equatorial filaments. A 'ghost' framework is thereby produced within which the exine may either be totally destroyed or partly preserved between the filaments. The equatorial margin has suffered from some degree of mechanical effects, but this is slight since the margins of the prominent embayments are lined with coccoïd cells and beaded filaments. Along the lower border the equatorial flange and part of the annulus have been destroyed, yet the line of the equatorial margin is preserved by a beaded filament in continuity with a well-preserved portion of the flange.

There is a remarkable similarity in the distribution and organization of this attack with that described for certain stages of attack on *Lycospora* and *Densosporites*, based as it is upon a similarity of spore structure. No other specimens indicated a more advanced stage of investment on this type of spore, and it was impossible to complete the comparison for all stages.

Auroraspora (Pl. 56, fig. 7)

The illustration represents the proximal surface of a large spore of this genus in which the focal plane is coincident with the equatorial margin of the spore. The characteristic features include a pale-yellow resinous central body carrying prominent trilete sutures. This body is enclosed by a thin-walled colourless saccus which extends beyond its periphery as a double layer of tissue uniting in the equatorial margin of the spore. The saprophytic action is directed upon the saccus and also upon the central body.

Saccus. This thin colourless membrane shows evidence of original ornamentation in the form of closely spaced granules, and the attack upon it is best seen in the outer zone consisting of the proximal and distal layers of the saccus alone. Coccoïd cells, beaded filaments, and branching filaments are common, the latter two form an irregular network of straight or curved, branching remains. The complexity suggested by Plate 56, fig. 7 is in part due to the superimposition of elements occurring on both surfaces of the saccus. There is a general radial direction in the filament distribution, and many are continuous from the marginal saccus on to its continuation over the surface of the central body. This is generally evident but particularly so where the influence of the haplotypic structures has affected the saccus (Pl. 56, fig. 7*a*). Over portions of the proximal surface the saccus has been removed from the central body by microbiological activity. Thus the greater part of the right-hand segment is free (paler coloured); the present margin of the saccus is represented by the dark line crossing the lower portion of this segment, which consists of a concentration of linearly arranged coccoïd cells and beaded filaments marking its edge (Pl. 56, fig. 7*b*).

The central body. The most prominent regions of attack are along the two margins of the triradiate ridges. The investment is principally concerned with the saccus, which is destroyed along such lines, and it extends into the exterior wing as seen along the north-east triradiate mark. The fact that this trilete mark on the central body is not accompanied by a double row of filaments follows from the destruction of the saccus along one side of this line and the retreat of its margin to the further dark line in the right-hand segment (Pl. 56, fig. 7*b*). The central body is only exposed in the right-hand segment; here its surface carries isolated cells and filaments, but no obvious pattern of distribution has

been established. While the margin of the central body carries a somewhat denser concentric distribution of elements, these are predominantly in the saccus and no unusual development is present.

The attack on this saccate spore appears to be relatively simple, and at the stage represented consists largely of the destruction or modification of the saccus. The prominent radial organization on this part of the spore may follow an original structure of the integument, either of ornamentation or radial folding. When compared with spores such as *Tenosporites*, which possess an inner thickened cingulum which is followed by annular concentric filaments, the contrast in the organization of attack on this saccate spore is well marked.

Diatomozonotriletes (Pl. 56, fig. 8)

The figure illustrates the proximal view of a typical spore of this genus characterized by a thick-walled trilete form with sharply rounded extremities and straight sides, the latter adorned by strong, pointed, spine-like processes. Attack on the proximal surface is very restricted and generally limited to the region of the trilete mark. The rays are attended by thick-walled filaments, with prominent swollen cells, which diverge from the margins of the ray on to the surrounding exine. The left-hand ray is followed by a filament which branches and recurves to enclose a small circular area at the radial extremity of the spore, from which the exine has been removed (Pl. 56, fig. 8a). Isolated clusters of cells are scattered over the surface.

Incertae sedis (Pl. 56, figs. 9, 10)

The remains represented by the above figures are common ingredients of the preparations and further illustrate the nature and association of the elements here described as *Palynomorphites*. They consist of that organism preserved in a skeletal network, and may be other examples of '*Palynomorphites* pseudomorphs' but with no indisputable indication of an original organism which may have been replaced; Plate 56, fig. 10 may possibly bear some resemblance to the 'pseudomorph after *Lycospora*'. These remains serve to illustrate the advanced degree to which microbiological action may progress under certain conditions without destruction of the evidence. The figures are of value in providing a comparative basis upon which the selection of material used in the other illustrations, indicating stages of attack, may be judged.

CONCLUSIONS

Spores of very divergent characters are invested by the organism *Palynomorphites diversiformis* gen. et sp. nov. under suitable environmental conditions. There is an organization in the nature and distribution of the elements which form the basis of the colonization or attack; this organization is not uniform but dependent either upon the major structural features or upon the ornamentation of the spore: the organism is therefore often selective in its distribution upon a given spore. The major structural features are important in controlling or modifying the organization of the attack, but in certain cases serious modification of a structural feature may result, culminating in its partial destruction or complete removal. The loss of a central body or flange, or the removal of

both structural features, exemplifies this modification as in *Densosporites* and *Lycospora*. One effect of the attack on the structural features results in the production of a 'Palynomorphites pseudomorph' of the spore in which the form of certain structural features is represented by the organism which has destroyed the original spore.

In the case of spores with few structural features and strong ornamentation, particularly that of rugulae on thick-walled spores such as *Convolutispora*, the attack is controlled by the surface ornament. The destruction of irregular or reticulate areas of the exine may follow and eventually result in the formation of a 'Palynomorphites skeleton' of the spore as in *Convolutispora* and *Leiotriletes*.

Where the spore has no marked structural features, and little or no well-defined surface ornamentation, as in the case of some forms of *Punctatisporites* described in this paper, there is little selectivity and a greater degree of uniformity in distribution results. The organization is more diverse, but tends to follow a reticulate or concentric pattern. The eventual degradation of the spore is followed by its disintegration into segments often controlled, but not necessarily so, by the haptotypic features (e.g. *Lycospora*).

A spore may be modified by the addition of *Palynomorphites* cells or filaments, and confusion with normal ornament may arise with the varied elements and organization of attack which *Palynomorphites* assumes. Thus the formation of radial, reticulate, or concentric patterns by filaments, and the absorption and pitting of the exine may severely affect the appearance of the spore.

While the attack on miospores by the agent, *Palynomorphites diversiformis*, has been established, it is not possible to provide reliable evidence as to whether this attack was preferential on certain groups of spores. All spores present show some degree of attack, and even within the same group there is wide diversity in the intensity of attack. The most commonly attacked spores are *Lycospora*, *Densosporites*, and *Schulzospora* in this order, the first two groups being most regularly and most seriously affected. Some substantiation for this statement follows from the larger number of recognizable fragments of these spores in the preparations. It is of interest to record that microbiological attack has largely destroyed wood cells; only algae of the *Botryococcus* type are less affected than the miospores.

The severity of attack on the miospores described may be regarded as unusual and possibly due to special circumstances of the environment. As described, the environment was abnormal, but similar attack by the same organism on spores isolated from other oil shales and organically rich sediments, has been noted by the writer. This has been particularly well seen where isolation by hydrofluoric acid alone has been used, or where calcareous sediments have been digested with hydrochloric acid and the organic material separated.

In conclusion, *Palynomorphites diversiformis* is not the only organism which attacks fossil spores; reference to Plate 54, fig. 1 indicates a further organism investing *Schulzospora*, and other presumed saprophytic organisms of a type similar to *Polymorphycetes* (Moore 1963).

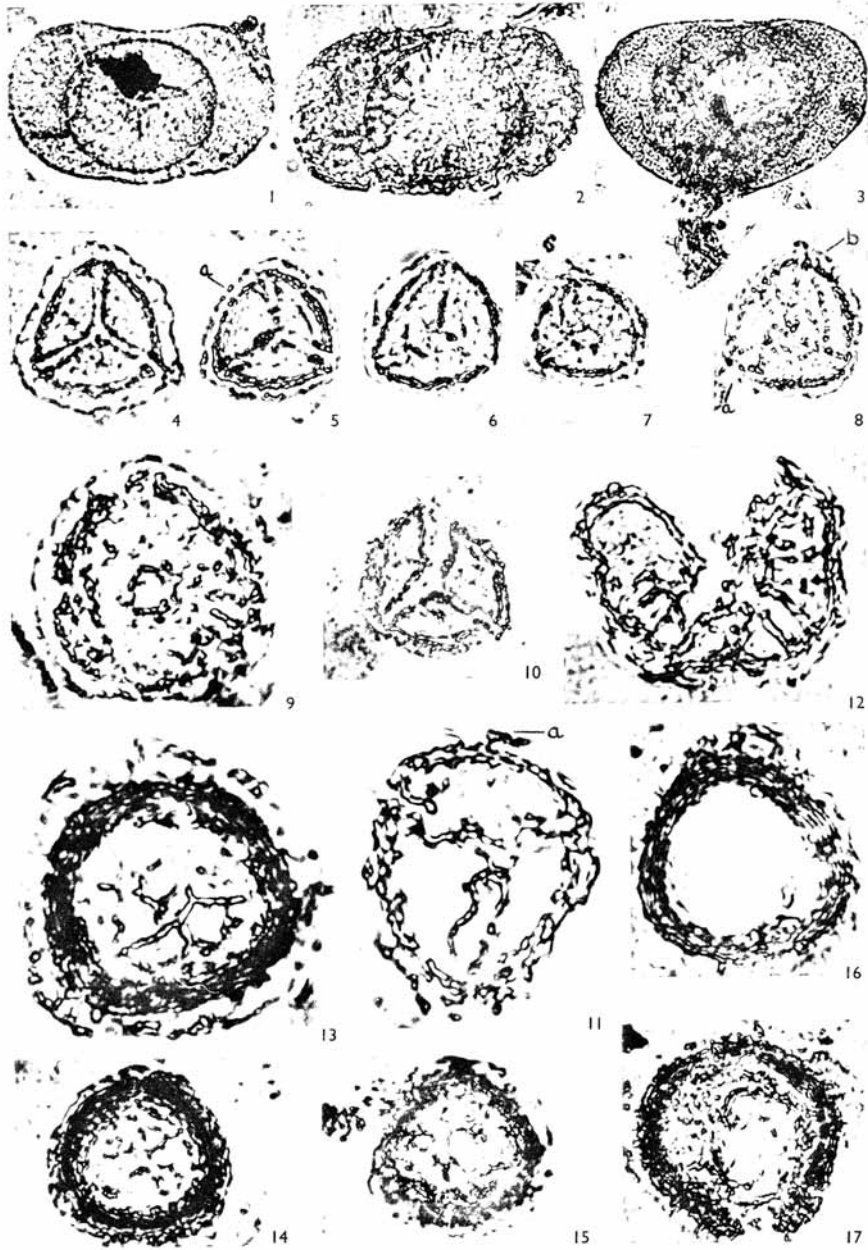
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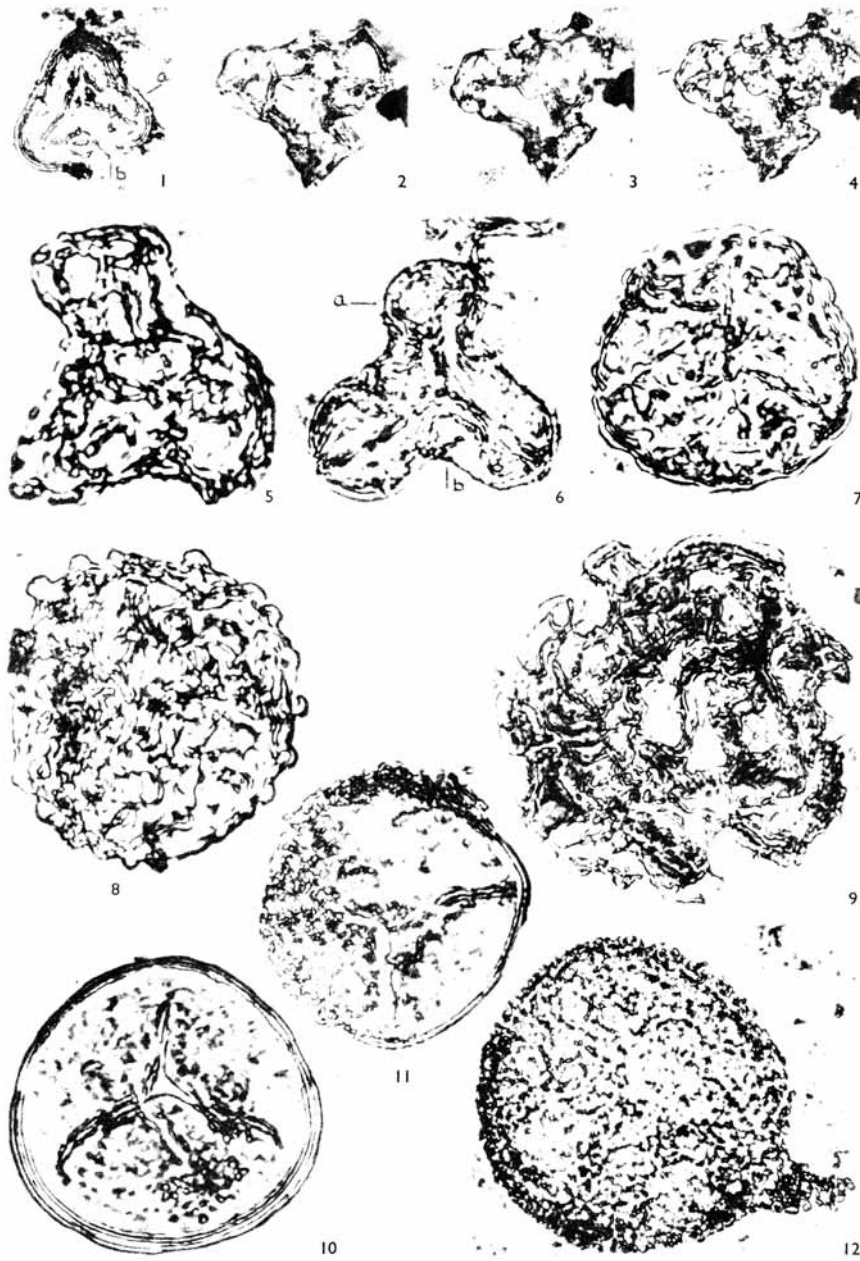
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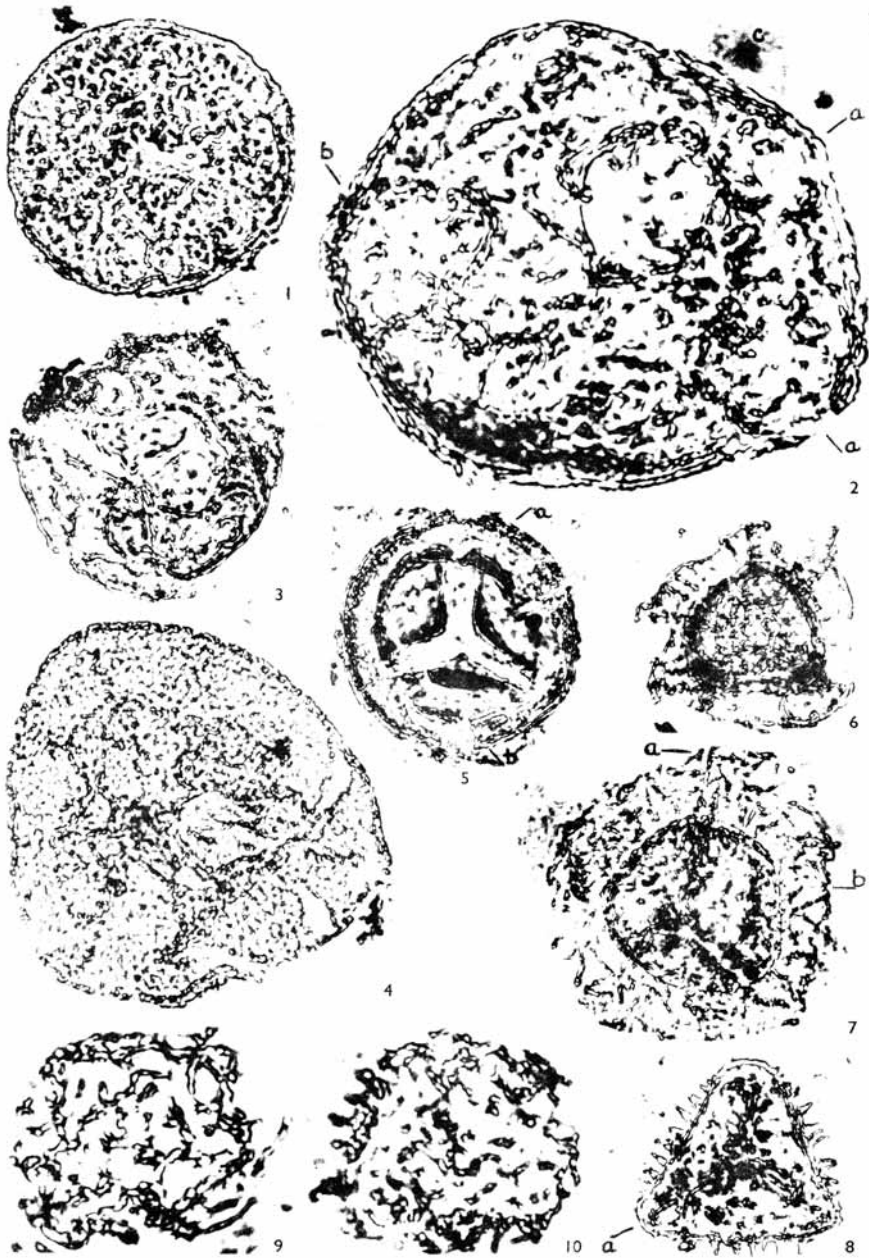
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