

BARREMIAN EARLIEST ANGIOSPERM POLLEN

by NORMAN F. HUGHES, GILLIAN E. DREWRY, and JOHN F. LAING

ABSTRACT. The first 'angiosperm' fossils from palaeolatitude Cretaceous 35° N. or more, appear to be tectate pollen from the English upper Wealden. This pollen with angiospermid characters is always less than 1% of Barremian palynomorph assemblages, and the usual grain diameter is less than 25 microns; it has, therefore, been necessary to study it by direct SEM search of strew mounts, enabling sculpture characters well below one micron to be used in correlation. Seven new fully described taxa and eight more candidate-taxa are presented from mid and late Barremian rocks of England; they have been described as biorecords and comparison records, the principal developments in this paper being the use of names instead of numbers for the records and a provision for the orderly mention of subordinate records. The records have also been referred to existing taxa in the few cases in which this has been possible. Although most of the records are from the upper Wealden Group, others are from fully marine strata; they also continue to be well represented into the Lower Greensand above. Comparison is made with fossils of lower Zone I of the Potomac Group of the eastern United States, and a preliminary correlation bracket is offered. The need for two separate but compatible systems of data-handling is discussed. Problems of extension of the evolutionary search both before and immediately after the mid Barremian are outlined.

THE dispersed tectate pollen grains here studied from the upper part of the Wealden appear to be the earliest fossils with angiospermid characters in the English succession. The age of these first records is now established as mid Barremian and there is every prospect of progressive refinement of this time-correlation as palynological observations are extended. Any such time-scale correlation advances will also serve to date the comparable pollen of the lowest part of the Potomac Group of the eastern United States, for which stratigraphic control is less clear. Some of these angiospermid pollen grains have now also been found in marine strata of eastern England, and they will be useful in the difficult time-correlation of the essentially non-marine Wealden with the European and global time-scale.

These English fossils from about palaeolatitude 35° KrN occur most usefully in a long continuous rock succession which provides scope for a search for the pollen of immediate gymnospermous ancestors, although we do not yet have any success to offer in this field. If, however, the suggestion that fossils in some lower palaeolatitudes might eventually prove to be slightly earlier (Doyle *et al.* 1977), the critical evolution may have taken place there (palaeo-equatorially) and the English succession might be recording only migration.

SEM studies have revealed unexpected diversity in these very small pollen grains at this early stage of their history. The purpose of this paper is to present firm neutral taxonomic and stratigraphic documentation of those taxa that have so far been recorded in adequate quantity.

MATERIAL AND METHODS

The presence of *Clavatipollenites* in upper Wealden strata has been known for twenty years (Couper 1958; Hughes 1958), and unpublished records have subsequently

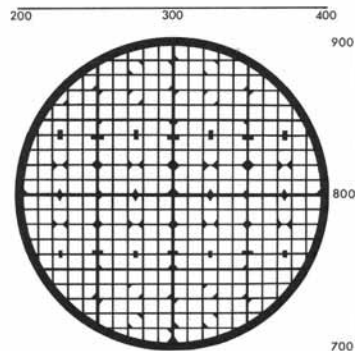
[*Palaeontology*, Vol. 22, Part 3, 1979, pp. 513-535, pls. 57-64.]

extended knowledge. However, light microscope searching for this relatively rare small pollen grain and making meaningful observations of it (Kemp 1968) proved laborious and inconclusive. Now that SEM study has greatly improved observation potential (Laing 1974, 1975), over 300 grains have been photographed in this Department in the last three years and it has become necessary to plan a new sequence of study of samples.

Initially most effort was put into core-samples from the Warlingham borehole (Worsam and Ivimey-Cook 1971) which provided a relatively continuous section of rocks from Berriasian to earliest Aptian age; this gave information on first occurrences and succession and can still eventually give more on precursors of *Clavati-pollenites*. The Isle of Wight (Atherfield) outcrop cliff section (White 1921) provided some check on the Warlingham succession and also a continuation into the Aptian where surprisingly the marine nature of the rocks did not decrease the number of records (see Kemp 1970). For marine correlation in Barremian time an extensive search of successions in Lincolnshire (Alford borehole; Swinnerton 1935), Yorkshire (Speeton), and Norfolk has begun; this will take longer if only because of the relative rarity of angiospermid pollen in these marine facies at a time when it was only just entering the Wealden succession.

The palynological samples that have been productive are mainly grey siltstones. They have been treated by a standard extraction method for light microscope study involving HCl, HF, centrifuging, and the use of zinc bromide (S.G. 2.0) as a heavy liquid; oxidation of unwanted organic matter was by concentrated HNO₃ for periods of from ten to thirty minutes with brief clearance by alkali using ammonium hydroxide (to avoid the exine swelling associated with use of KOH). A few samples very recently prepared specifically for SEM were not oxidized, or were treated for only one to two minutes. Some residues of preparations from more than fifteen years ago were stored in glycerine jelly; this was dispersed without difficulty by hot water; a few of these older preparations had been oxidized for longer periods but could not be remade for lack of sample.

SEM stubs were equipped with nickel grids (see Laing 1974) of a new design (by G. E. D.) with sufficient identification marks (text-fig. 1) for rapid relocation at high



TEXT-FIG. 1. Cambridge Geology Mark 2 nickel grid (photo by courtesy of Mr. Smethurst) used on standard SEM stubs. Co-ordinate pattern of 'eastings' and 'northings' used for locating all specimens; data stored with film negatives. A selection of marks on the grid provide orientation and also location without frequent changes of scale.

magnifications. They are obtainable as Cambridge Geology Mark 2 nickel grids from Smethurst High-Light Ltd., 420 Chorley New Road, Bolton, Lancs., BL1 5BA. Adhesive for the grid to the stub is Reeves Acrylic Polymer Varnish Code 11409. Material from preparation residue (in distilled water) was strewn evenly over the whole stub. Specimens were coated with gold/palladium in the standard way. The gridded stub was traversed systematically, and co-ordinate readings were kept for photographing selected specimens. The stubs were stored, and are re-coated if observed again, but the negatives on 70 mm film (Ilford FP4) form the effective record. The SEM is a Cambridge S600.

DATA-HANDLING OPTIONS

Under the current pressures both on man hours available for study of such microfossils and on publication of the results, it is tempting to shorten the procedure and to abandon the use of taxa altogether in favour of simply obtained and reproduced records of the appearance of new characters. We have resisted this step and erected taxa because we prefer to keep our records compatible with past work and with generally accepted traditions.

The International Code of Botanical Nomenclature (ICBN) is ostensibly only concerned with names, but it presumes use of a Linnean system of taxonomy, and its protagonists have come over the years to attempt to make that use obligatory. This system is adequate for organisms from the single (Recent) time plane and, because of its cluster basis, works well enough for 'lumping' of organisms or taxa (even of fossils) for biological interpretation purposes (option LL—'Linnean lumping'). Perhaps its single greatest disadvantage is the type and synonymy arrangement which always requires good new 'wine' of more detailed scientific description to be submerged in outmoded jumbles of old 'bottles' of previous taxa which have to be retained for their antique priority of names.

For stratigraphical purposes, the need is for identification and labelling of differences (i.e. option SS—stratigraphic 'splitting') which logically requires an entirely opposite approach.

PALAEONTOLOGICAL DATA-HANDLING SYSTEM SS

The data-handling system used below was described by Hughes (1975, 1976, p. 26). The principal developments in this paper are the use of names instead of numbers for the records (see Hughes and Croxton 1973), and a provision for the orderly mention of subordinate records which may be important but which have not yet been brought up to the data-base standards we are attempting to establish.

Reference taxa and filing. The reference taxa are *biorecords* that are comparable in scope with species, but each consists of a stated number of fossils from a stated unit of rock (usually a single sample). A biorecord once made, cannot be changed in circumscription or in name; it has no type, nor priority; it may be used, or ignored without formality, by subsequent workers. A biorecord must be accommodated in a *genusbox*, which is essentially a file for search purposes which has morphologic limits

TABLE 1. Sample, preparation, SEM stub and film data relating to biorecords of Barremian angiospermid pollen.

Sample number	Oxidation minutes	Preparation number	Stub number	Film numbers	Biorecords	Comparison records
F317	10	F317	GD180	B127-156	-DIDENT	cfA-MONBAC, -BACCAT cfA-NEWLING, -TRIANG
B38	30	V081	GD136	B73		cfA-DIDENT
B44	10 15	X272 X290	GD150 GD173,174	B87,88 120-123		cfA-DENTAT
K469	5	X306	GD165	B108		-CAND(SUBDENT) PERPOTROT-SPOT
K474	5	X307	GD167,168	B31,32 77,78	-CROTON -TRIANG	-CAND(SUBCROT) -CAND(KRIKSEL)
K475	5	X081	JL47,48	115,118	-MONBAC	-CAND(TERRAC) -CAND(CROCHET)
WM129B/4	15	W116	JL37/3B	B14,15		cfA-BACCAT
WM1333/10	20	W106	JL22,35,36 49,50,52	B3,8,9,18,19 21-26,33,34 100	-BACCAT, -NEWLING	cfA-CROTON cfB-NEWLING
WM1345	30	W072	GD73	B46		cfA-NEWLING
WM1353/6	5	X078	JL45	B27,28		cfA-BACCAT cfA-DENTAT
WM1394/1	30	W055	JL41,42	B15		cfA-NEWLING
WM1415/6	5	X105	JL55,56	B38-41,103- 105	-DENTAT	cfA-NEWLING -CAND(LAEVOAT)
WM1423/2	25	V960	JL43,44	B16,17		cfA-DENTAT
WM1488/7	25	V957	GD81	B48,49		cfA-NEWLING
Iirg	20	W415	GD125,126	B70,71,124 125,126		cfA-BACCAT cfA-CROTON

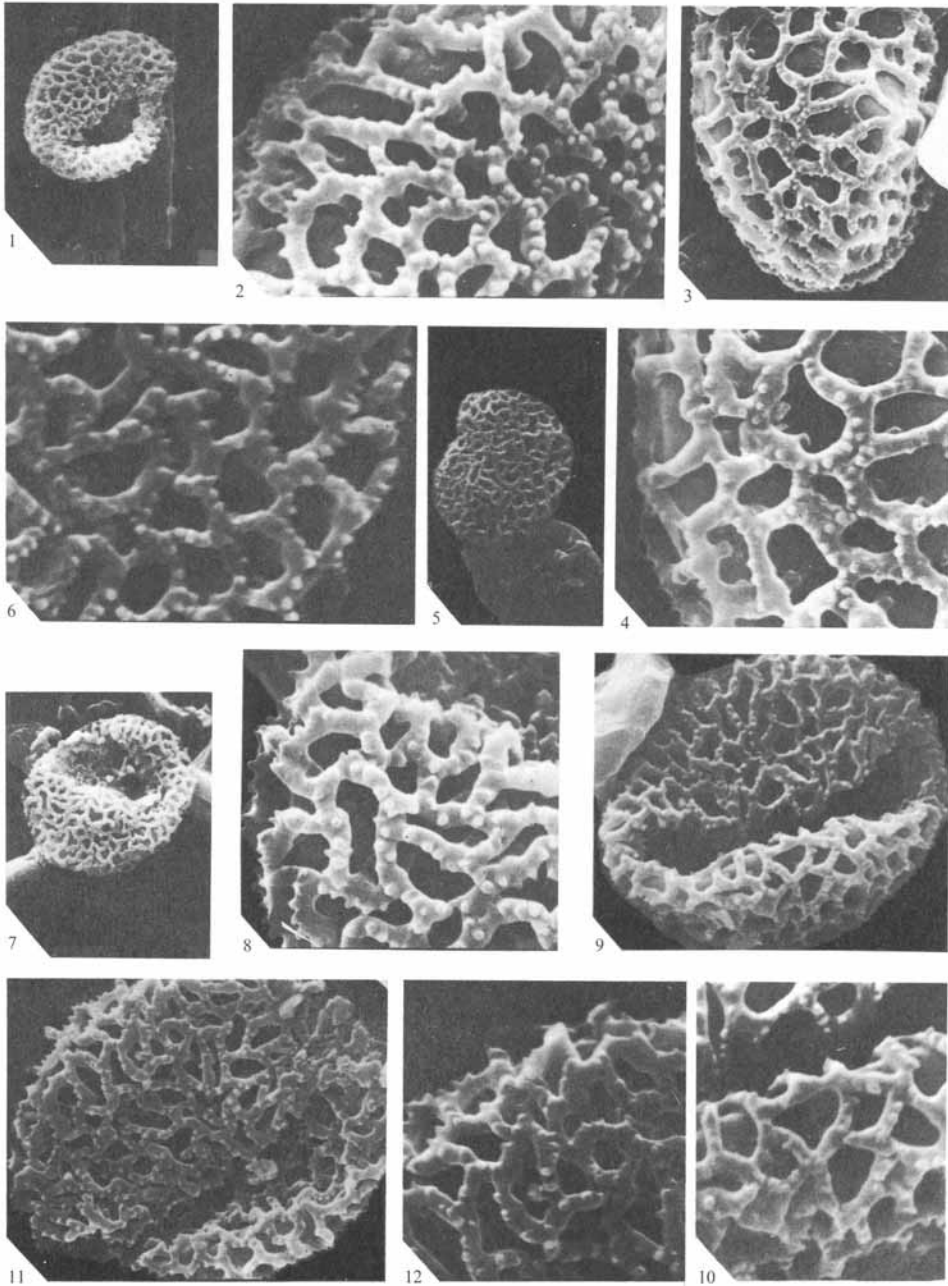
All materials stored in Department of Geology, Sedgwick Museum, Cambridge. Sample key: K = Kingsclere borehole; WM = Waringham borehole; Iirg from Alford borehole, Lincolnshire; F and S = outcrop samples, Isle of Wight (see text-fig. 2).

against adjacent genusboxes. A superior file, known as a *group*, is organized on a stratigraphic time basis; we believe that because this is only a filing device, intermediate hierarchical terms are not necessary.

Comparison taxa. All other relevant assemblages of fossils that are considered significant are placed in taxa known as *comparison records*, for which a degree of comparison with a biorecord (expressed as cfA, cfB) is required from the observer; the presence of such a comparison record is then of direct application in stratigraphic correlation (Hughes and Moody-Stuart 1969).

EXPLANATION OF PLATE 57

Figs. 1-12. Cretaceous (angiospermid) pollen; RETISULC-DENTAT biorecord: Barremian age; Upper Wealden, Waringham borehole, depth 1415 feet; preparation no. X105; Films B39, B40, B103, and B105 (GED); Stub JL55 (JFL). 1-2, Ref. 350728; 1, B103/1, $\times 2000$; 2, B103/3, $\times 10000$. 3-4, Ref. 345814; 3, B40/106, $\times 5000$; 4, B40/107, $\times 10000$. 5-6, Ref. 302707; 5, B105/21, $\times 2000$; 6, B105/23, $\times 10000$. 7-8, Ref. 281754; 7, B39/27, $\times 2000$; 8, B39/29, $\times 10000$. 9-10, Ref. 360819; 9, B103/24, $\times 5000$; 10, B103/26, $\times 10000$. Film B41 (GED), Stub JL56 (JFL). 11-12, Ref. 282814; 11, B41/27, $\times 5000$; 12, B41/28, $\times 10000$.



HUGHES *et al.*, Cretaceous angiospermid pollen

Nomenclature. The biorecord trivial name is intended to be pronounceable but does not normally exceed two syllables or seven letters; in order to be distinct from existing names, it is *not* latinized, and is set in one case of type, here capitals. The genusbox name is also pronounceable, with a normal limit of three syllables or eight letters. Trivial and genusbox names are always linked by a hyphen; trivial names appearing alone bear a hyphen in front of the word, e.g. -BACCAT; genusbox names bear a hyphen at the end of the word, e.g. RETICHOT-.

Subordinate records. RETISULC-CAND(LAEGVAT) indicates an intended biorecord with trivial name -LAEGVAT which has as yet an insufficient number of specimens from any one sample for formal description, although numerous specimens may be known from a scatter of samples. PERFOTECT-SPOT represents interesting specimens with morphology within the limits of PERFOTECT- genusbox.

Standards. Our aim has been to obtain twenty specimens from one sample for a biorecord, but we accept eight; for a comparison record, a quarter of these numbers is theoretically suitable, i.e. aim for five, accept two. The biorecord -CROTON is an exception (Table 2), made because of the existence of numerous comparison records of this taxon. However, as long as the facts are provided, subsequent workers can decide whether to jettison a biorecord.

SYSTEMATIC DESCRIPTIONS

As many details as possible of the biorecords and of some sub-taxa are shown on Tables 1 and 2. Comparison records are not described or figured.

Group EARLYCRETPELL

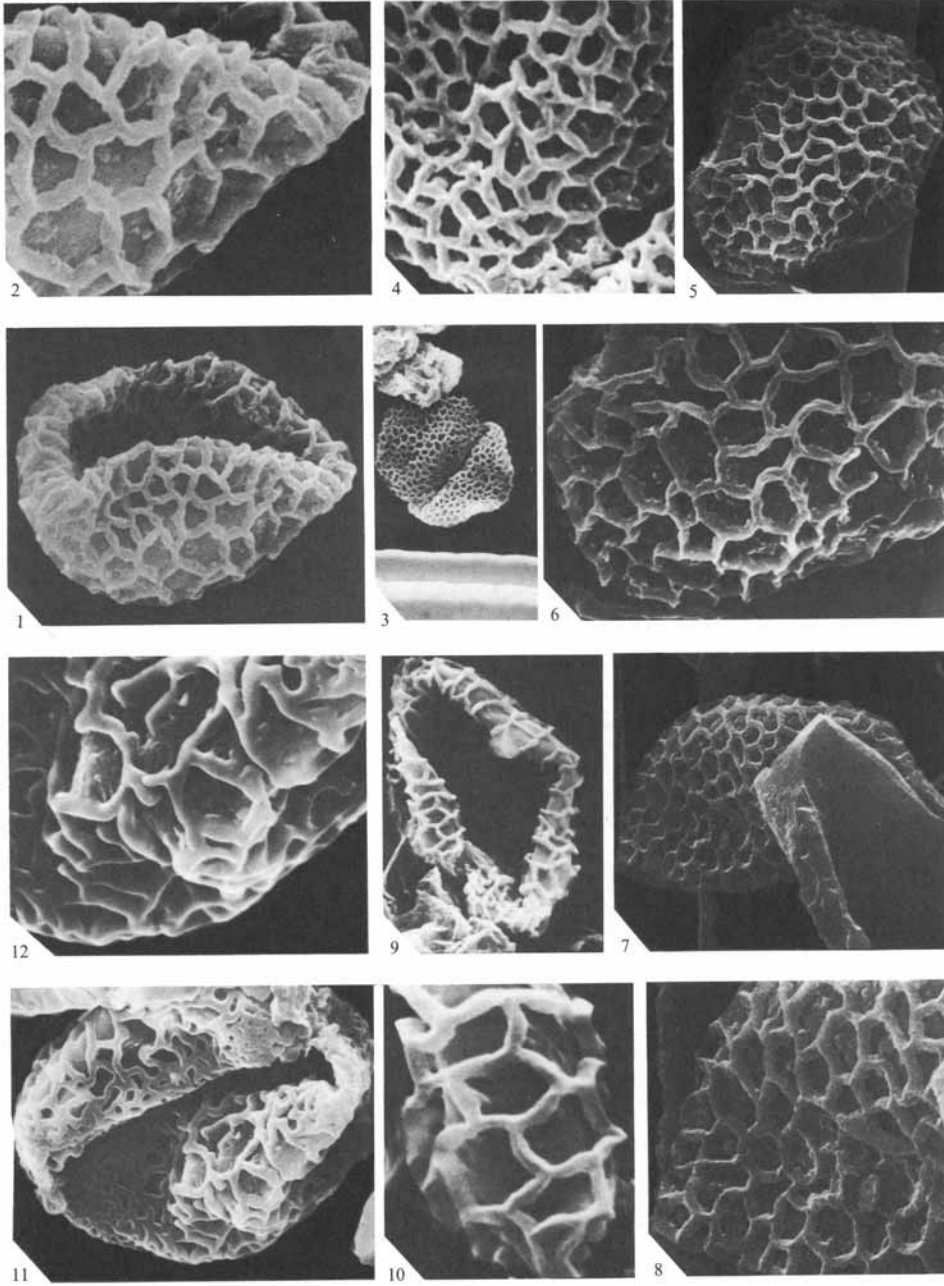
Nature of file. To contain all fossil pollen, or supposed pollen, of early Cretaceous age. Subgroups may subsequently be erected for time-divisions within the early Cretaceous. Morphological groupings should be expressed in genusbox or genus.

Genusbox RETISULC-

Descriptive limits. Monosulcate semitectate columellate pollen, excluding biorecords in which other aperture arrangements, or in which full tecta, may predominate. The tectum appears as a continuous reticulum, described in terms of muri and lumina; muri with expanded suprategal processes as in SUPERRET- are excluded.

EXPLANATION OF PLATE 58

Figs. 1-12. Cretaceous (angiospermid) pollen; Barremian age; Upper Wealden, Warmingham borehole. RETISULC-NEWLING biorecord: depth 1333/10 feet; preparation no. W106; Film B21, Stub JL49 (JFL); Films B25, B33, and B34 (JFL), Stub JL35 (JFL); Film B100 (GED), Stub JL52 (JFL). 1-2, Ref. 283848; 1, B34/1, $\times 5000$; 2, B34/3, $\times 10000$. 3-4, Ref. 258841; 3, B33/13, $\times 2000$; 4, B33/12, $\times 10000$. 5-6, Ref. 340705; 5, B25/3, $\times 5000$; 6, B25/4, $\times 10000$. 7-8, Ref. 341840; 7, B21/15, $\times 5000$; 8, B21/16, $\times 10000$. 9-10, Ref. 252782; 9, B100/27, $\times 5000$; 10, B100/29, $\times 20000$. RETISULC-CAND(LAEGVAT): depth 1415/6 feet; preparation no. X105; Film B40 (GED); Stub JL55 (JFL). 11-12, Ref. 333828; 11, B40/94, $\times 5000$; 12, B40/95, $\times 10000$.



HUGHES *et al.*, Cretaceous angiospermid pollen

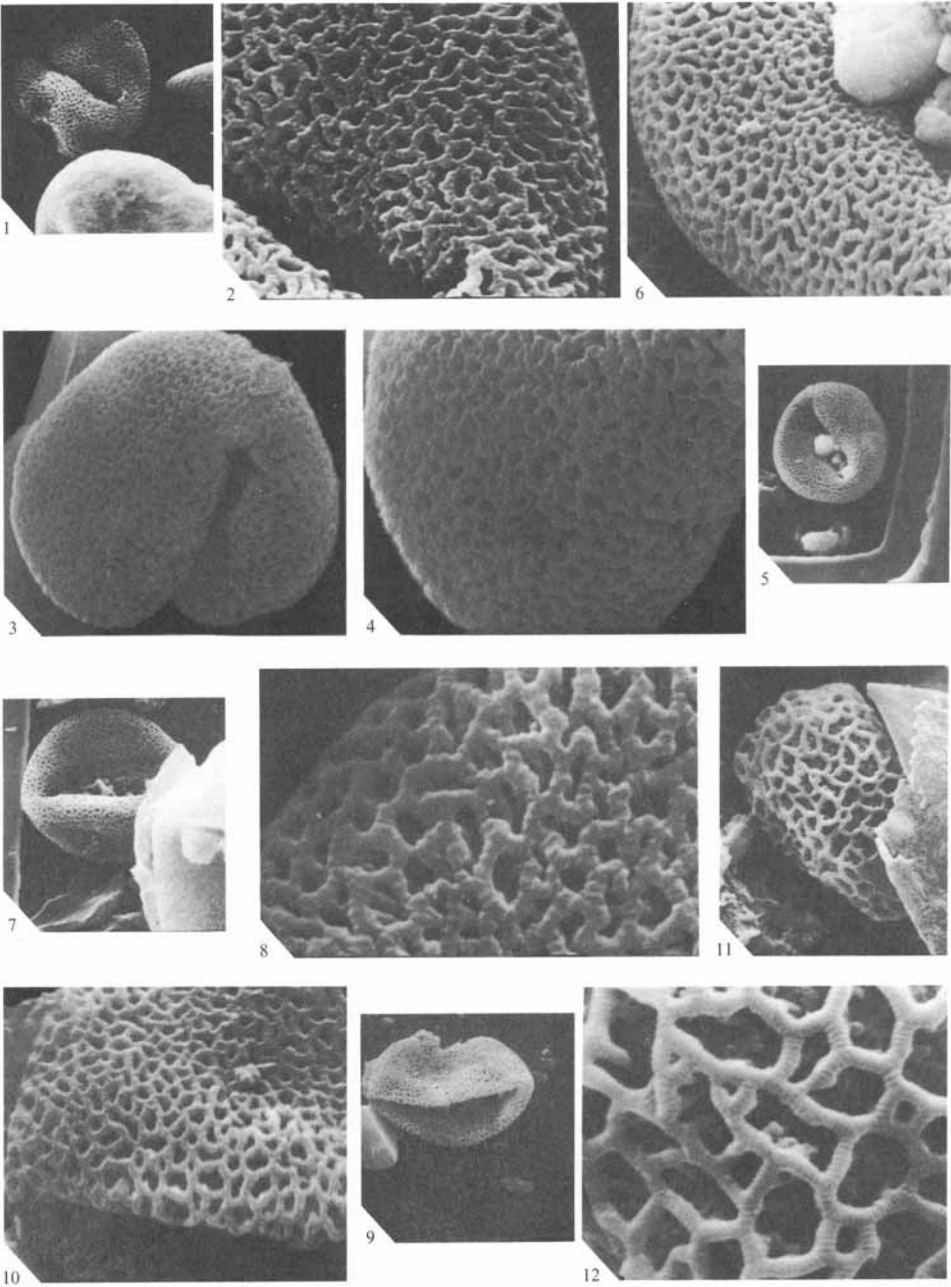
TABLE 2. Descriptive data for comparison of all figured biorecords and sub-taxa mentioned in the text section on systematics.

Name and status	Number of specimens	Maximum diam. μm	Aperture	Shape	No. lumina in 4 μm square	Columnella Height μm	Columnella Width μm	Murus Depth μm	Murus Width μm	Suprotestal processes Height μm	Suprotestal processes Width μm
<i>BIORECORD</i>											
DENTAT	24	19 (5-21; 20-72; 37)	MONOSULC.	ELLIPSOID	(4) 6.5 (9)	10 (0-4) 0.56 (0.8)	12 (0.3) 0.47 (0.6)	(0-2) 0.39 (0.5)	(0-4) 0.45 (0.6)	0.0 0.22 (0.3)	(0.2) 0.24 (0.3)
BACCAT	13	9.6 (5-8-9; 2)	3-4 CHOTOMO-SULCATE	SUB-SPHEROID	(3) 2.2 (2.8)	5 (0.3) 0.4 (0.6)	5 (0.2) 0.3 (0.4)	(0-2) 0.28 (0.3)	(0.3) 0.32 (0.4)	(0-1) 0.1 (0.0)	(0-1) 0.13 (0.2)
MONBAC	8	94-118-322 (0)	MONOSULC.	SUB-SPHEROID	(4) 5.6 (8.5)	7 (0.3) 0.34 (0.5)	7 (0.2) 0.2 (0.2)	(0-2) 0.27 (0.4)	(0-2) 0.27 (0.4)	(0-1) 0.11 (0.2)	(0-2) 0.23 (0.3)
DIDENT	15	13 (5-21; 18-62; 21.5)	MONOSULC.	SUB-SPHEROID	(22) 4.1 (7.8)	4 (0.2) 0.32 (0.4)	12 (0.17) 0.28 (0.3)	(0-2) 0.2 (0.2)	(0-2) 0.2 (0.2)	(0-2) 0.2 (0.2)	(0-2) 0.2 (0.2)
NEWLING	14	13-116-619 (6)	MONOSULC.	ELONGATE	(7) 10 (6)	(0-1) 0.13 (0.2)	(0-1) 0.14 (0.2)	(0-1) 0.3 (0.2)	(0-2) 0.3 (0.4)	0	0
CROTON	5	29-133-538 (0)	MONOSULC.	ELLIPSOID	(4) 7.5 (12)	(0-1) 0.12 (0.2)	(0-1) 0.12 (0.2)	—	(0-3) 0.35 (0.47)	3 (0-4) 0.47 (0.6)	(0-6) 0.76 (1.0)
TRIANG	9	29-130-633 (5)	MONOSULC.	ELLIPSOID	(3) 4.5 (7)	(0-1) 0.17 (0.3)	(0-1) 0.13 (0.2)	—	(0-3) 0.38 (0.5)	(0-5) 0.58 (0.7)	(0-9) 0.97 (1.1)
<i>CAND</i>											
LAEVGAT	5	19.1	MONOSULC.	ELLIPSOID	4 12.75	3 0.26	3 0.26	0.3	0.38	0	0
CROCHET	3	17.3	MONOSULC.	ELLIPSOID	2.0	0.23	0.21	0.26	0.3	0	0
TEEBAC	3	15.0	MONOSULC.	ELLIPSOID	14.5	0.3	0.21	0.28	0.31	0.05	0.05
SUBCROT	3	18.0	3-CHOTOMO-SULCATE	SPHEROID	5.5	—	—	—	—	0.4	0.4
KRINKEL	2	3.9	MONOSULC.	ELLIPSOID	2.4	0.4	0.2	—	0.2	0.45	0.5
DUBDENT	2	16.0	MONOSULC.	ELLIPSOID	3.5	—	—	0.4	0.55	0.25	0.25
<i>SPOT</i>											
PERFOTECT	2	15.5	MONOSULC.	ELLIPSOID	3.8	—	—	0.55	0.4	0	0

Mean values are given where appropriate with maximum and minimum observations in parentheses. Number placed above in certain boxes indicates the number of observations made when it was less than the number of specimens. For other data see appropriate plates and text. Key: 0 refers to specimens without processes; — = observation could not be made.

EXPLANATION OF PLATE 59

Figs. 1-12. Cretaceous (angiospermid) pollen; RETISULC-MONBAC biorecord: Barremian age; Upper Wealden. 1-2, Kingsclere borehole, depth 475 feet; preparation no. X081; Film B77 (GED); Stub JL48 (JFL). 1-2, Ref. 236865; 1, B77/28, $\times 2000$; 2, B77/30, $\times 10000$. 3-4, Film B32 (JFL); Stub JL47 (JFL); Ref. 340848; 3, B32/31, $\times 5000$; 4, B32/32, $\times 10000$. 5-8, Kingsclere borehole, depth 474 feet; preparation no. X307; Film B115 and B116 (GED); Stub GD167 (GED). 5-6, Ref. 349851; 5, B116/15, $\times 2000$; 6, B116/17, $\times 10000$. 7-8, Ref. 291813; 7, B115/11, $\times 2000$; 8, B115/14, $\times 20000$. 9-10, Kingsclere borehole, depth 475 feet; preparation no. X081; Film B32 (JFL); Stub JL47 (JFL). Ref. 275710; 9, B32/3, $\times 2000$; 10, B32/2, $\times 10000$. 11-12, RETISULC-CAND(TEEBAC); Kingsclere borehole, depth 474 feet; Film B115 (GED); Stub GD167; Ref. 312787; 11, B115/26, $\times 5000$; 12, B115/28, $\times 20000$.



HUGHES *et al.*, Cretaceous angiospermid pollen

Biorecord RETISULC-DENTAT: Plate 57

Description. Processes in a single row on murus; processes pointed with round base diameter less than murus width.

Comparison records. cfA: WM1423/2, WM1353/6, WM1333/10; S44.

Biorecord RETISULC-NEWLING: Plate 58 (1-10)

Description. Murus smooth but ridged, like a roof.

Comparison records. cfA: WM1488/7, WM1415/6, WM1394/1, WM1345.
cfB: F317.

Biorecord RETISULC-MONBAC: Plate 59 (1-10)

Locality. K474+K475.

Description. Processes low rounded, across full width of murus.

Comparison record. cfA: F317.

Biorecord RETISULC-DIDENT: Plate 60

Description. Low rounded processes in two lines, one along each side of the murus top. Some development of muri ending blindly within lumina.

Comparison record. cfA: S38.

RETISULC-CAND(LAEVGAT): Plate 58 (11-12)

Character. Muri entirely smooth (laevigate), and flat-topped.

RETISULC-CAND(CROCHET): Plate 63 (10-12)

Character. Laevigate muri with two sizes of lumina, evenly distributed (unlike *Liliacidites* of Doyle and Robbins 1977).

RETISULC-CAND(TEEBAC): Plate 59 (11-12)

Character. Muri appear to be closely cross-segmented throughout.

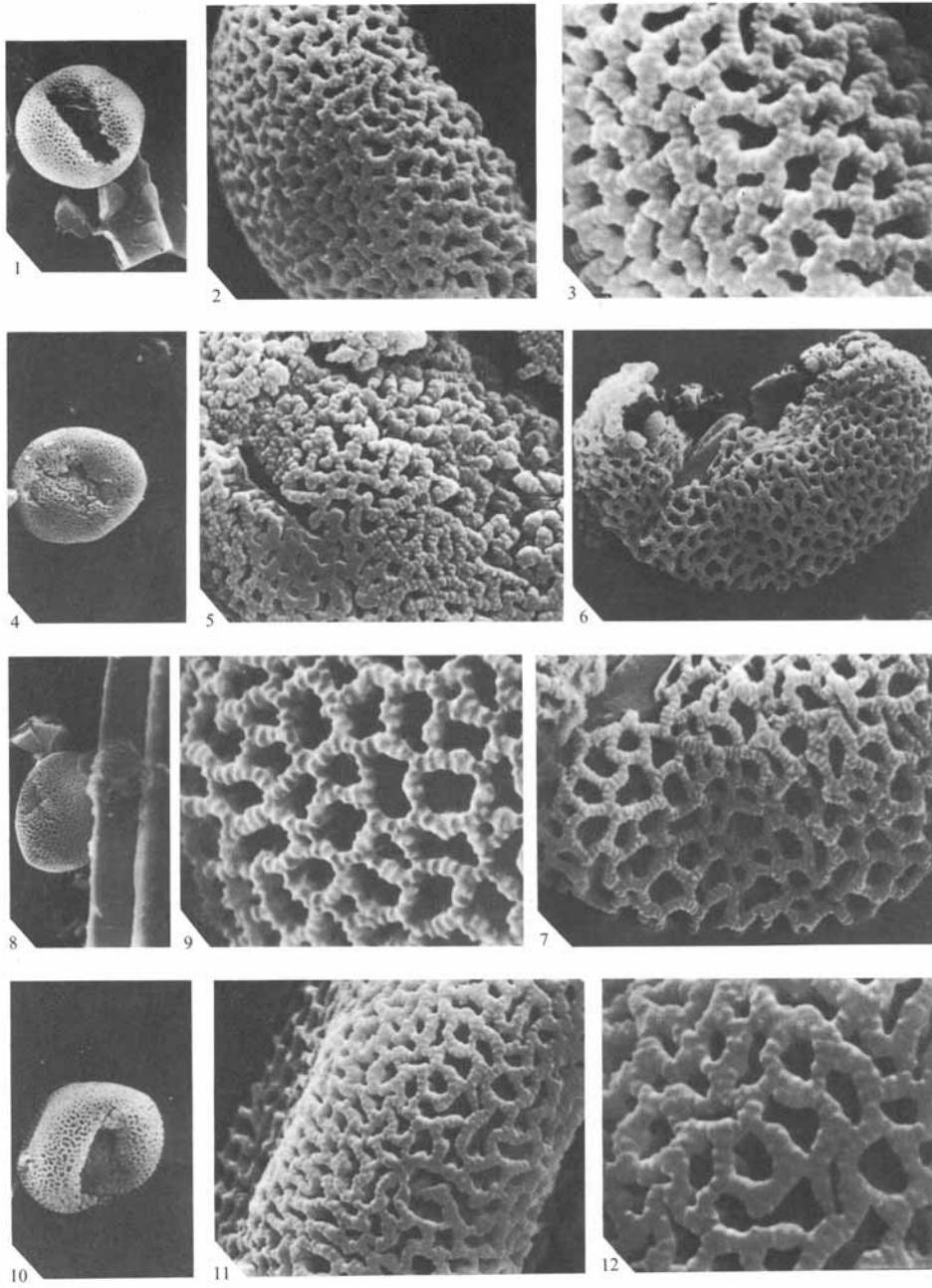
RETISULC-CAND(DUBDENT): Plate 64 (1-4)

Locality. K469 and F317; early Aptian.

Character. Supratectal coni in two rows, one along either side of each murus. Reticulum loosely attached to smooth exine, with short basal remnants of columellae.

EXPLANATION OF PLATE 60

Figs. 1-12. Cretaceous (angiospermid) pollen; RETISULC-DIDENT biorecord: Aptian age; Lower Greensand, Crackers Bed, Atherfield, Isle of Wight; 94 feet above Perna Bed (see Kemp 1970); preparation no. F317; Films B132, B133, B134, and B136 (GED); Stub GD180 (GED). 1-3, Ref. 363736; 1, B134/14, $\times 2000$; 2, B134/16, $\times 10000$; 3, B134/17, $\times 20000$. 4-5, Ref. 323857; 4, B132/10, $\times 2000$; 5, B132/12, $\times 10000$. 6-7, Ref. 323848; 6, B132/7, $\times 5000$; 7, B132/8, $\times 10000$. 8-9, Ref. 239827; 8, B136/17, $\times 2000$; 9, B136/20, $\times 20000$. 10-12, Ref. 358733; 10, B133/37, $\times 2000$; 11, B133/39, $\times 10000$; 12, B133/40, $\times 20000$.



HUGHES *et al.*, Cretaceous angiospermid pollen

Genusbox RETICHOT-

Descriptive limits. Trichotomosulcate, or tetra-, or penta-; semitectate columellate pollen.

Biorecord RETICHOT-BACCAT: Plate 61

Description. Processes low rounded; across full width of murus as in RETISULC-MONBAC.

Comparison records. cfA: WM1356/6, WM1298/4; Ilrg(Alford).
cfB: F317.

Genusbox SUPERRET-

Descriptive limits. Semitectate columellate pollen; monocolpate. Supratectal elements transverse to muri (crotonoid pattern).

Biorecord SUPERRET-CROTON: Plate 62

Locality. K474+K475.

Description. Triangular and rectangular plan supratectal elements (Pl. 62, fig. 6).

Comparison records. cfA: WM1333/10; S38(IOW); Ilrg(Alford).

Biorecord SUPERRET-TRIANG: Plate 63 (1-9)

Locality. K474+K475.

Description. Triangular plan supratectal elements only (Pl. 63, fig. 7; compare with Pl. 62).

Comparison records. cfA: S38(IOW), F317(IOW).

SUPERRET-CAND(SUBCROT): Plate 64 (9-12)

Character. Closely packed crotonoid supratectal elements; this pollen may be trichotomosulcate.

SUPERRET-CAND(KRINKEL): Plate 62 (11-12)

Character. Supratectal elements with crenulated margins.

Genusbox PERFOTECT-

Descriptive limits. Tectate columellate pollen. Lumina smaller than 'murus' width.

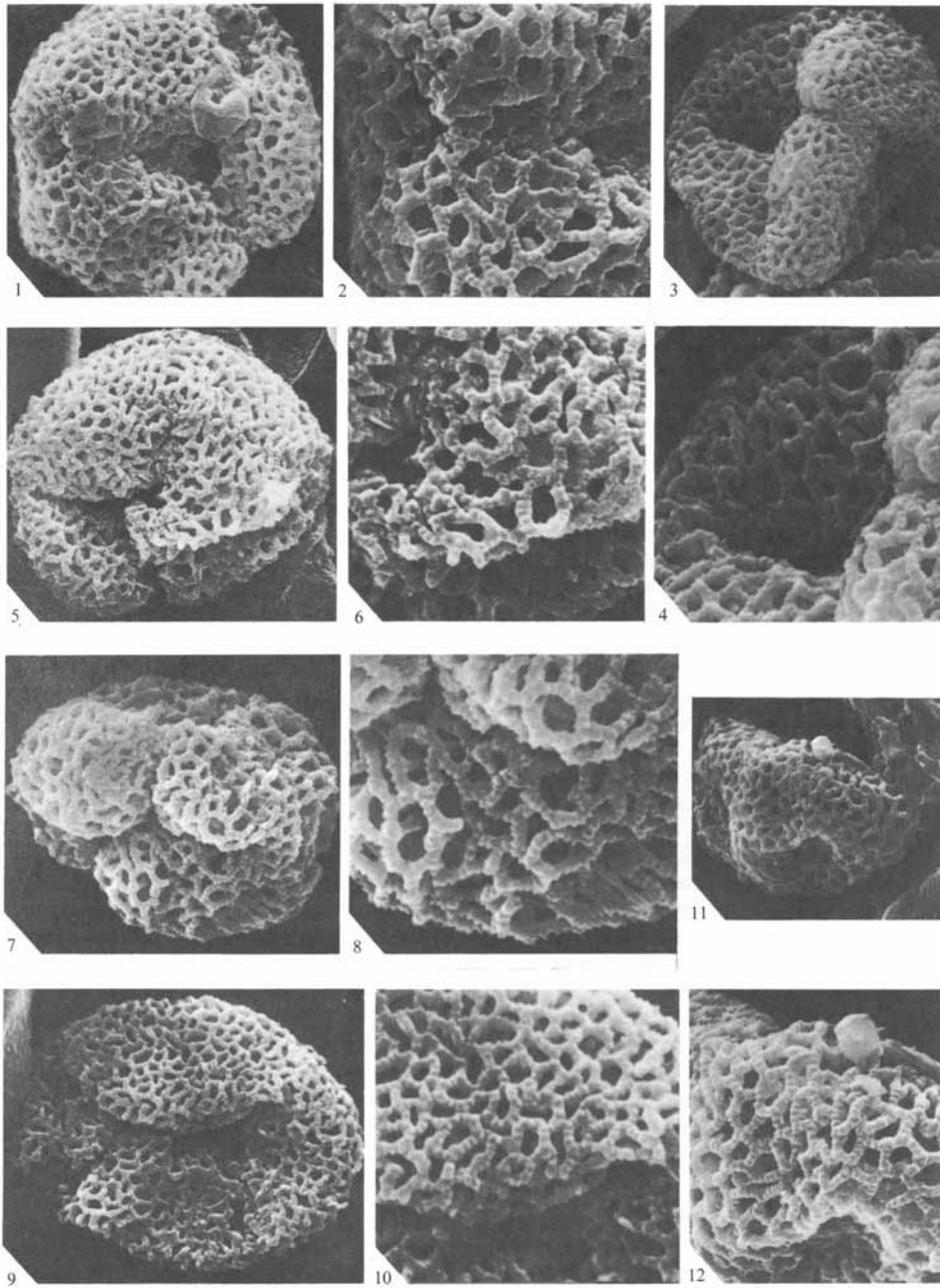
PERFOTECT-SPOT: Plate 64 (5-8)

Locality. K469 and K474.

Character. Believed to be tectate but not yet sectioned.

EXPLANATION OF PLATE 61

Figs. 1-12. Cretaceous (angiospermid) pollen; RETICHOT-BACCAT biorecord: Barremian age; Upper Wealden, Warlingham borehole, depth 1333/10 feet; preparation no. W106; Films B8 and B33 (JFL), Stub JL35 (JFL); Films B18 and B19 (JFL), Stub JL49 (JFL); Film B23 (JFL), Stub JL50 (JFL); Film B25 (JFL), Stub JL36 (JFL). 1-2, Ref. 268776; 1, B18/33, $\times 5000$; 2, B18/34, $\times 10000$. 3-4, Ref. 263811; 3, B23/7, $\times 5000$; 4, B23/8, $\times 10000$. 5-6, Ref. 298731; 5, B19/5, $\times 5000$; 6, B19/6, $\times 10000$. 7-8, Ref. 230774; 7, B33/1, $\times 5000$; 8, B33/3, $\times 10000$. 9-10, Ref. 285728; 9, B8/21, $\times 5000$; 10, B8/22, $\times 10000$. 11-12, Ref. 325709; 11, B25/21, $\times 5000$; 12, B25/22, $\times 10000$.



HUGHES *et al.*, Cretaceous angiospermid pollen

STRATIGRAPHIC RECORD

As indicated on Table 1, the biorecords, candidate records, and a large number of comparison records have been taken from eleven borehole and four outcrop samples. The preparations of many more samples in these rock sequences are in the reconnaissance stage of study, and they are expected to provide numerous further comparison records in due course. To save space, we have deferred detailed use of the comparison records to arrive at correlation brackets (as in Hughes and Moody-Stuart 1969; Hughes and Croxton 1973). The purpose here is to document the reference taxa and main framework, both for stratigraphical correlation which is promising although laborious, and for evolutionary work in which plant affinities have to be found for the pollen and in which extensive further exploration is obviously required.

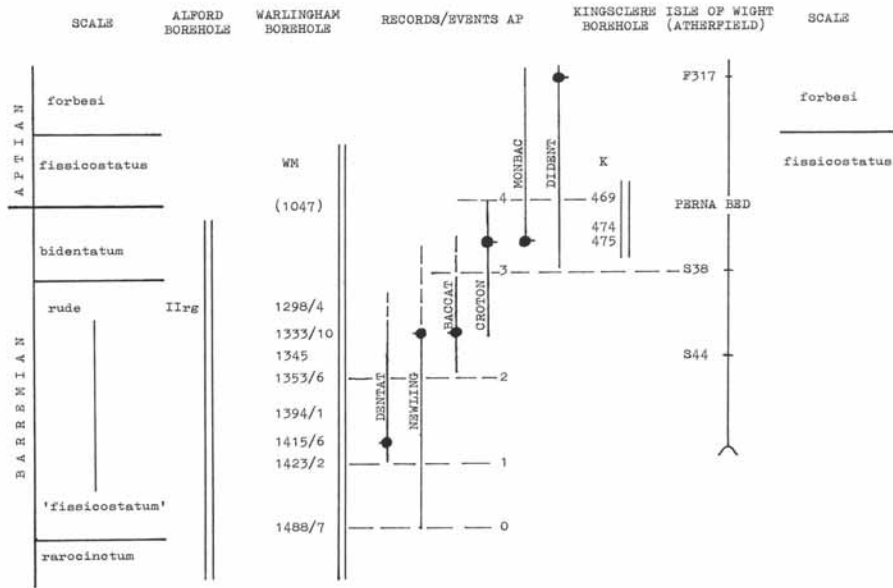
Biorecord sites are selected after reaching adequate abundance and quality but, where there is choice, they are taken low in their apparent comparison-range as known at the time of observation; as suggested above, they will be superseded by better biorecords if opportunity offers.

Text-fig. 2 shows the stratigraphic position of samples which mostly fall within the rude-'fissicostatum' zones (mid Barremian) of Rawson *et al.* (1978). Suggested intersection correlations are shown by the relative positions of the sample numbers; the only direct correlations with the reference scale are from the Alford (Lincolnshire) sample from the Fulletby Beds, and from F317 in the Isle of Wight Lower Greensand. Further Norfolk, Lincolnshire, and Yorkshire samples have yielded angiosperm pollen specimens, but so far mostly as single grains. The angiosperm pollen (AP) Events O-4 are recognized as a rough guide to sequence but are not intended to serve yet as biozones of any kind.

TIME-CORRELATION OF THE LOWEST PART OF THE POTOMAC GROUP

The lower Zone I rocks (Doyle 1969, 1973, 1977a, 1977b) will remain difficult to date because they were probably laid down patchily over an irregular surface of unconformity. They also show little outcrop, and the interesting palynomorphs are rare. We believe therefore that the best policy is to erect firm unambiguous taxa in the English succession which is more complete; substantial comparison records can then eventually be created in the Patuxent.

From the present evidence, it appears that Delaware City D12-770 (Doyle and Robbins 1977) could be just later than Kingsclere K474, and distinctly earlier than F317, which could mean lowermost Aptian age. This is suggested by the presence of *Retimonocolpites peroreticulatus*, and less valuably the absence of the several English Barremian taxa of Events AP1 and AP2. In reality, however, this can be no more than a framework for further investigation of the succession after Event AP3 in Britain (text-fig. 2), and of lower Zone I of the Potomac Group.



TEXT-FIG. 2. Diagram (thickness of beds not to scale) showing position of fifteen samples, inter-sequence correlations, and correlations to Boreal stratigraphic scale. AO-4 = successive angiospermid pollen assemblages. Samples: IIrg = 146 feet in Alford borehole (Swinerton 1935), Lower Roach (Fulley Beds); F317 = Crackers Bed (Kemp 1970), 30 feet below top of Atherfield Clay formation; S38 = Atherfield Bed 35 (White 1921), base of Weald Shales, foot of Cowleaze Chine; S44 = just below Atherfield Bed 1 (White 1921), Weald Marls, Sedmore Point.

'LINNEAN' TAXONOMY LL

As mentioned above under 'data-handling options', the Linnean taxonomy LL which is dependent on ICBN, is in current use by other authors. Both the genera (below) and the species (next section) suffer greatly from lack of agreed definition, and the principal reason for this is the difficulty of effectively accommodating modern accurate descriptive characters in old taxa that are already widely used but unavoidably ill-defined (even over as little time as twenty-five years).

Genera in use. Most of the types of the relevant published taxa were originally studied on light microscopes, and the detail of sculpture was as a result unclear. Doyle and Robbins (1977) and Doyle (1975, not 1973) have developed a consistent policy of using four genera:

Stellatopollis Doyle *et al.* 1975: discrete suprategal elements (crotonoid); SEM study.

Liliacidites Couper 1953: reticulum of two lumen sizes with smaller lumina concentrated at poles or sulcus.

Retimonocolpites Pierce 1961: coarsely reticulate, i.e. lumina greater than 2 μm diameter.

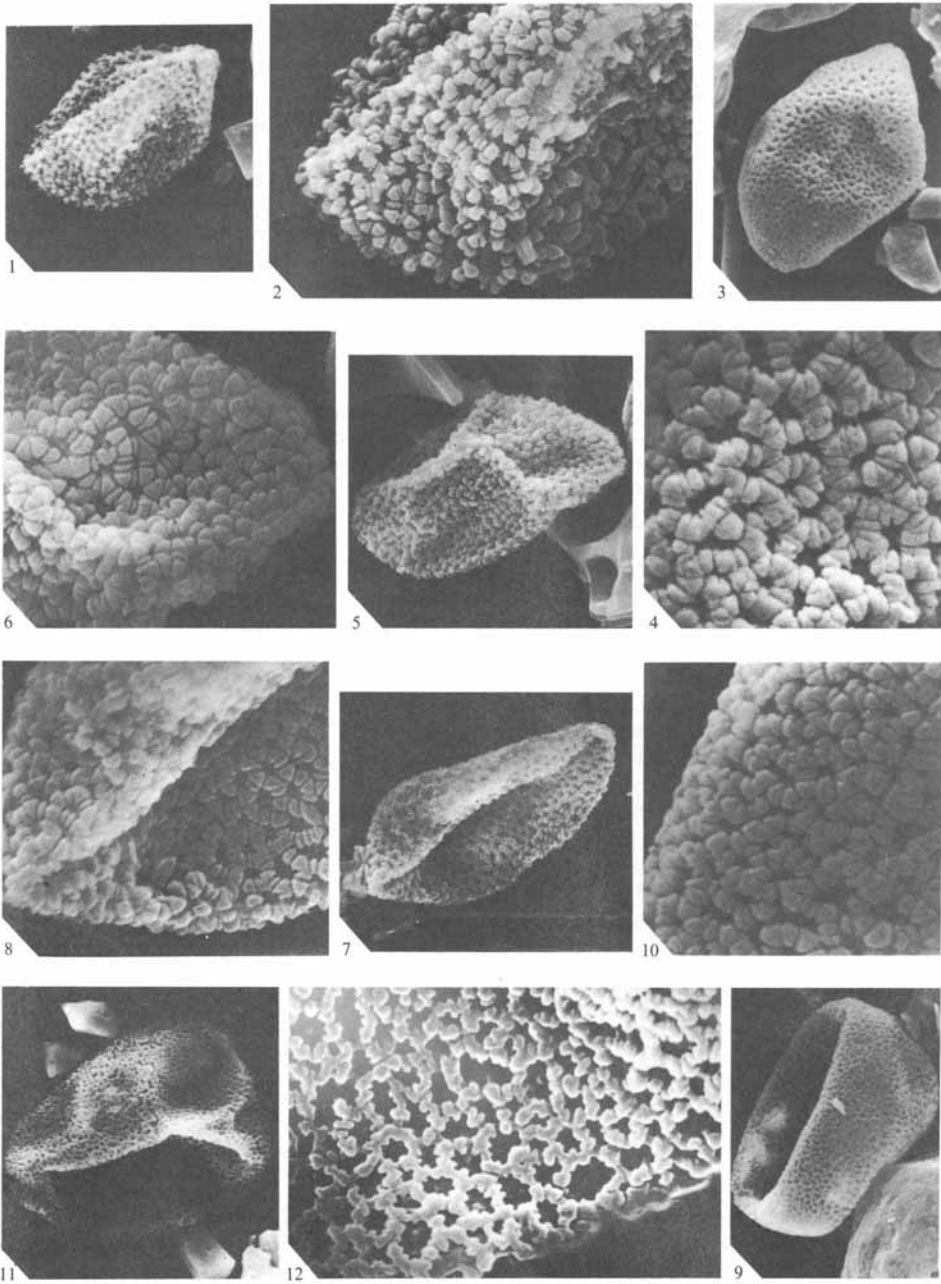
Clavatipollenites Couper 1958: finely columellar, finely reticulate; granular sulcus membrane.

Other authors such as Brenner (1963), Kemp (1968), Singh (1971), Dettmann (1973), and Laing (1975) had each used the three earlier genera in different ways, usually reducing their number in synonymy on grounds of priority. This amounted to normal palaeontological practice and was understandable, although as a whole confusing. Doyle and Robbins (1977) sensed from SEM observations that there was great variety in the material; thus they rightly sought uses for all the existing names. Unless, however, the genera are all redescribed and diagnosed with limits against each other, the confusion and probably even the attempts to construct synonymies will continue.

Stability of genera. A central problem is that the holotype of *C. hughesii* Couper 1958 is an overmacerated (20 μm) specimen in a glycerine jelly strew mount which also contains holotypes of other palynomorph taxa; it would be wrong to disturb the preparation even if one could be certain of successfully extracting the specimen, washing it, and re-examining it on an SEM stub. Additionally, we now know from SEM study that the sample (K475) has yielded at least seven kinds (see Table 1) of tectate pollen; the assemblages of six specimens (Couper 1958) or of a hundred (Kemp 1968) will have included unknown proportions of all seven and probably more. The holotype seems as likely from size and appearance to have been a small crotonoid as a reticulate type. Otherwise, in the context of present knowledge, *Clavatipollenites* lacks sufficiently clear meaning to be used at all as a genus but could be used as a supra-generic group based on Doyle and Robbins's (1977) interpretation of Couper's (1958) diagnosis. *Liliacidites* was not erected for early Cretaceous pollen, and in fact its author declined in 1958 to use it for his own newly discovered and distinct early tectate pollen; its use now is understandable in an LL context but perhaps Couper's (1958) decision should be respected. *Retimonocolpites* alone retains a clear use for reticulate forms with lumina and muri large enough to be resolved on a light microscope, although the character appears to be combined with a lack (? loss) of actual columellae and a consequent looseness of fitting of the tectum on the nexine.

EXPLANATION OF PLATE 62

Figs. 1-12. Cretaceous (angiospermid) pollen; SUPERRET-CROTON biorecord: Barremian age; Upper Wealden. 1-4, Kingsclere borehole, depth 474 feet; preparation no. X307; 1-2, Film B115 (GED); Stub GD 167 (GED); Ref. 328815; 1, B115/37, $\times 2000$; 2, B115/38, $\times 5000$; 3-4, Film B118 (GED); Stub GD168 (GED); Ref. 340753; 3, B118/27, $\times 2000$; 4, B118/29, $\times 10000$. 5-12, Kingsclere borehole, depth 475 feet; preparation no. X081; Film B31 and B32 (JFL), Stub JL47 (JFL); Film B77 (GED), Stub JL48 (JFL). 5-6, Ref. 339728; 5, B32/25, $\times 2000$; 6, B32/23, $\times 5000$. 7-8, Ref. 228799; 7, B31/3, $\times 2000$; 8, B31/1, $\times 5000$. 9-10, Ref. 294793; 9, B32/15, $\times 2000$; 10, B32/14, $\times 10000$. 11-12, SUPERRET-CAND(KRINKEL), Ref. 267841; 11, B77/8, $\times 2000$; 12, B77/10, $\times 10000$.



HUGHES *et al.*, Cretaceous angiospermid pollen

EXISTING SPECIES AND NEW BIORECORDS

As will be seen below, the existing relevant taxa used for specimens from the Potomac Group lower Zone I are few and poorly defined. This is partly because of the small number of specimens so far discovered and figured, and partly because none of the taxa concerned are based in these strata. The rocks concerned are from Delaware City well D12 depths 765–70 feet, and a few Patuxent outcrops such as Dutch Gap Canal and Baltimore–Susquehanna Aqueduct. (Upper Zone I records are from above 745 feet in the well and from the Arundel Formation; they are richer in specimens but are probably of earliest Albian age and are quite distinct.)

Each taxon is separately discussed from the point of view of which English specimens could be accommodated in it:

1. cf. *C. hughesii*. Doyle and Robbins (1977) have used this form of the name, while Doyle *et al.* (1975) used *C. cf. hughesii* for some excellent SEM and TEM figures. In view, however, of the difficulties about the holotype mentioned in the last section, neither subtlety is effective and such nomenclature is bound to be both cumbersome and indefinite. The biorecord RETISULC-MONBAC compares closely with the specimens of Doyle *et al.* (1975) except that it is smaller, but to place it under this name cannot be meaningful.

2. *Clavatipollenites* sp. A. Doyle and Robbins (1977, pl. 1, figs. 4–5) record a large grain (30 μm) which we have not yet observed.

3. aff. *C. minutus* Brenner. Doyle and Robbins (1977, pl. 1, figs. 6–8) provide only a light micrograph of this small grain (19 μm); it cannot therefore be matched.

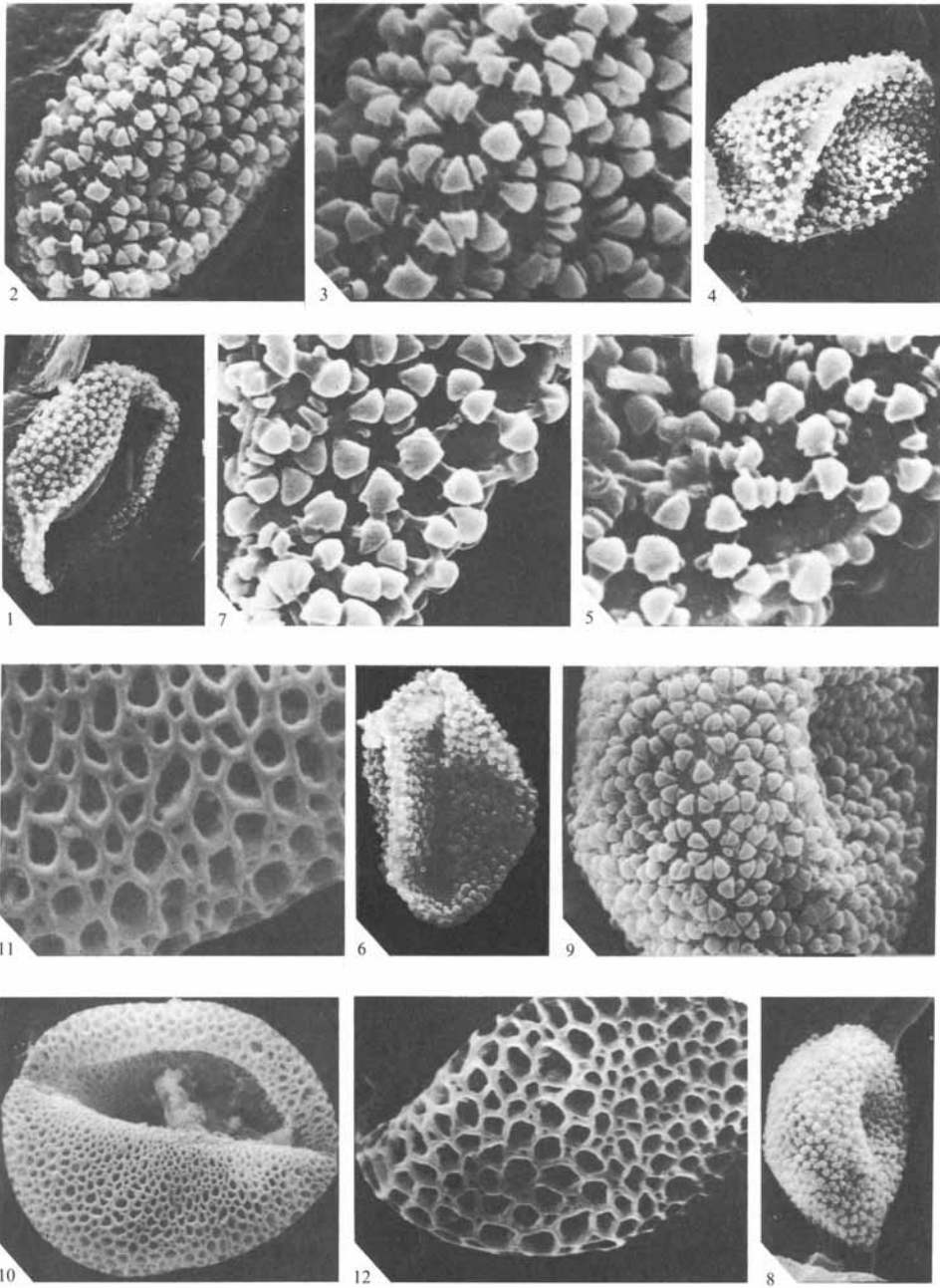
4. *R. peroreticulatus* (Brenner) Doyle, as figured by Doyle and Robbins (1977, pl. 1, figs. 9–11) could well include RETISULC-CAND(DUBDENT) from the sample K469 and some similar specimens we have from outcrop samples of early Aptian age. The effective description of this species is, however, from late Zone I.

5. *Liliacidites* sp. B. Doyle and Robbins (1977, pl. 1, figs. 12–14) only provide a light micrograph. RETISULC-CAND(CROCHET) is smaller but may compare if the muri of the Potomac specimens prove to be unsculptured.

6. *Stellatopollis* sp. Two figured specimens from Fish Hut are in (a) Doyle *et al.* (1975, pl. 8, figs. 6–8), and (b) Hickey and Doyle (1977, fig. 4j). Biorecord SUPERRET-CROTON probably compares.

EXPLANATION OF PLATE 63

Figs. 1–12. Cretaceous (angiospermid) pollen; Barremian age; Upper Wealden. SUPERRET-TRIANG biorecord: 1–7, Kingsclere borehole, depth 475 feet; preparation no. X081; Film B31 (JFL), Stub JL47 (JFL); Film B77 (GED), Stub JL48 (JFL). 1–3, Ref. 257794; 1, B31/17, $\times 2000$; 2, B31/15, $\times 5000$; 3, B31/16, $\times 10000$. 4–5, Ref. 236859; 4, B31/7, $\times 2000$; 5, B31/6, $\times 10000$. 6–7, Ref. 260857; 6, B77/12, $\times 2000$; 7, B77/14, $\times 10000$. 8–9, Kingsclere borehole, depth 474 feet; preparation no. X307; Film B115 (GED); Stub GD167 (GED); Ref. 320816; 8, B115/29, $\times 2000$; 9, B115/30, $\times 5000$. RETISULC-CAND(CROCHET): 10–12, Kingsclere borehole. 10–11, depth 474 feet; preparation no. X307; Film B115 (GED); Stub GD167 (GED); Ref. 299836; 10, B115/19, $\times 5000$; 11, B115/21, $\times 20000$. 12, Film B78 (NFH); Stub 48 (JFL); Ref. 303826, B78/15, $\times 10000$.



HUGHES *et al.*, Cretaceous angiospermid pollen

Thus some of our biorecords could be assembled in the generic taxa of Doyle in an LL context for general palaeobiological interpretative purposes, the two systems being adequately compatible.

PALAEOBIOLOGICAL INTEREST IN ANGIOSPERM ORIGINS

If a semitectate sexine together with a non-laminated interapertural nexine (Doyle *et al.* 1975) are to be taken as indicative angiosperm characters, they must have arisen in early Barremian or just earlier time from characters acknowledged as gymnospermous. Because these angiosperm characters appear first in exclusively monosulcate grains (Hughes and Drewry 1978; event AP1), gymnospermous monosulcates come under scrutiny as precursors of RETISULC-DENTAT, which is the earliest tectate grain observed in quantity. Even the very few earlier records, single grains of quite different sculpture (Hughes 1977*b*, pl. 1), were probably monosulcates. It also seems possible that RETISULC-CAND(TEEBAC) on Plate 3 (11–12) may be an important type with the tectum muri apparently segmented; specimens have been seen in several other samples and more may be recorded when good preservation and better than normal SEM resolution coincide.

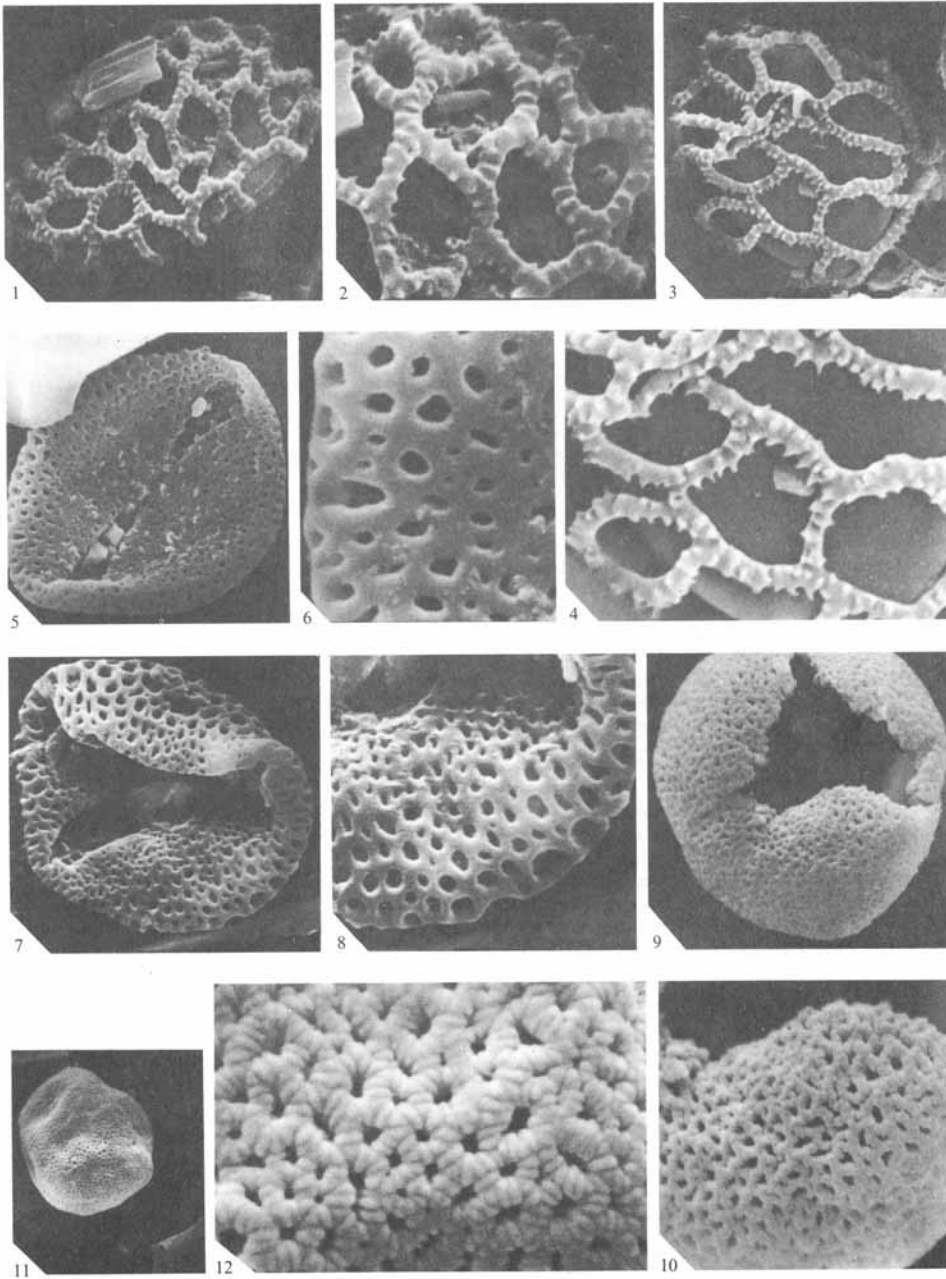
Similar exine patterns were developed in tricolpates, but later, in Albian time. RETICHOT-BACCAT appears to be trichotomosulcate but is not obviously or necessarily connected with either monosulcate or tricolpate evolution.

The SEM strew study of samples below WM1488/7 is slow because it lacks such a clear positive search element. SEM magnifications have revealed unsuspected sculptural variety in monosulcates that presumably belonged to Nilssoniales (see Krassilov 1975, 1977), Bennettitales, Czekanowskiales, or Ginkgoales, but none have yet been brought to biorecord standard. We have also recorded interesting sculpture in *Eucommiidites* and *Classopollis* under the same conditions. It is not known whether evolution or immigration controlled events in this area. SEM strew search of late Barremian to mid Aptian available samples is simply a matter of man-hours and organization of data.

The rapidly increasing volume of records of tectate pollen now provide a very firm basis of timing of the origin of the angiosperms. Building up associated and integrated records of leaves, wood, and seeds will again be a matter of effort and organization but there is no longer any question of 'mystery' in this topic.

EXPLANATION OF PLATE 64

Figs. 1–12. Cretaceous (angiosperm) pollen. 1–4, Barremian–Aptian age; RETISULC-CAND(DUBDENT); 1–2, Upper Wealden, Kingsclere borehole, depth 469 feet; preparation no. X306; Film B108 (GED); Stub GD165 (GED); Ref. 249783; 1, B108/8, $\times 5000$; 2, B108/10, $\times 10000$. 3–4, Lower Greensand, Crackers Bed, Atherfield, 94 feet above Perna Bed, Isle of Wight; preparation no. F317; Film B129 (GED); Stub GD180 (GED); Ref. 291877; 3, B129/42, $\times 5000$; 4, B129/44, $\times 10000$. 5–8, PERFOTECT-SPOT, depth 474 feet; preparation no. X307; Film B116 (GED); Stub GD180 (GED); Ref. 378798; 5, B116/31, $\times 5000$; 6, B116/33, $\times 20000$. 7–8, Kingsclere borehole, depth 469 feet; preparation no. X306; Film B108 (GED); Stub GD165 (GED); Ref. 255801; 7, B108/13, $\times 5000$; 8, B108/15, $\times 10000$. 9–12, Barremian age; Upper Wealden; Kingsclere borehole, depth 474 feet; preparation no. X307; SUPERRET-CAND(SUBCROT); Films B117 and B118 (GED); Stub GD168 (GED). 9–10, Ref. 284807; 9, B117/30, $\times 5000$; 10, B117/31, $\times 10000$. 11–12, Ref. 316773; 11, B118/7, $\times 2000$; 12, B118/10, $\times 20000$.



HUGHES *et al.*, Cretaceous angiospermid pollen

Acknowledgements. We are grateful for support from N.E.R.C. under grants 3/2106 and 3/2969. We thank Mr. David Newling for his invaluable assistance with SEM work and photography.

REFERENCES

- BRENNER, G. J. 1963. The spores and pollen of the Potomac Group of Maryland. *Bull. Md Dep. Geol. Mines*, **27**, 215 pp., 43 pls.
- 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. In BECK, C. B. (ed.), *Origin and early evolution of angiosperms*, pp. 23–47. Columbia University Press, New York.
- COUPER, R. A. 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. *Palaeont. Bull. geol. Surv. N.Z.* **22**, 1–77, 9 pls.
- 1958. British Mesozoic microspores and pollen grains. *Palaeontographica*, **B103**, 75–179, 16 pls.
- DETTMANN, M. E. 1973. Angiospermous pollen from Albian to Turonian sediments of eastern Australia. *Geol. Soc. Aust. Spec. Publ.* **4**, 3–34, 6 pls.
- DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. *J. Arnold Arbor*, **50**, 1–35.
- 1973. Fossil evidence on early evolution of the monocotyledons. *Quart. Rev. Biol.* **48**, 399–413.
- 1977a. Spores and pollen: the Potomac Group (Cretaceous) angiosperm sequence. In KAUFFMAN, E. G. and HAZEL, J. E. (eds.), *Concepts and methods of biostratigraphy*, pp. 339–363. Dowden, Hutchinson, and Ross, Stroudberg.
- 1977b. Patterns of evolution in early angiosperms. In HALLAM, A. (ed.), *Patterns of evolution*, 501–546. Elsevier, Amsterdam.
- BIENS, P., DOERENKAMP, A. and JARDINÉ, S. 1977. Angiosperm pollen from the pre-Albian Lower Cretaceous of equatorial Africa. *Bull. Centr. Rech. Explor.-prod. Elf-Aquitaine* **1** (2), 451–473, 2 pls.
- and HICKEY, L. J. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on angiosperm evolution. In BECK, C. B. (ed.), *Origin and early evolution of angiosperms*, pp. 139–206. Columbia Univ. Press, New York.
- and ROBBINS, E. I. 1977. Angiosperm pollen zonation of the continental Cretaceous of the Atlantic Coastal Plain and its application to deep wells in the Salisbury Embayment. *Palynology*, **1**, 43–78, 7 pls.
- VAN CAMPO, M. and LUGARDON, B. 1975. Observations on exine structure of *Eucommiidites* and Lower Cretaceous angiosperm pollen. *Pollen et Spores*, **17**, 429–486, 11 pls.
- HICKEY, L. J. and DOYLE, J. A. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev.* **43**, 3–104.
- HUGHES, N. F. 1958. Palaeontological evidence for the age of the English Wealden. *Geol. Mag.* **95**, 41–49.
- 1974. Angiosperm evolution and the superfluous upland origin hypothesis. *Birbal Sahni Inst. Palaeobotan. Spec. Publ.* **1**, 25–29. Lucknow.
- 1975. The challenge of abundance in palynomorphs. *Geoscience and Man*, **11**, 141–149.
- 1976. *Palaeobiology of angiosperm origins*, 242 pp. Cambridge University Press.
- 1977a. Mid-Cretaceous seed plants. *Sixth Birbal Sahni Memorial Lecture*, 11 pp., 3 pls. Birbal Sahni Inst., Lucknow.
- 1977b. Palaeo-succession of earliest angiosperms. *Bot. Rev.* **43**, 105–127, 3 pls. New York.
- and CROXTON, C. A. 1973. Palynologic correlation of the Dorset 'Wealden'. *Palaeontology*, **16**, 567–601, 10 pls.
- and DREWRY, G. E. 1978. Cretaceous Barremian tectate pollen from southern England. *Cour. Forsch.-Inst. Senckenberg* **30**, 62–69. Frankfurt-am-Main.
- and MOODY-STUART, J. C. 1969. A method of stratigraphic correlation using early Cretaceous microspores. *Palaeontology*, **12**, 84–111, 10 pls.
- KEMP, E. M. 1968. Probable angiosperm pollen from the British Barremian to Albian strata. *Ibid.* **11**, 421–434, 3 pls.
- 1970. Aptian and Albian microspores from southern England. *Palaeontographica*, **B131**, 73–143, 20 pls. Stuttgart.
- KRASSILOV, V. A. 1975. Dirhopalostachyaceae—a new family of proangiosperms and its bearing on the problem of angiosperm ancestry. *Ibid.* **B153**, 100–110.
- 1977. The origin of angiosperms. *Bot. Rev.* **43**, 143–176.

- LAING, J. F. 1974. A specimen location technique for SEM strew mounts. *Palaeontology*, **17**, 435-436.
- 1975. Mid-Cretaceous angiosperm pollen from southern England and northern France. *Ibid.* **18**, 775-808, 5 pls.
- 1976. The stratigraphic setting of early angiosperm pollen. In FERGUSON, I. K. and MULLER, J. (eds.). *The evolutionary significance of the exine*, pp. 15-26. Linn. Soc. Symp. Ser. 1.
- PIERCE, R. L. 1961. Lower Upper Cretaceous plant microfossils from Minnesota. *Bull. Minn. geol. Surv.* **42**, 1-86.
- RAWSON, P. F. *et al.* 1978. A correlation of Cretaceous rocks in the British Isles. *Geol. Soc. Lond., Special Report* **9**, 70 pp.
- SINGH, C. 1971. Lower Cretaceous microfloras of the Peace River area, north-western Alberta. *Bull. res. Coun. Alberta*, **28**, 542 pp., 8 pls.
- SWINNERTON, H. H. 1935. The rocks below the Red Chalk of Lincolnshire and their cephalopod faunas. *Quart. Jl geol. Soc. Lond.* **91**, 1-46, 4 pls.
- WORSSAM, B. C. and IVIMEY-COOK, H. C. 1971. The stratigraphy of the Geological Survey borehole at Warlingham, Surrey. *Bull. Inst. geol. Surv. Gt. Br.* **36**, 1-176.
- WHITE, H. J. O. 1921. A short account of the geology of the Isle of Wight. *Mem. geol. Surv. Gt. Br.* 219 pp.

NORMAN F. HUGHES
GILLIAN E. DREWRY

Department of Geology
Sedgwick Museum
Cambridge CB2 3EQ

JOHN F. LAING

Robertson Research
Petroleum Services Ltd.
Llanrhos
Llandudno LL30 1SA

Typescript received 20 April 1978

Revised typescript received 4 December 1978