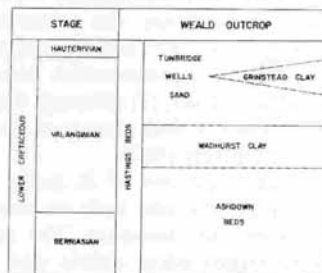


PALYNOLOGY OF EARLY CRETACEOUS SOIL BEDS AND ASSOCIATED STRATA

by D. J. BATTEN

ABSTRACT. A distinctive palynologic assemblage is associated with *Equisetites* soil beds and fragment partings in the Wadhurst Clay of south-east England. Some of the components are probably the products of a local flora which grew in or near the *Equisetites* communities. Palynologic and palaeobotanic data suggest that the communities were isolated from the 'homogeneous Wealden delta flora', probably offshore from the delta complex. New taxa have been recorded from the assemblages. *Converrucosporites venitus*, *Regresporites lophus*, *Retitriletes* sp., *Triobosporites ivanovae*, and *Admolia amphidoxa* are described.

Equisetites ('horsetail') soil beds are common in the Wadhurst Clay (Lower Cretaceous; text-fig. 1) of south-east England. They constitute combinations of roots, rhizomes, and stems of the plant preserved *in situ*, generally in a matrix of inter-laminated clays and fine-medium silts. They are the only truly autochthonous plant beds of botanic value in the Wealden. Some of the *Equisetites* fragment partings which occur above and occasionally within the soil beds are probably parautochthonous. The majority of the rootlet beds in the succession have, however, been truncated and there is nothing to indicate to which plants the roots were attached (although in the Wadhurst Clay they may frequently belong to *Equisetites*). It has proved difficult to determine both the environments of deposition in which *Equisetites* thrived and the factors which controlled its distribution. The Hastings Beds succession accumulated in an essentially non-marine basin (the Anglo-Paris Basin) with the result that similar aquatic faunas and floras lived both on the delta complex and offshore (Allen 1959, 1967). Although the properties of many of the sediment types are probably characteristic for special areas of formation, these areas are difficult to delimit. Four possible interpretations of the standard Hastings Beds megacyclothem, in which *Equisetites* soil beds play an important part, have been proposed by Allen (summarized 1967, text-fig. 1). The distribution of palynomorphs in samples from horizons within and adjacent to some of the Wadhurst Clay soil beds is considered here both in the light of these interpretations and with regard to the distribution of local flora.



TEXT-FIG. 1. Correlation of the Hastings Beds in south-east England (after Harland *et al.* 1967, and latest published information). Lithological boundaries are indicated by broken lines. Thickness of Wadhurst Clay varies from 30 to 70 m.

MATERIAL

The samples came from the Wadhurst Clay in the Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2962 2729, first redrilling, and TQ 2961 2731, second redrilling); Warlingham Borehole, Surrey

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(TQ 3476 5719); Railway Brickyard, Sharpthorne, Sussex (TQ 3740 2729); and Freshfield Lane Brickworks, Danehill, Sussex (TQ 3813 2659). Most of the sampling horizons are figured in Batten (1968, text-figs. 1 and 2). Approximately 15 g of each sample from not more than 2 cm stratigraphic thickness were subjected to a standard preparation procedure (see Batten 1973) employing 50% hydrochloric acid, HF, nitric acid (< 30 minutes) or Schulze solution (< 10 minutes), ammonium hydroxide (5 minutes), and zinc bromide (sp. gr. c. 2.2). Strew slides were made with Clearcol; Euparal sealed the cover-slips to the slides.

WADHURST CLAY *EQUISETITES*

Rootlets preserved as casts and infilled rhizomes are usually all that remain of Wadhurst *Equisetites* communities. Infilled stems in position of growth occur less often and rhizomes preserved as carbonaceous compressions are rare. The species preserved in the soil beds examined is *Equisetites lyellii* (Mantell) (1833). Since the species was erected, it has been consistently referred to as *lyelli*. Mantell's spelling is correct and is here reverted to (see Lanjouw *et al.* 1966, Recommendation 73C). *E. lyellii* is the only common plant megafossil in the Wadhurst Clay. *E. burchardti* Dunker and *E. yokoyamae* Seward, both tuber-bearing forms, were not encountered; they tend to occur in the more arenaceous facies of the succession (cf. Allen 1962).

The scarcity of other plants in the Wadhurst Clay suggests: (1) that most of the plant material derived from the lowland flora bordering the basin of deposition was deposited or comminuted before it reached the Wadhurst zone of deposition, (2) that the horsetail communities were isolated in some way from the bulk of the lowland flora. In addition, the preservation of *E. lyellii* may have been enhanced by two factors: (1) it was not dependent on chance deposition in an aqueous environment conducive to preservation because it probably grew in the shallow waters of the Wadhurst Clay, (2) although there is no direct evidence, the plants may have accumulated silica in their tissues as do species of extant *Equisetum* (e.g. *E. hyemale*; Lovering and Engel 1967).

Stem fragments of *E. lyellii* may be scattered through the clays and silts above or within the soil beds or concentrated in thin bands separated by more or less fragment-free horizons. The concentrations represent periods when deposition of waterlogged plant debris was more rapid than that of sediment deposition, and are probably the product of destruction of *E. lyellii* communities by water disturbance (Allen 1941; Batten 1968). The preservation state varies, but the accumulations which are well preserved may be nearly autochthonous. The absence of any large accumulations of *Equisetites* suggests that the communities were short lived (Allen 1941, 1960) and that *E. lyellii* was a pioneer coloniser (Hughes and Moody-Stuart 1967a); their existence was probably terminated by deepening water. Had the communities existed for many more than a few years, thin coal seams like those in the Yorkshire Jurassic (Harris 1953) might have been formed.

SOIL BED AND FRAGMENT PARTING PALYNOLOGY

Soil beds and fragment partings often yield a distinctive palynologic assemblage. This assemblage is here designated as the SF (soil bed/fragment parting) type. During a routine examination of Wadhurst preparations most were assigned (at

the specific level) to assemblage-types 8 and/or 16 (Table 1 and Batten 1973). Important characters are: (1) the miospore *Pilasporites allenii* (described from a Wadhurst Clay soil bed preparation (CUC 792) and attributed by Batten 1968 to *Equisetites*) is abundant (V or F on Table 1), (2) there is usually a large amount of plant debris comprising brown 'wood' (probably mostly degraded *Equisetites* material) and *Equisetites* cuticle, (3) the general state of preservation of the miospores is usually fair to good.

Certain miospore taxa, viz. *Retitriletes* sp., *Regresporites lophus* gen. et sp. nov., *Ischyosporites arkealii* (Pocock 1970) comb. nov., and *Admolia amphidoxa* gen. et sp. nov. appear to be significantly associated. *I. arkealii* and *A. amphidoxa* occur more often and in greater abundances in SF assemblages than elsewhere, and *Retitriletes* sp. and *Regresporites lophus* have only been recorded from the SF type. *Trilobosporites ivanovae* sp. nov. and *Patellasporites* spp. occur more frequently associated with *Equisetites* than elsewhere in the Wadhurst Clay (although the former is more numerous and better preserved in the described Grinstead Clay sample). The frequency of occurrence of *Pilosporites* spp., *Converrucosisporites venitus* sp. nov., *Staplinisporites* spp., *Classopollis* spp., and most of the other taxa recorded from soil beds and associated strata differs little from their frequency in the rest of the Wadhurst. However, megaspores have not been recovered, and the following are notably less common: *Inapertisporites* sp., *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958, *Couperisporites* spp., *Vitreisporites pallidus* (Reissinger 1938) Nilsson 1958, *Ceratosporites* spp., and *Celyphus rallus* Batten 1973. Some soil bed and fragment parting samples do not yield an SF kind of assemblage (Table 1). Instead, the assemblages show little diversity and poor preservation and have (see below) a typical 'Wadhurst aspect' (assemblage-types 1, 4, 7, 9, 10, and 12 in Batten 1973).

NUMERICAL COMPARISON OF ASSEMBLAGES

The relationships between forty-two selected assemblages recovered from soil beds and adjacent strata were determined by using both cluster analysis and non-metric multidimensional scaling (see Kruskal 1964*a, b*). For cluster analysis both weighted and unweighted pair-group linkage methods were used (Sokal and Michener 1958; Sokal and Sneath 1963). The cluster program operated on matrices of coefficients of association derived by comparing data from counts of both 500 (Table 1) and 200 miospores, with and without other data (on preservation, abundance of wood, cuticle, etc.). The coefficients of association used were those of proportional similarity ($\text{Cos } \theta$) of Imbrie and Purdy (1962), the Jaccard, and Sokal and Michener (see Cheetham and Hazel 1969). The multivariate data were converted to binary form to use the Sokal and Jaccard coefficients. The nonmetric multidimensional scaling program employed $\text{Cos } \theta$ converted to a distance coefficient. Both procedures yielded similar results but those from the cluster analysis were more clear cut than the multidimensional scaling. Assemblages with an SF aspect formed one grouping and those identified as 'typical Wadhurst type' formed another. 'Borderline' assemblages which show only some of the characters of the SF type (i.e. those from samples CUC 792/1, CUC 792/4, CUC 792/6, DJB 329, and DJB 368;

Table 1) tended not to be well linked with either group. The records of *Regresporites lophus*, *Ischyosporites arkellii*, *Admolia amphidoxa*, *Pilasporites allenii*, *Classopollis* spp., *Ceratosporites* spp., and *Gleicheniidites* spp. were important in determining the grouping of the assemblages. The state of preservation and the abundance of brown wood and cuticle fragments were also important when all the data, not just the miospore content, were taken into account.

PALAEOECOLOGY

Both onshore and offshore habitats have been postulated for the *Equisetites* communities (Allen 1959, 1967, text-fig. 1). On the delta top they could have thrived on levées and in backswamps and shallow ponds (Allen 1949, 1959, megacyclothem interpretations 1 and 2); offshore they could have become established in a band along much of the length of the delta shore-face and in other areas of shallow water (shoals) (Allen 1959, 1967, interpretations 3 and 4). Most Wadhurst Clay palynologic assemblages reflect the homogeneous delta flora in their composition. They are composed mainly of pteropsid and coniferopsid elements. Fern spores, especially the families Schizaeaceae and Gleicheniaceae, are prominent and, in the former, diverse. The miospores are, however, generally in a poor state of preservation, and when compared with the whole Wealden succession, show below average diversity. The general aspect of the assemblages, and the scarcity of both megaspores (Batten 1969) and determinable megascopic plant remains, apart from those of *Equisetites*, in the Wadhurst suggest that deposition took place far from source. The poor preservation of the palynomorphs can be accounted for by prolonged aerobic decay and reworking. All but the more resistant spores and plant fragments (fusain) would have been destroyed by the alternations of erosion and deposition on the delta complex.

The SF kind of assemblage has, however, a different aspect. The homogeneous delta flora forms only a background component. The better preservation suggests that some of the elements were not transported over long distances but were deposited in an environment where water transport was restricted to some extent, and where the duration of their exposure to aerobic decay depended on the rate at which they

TABLE 1. Plant megafossil and miospore content of 42 selected samples from *Equisetites* soil beds and associated strata. Sample numbers on left-hand side of table: prefix DJB = field sample, CUC = core sample from Cuckfield No. 1 Borehole, WM = core sample from Warringham Borehole. On extreme right, record of assemblage-type assignments (see Batten 1973) noted during routine examination of Wadhurst Clay preparations (before counts of 500 miospores), and of SF kinds of assemblages (B = 'borderline' type).

Miospore taxa: P = present (< 3% after count of 500), C = common (3-14.5%), V = very common (15-29.5%), F = frequent (30% or more). Taxa grouped within suprageneric categories except where indicated by solid line. Elements recorded subsequent to completion of count not included. Rootlets, rhizomes, and stems, X if recorded. Megascopic fragments of *Equisetites*: C = common, F = frequent. 1. *Cyclogranisporites* Pot. and Kr./*Granulatisporites* Ibr. emend. Pot. and Kr. 2. *Corrugatisporites* Th. and Pfl. ex Wey. and Greif./*Rugulatisporites* Th. and Pfl. 3. *Foveosporites* Balme/*Foveotriletes* v.d. Hammen ex Pot./*Sestrosporites* Dett. 4. *Lycopodiumsporites* Thierg. ex Del. and Spr./*Reticulispores* Pot. and Kr. in Wey. and Krieg. 5. *Tauocusporites* Stover emend. Play. and Dett./*Polycingulatisporites* Simonc. and Kedv. emend. Play. and Dett.

SAMPLES		TAXA
CUC 7810/11A	U	<i>Auriculatisporites</i> NILSSON
CUC 7810/11B	U	<i>Conosporites</i> NILSSON
CUC 7810/11C	U	<i>Strepisporites</i> PFL in TN and PFL
CUC 7810/11D	U	<i>P. Strepisporites</i> sp. (undescribed)
CUC 7810/11E	U	<i>Lindulatisporites</i> PFL in TN and PFL
CUC 7810/11F	U	TOTAL SMOOTH WALLED TRILETES
CUC 7810/11G	U	<i>Acanthosporites</i> NAUM emend POT and KR
CUC 7810/11H	U	<i>Apiculatisporis</i> POT and KR
CUC 7810/11I	U	<i>Leucosporites</i> TN and PFL
CUC 7810/11J	U	<i>Ceratopores</i> COOK and DETT
CUC 7810/11K	U	<i>Convolvulites</i> DEL and SPR emend DEL et al
CUC 7810/11L	U	<i>Convolvulites</i> POT and KR
CUC 7810/11M	U	<i>C. vexus</i> SP NOV
CUC 7810/11N	U	<i>Cystosporites</i> / <i>Stenotriporites</i> 1
CUC 7810/11O	U	<i>Vernemiasporites</i> KRUYFSCHE
CUC 7810/11P	U	<i>Dumaliolites</i> COUPER
CUC 7810/11Q	U	<i>Plicisporites</i> DEL and SPR
CUC 7810/11R	U	<i>Verrucosporites</i> (B) emend SMITH and B'WORTH
CUC 7810/11S	U	<i>Verrucosporites</i> sp. (undescribed)
CUC 7810/11T	U	<i>Cicatriculites</i> POT and GELL
CUC 7810/11U	U	<i>Corrugatisporites</i> / <i>Rugulatisporites</i> 2
CUC 7810/11V	U	<i>Foveosporites</i> / <i>Foveatrilites</i> / <i>Zestrosporites</i> 3
CUC 7810/11W	U	<i>Miculisporites</i> COUPER
CUC 7810/11X	U	<i>Lycopodiumsporites</i> / <i>Petalosporites</i> 4
CUC 7810/11Y	U	<i>Lycopodiumsporites</i> austroriparianus (COOK) POCKOCK
CUC 7810/11Z	U	<i>Microriparianites</i> KINX emend POT and KR
CUC 7810/12A	U	<i>Microriparianites</i> subreticulatus (BURGER) NORRIS
CUC 7810/12B	U	<i>Microriparianites</i> ex HAMMEN ex PIERCE
CUC 7810/12C	U	<i>Microriparianites</i> sp.
CUC 7810/12D	U	<i>Negetosporites</i> raphus GEN and SP NOV
CUC 7810/12E	U	<i>Stegalisporites</i> POCKOCK / <i>Coronatispora</i> DETT
CUC 7810/12F	U	<i>Tropocarpusporites</i> / <i>Polycingulatisporites</i> 5
CUC 7810/12G	U	<i>Triporites</i> MALM ex POT
CUC 7810/12H	U	<i>Uchysporites</i> BALME
CUC 7810/12I	U	<i>Larkelia</i> (POCKOCK) comb. nov.
CUC 7810/12J	U	<i>Metasporites</i> COUPER emend DETT
CUC 7810/12K	U	<i>Trilobosporites</i> PANT ex POT
CUC 7810/12L	U	<i>T. immanis</i> SP NOV
CUC 7810/12M	U	<i>Gleichenites</i> ROSS ex DEL & SPR emend DETT THIRASSATI
CUC 7810/12N	U	<i>Gleichenites</i> apiculatus BRENNER
CUC 7810/12O	U	<i>Cingulites</i> PIERCE emend DETT
CUC 7810/12P	U	<i>Contigiosporites</i> DETT
CUC 7810/12Q	U	<i>Contigiosporites</i> WEX and KRIG emend DETT
CUC 7810/12R	U	<i>Petalosporites</i> GROOT and BRODT emend KEMP
CUC 7810/12S	U	<i>Petalosporites</i> sp. (undescribed)
CUC 7810/12T	U	INDEX SCULPTURED TRILETES
CUC 7810/12U	U	<i>Magdalenites</i> DEL and SPR emend COOK and DETT
CUC 7810/12V	U	<i>Magdalenites</i> POCKOCK emend DETT
CUC 7810/12W	U	<i>Couperisporites</i> complexus (COUPER) POCKOCK
CUC 7810/12X	U	<i>Couperisporites</i> sp. (undescribed)
CUC 7810/12Y	U	<i>Mousetisporites</i> POCKOCK
CUC 7810/12Z	U	<i>Mousetisporites</i> COUPER
CUC 7810/13A	U	<i>Peromorphites</i> ERST ex COUPER
CUC 7810/13B	U	<i>Aracariolites</i> COOK ex COUPER
CUC 7810/13C	U	<i>Imperisporites</i> ud HAMMEN ex ROUSE
CUC 7810/13D	U	<i>Imperisporites</i> PFL ex TN and PFL emend POT
CUC 7810/13E	U	<i>Pilularia</i> BATTEN
CUC 7810/13F	U	<i>Reticulatisporites</i> (B) emend POT and KR
CUC 7810/13G	U	<i>Tetradicoccolites</i> KR
CUC 7810/13H	U	<i>Ceratocollites</i> mesoleucus (COUPER) NILSSON
CUC 7810/13I	U	<i>Tropocarpus</i> POT and VEN emend POT
CUC 7810/13J	U	DISACCATES, excluding <i>Vireosporites</i>
CUC 7810/13K	U	<i>Vireosporites</i> LESCHNIK emend JANSOHN
CUC 7810/13L	U	<i>Eucammiolites</i> ENDY emend HUGHES
CUC 7810/13M	U	<i>Cyclophorus</i> WÖGEN ex WILS and WEBST
CUC 7810/13N	U	<i>Classosporis</i> PFL emend RETW.
CUC 7810/13O	U	<i>Classosporis</i> sp. (undescribed)
CUC 7810/13P	U	<i>Exosporites</i> BALME
CUC 7810/13Q	U	<i>Perisporites</i> COUPER
CUC 7810/13R	U	<i>Sphaerospores</i> COUPER
CUC 7810/13S	U	<i>S. subgraminis</i> COUPER
CUC 7810/13T	U	<i>Sclerospores</i> COOK and DETT
CUC 7810/13U	U	<i>Calypha</i> retusa BATTEN
CUC 7810/13V	U	TRILETES
CUC 7810/13W	U	TRILETES (AND STEMS)
CUC 7810/13X	U	MEGASCOPIC FRAGMENTS (C or F)
CUC 7810/13Y	U	SP TYPE
CUC 7810/13Z	U	ASSEMBLAGE - TYPE RECORD

For explanation of Table 1 see opposite.

were buried. The relative abundance of *Pilasporites allenii* and to a lesser extent of *Ischyosporites arkellii*, *Admolia amphidoxa*, and *Regresporites lophus* suggests both local production and some kind of ecological association between the parent plants. *R. lophus*, a relatively large thick-walled spore, and *A. amphidoxa*, another thick-walled palynomorph, could not have been produced by plant species constituting part of the homogeneous delta flora. If they had been, they would have been recovered from sediments deposited closer to this source, particularly in medium and coarse siltstones of near-shore and back-delta facies. Thus *Equisetites* appears not to have been an important component of the onshore flora but probably thrived offshore in the pro-delta. This supports interpretations 3 and 4 of Allen (1959, 1967).

The local flora may be poorly represented in the soil beds and fragment partings. Possible reasons for the fluctuations in abundances include depositional environments unfavourable for preservation, winnowing, low rate of spore production, seasonal production, and variable rate of sedimentation (Batten 1968). Fragment partings yield *P. allenii* abundances more consistently than soil beds, probably because they contain a greater number of dispersed *E. lyellii* sporangia. Allen has suggested (*Pal. Ass. Circ.* 64, 1971, unpublished) that the larger Hastings Beds *Equisetites* (i.e. *E. lyellii*) may have flourished during periods of low salinity (cf. Anderson *et al.* 1967), that low salinity transgressions might have been followed by offshore *Equisetites*, and that brackish transgressions might not. The lack of dinoflagellates and acritarchs in soil beds and adjacent strata suggests that *Equisetites* flourished in fresh or only weakly saline waters. However, disagreement over the salinity ranges of several of the fossils of the Wadhurst Clay confuses the picture.

The *Classopollis* group of species is an important component of many Wadhurst assemblages. Hughes and Moody-Stuart (1967a) proposed that the group was not available for deposition in back-delta environments but that the parent plants were favourably placed for their pollen to be preserved in offshore deposits; they suggested a coastal swamp habitat comparable with the Tertiary and Recent mangroves. There is, however, no direct (megafossil) evidence for this and by contrast, Vakhrameev (1970) has suggested that the parent plants of *Classopollis* were psammophilic, preferring upland slopes, and able to tolerate drought conditions. An attempt to determine the relationship between *Classopollis* producers and *Equisetites* using palynology has merely shown that the *Classopollis* parent plants are not significantly associated with *Equisetites*, nor do they show an antipathetic relationship. There are some roots of unknown origin, which are larger than those of *Equisetites*, preserved in the coarse-grained Ashdown and Tunbridge Wells Sand facies (e.g. at Hastings, East Grinstead, and Pembury; White 1928, Allen 1959); Hughes and Moody-Stuart (1967a) suggested that *Classopollis* plants might have borne them, but attempts to prove this by palynologic association have been unsuccessful.

The affinities of the palynomorph taxa associated with *Pilasporites allenii* are uncertain because it is hazardous to compare them either with the spores of modern plants or with modern plant associations. It is probable that *Ischyosporites arkellii* is a filiclean spore (produced by a member of the Schizaeaceae?). *Regresporites lophus* is probably a fern spore, but *Retriletes* sp. could have been produced by a member of the Lycopodiaceae or of the Bryophyta, and the affinities of *Admolia*

amphidoxa can only be guessed at (Thallophyta (Algae)?, Bryophyta?). However, the palynologic record does suggest that other plants grew, if not amongst the *Equisetites*, at least near by. That remains of the parent plants have not been recorded may be due either to non-preservation or lack of recognition. The only other record of plants suggested as being ecologically associated with *Equisetites* is that of 'doubtful leafy liverworts' (Allen 1959, p. 295).

TABLE 2A. Records of miospores tentatively attributed to the Equisetaceae (*Equisetites*/*Equisetum*) or compared with the spores of *Equisetum* (see *Pilasporites allenii* discussion). The spores that Rogalska (1962) attributed to cf. *Equisetum* differ from her earlier assignments (1954, 1956) in lacking a 'perisporium'. She noted that the earlier records may represent another genus.

Author	Record	Age
Rogalska 1956	<i>Equisetum</i> sp.	Lower Jurassic
Rogalska 1962	Cf. <i>Equisetum</i>	Jurassic
Góczán 1956	<i>Calamospora</i> cf. 'cf. <i>C. pallida</i> Schemel'	Lower Jurassic
Nagy 1958	Cf. <i>Equisetum</i>	Pliocene
Kara-Murza 1960	<i>Leiotriletes</i> spp.	Mesozoic
Chun'-Bin Chzhan 1962	<i>Equisetum</i> sp.	Lower Cretaceous
Verbitskaja 1962	<i>Leiotriletes</i> spp.	Cretaceous
Simoncsics 1964	<i>Perinosporites sphaericus</i> Simoncsics 1964	Miocene
Voevodova (in Pokrovskaja and Stel'mak) 1964	<i>Equisetum chassynense</i> Voevodova 1964	Lower Cretaceous
Piel 1971	? <i>Equisetum</i> sp.	Oligocene

TABLE 2B. Dispersed spores which bear some resemblance to *Pilasporites allenii*.

Author	Record	Age
Nakoman 1964	<i>Inaperturopollenites problematicus</i> Nakoman 1964	Oligocene
Wall 1965	<i>Concentrisporites hallei</i> (Nilsson 1958) Wall 1965	Lower Jurassic
Goubin 1965	<i>Inaperturopollenites</i> cf. <i>orbicularis</i> Nilsson 1958	Middle Jurassic
Goubin 1965	<i>Laricoidites desquamatus</i> Goubin 1965	Upper Triassic
Volkheimer 1968	<i>Inaperturopollenites velatus</i> Volkheimer 1968	Jurassic

SYSTEMATIC PALAEOLOGY

Ischyosporites arkellii (Pocock 1970) comb. nov., recorded in graded comparison form (see Hughes and Moody-Stuart 1967b, p. 355), *Retitriletes* sp., and the four new taxa referred to in the text are here described and compared. *Pilasporites allenii* Batten 1968 is also discussed. Assemblage-type identifications (see Batten 1972, 1973) are given for the assemblages from which the taxa are described. The age/stage from which a compared species was described is given if it came from outside the Cretaceous period.

Miospores examined with the scanning electron microscope were individually mounted on 'Durofix' or double-sided 'Sellotape' on 12-mm diameter stubs, or strew mounted on stubs without adhesive. Most mounts were coated with carbon but gold-palladium was also used. The assemblage slides are labelled with the preparation number prefixed by 'T'. A holotype specimen is present with topotypes on a strew slide of a single preparation. The slides containing the figured specimens are in the Sedgwick Museum, Cambridge. Representative specimens of the new species are in the Institute of Geological Sciences, Leeds. Stage co-ordinates given refer to Leitz Laborlux (LI) microscope, number 557187, Sedgwick Museum.

Turma TRILETES Reinsch emend. Dettmann 1963

Infraturma APICULATI Bennie and Kidston emend. Potonié 1956

Genus CONVERRUCOSISPORITES Potonié and Kremp 1954

Converrucosisporites venitus sp. nov.

Plate 41, figs. 1-9; Plate 42, figs. 1-5

Type sample. CUC 924, Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2961 2731), depth 924 ft (281.6 m); upper Ashdown Sand, Valanginian? Grey (N5-N7) laminated fine siltstone, sedimentary mica, bedding disturbed, rootlets *in situ*. Preparation T206; ten minutes Schulze solution, cleared in dilute NH₄OH, mineral separation, strew slides with Clearcol. AT1.

Holotype. Slide T206/3, L1 48-4 125-2; Pl. 41, fig. 3.

Diagnosis. Miospore, trilete, mean maximum diameter 41.5 μ m, standard deviation 4.1 μ m (100 specimens). Amb triangular; concave, straight or slightly convex sides, rounded angles. Proximal face slightly convex, may be raised up along margins of laesurae; distal surface convex. Laesurae distinct, $> \frac{1}{3}$ radius. Exine two-layered, total thickness 1-2 μ m. Inner layer smooth 0.75-1.5 μ m thick. Outer layer 0.5-1 μ m thick, carries sculpture on both proximal and distal surfaces. Sculpture, which may be only weakly developed on proximal face, generally consists of grana and verrucae of low elevations ($< 1-2 \mu$ m high) and variable maximum diameter (up to 6 μ m). Elements spaced $< 1-2 \mu$ m (sometimes up to 4 μ m) apart; bases rounded to irregular in outline, distinct or (more usually) partially fused, leading to the formation of irregular rugulae.

Description. The observed limits of the maximum diameter of the spores are 33-53 μ m (coefficient of variation 9.8%). Fifty per cent of the specimens are in polar aspect; none are in equatorial view. Proximal arcuate folds resulting from compression of the raised up area of the proximal face may be present (Pl. 41, fig. 5). The sculptural elements are sparsely distributed on four specimens (Pl. 41, fig. 6), and predominantly dome shaped on seven (Pl. 41, fig. 3). Four show isolated clavae or dome shaped verrucae up to 6 μ m high (Pl. 41, fig. 1) and two have almost smooth proximal

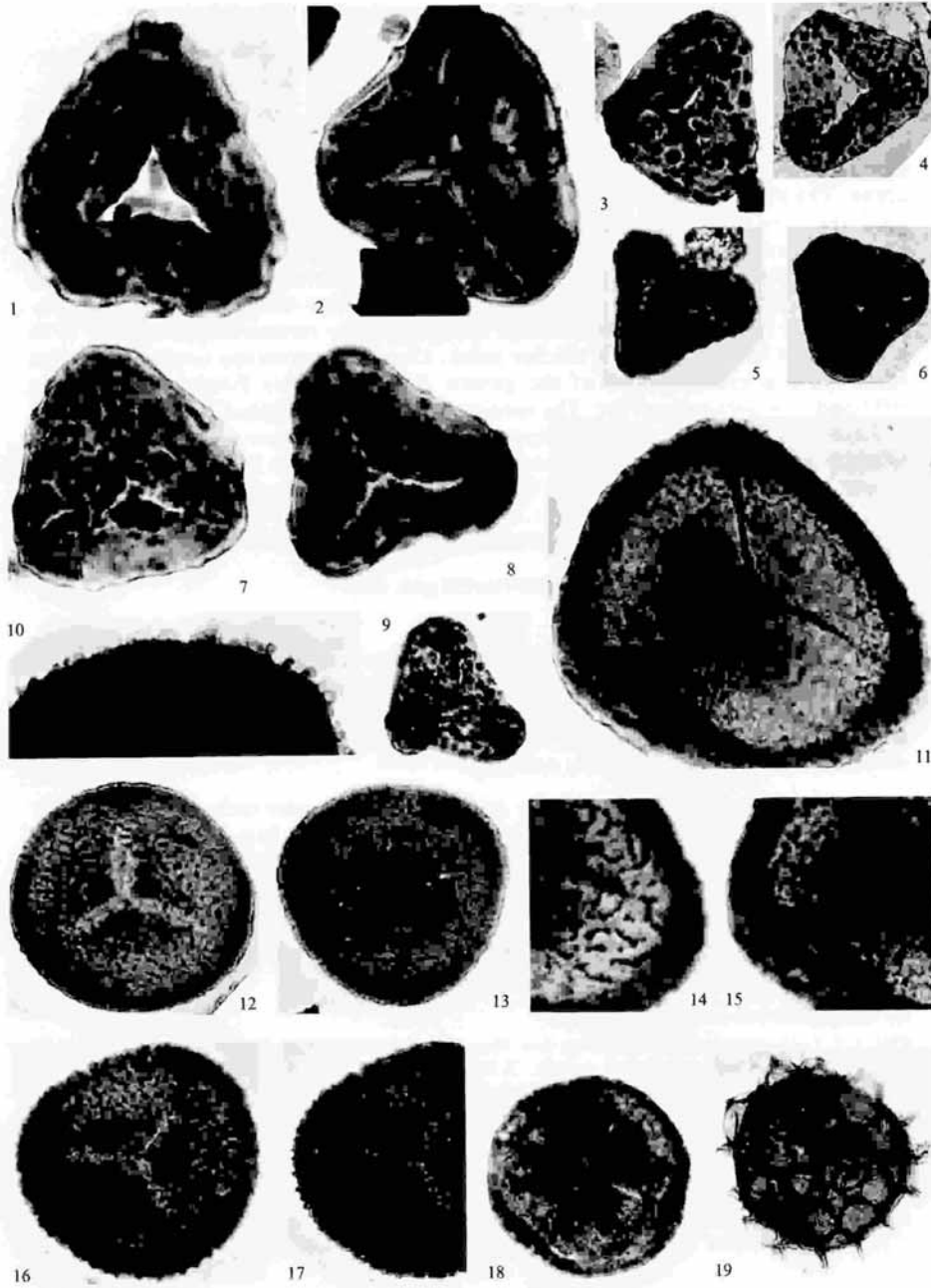
EXPLANATION OF PLATE 41

Figs. 1-9. *Converrucosisporites venitus* sp. nov. Preparation T206. 1, Showing variable shape and distribution of sculptural elements and two layered exine, T206/1, L1 54-1 123-2, $\times 1000$. 2, Proximal surface almost smooth, T206/1, L1 58-7 116-6, $\times 1000$. 3, Holotype, T206/3, L1 48-4 125-2, $\times 500$. 4, T206/3, L1 42-9 118-2, $\times 500$. 5, Proximal kyrtoles, T206/1, L1 38-7 120-2, $\times 500$. 6, Sparsely distributed sculptural elements, T206/2, L1 40-3 118-7, $\times 500$. 7, T206/1, L1 53-3 118-2, $\times 1000$. 8, T206/1, L1 43-3 118-1, $\times 1000$. 9, T206/3, L1 41-6 118-8, $\times 500$.

Figs. 10-17. *Regresporites lophus* gen. et sp. nov. Preparation T209. 10, Equatorial sculpture, T209/1, L1 57-0 129-1, $\times 1000$. 11, 14, 15, Same specimen. 11, Raised lips; 14, distal sculpture; 15, proximal sculpture; T209/1, L1 61-7 129-1, $\times 1000$. 12, T209/1, L1 63-3 125-7, $\times 500$. 13, T209/3, L1 58-4 126-0, $\times 1000$. 16, 17, Same specimen, holotype. 16, Distal focus; 17, equatorial focus; T209/1, L1 41-5 126-4, $\times 500$.

Fig. 18. cfA. *Regresporites lophus* gen. et sp. nov. Specimen corroded, preparation T210/13, L1 58-7 123-2, $\times 500$.

Fig. 19. *Retitriletes* sp. Preparation T210/13, L1 54-3 115-7, $\times 500$.



BATTEN, Cretaceous spores

surfaces (Pl. 41, fig. 2). Predepositional and diagenetic corrosion is shown by tearing and pitting of the exine of some specimens.

Discussion. The sculptural elements of *Converrucosisporites cameroni* (de Jersey 1962) Playford and Dettmann 1965 (Triassic) rarely coalesce, and although they consist mostly of verrucae, they may also comprise some bacula, spinae, conii, and grana. The closely spaced verrucae on the exine of *C. geniculatus* Deák and Combaz 1967 are more rounded and more strongly developed. '*Trilitisporites*' *rariverrucatus* Danzè-Corsin and Laveine 1963 (lower Lias) has more or less rounded verrucae 1–3 μm high scattered widely over its surface. *Concavissimisporites southeyensis* Pocock 1970 (lower Bajocian) is larger and has a sexine which is thicker in equatorial radial regions than interradially. *Concavissporites variverrucatus* Couper 1958 is somewhat larger and has a thicker exine. *Converrucosisporites venitus* resembles some Carboniferous species of the genera *Pustulatisporites* Potonié and Kremp 1954 and *Converrucosisporites*. The specimens ascribed by Lantz (1958, pl. 1, fig. 12) to *Leptolepidites* cf. *verrucatus* Couper 1953 are similar. Forms recorded as *Converrucosisporites venitus* have been recovered from the Ashdown Beds, Wadhurst Clay, Lower Tunbridge Wells Sand, and Grinstead Clay (Berriasian–Valanginian?).

Infraturma MURORNATI Potonié and Kremp 1954

REGRESPORITES gen. nov.

Type species. *R. lophus* sp. nov.

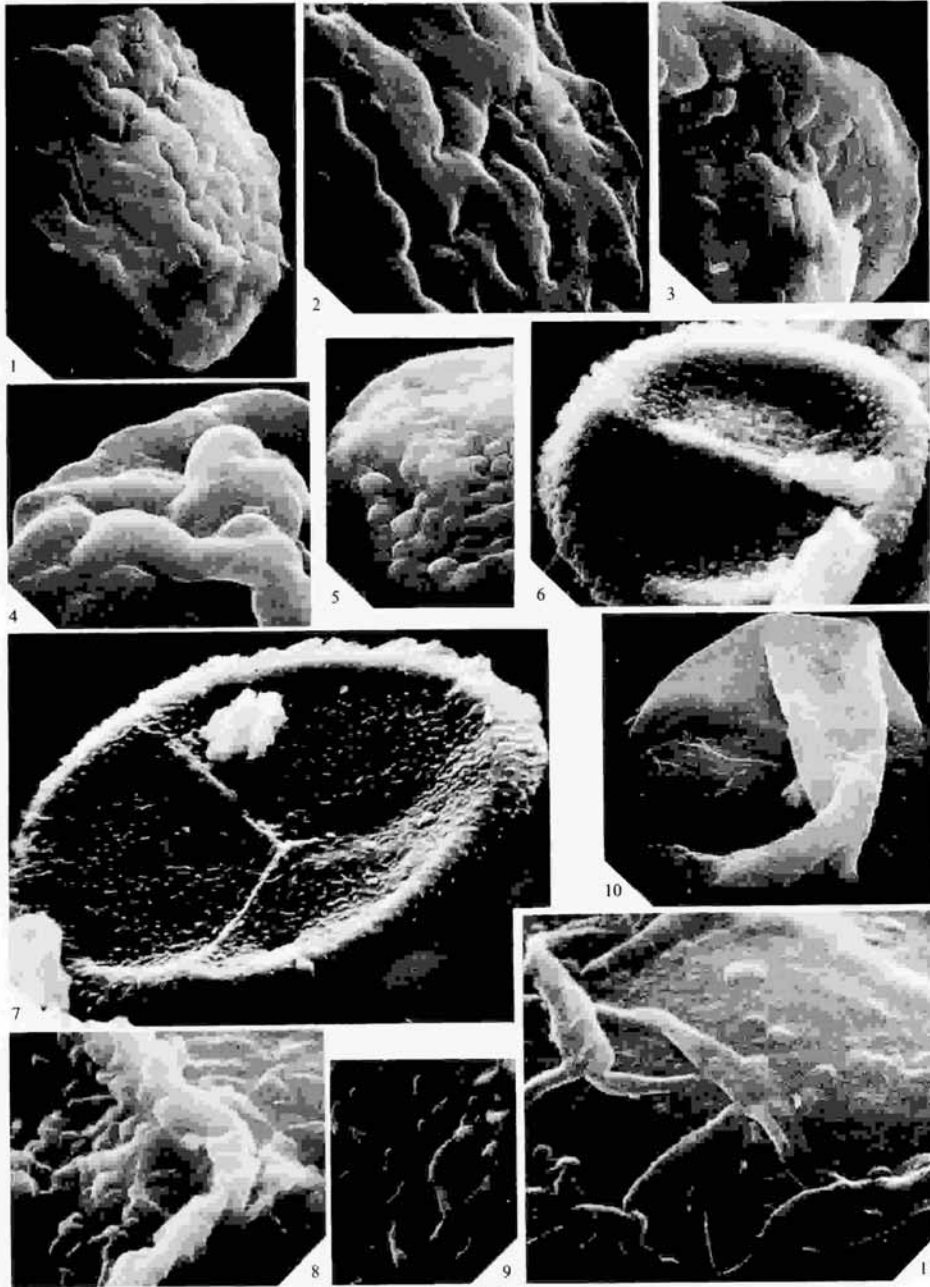
Diagnosis. Miospore, trilete, rounded triangular to subcircular in equatorial outline. Extremities of laesurae usually merge with equatorial or proximal subequatorial exine thickening. Distal sculpture of irregular, occasionally anastomosing rugulae \pm scattered grana, verrucae, clavae, or bacula. Proximal sculpture similar but reduced, may consist only of grana, rarely scabrate.

Discussion. Spores which structurally resemble *Regresporites* include *Retusotriletes* Naumova 1953 emend. Streel 1964 and related genera (e.g. *Apiculiretusispora* Streel 1964) described from the Palaeozoic. *Rugulatisporites* Thomson and Pflug 1953 is used for rugulate Mesozoic spores but the diagnosis of the genus does not allow for the inclusion of forms which show modifications of the exine in equatorial

EXPLANATION OF PLATE 42

All scanning electron micrographs.

- Figs. 1–5. *Converrucosisporites venitus* sp. nov. Preparation T206. 1, 2, Specimen on stub (SH) DB 44. 1, Specimen obliquely compressed, $\times 1500$. 2, Detail of distal sculpture, $\times 3500$. 3, Second specimen, distal view, $\times 1500$, (SH) DB 50. 4, Third specimen, detail of proximal radial region, $\times 3500$, (SH) DB 44. 5, Part of distal surface of fourth specimen, $\times 1500$, (SH) DB 44.
- Figs. 6–9. *Regresporites lophus* gen. et sp. nov. Preparation T209. 6, Slightly oblique compression, $\times 1000$, (SH) DB 36. 7, Second specimen showing raised lips and thickened proximal equatorial regions, $\times 1000$, (SH) DB 1a. 8, Third specimen, detail of proximal pole, $\times 4000$, (SH) DB 34. 9, Distal sculpture detail of fourth specimen, $\times 2000$, (SH) DB 36.
- Figs. 10–11. *Pilasporites allenii* Batten 1968. Preparation T210. Specimen on (SH) DB 47. 10, $\times 1500$. 11, Detail of loosened η ektexine showing crinkling and attached globules, $\times 7500$.



BATTEN, Cretaceous spores

or subequatorial regions. *Lycopodiacidites* Couper 1953 emend. Potonié 1956 is generally used for azonate miospores which are verrucate to rugulate on their distal surface. *Hamulatisporis* Krutzsch 1959, erected from the Tertiary, is a subtriangular spore with hamulate sculpture.

Regresporites lophus sp. nov.

Plate 41, figs. 10–17; Plate 42, figs. 6–9; Plate 44, figs. 1–6

Type sample. CUC 791/11, Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2962 2729), depth 791 ft 11 in (241.4 m), Wadhurst Clay, Valanginian? Medium grey (N5) clay, thin fine silt laminations, *Equisetites in situ* and fragments of same. Preparation T209; 10 minutes Schulze solution, cleared in dilute NH₄OH, mineral separation, strew slides with Clearcol. AT8. Holotype slide T209/1, LI 41.5 126.4; Pl. 41, figs. 16, 17.

Diagnosis. Miospore, trilete, mean maximum diameter 62.6 μ m, standard deviation 5.5 μ m (100 specimens). Amb rounded triangular to subcircular. Distal surface (when uncompressed) more strongly convex than proximal. Laesurae length $\frac{3}{4}$ spore radius or more, straight or (rarely) slightly sinuous. Lips may be raised, 0.5–2 μ m wide at base on each side of laesurae and up to 5 μ m high (measured on thirty-eight specimens). Extremities of laesurae usually merge with equatorial or subequatorial exinal thickening which appears as a dark zone in transmitted light. Width of this zone usually 5–7 μ m interradially and 6–11 μ m radially; inner margin usually indistinct.

Exine 2–3 μ m thick except near equator where it may be up to 4.5 μ m thick in interradiial regions and up to 5 μ m thick at angles, probably two-layered; outer layer thin (c. 1 μ m?), carries sculpture. A subcircular area (outline indistinct) at proximal pole may be slightly darkened in transmitted light (= slight thickening of exine); observed limits of maximum diameter 19–36 μ m, mean 26.3 μ m (sixty-six specimens).

Proximal sculpture usually of small grana and/or occasionally anastomosing irregular rugulae (up to 1 μ m high, < 4 μ m in length, up to 3 μ m apart). Distal and equatorial sculpture of rugulae \pm scattered grana, verrucae, clavae, and baculae; rugulae irregular, occasionally anastomosing, up to 4 μ m apart, 4–10 μ m long, usually 0.5–2 μ m (rarely up to 3.5 μ m) wide, and < 2 μ m (rarely up to 4 μ m) high.

Description. The observed limits of the maximum diameter of these spores are 51–80 μ m (coefficient of variation 8.7%). Seventy-five of the specimens are in polar aspect but none are in equatorial view. The laesurae are sometimes only weakly developed (Pl. 42, fig. 6 in part; Pl. 44, fig. 4). The dimensions of the sculptural elements on the proximal face tend to increase towards the equator. Eighty-two specimens have both grana and rugulae proximally (Pl. 41, fig. 15; Pl. 42, fig. 7). Most specimens are very compressed, usually in polar orientation or slightly obliquely. The proximal face is often concave (Pl. 42, figs. 6, 7; Pl. 44, fig. 4). The sculptured layer of the exine has been loosened on, and partially removed from, some specimens. Twenty-four specimens show a single fold which in most cases is developed subparallel to the equator.

Discussion. Forms identified as *Regresporites lophus* have only been recorded from the Wadhurst and Grinstead Clays (Valanginian?).

Genus RETITRILETES van der Hammen *ex* Pierce 1961*Retitriletes* sp.

Plate 41, fig. 19; Plate 43, fig. 1

Description. The observed limits of the maximum diameter of this miospore, excluding sculpture, are 40–75 μm (twenty specimens). The amb is circular or subcircular in outline. An irregular weakly developed (discontinuous) triradiate ridge may be present on the proximal face extending to the equator of the spore body. The exine is 2–3 μm thick and sculptured with a reticulum both on the distal face and equatorially. On the proximal face the sculpture is reduced, sometimes to a low reticulum, but more often to irregular grana, and muri < 3 μm high. Near the trilete mark the exine may be scabrate. The distal and equatorial muri are 0.5–1.5 μm wide at their bases but rapidly become membraneous above and are up to 12 μm high. The lumina are 4–21 μm in maximum diameter and circular to polygonal in outline.

Discussion. Species of *Januasporites* Pocock 1962 emend. Singh 1964 are alete miospores possessing a two-layered exine. The outer layer is absent over a more or less circular area on the distal face. The muri of *Reticulatisporites arcuatus* Brenner 1963 are thicker and more irregular in width. The proximal sculpture of *Hymenoreticulispores altimuronatus* Döring 1964 (Jurassic; Upper Malm) is not reduced. The laesurae of *R. castellatus* Pocock 1962 are not visible and the proximal sculpture is not reduced. *Woodsia reticulata* Bolkhovitina 1953 appears to possess a clearly defined triradiate mark. *R. incomptus* Manum 1962 (Tertiary) has muri of lower elevations and is clearly triradiate. *Zlivisporis blanensis* Pacltová 1961 is clearly trilete, lacks sculpture on the proximal face, and the arrangement of the muri is different. *Lycopodiumsporites marginatus* Singh 1964 differs chiefly in having a stronger trilete mark. *Retitriletes* sp. bears some resemblance to palynomorphs which have been referred to species of the acritarch genus *Cymatiosphaera* (cf. Wall 1965, pl. 9, fig. 8). *Retitriletes* sp. has only been recorded from the Wadhurst Clay (Valanginian?).

Infraturma AURICULATI Schopf emend. Dettmann 1963

Ischyosporites arkellii (Pocock 1970) comb. nov.1970 *Dictyotriletes arkelli* Pocock, p. 52, pl. 9, fig. 16A; *D. arkellii*, p. 119.Pocock's species is included here in *Ischyosporites* because it has a valvate exine.Cf. B. *Ischyosporites arkellii*

Plate 43, figs. 2–14; Plate 44, figs. 7–11; Plate 46, fig. 2

Sample. CUC 792, Cuckfield No. 1 Borehole, Sidnye Farm, Sussex (TQ 2962 2729), depth 792 ft (241.4 m); Wadhurst clay, Valanginian? Medium dark grey (N4) clay, thin fine silt laminations. *Equisetites in situ* and fragments of same. Preparation T210; 10 minutes Schulze solution, cleared in dilute NH_4OH , mineral separation, strew slides with Clearcol. AT8/16.

Description. A trilete miospore with a mean maximum equatorial diameter of 43.6 μm

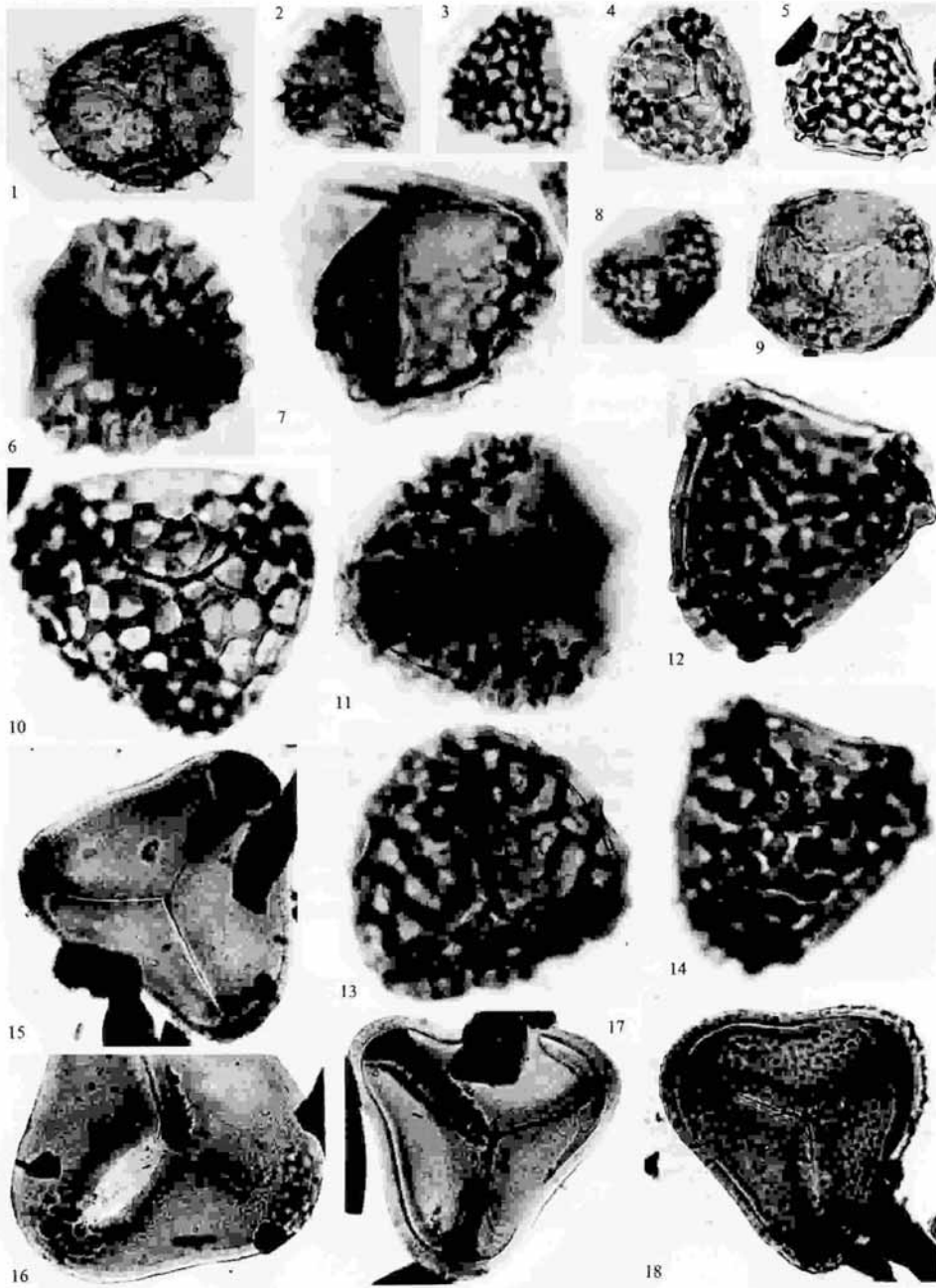
(standard deviation $5.1 \mu\text{m}$, observed limits $32\text{--}57 \mu\text{m}$, coefficient of variation 11.7% (100 specimens)) and a mean maximum polar diameter (including membranous lips of trilete mark) of $45 \mu\text{m}$ (twenty-two specimens). The amb has straight to slightly convex sides and rounded angles. The proximal face is slightly, and the distal face markedly, convex. The laesurae are straight or slightly sinuous and are longer than three-quarters of the spore radius. The membranous lips of the trilete mark are up to $5 \mu\text{m}$ high and have a basal width of $1.5\text{--}2 \mu\text{m}$. The (perfect or imperfect) distal reticulum encroaches on to the otherwise smooth proximal face at the angles. The muri are rounded or (sometimes) flat-topped, $0.5\text{--}3.5 \mu\text{m}$ (usually $1\text{--}2.5 \mu\text{m}$) high, highest where they join and at the angles. They are $1\text{--}2.5 \mu\text{m}$ wide except at intersections where the width may increase to $4 \mu\text{m}$. The lumina are generally subcircular to polygonal and $2\text{--}7 \mu\text{m}$ in diameter but may be larger and irregular if the reticulum is imperfect. They tend to be smallest in equatorial radial regions.

Thirty-two specimens are in polar and twenty-two in equatorial aspect. One weakly sculptured specimen has unusually convex sides (Pl. 43, fig. 9) but this is probably because the triradiate lips have parted. The compression of the specimens varies from relatively uncompressed to very compressed. A few show signs of corrosion in the form of pitting of the exine.

Discussion. The lumina of *Ischyosporites crateris* Balme 1957 are larger and the exine is thicker. *I. punctatus* Cookson and Dettmann 1958 has a thicker exine, foveoreticulate sculpture and wider muri. *I. marburgensis* de Jersey 1963 (Jurassic) has a different sculpture and a thicker exine. '*Lycopodiacidisporites*' *cerniidites* (Ross 1949; Delcourt and Sprumont 1955) Danz -Corsin and Laveine 1963 (*in Briche et al.* 1963; Lower Lias), has cristate sculpture disposed more or less concentrically and not forming a true reticulum. *Lycopodiumsporites crassimacerius* Hedlund 1966 has a thicker exine, is sculptured with a polygonal reticulum, and has higher muri. The distal sculpture of '*Ischyisporites*' *puzzlei* Levet-Carette 1966 consists of little cavities, rounded or more often vermiform in shape, separated by muri $3\text{--}5 \mu\text{m}$ wide. *Ischyosporites disjunctus* Singh 1971 is larger, and the muri are wider and the exine thicker. The nature of the murornate sculpture and/or other features distinguishes *I. arkellii* from the following: *L. dentimuratus* Brenner 1963, '*Ischyisporites*' *surangulus* Levet-Carette 1964 (Bajocian), *Foveosporis microfovearis* Krutzsch 1959 (Tertiary), *Ischyosporites asolidus* (Krutzsch 1959) Krutzsch 1967 (Tertiary), *I. foveasolidus*

EXPLANATION OF PLATE 43

- Fig. 1. *Retitriletes* sp. Preparation T210/14, L1 47.9 123.0, $\times 500$.
 Figs. 2-14. cfB. *Ischyosporites arkellii* (Pocock 1970) comb. nov. Preparation T210. 2, 3, Same specimen. 2, Proximal focus; 3, distal focus; T210/14, L1 30.3 121.6, $\times 500$. 4, T210/11, L1 35.6 121.2, $\times 500$. 5, T210/2, L1 42.7 118.0, $\times 500$. 6, Lateral view, T210/2, L1 28.7 118.7, $\times 1000$. 7, Oblique view, T210/1, L1 48.3 115.8, $\times 1000$. 8, T210/14, L1 25.2 119.7, $\times 500$. 9, Specimen weakly sculptured, unusually convex sides, T210/2, L1 46.0 122.8, $\times 500$. 10, Distal focus, T210/13, L1 60.7 123.7, $\times 1000$. 11, Lateral view, T210/14, L1 48.6 123.0, $\times 1000$. 12, 14, Same specimen. 12, Proximal focus; 14, distal focus; T210/3, L1 48.0 122.2, $\times 1000$. 13, Oblique view, T210/14, L1 47.5 122.0, $\times 1000$.
 Figs. 15-18. *Trilobosporites ivanovae* sp. nov. Preparation T061. 15, Holotype T061/1, L1 43.6 109.8, $\times 500$. 16, T061/1, L1 37.3 111.8, $\times 500$. 17, Margins of laesurae thickened, T061/1 L1 52.7 113.0, $\times 500$. 18, T061/1, L1 27.0 113.8, $\times 500$.



BATTEN, Cretaceous spores

Krutzsch 1967 (Tertiary), *I. tuberosus* Döring 1965, and *F. triangulus* Stanley 1965 (Paleocene).

The spores *Dictyotriletes arkelli* Pocock 1970 from the lower Bajocian of western Canada (not recorded from younger strata) are similar to those described here. Some characters differ slightly, but there are not sufficient criteria for the erection of a new species for the Wealden spores. The illustrations of *Klukisporites pseudoreticulatus* Couper 1958 in Agasiz (1969) resemble some of those of *I. arkellii* shown here. Forms comparable with *I. arkellii* have been recorded from the Ashdown Beds, Wadhurst Clay, Lower Tunbridge Wells Sand, and Grinstead Clay (Berriasian-Valanginian?).

Trilobosporites ivanovae sp. nov.

Plate 43, figs. 15-18; Plate 45, figs. 1-8; Plate 46, figs. 1, 5-9

Type sample. DJB 18, Philpots Quarry, West Hoathly, Sussex (TQ 3592 3221), 5.4 m above base of Grinstead Clay, Valanginian? Light brown (5YR 6/4) medium silt, plant fragments. Preparation T061; 20 minutes HNO₃, cleared in dilute NH₄OH, mineral separation, strew slides with Clearcol. AT13/14; S4, 5. Holotype slide T061/1, Ll. 43-6 109-8; Pl. 43, fig. 15.

Diagnosis. Miospore, trilete, mean maximum diameter 92 μ m, standard deviation 8.3 μ m (100 specimens). Amb triangular with slightly concave, straight or slightly convex sides and rounded angles. Distal surface more convex than proximal. Laesurae about $\frac{3}{4}$ spore radius, may divide near extremities, bordered by simple membraneous lips 1-2.5 μ m high. Exine may be slightly thickened for 4-7 μ m on each side of laesurae (forty-four specimens). Width of thickened zone may increase slightly near equatorial radial regions and merge with equatorial radial thickenings.

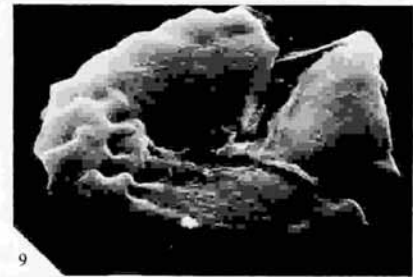
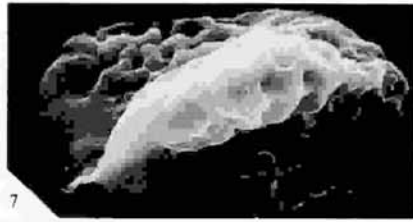
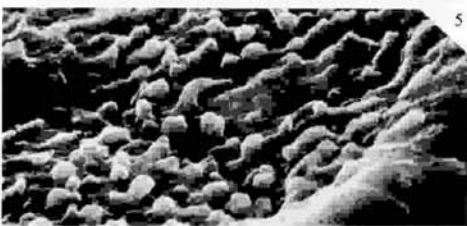
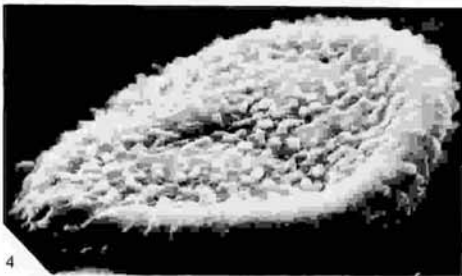
Exine mainly 3-5 μ m thick but generally thicker (up to 8 μ m) in equatorial radial regions; increase in thickness varies from 0.5 to 4 μ m. Thickened areas extend from 14 to 25 μ m over proximal and distal faces; boundaries usually indistinct. Exine scabrate, maculate, or sculptured with closely spaced (0.25 μ m or less apart) grana and/or verrucae. Verrucae subcircular, polygonal, or somewhat irregular in shape, usually < 1 μ m high and with a diameter of < 3 μ m interradially and < 5 μ m at the angles, may form a negative reticulum. Sculpture often more strongly developed on distal face and/or near equatorial radial regions. Forms with verrucate distal exines are usually maculate or scabrate in vicinity of proximal pole and in proximal interradiial regions.

EXPLANATION OF PLATE 44

All scanning electron micrographs.

Figs. 1-6. *Regresporites lophus* gen. et sp. nov. 1, 2, 3, Fifth specimen, on stub (SH) DB 36. 1, Part of distal surface, $\times 1000$. 2, Sculpture detail, $\times 1500$. 3, Sculpture detail, $\times 4000$. 4, 5, 6, Sixth specimen, (SH) DB 36. 4, Proximal surface, trilete mark weakly developed, $\times 1000$. 5, Sculpture detail, $\times 2000$. 6, Sculpture detail, $\times 5000$.

Figs. 7-11. cfB. *Ischyosporites arkellii* (Pocock 1970) comb. nov. Preparation T210. 7, 8, Specimen laterally compressed, (SH) DB 46. 7, $\times 1500$. 8, Sculpture detail, $\times 3500$. 9, Second specimen, proximal surface, $\times 1500$, (SH) DB 44. 10, Third specimen, lateral view, $\times 1500$, (SH) DB 46. 11, Fourth specimen, $\times 1500$, (SH) DB 44.



BATTEN, Cretaceous spores

Description. The observed limits of the maximum equatorial diameter of this microspore are 75–126 μm (coefficient of variation 9%) and of the maximum polar diameter are 62–80 μm (seven specimens). Although the increase in thickness of the exine from interradial to radial regions is usually about the same at each angle, differences of up to 3.5 μm have been noted. There is no increase in thickness at one or two of the angles of three specimens (Pl. 45, fig. 6). Three specimens which are sculptured with a few verrucae up to 7 μm in diameter and 3 μm in height (Pl. 45, figs. 10–12) are considered to be extreme variants.

Discussion. *Trilobosporites (Trilobosporites) tenuiparietalis* Döring 1965 has a thinner exine and more strongly concave sides. *Maculatisporites microverrucatus* Döring 1964 and *M. undulatus* Döring 1964, both from the Wealden A of Westmecklenburg, lack thickening of the exine in equatorial radial regions and are somewhat smaller; the exine of *M. microverrucatus* is also thinner. Rare specimens of *T. ivanovae* resemble *Lygodium (Tuberculata) triangulatum* E. Ivanova 1961 but the latter has a thinner exine.

The descriptions and illustrations of both *Lygodium (Cavernosotriangulata) cavernosum* E. Ivanova 1961 and *L. (C.) cavernosum* var. *tuberculatum* E. Ivanova 1961 (in Samoilovitch *et al.* 1961; Cenomanian) suggest that these taxa may fall within *T. ivanovae*, but in Ivanova's descriptions are insufficient to confirm this. Some of the weakly sculptured specimens of *T. ivanovae* resemble both *T. (Trilobosporites) aornatus* Döring 1965 (Upper Malm) and *T. (T.) crassiangularis* Döring 1965 (German Wealden A).

Forms comparable with *T. ivanovae* have been recorded from the Wadhurst Clay, Lower Tunbridge Wells Sand, and Grinstead Clay (Berriasian–Valanginian?).

Turma ALETES Ibrahim 1933

Subturma AZONALETES Luber emend. Potonié and Kremp 1954

Genus PILASPORITES Balme and Hennelly 1956

Pilasporites allenii Batten 1968

Plate 42, figs. 10, 11

A specimen of *Pilasporites allenii* from the type sample (CUC 792) was illustrated in Batten (1968, pl. 123, fig. 11) and described as having granules and small verrucate

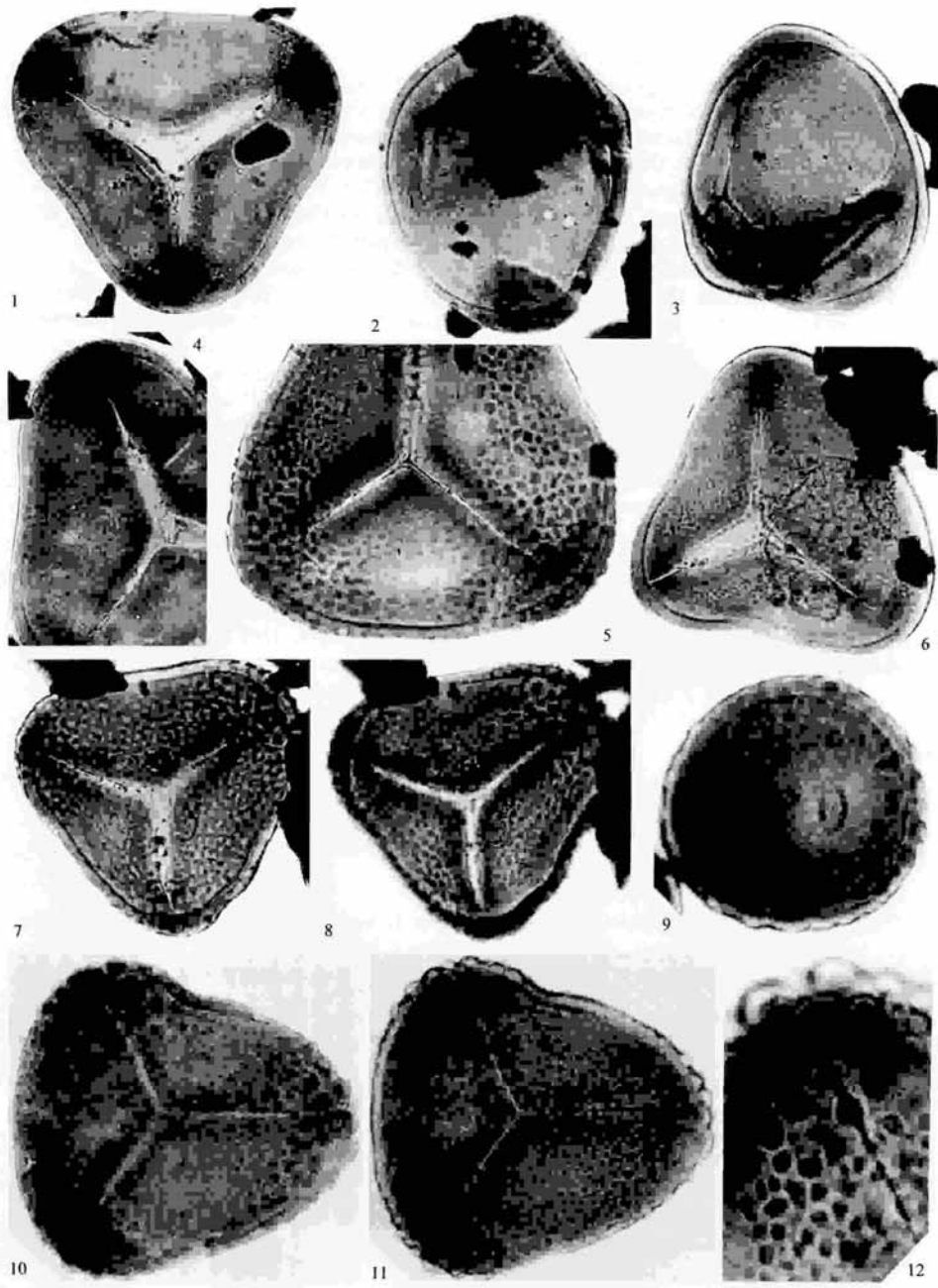
EXPLANATION OF PLATE 45

All figures $\times 500$ unless otherwise specified.

Figs. 1–8. *Trilobosporites ivanovae* sp. nov. Preparation T061. 1, Specimen with scabrate exine and scattered corrosion pits, T061/1, L1 35-1 112-2. 2, Lateral view showing equatorial radial thickenings, T061/1, L1 57-1 111-1. 3, Oblique orientation, T061/1, L1 35-7 114-3. 4, Small verrucae on distal face near equatorial radial thickening, T061/1, L1 43-0 111-1. 5, Unusually large specimen, T061/1, L1 44-9 114-2. 6, Exine weakly thickened in equatorial radial regions, T061/1, L1 35-3 113-7. 7, 8, Same specimen, strongly sculptured. 7, Equatorial focus; 8, distal focus; T061/1, L1 41-9 121-0.

Fig. 9. *Admolia amphidoxa* gen. et sp. nov. Preparation T209/2, L1 39-9 124-2, $\times 1000$.

Figs. 10–12. cfA. *Trilobosporites ivanovae* sp. nov., showing strongly developed sculpture in equatorial radial regions. 10, Equatorial focus; 11, proximal focus; 12, detail, $\times 1000$; preparation T053/2, L1 36-0 114-3.



BATTEN, Cretaceous spores

elements attached to a closely adhering perine. These elements (Pl. 42, fig. 11) are similar to the 'resin droplets' observed by Smith and Butterworth (1967, p. 145) on the Carboniferous miospore *Cadiospora magna* Kosanke 1950, and to the 'globules of ?tapetal material' (Evans 1970, p. 65) characteristically attached to the 'exoexine' of species of *Diaphanospora* Balme and Hassell 1962 emend. Evans 1970. They may also be comparable with Ubisch bodies (cf. Rowley 1963; Pettitt 1966). Lugardon (1969) showed similar bodies adhering to the perispore of spores of *Equisetum maximum* Lamk. Abnormal spores (not Ubisch bodies) attached to *P. allenii* exines occasionally occur in Wealden dispersed spore preparations. They are comparable with those of Gould (1968, pl. 2, fig. 11). Specimens of *P. allenii* may pseudomorph *Cycadopites* or *Taxodiaceapollenites* and resemble probable algal bodies, e.g. *Halosphaeropsis liassica* Mädlér 1963 (Lias) and *Leiosphaeridia pusilla* Mädlér 1963 (Lias). Species of *Inaperturopollenites* generally have thinner exines containing many more secondary folds than is usual in *P. allenii*.

P. allenii was compared by Batten (1968) with other miospore species, some attributed to the Equisetaceae (*Equisetites*/*Equisetum*). Additional records of dispersed miospores which have been (tentatively) attributed to the family or genera or compared with the spores of *Equisetum* are listed on Table 2. Other dispersed spore species resembling *P. allenii* are also listed. Perhaps most closely comparable with *P. allenii* is *P. marcidus* Balme 1957 (Batten 1968, p. 641), from the Lower Jurassic of Western Australia, and recorded from both the Jurassic and Cretaceous. It may have affinities with the Equisetaceae (Balme 1957, p. 28) but other species of *Pilasporites* (including the type species *P. calculus* Balme and Hennelly 1956, *P. plurigenus* Balme and Hennelly 1956, and others) are unlikely to be so related.

INCERTAE SEDIS

ADMOLIA gen. nov.

Type species. A. amphidoxa sp. nov.

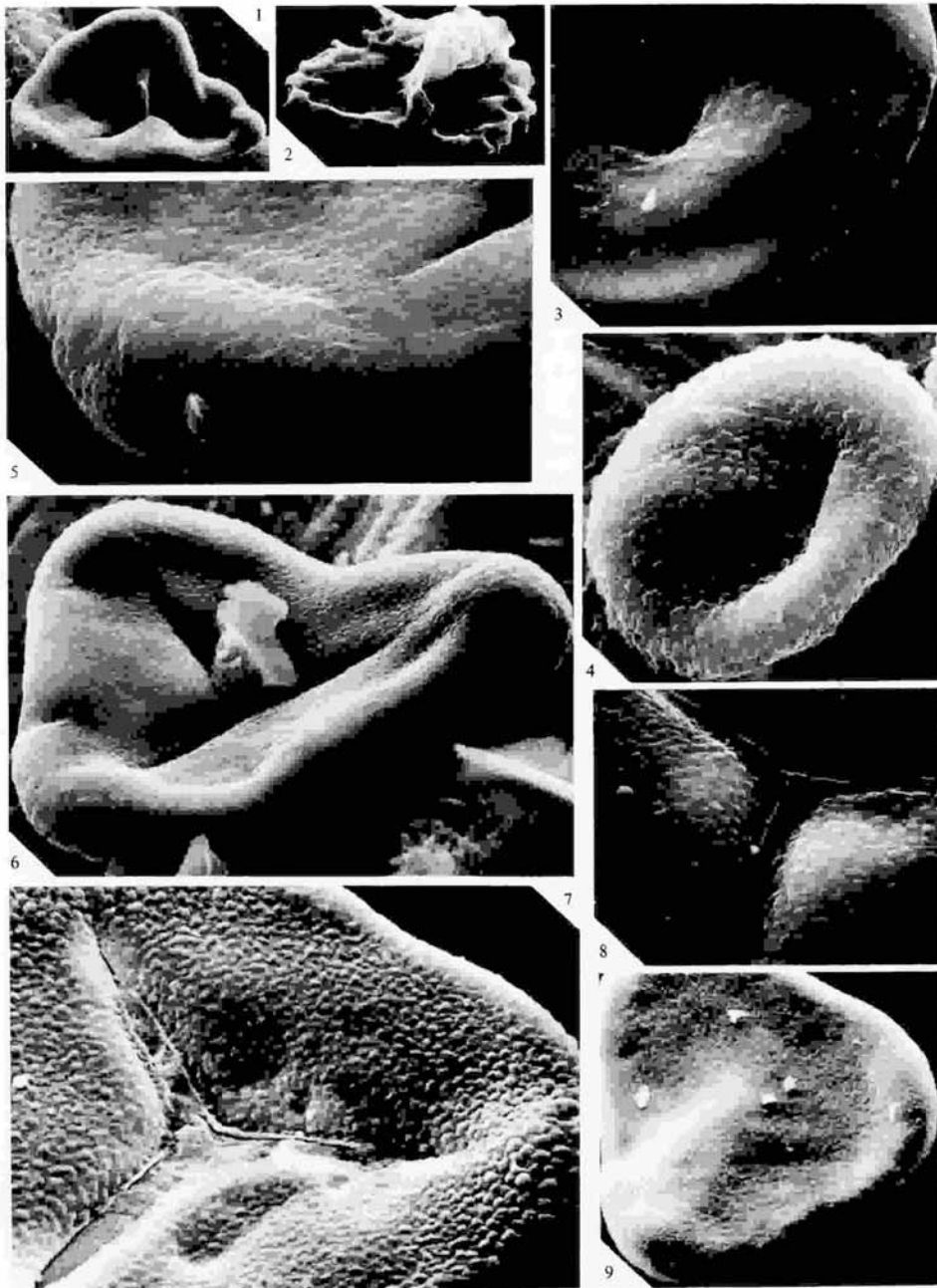
Diagnosis. Spherical or subspherical body in uncompressed state. Exine differentially thickened, smooth or sculptured, may show a circular or subcircular perforation (rarely a pore) on thinnest part.

Discussion. Forms referable to *Exesipollenites* have a circular depression, which probably represents a pore, surrounded by exine thickening. The wall of *Discoperculina* Phillips 1971 is thickest by the operculum; this palynomorph also has a thin-

EXPLANATION OF PLATE 46

All scanning electron micrographs.

Figs. 1, 5-9. *Trilobosporites ivanovae* sp. nov. Preparation T061. 1, 5, Specimen on stub (SH) DB 33. 1, Proximal view, $\times 400$. 5, Detail of radial equatorial region, $\times 2000$. 6, Second specimen, $\times 1000$, (SH) DB 33. 7, Third specimen, part of proximal exine, $\times 1000$, (SH) DB 8. 8, Fourth specimen, detail of proximal pole, $\times 2000$, (SH) DB 33. 9, Fifth specimen, distal surface, $\times 500$, (SH) DB 8.
Fig. 2. cfB. *Ischyosporites arkellii* (Pocock 1970) comb. nov. Fifth specimen, $\times 750$, (SH) DB 46.
Figs. 3-4. *Admolia amphidoxa* gen. et sp. nov. Preparation T209. 3, Specimen with pore, $\times 2000$, (SH) DB 34. 4, Second specimen, $\times 1500$, (SH) DB 36.



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walled inner body. *O. carbonis*, of the monotypic genus *Operculites* Newman 1965 is smaller than *A. amphidoxa*, bears a rounded or helicoidal operculum of width about $\frac{1}{3}$ – $\frac{2}{3}$ grain diameter attached at one side when in place, and the exine is thinner and not differentially thickened.

Admolia amphidoxa sp. nov.

Plate 45, fig. 9; Plate 46, figs. 3, 4; Plate 47, figs. 1–14

Type sample. CUC 791/11, preparation T209; details under *Regresporites lophus* sp. nov. Holotype slide T209/2, LI 27.4 115.1; Pl. 47, fig. 5.

Diagnosis. Mean maximum diameter of grain $42.5 \mu\text{m}$, standard deviation $4.7 \mu\text{m}$ (200 specimens). Amb circular or subcircular. A circular or subcircular perforation of exine (rarely a pore or tear) $5\text{--}8 \mu\text{m}$ in diameter, may be present on thinnest part of differentially thickened exine. Perforation frequently only partially separates (sub)circular area of exine (operculum) from surrounding exine, but separation may be as much as $3 \mu\text{m}$. Thickness of exine mainly between 2 and $4.5 \mu\text{m}$; difference between thinnest and thickest parts varies considerably (from < 0.5 to $3 \mu\text{m}$), thickest on face opposite perforation. Exine smooth, gently undulating, or scabrate, or sculptured with micrograna, grana, or dome-shaped verrucae or combinations of these. Sculpture often more weakly developed on thinnest part of wall. Height of verrucae usually $1 \mu\text{m}$ or less, but may be as much as $3 \mu\text{m}$. Elements sometimes separated by distances greater than their diameter but usually closely spaced and partially coalescent, may form a negative reticulum.

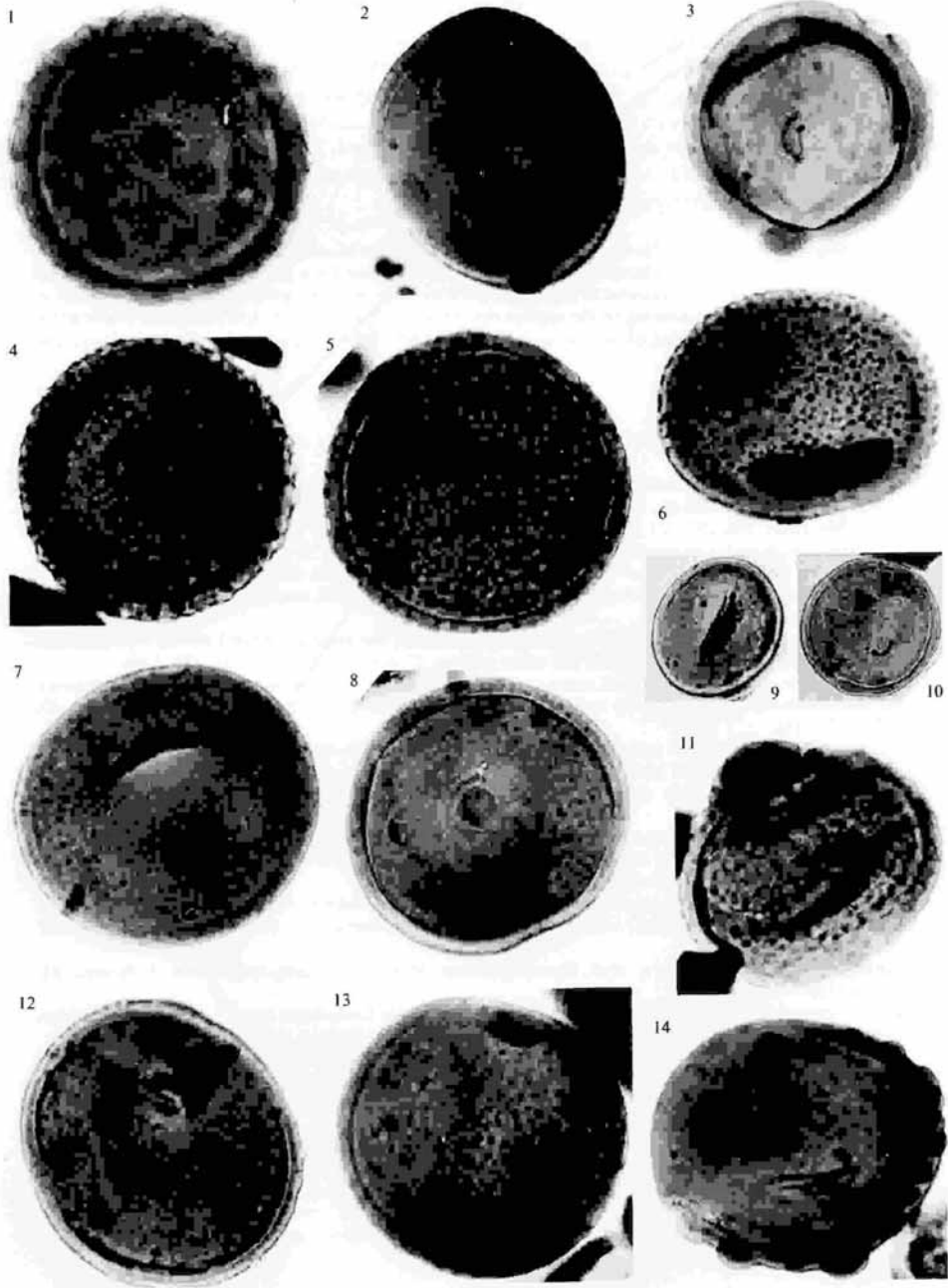
Description. The observed limits of the maximum diameter of the body of this palynomorph are $33\text{--}57 \mu\text{m}$ (coefficient of variation 11.1%). The exine of seven specimens is *c.* $1.5 \mu\text{m}$ around the perforation. One-hundred-and-two specimens show a small circular or subcircular perforation in the exine (Pl. 47, fig. 8), eight show a pore or tear (Pl. 46, fig. 3). The perforation may be obscured by a small fold developed on the thin area, and it is invisible in some compression states or orientations. Discrete grana, bacula, or verrucae may be superimposed on low verrucae. The specimens are compressed but generally well preserved.

Discussion. *Foveinaperturites paucipunctatus* Pierce 1961 is larger and has an infra-punctate, sparsely foveolate exine. Some phytoplankton show a naturally constituted exit hole. Forms probably comparable with *A. amphidoxa* have been seen in the Tertiary (A. E. González Guzmán, pers. comm.). The relatively small size variation

EXPLANATION OF PLATE 47

All figures $\times 1000$ unless otherwise specified.

Figs. 1–14. *Admolia amphidoxa* gen. et sp. nov. Preparation T209. 1, T209/2, LI 37.7 109.3. 2, Showing perforation of thinnest part of differentially thickened exine, T209/2, LI 52.1 113.0. 3, T209/2, LI 25.3 117.8. 4, T209/1, LI 54.6 116.7. 5, Holotype, T209/2, LI 27.4 115.1. 6, T209/2, LI 29.0 123.8. 7, Perforated area of exine on fold, T209/2, LI 38.3 119.6. 8, T209/2, LI 42.2 124.2. 9, Smooth exine, T209/2, LI 28.8 114.1, $\times 500$. 10, Partial separation of circular area from surrounding exine, T209/2, LI 25.8 118.9, $\times 500$. 11, Large verrucae, T209/2, LI 33.6 115.3. 12, T209/2, LI 34.7 124.7. 13, T209/2, LI 51.1 118.0. 14, Large dome-shaped verrucae, T209/1, LI 47.2 129.6.



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and the variety of sculpture observed in this population is usual. DJB 294, a sample from the Wadhurst Clay of the High Brooms Brick and Tile Company's pit at Southborough, Kent (TQ 5948 4189), however, yielded an assemblage composed almost entirely of smooth forms. The High Brooms assemblages are mostly smaller and darker in colour than the population on which this species is based. Specimens identified as *A. amphidoxa* have so far only been recorded from the Wadhurst and Grinstead Clays (Valanginian?).

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D. J. BATTEN
Robertson Research International Ltd.
'Ty'n-y-Coed'
Llanrhos, Llandudno
Caernarvonshire