PROBABLE ANGIOSPERM POLLEN FROM BRITISH BARREMIAN TO ALBIAN STRATA

by ELIZABETH M. KEMP

ABSTRACT. Two species of the genus *Clavatipollenites* Couper are described. One is a redescription of the type species, *Clavatipollenites hughesii*, from the Upper Barremian part of the Wealden Series. The other, *Clavatipollenites rotundus*, is a new species from the Middle Albian Lower Gault. Three species of tricolpate angiospermous grains are described. Only one of these, *Tricolpites albiensis*, from the Upper Albian, occurs in sufficient quantity to be formally named as a new species. These forms constitute the earliest record of recognizable angiosperm grains from England.

DURING an investigation into the spore and pollen assemblages of the marine Lower Greensand and Gault of southern England, several pollen species were recovered which are of particular botanical and stratigraphical interest. Two of these are monosulcate pollens referable to the genus *Clavatipollenites* Couper; the others are tricolpate angiospermous forms, the earliest undoubted pollen of this group from England. Of these last forms, only one was recovered in sufficient quantity to permit formal designation as a new species. The monosulcate pollens described here are of interest in that they possess some angiosperm characters and their appearance slightly predates that of grains of undoubted angiospermous affinity.

Acknowledgements. Research facilities in the Department of Geology, Sedgwick Museum, Cambridge, were made available by Professor O. M. B. Bulman. Mr. N. F. Hughes took a constant interest in the course of this work and provided the sample from the Kingsclere Borehole. Financial assistance was provided by a British Commonwealth Scholarship from 1963 to 1966.

LOCATION AND STRATIGRAPHY OF SAMPLES

The samples yielding the type material of the new species described here are part of a more extensive collection of Lower Greensand, Gault and Upper Greensand. The systematic and stratigraphic palynology of these sediments has been investigated in detail for an unpublished thesis. The sediments are of Aptian and Albian age, with a rich fauna which permits their subdivision in terms of ammonite zones.

The Lower Greensand samples have been collected chiefly from the Isle of Wight, with minor sampling in the Weald and in the northern sedimentary basin near Leighton Buzzard. The Gault and Upper Greensand have been collected over a wider geographic area, extending from near Leighton Buzzard, through sections in the northern Weald to the Isle of Wight and the Dorset coast in the south and south-west. In addition, the sample from 475 ft. in the Kingsclere Borehole, previously studied by Couper (1958), has been re-examined as it provided the type material of the species *Clavatipollenites hughesii*. This species persists into younger strata. The type sample comes from the Wealden, and is probably of Upper Barremian age.

[Palaeontology, Vol. 11, Part 3, 1968, pp. 421–34, pls. 79–81.]

More detailed references to the samples used in this study and to the sections from which they were collected are given below:

Sample F154—Calcareous pale yellowish-grey clay with shell fragments. Gault at Ford Place, Wrotham (Nat. Grid. reference 51/636591). Bed 20, near base; *niobe* Subzone of the *dentatus* Zone; Middle Albian. The detailed stratigraphy of this clay pit is given by Milbourne (1963), who subdivided the section into 82 beds on the basis of lithology.

Sample K475—Medium-grey siltstone with small dark patches, possibly plant fragments. Wealden Series, 475 ft. in the D'Arcy Exploration Company's Kingsclere No. 1 Borehole; probably Upper Barremian. Further details of the palynology and stratigraphic position of this sample are given by Hughes (1958) and Couper (1958).

Sample F312—Calcareous friable pale yellowish-green silty sandstone. Upper Greensand, west side of Lulworth Cove, Dorset (Nat. Grid reference 30/825799). 18 ft. beneath the base of the *Exogyra* Rock, which underlies a series of stone bands at the top of the Upper Greensand and serves as a convenient local marker (Wright, in Arkell 1947). Beds above the *Exogyra* Rock can be referred to the *dispar* Zone. The zonal position of the beds below is less certain, but they are probably of Upper Albian age.

Sample F270—Grey and cream mottled sandstone with ferruginous pebbles and patchy iron staining. Munday's Hill pit, Leighton Buzzard (Nat. Grid reference 42/930265). 6 in. beneath base of Carstone Breccia in the upper part of the Woburn Sands. The precise age of the sample is unknown. The Carstone Breccia is partly of Lower Albian age; the sample in question comes probably from the Lower Albian.

Location of type material. Rock samples, strew slides and individual mounts made from preparations are lodged in the Sedgwick Museum, Cambridge. Slides are deposited in the Palynology Collection of that museum. Formally named species are based on examination of 100 specimens in each case, and all of these are available for restudy. The co-ordinates quoted are those of the Leitz Dialux microscope Serial No. 526724 in the Sedgwick Museum.

Preparation procedures. Spore assemblages were extracted by solution of silicates in cold hydrofluoric acid following the removal of carbonates, where necessary, with 10–15 per cent. HCl. Residues were oxidized in Schulze solution, two short periods of oxidation usually being used. The total oxidation time did not in any case exceed twenty minutes. Residues were briefly cleared in less than 1 per cent. NH_4OH and the microfossils separated from the remaining mineral debris by centrifuging in zinc bromide solution.

SYSTEMATIC PALYNOLOGY

Anteturma POLLENITES Potonié 1931
Turma PLICATES Naumova 1939 emend. Potonié 1960
Subturma MONOCOLPATES Iversen and Troels-Smith 1950
Genus CLAVATIPOLLENITES Couper 1958

1958 *Clavatipollenites* Couper, p. 159.
1961 *Retimonocolpites* Pierce, p. 47.

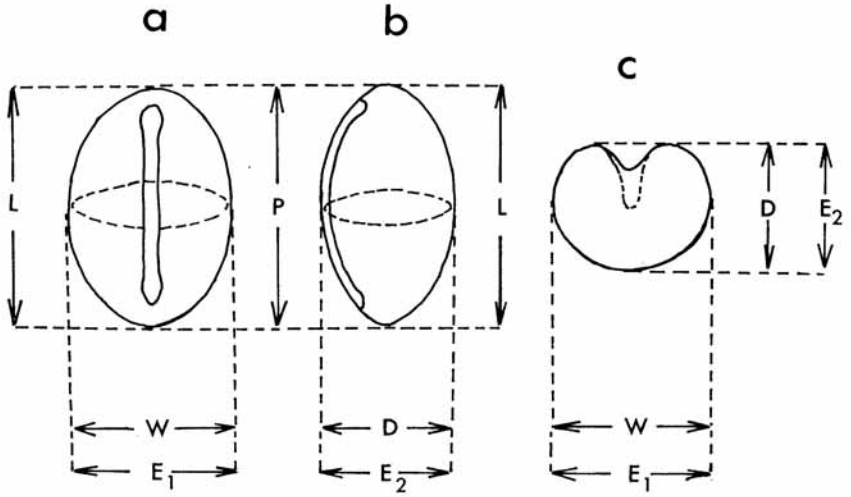
Type species. Clavatipollenites hughesii Couper 1958, p. 159, pl. 31, figs. 19–22.

Diagnosis. As given by Couper (1958).

Remarks. On a morphological basis *Clavatipollenites* resembles *Liliacidites* Couper (1953, p. 56) which was proposed to incorporate monosulcate grains of reticulate exine pattern, or, more precisely, 'for the reception of fossil pollens of liliaceous affinities that

cannot be more accurately placed'. The species originally referred to *Liliacidites* formed part of an Upper Cretaceous and Tertiary complex which had a large component of grains of unquestionably angiospermous origin. It would seem that the retention of a separate genus is valuable for Lower and lower Upper Cretaceous forms the affinity of which is in question.

Species from several widely separated localities have been referred to *Clavatipollenites*. Not all of these, however, conform to the diagnosis of the genus. Pocock (1962, p. 74,



TEXT-FIG. 1. Grain orientation in *Clavatipollenites*. L = length, W = width, D = depth. Designations P, E_1, and E_2 correspond with those of Couper (1958) for describing monosulcate and tricolpate pollens. Orientation: *a*, polar view; *b*, equatorial longitudinal view; *c*, equatorial transverse view.

pl. 12, figs. 190–2) described a large form which he named *Clavatipollenites couperi*, from the Upper Jurassic–Neocomian Vanguard Formation of western Canada. The specimens he figured do not show the presence of a tectate exine convincingly, and the species may perhaps be more accurately referred to *Monosulcites* or *Ginkgocycadophytus*. Helal (1965, pl. 17, fig. 19; 1966, pl. 34, figs. 54, 55) recorded both *C. couperi* and *C. hughesii* from subsurface Jurassic sediments in the Western Desert, Egypt. Both of the grains figured by this author appear to be distinctly three-furrowed, suggesting *Eucommiidites* rather than *Clavatipollenites*.

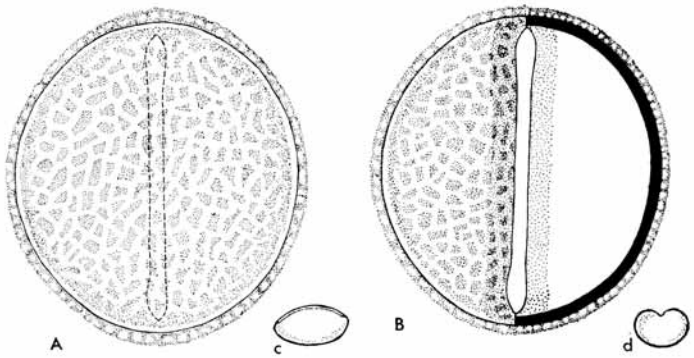
The type species, *C. hughesii*, has been recorded by Brenner (1963) together with a smaller form which he designated *C. minutus*, from Potomac Group sediments in Maryland. Von der Brelie (1965, p. 151, pl. 13, figs. 6–8) found *C. hughesii* in sediments of probable Aptian–Albian age in Germany. Archangelsky and Gamerro (1967) reported the presence of the species in assemblages of probable Barremian age in southern Argentina.

Pierce (1961, p. 47, pl. 3, fig. 87) described a monosulcate pollen from Çenomanian clays and lignites in Minnesota. This species, which he named *Retimonocolpites dividuus*,

Pierce designated as type species of the genus *Retimonocolpites*. This genus is regarded as synonymous with *Clavatipollenites* on the basis of Pierce's definition.

Both the type species, *C. hughesii*, and a new species, *C. rotundus*, were recorded from samples investigated during the present study. The expanded description of *C. hughesii* given below is based on re-examination of specimens from Couper's type sample.

The terminology of the grain dimensions and orientations used in the descriptions is shown in text-fig. 1. Comparisons of the size and shape of grains assigned to the two species are shown in the scatter diagram text-fig. 4, histograms of size frequency distributions in text-fig. 5.



TEXT-FIG. 2. Diagrammatic representation of *Clavatipollenites rotundus* sp. nov. Large figures, ×2,000. A, proximal face, LO pattern, position of sulcus dotted. B, distal face, left-hand side showing reticulum, right-hand side showing exine stratification in section. Dark zone adjacent to the sulcus is stippled. *c*, equatorial longitudinal view. *d*, equatorial transverse view.

Clavatipollenites rotundus sp. nov.

Plate 79, figs. 1–19; Plate 80, figs. 1–8; text-fig. 2

Diagnosis. Monosulcate pollen grains of subcircular to elliptical outline, with a distinctly tectate exine. The sulcus is conspicuous, round-ended, and bordered by thicken-

EXPLANATION OF PLATE 79

All figures at magnification ×1,000 unless otherwise stated.

Figs. 1–19. *Clavatipollenites rotundus* sp. nov. All specimens from sample F154, *niobe* Subzone of the *dentatus* Zone, Lower Gault at Ford Place, Wrotham. 1–5, F154/2; 35·0, 92·7. 1, Median focus showing tectate exine in section at equator (×2,000). 2, High focus on sulcus. 3, 4, Deeper foci. 5, Proximal focus on reticulum with sexine partly detached. 6, 7, F154/11; 27·0, 108·2; grain obliquely compressed. 6, Deep focus. 7, High focus showing end of sulcus and darkened zone. 8, F154/Separate 15, 40·0, 97·6; grain showing pronounced infolding associated with sulcus. 9–11, F154/Separate 1; 38·3, 99·2. 9, Proximal focus showing reticulum. 10, Median focus on sulcus and associated structure. 11, Distal focus. 12, 13, F154/10; 34·2, 90·2. 12, High focus on proximal face, sexine partly removed. 13, Equatorial focus. 14, 15, F154/12; 35·8, 89·8. 14, Median focus of specimen in end-on view. 15, High focus on reticulum. 16, F154/Separate 8; 39·0, 98·1; median focus showing folding adjacent to sulcus. 17–19, F154/Separate 9; 39·2, 98·5; Holotype. 17, High focus on distal face. 18, Median focus on sulcus with exine stratification distinct at equator. 19, Proximal focus.

ings or infoldings of the nexine. The reticulate pattern of the sexine is formed from the fused tips of bacula; the mesh diameter is from 0·7 to 2·0 μ. The mean grain width lies in the range 22–27 μ, mean grain length 25–30 μ. Sexine shows a tendency to separate from nexine.

Holotype. Sample F154, separate mount 9; 39·2, 98·5. Plate 79, figs. 17–19. Lower Gault, Ford Place, Wrotham; Middle Albian. Grain orientated with sulcus uppermost, extending full length of grain, bordered by darkened zone 2·4–2·5 μ wide on either side. Sulcus slightly expanded and rounded at extremities. Nexine 0·8 μ thick, sexine 1·2 μ. Length $\times$ width 26 $\times$ 25 μ.

Dimensions. (Measured on 100 specimens from Sample F154; see text-fig. 5.) Grain length 20(27)32 μ, grain width 18(25)31 μ, grain depth 17(22)28 μ.

Orientation. (For grain positions see text-fig. 1.) Grains in position *a*—68 per cent., position *b*—7 per cent., position *c*—25 per cent.

Description. The original grain shape, as deduced from measurements and from grain orientations appears to have been subspheroidal to oblate spheroidal. The ratio grain length to grain width is shown in the scatter diagram text-fig. 4.

The sulcus extends for almost the full length of the grain and is parallel-sided throughout most of its length, but frequently shows slight expansion at the extremities. The ends are usually rounded. Most specimens show a darkened zone 1·5–2·0 μ wide on either side of the sulcus throughout its length. This either represents a thickening of the nexine adjacent to the sulcus or a doubling of this layer caused by infolding consequent on rupture of the grain along the sulcus. Optical sections of grains (text-fig. 3) suggest that the last interpretation is more likely to be correct. Some specimens, for example, that illustrated in text-fig. 3*b*, show a small gap in the thickened nexine layer adjacent to the sulcus, suggestive of breakage during infolding and compression. These sections also demonstrate that the sexine is not involved in the infolding.

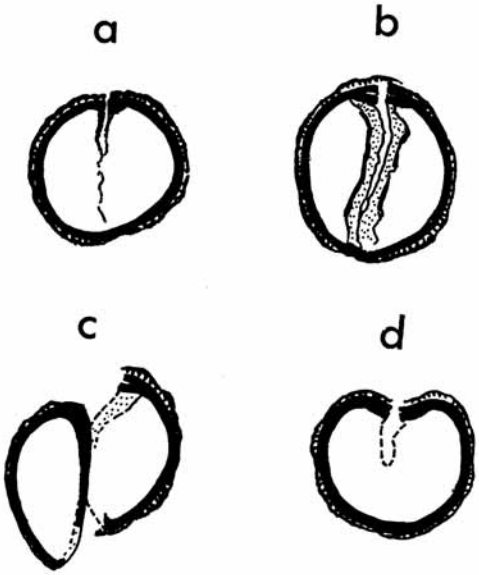
The stratification of the exine is distinct. The nexine is 0·8–1·8 μ thick. The bacula arising from this layer expand and coalesce at their tips to form the reticulum of the ectosexine. The meshes of the reticulum are irregularly polygonal, separated by muri 0·3–0·5 μ wide, which are formed from single rows of fused bacula. The meshes are generally of uniform size over the entire grain surface. The sexine characteristically separates from the nexine; separation is usually more extreme at the grain ends. Some grains were observed in which the sexine had been entirely removed.

Remarks. Clavatipollenites rotundus appears similar to Pierce's species *Retimonocolpites dividuus*, although the single illustration given by Pierce (1961, pl. 3, fig. 87) makes comparison difficult. Pierce does, however, mention the tendency for the exine layers to separate. Brenner (1963) recombined Pierce's species with *Liliacidites*, with little descriptive comment. The specimens from the Patapsco Formation show some evidence of infolding adjacent to the sulcus but not to the degree seen in the English forms. The American species appears less spherical and thinner and consequently tends to fold more readily than its English counterpart.

Distribution. In England *C. rotundus* is confined to Albian sediments. Its earliest recorded appearance is in Sample F270, which is probably of Lower Albian age. This occurrence is the only one observed beneath the base of the Gault. The species was noted in greatest abundance in the vicinity of the *niobe*

Subzone at Wrotham and at Folkestone, although it persists throughout the Albian. These concentrations, which do not in any case exceed 5 per cent. of the total spore and pollen content, may be due to a facies factor as they are associated with a rich benthonic fauna and ferruginous bands.

The distribution in time of *C. dividuus* is similarly restricted in America. Brenner (1963) records the species as being confined to the Patapsco Formation (Albian).



TEXT-FIG. 3. Optical sections of specimens of *Clavatipollenites rotundus* sp. nov., drawn from photographs to show the structure associated with the sulcus. All × 1,000. Nexine shown solid black. *a*, F154/Separate 8; 39·0, 98·1; nexine appears as thickening adjacent to sulcus. *b*, F154/Separate 1; 38·3, 99·2; optical section of grain in equatorial view. Slight obliquity causes sulcus to appear in section at top of drawing. Sexine is detached, not involved in infolding; the nexine adjacent to the sulcus appears split. Darkened zone next to the remainder of sulcus shown stippled. *c*, F154/10; 36·6, 106·0; split grain showing a similar structure to *b*. *d*, F154/2; 32·0, 100·1; grain in end-on view.

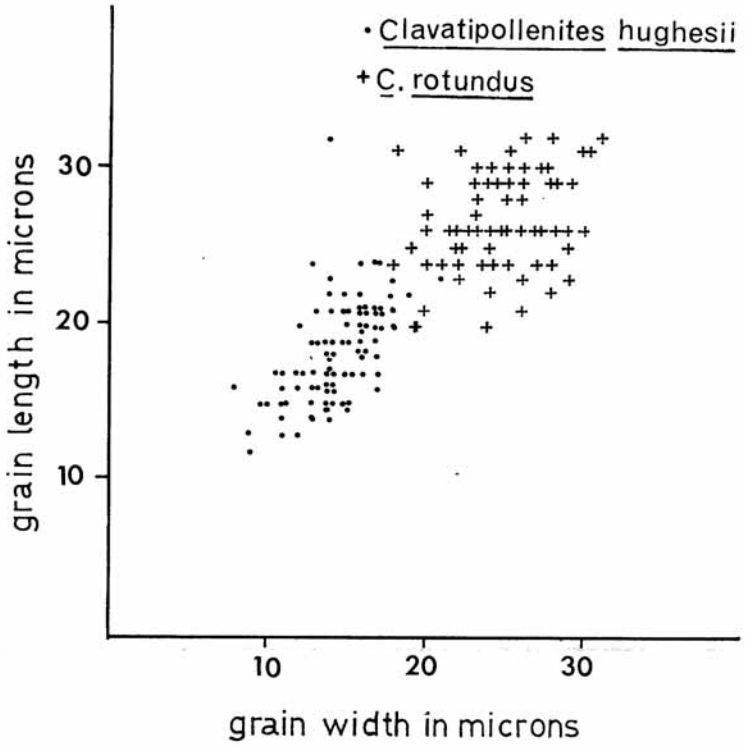
Clavatipollenites hughesii Couper emend.

Plate 80, figs. 9–19

Remarks. Couper (1958) gave no separate diagnosis for *C. hughesii*, so his description has been emended slightly and is here restated as a diagnosis.

Emended diagnosis. Monosulcate pollen grain, sulcus extending full length of grain, gaping in its central region and tapering slightly towards extremities. Equatorial outline elliptical to subcircular. Exine consisting of an inner unsculptured nexine 0·5–1·0 μ thick

and a sexine formed of baculate projections approximately 1·0 μ long, which either remain discrete or fuse at their tips to form a microreticulum. Lumina of reticulum irregularly polygonal, 1·0–2·0 μ in diameter.

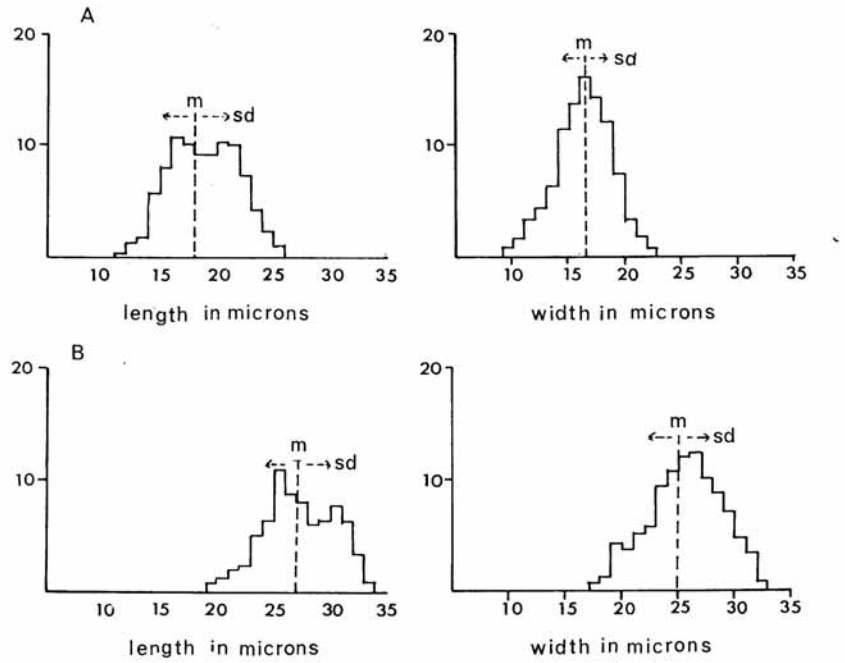


TEXT-FIG. 4. Scatter diagram showing differences of shape and size between *Clavatipollenites hughesii* Couper and *C. rotundus* sp. nov. Based on 100 specimens from each of the type samples, K475 Kingsclere Borehole, and F154, Ford Place, Wrotham.

Holotype. Couper (1958, pl. 31, figs. 21, 22). Slide C128/9, specimen K5087; 35·8, 114·2. Kingsclere Borehole at 475 ft. Grain orientated with sulcus uppermost. Length × width 28·0 × 17·5 μ.

Dimensions. (Measured on 100 specimens from the type sample.) Histograms of size frequency distributions are shown in text-fig. 5. Grain length 12(18)30 μ, width 8(16)19 μ, depth 12(13)17 μ.

Description. The outline of the grains is variable, ranging from almost circular to strongly elliptical. Margin of sulcus often ragged. The sulcus is frequently indistinct, or represented as an indeterminate tear in the exine. The grains are often folded with the long axes of the folds parallel to the sulcus.



TEXT-FIG. 5. Histograms showing frequency distribution of grain lengths and widths in A, *Clavatipollenites hughesii* and B, *C. rotundus* sp. nov. Graphs smoothed using a three-point moving average.

EXPLANATION OF PLATE 80

All figures at magnification ×1,000, unless otherwise stated.

Figs. 1–8. *Clavatipollenites rotundus* sp. nov. All specimens are from sample F154, *niobe* Subzone of the *dentatus* Zone. Lower Gault at Ford Place, Wrotham. 1, 2, F154/2; 32·2, 100·1. 1, Median focus, end-on view. 2, High focus on reticulum and extremity of sulcus. 3, F154/10; 36·6, 106·0; specimen split along sulcus, infolded zone adjacent to sulcus visible. 4, F154/7; 27·3, 91·8; sexine has been partly removed. 5, F154/7; 26·6, 101·1; sexine partly removed. 6, F154/Separate 4; 39·9, 97·3; part of grain in equatorial focus, sexine loose. 7, 8, F154/4; 39·9, 94·2; specimen from which sexine has been completely lost. 7, High focus showing dark zone adjacent to sulcus. 8, Median focus.

Figs. 9–19. *Clavatipollenites hughesii* Couper. 9, 10, Slide BP174A (IX); 60·0, 104·4 (N. F. Hughes Coll. No.). 9, High focus showing bacula in surface view. 10, Deep focus showing sulcus and exine stratification. Kingsclere Borehole at 475 ft. 11, 12, F154/1; 26·7, 107·0. 11, Median focus showing sulcus and exine stratification. 12, The same at ×2,000. 13, F154/5; 28·1, 92·5; median focus, sulcus and exine stratification shown. Ford Place, Wrotham; Middle Albian. 14, 15, K475/2; 23·2, 101·1. 14, Equatorial focus showing bacula in section. 15, High focus showing surface pattern; Kingsclere Borehole at 475 ft. 16, 17, F154/2; 54·2, 92·8. 16, High focus showing sulcus. 17, Equatorial focus showing exine stratification. Ford Place, Wrotham; Middle Albian. 18, F154/5; 23·9, 90·0; median focus on compressed grain. Ford Place, Wrotham. 19, F099/1; 55·0, 104·0; high focus on grain with irregular, gaping sulcus. Compton Bay, Isle of Wight; Middle Albian.

Remarks and comparison. The dimensions quoted are smaller than those quoted by Couper and cover the range of the species *C. minutus* Brenner, which may be conspecific with *C. hughesii*. The histograms of size-frequency distribution do not suggest any ready subdivision of the species on a size basis. The larger size quoted by Couper may be due to some extent to the maceration technique employed. The specimens measured in the present study were isolated from a fresh preparation of the type material which was subjected to only fifteen minutes oxidation time in contrast to the minimum of six hours quoted by Couper.

C. hughesii and *C. rotundus* are readily separable on the basis of their size ranges and on the shape of the grains. Text-fig. 4 illustrates these differences. In *C. hughesii* most grains are longer than they are wide. *C. rotundus* shows greater variation in the ratio length to width, with slightly less than half the grains being wider than long.

In *C. rotundus* the sulcus is a conspicuous feature, rounded at the extremities and modified by probable infolding at its margins. In some of the grains referred to *C. hughesii* the sulcus is barely discernible. Where visible it is a ragged opening, tapering towards its extremities and lacking the marginal rigidity of that in *C. rotundus*.

A third feature which separates the species is the degree of development of the ectosexinous reticulum. The bacula of the sexine in *C. rotundus* almost invariably unite at their tips to form the muri of an unbroken reticulum; in *C. hughesii* they often remain discrete or unite in short broken rows only to form an imperfect reticulum.

Distribution. The first occurrence of *Clavatipollenites hughesii* in the Barremian has been recorded by Hughes (1958). In about half the Lower Greensand samples examined during the present study it occurred in concentrations somewhat less than 1 per cent. of the total spore and pollen assemblages. It persists throughout the Gault to Upper Albian horizons, although with a much lower sample frequency. The highest recorded concentrations occur near the top of the Atherfield Clay (up to 10 per cent.).

Affinity of Clavatipollenites. The feature of greatest botanical interest in fossil pollen of the *Clavatipollenites* type is the presence of a tectate exine. It was this feature which led Couper (1958) to suggest an angiospermous origin. He compared *C. hughesii* to grains of the extant dicotyledon *Ascarina lucida* and also drew attention to structural similarities of pollen of certain members of the Liliaceae. *C. hughesii* represents, to present knowledge, the earliest record of this type of exine organization, although it may be argued that parallels exist among disaccate pollens. *Clavatipollenites* first appears in spore and pollen assemblages which lack any other obvious angiosperm elements, a fact which justifies close attention being paid to the genus.

In spite of the angiospermous character of some of the features of *Clavatipollenites* it still remains possible that the grains were produced by a member of some extinct gymnosperm group. The over-all shape of the grains resembles that of both living and fossil cycadophyte pollen. The form of the sulcus, particularly where this is rounded at its extremities, is closer to that of living cycad pollens than to most angiosperm pollen.

The orientation of the grains observed in *C. rotundus* shows a pronounced tendency towards proximo-distal compression. This suggests that the proximo-distal axis E_2 (designations as used by Couper, 1958, pp. 162–3) is shorter than the other equatorial axis E_1. This observation indicates a similarity of shape to that of the grains of *Androstrobus manis* and *Gingko huttoni* as these were analysed and presented by Couper.

It is apparent that species referred to *Clavatipollenites* are characterized by features suggesting the possibility of either angiosperm or gymnosperm parentage. All discussion of affinity is, however, purely speculative, and the problem can only be resolved by discovery of the grains in association with other reproductive structures.

Subturma TRIPTYCHA Naumova 1939

Remarks. Potonié (1960, p. 92) has treated Naumova's category as a subturma, although it was originally intended as a broadly defined form genus. Potonié has remarked that the category is used as Tricolpites in Erdtman's (1947) sense; i.e. as a broad supra-generic category incorporating tricolpate grains of indeterminate affinity.

Genus TRICOLPITES Cookson ex Couper 1953

Type species. Tricolpites reticulatus Cookson 1947, p. 134, pl. 15, fig. 45. (Subsequent designation, Couper 1953.)

Remarks. The use of a broadly circumscribed form genus for early tricolpate pollens is considered adequate and non-committal. The diagnosis of *Tricolpites* given by Couper (1953, p. 61) is as follows: 'Grains free, anisopolar, tricolpate. Exine variable in thickness and sculpture. Size variable.'

Other authors dealing with early tricolpate pollens have referred them to *Tricolpopollenites* Thomson and Pflug (see Groot and Penny 1960, Brenner 1963). The diagnosis of this form genus implies the presence of some form of germinal structure in the equatorial region of the colpi, although it is not precise as to the form of this feature; 'Exitus nur als meridionale Colpen ausgebildet' (Thomson and Pflug 1953, p. 95).

Pierce (1961) referred Cenomanian tricolpate grains to *Retitricolpites* van der Hammen, but this genus is not regarded as valid under the International Rules of Nomenclature since the type of *R. vulgaris*, the type species, is a grain of the extant species *Neea macrophylla*.

Tricolpites albiensis sp. nov.

Plate 81, figs. 1–22. text-fig. 6

Diagnosis. Small (less than 20 μ diameter) tricolpate pollen grains in which the ratio of polar to equatorial diameter lies between 2:1 and 1:1. The bacula of the sexine form an imperfect microreticulum. The total exine thickness is around 1·0 μ.

Holotype. Sample F312/4; 46·8, 90·0. Plate 81, figs. 2–4. From 18 ft. below the base of the *Exogyra* Rock, Upper Greensand, Lulworth Cove, Dorset. Probably Upper Albian, zonal position uncertain. Grain in obliquely polar orientation, with three colpi almost meeting at pole. Grain diameters 16× 17 μ. Exine slightly less than 1 μ thick, microreticulate.

Dimensions. Equatorial diameter 7·0(11·4)14·5 μ, polar diameter 10·5(13·5)17·5 μ, ratio of polar to equatorial diameter 1·0(1·35)1·65 (based on measurement of 100 specimens from the type sample).

Orientation. Grains in polar view—73 per cent., equatorial view—19 per cent., oblique view—8 per cent.

Description. Grains are tricolpate, trilobate and radially symmetrical in polar view, oval in equatorial view. The colpi are narrow and the acolpia small in relation to the rest of

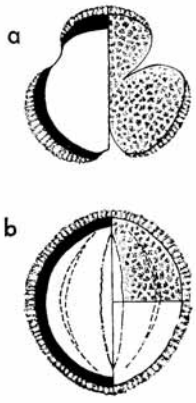
the grain; rare grains are almost syncolpate. The margins of the colpi are slightly ragged. The sexine and nexine are of approximately equal thickness. Diameter of meshes of microreticulum 0·3–0·4 μ.

Comparison. In its general form and size *Tricolpites albiensis* resembles *Tricolpopollenites micromunus* Groot and Penny. The original description of the species was brief, so close comparisons are difficult. *T. micromunus*, however, was described as having a coarsely reticulate exine, which justifies the separation of the English species from it. Brenner (1963, p. 93, pl. 39, fig. 7; pl. 40, fig. 1) gave a fuller description of specimens of *T. micromunus* from the Patapsco Formation, for which he quoted a mean polar diameter of 16 μ, and an equatorial one of 13 μ, which indicates that the American species is slightly larger.

It is possible that the species *Tricolpites minutus* Brenner is conspecific with *T. albiensis* although it appears to be slightly smaller and more spherical than the last species.

Affinity. Speculation as to the affinity of dispersed angiospermous grains of the generalized form of *Tricolpites* cannot be meaningful. Brenner (1963) compared the pollen of the extant species *Tetracentron sinense* to the dispersed species *Tricolpopollenites micromunus*. Similar small tricolpate grains occur in the families Trochodendraceae, Ranunculaceae, Salicaceae, etc.

Distribution. No specimens of *T. albiensis* have been recorded from the Lower Greensand. Rare specimens have been recovered from the Gault (Middle and Upper Albian). In the type locality, the Upper Greensand at Lulworth Cove, the species represented 15 per cent. of the total spore and pollen assemblage.



TEXT-FIG. 6. Diagrammatic representation of *Tricolpites albiensis* sp. nov., ×2,000. *a*, polar view with exine shown in section on left, nexine black. Surface view of reticulum on right, LO pattern. *b*, equatorial view, exine in section on left, one colpus shown in centre. Reticulum in surface view on right.

Tricolpites sp. 1

Plate 81, figs. 25, 26

Description. Grains tricolpate, oval in equatorial view, polar views not observed. Colpi distinct, open to a width of 2–3 μ in their equatorial regions and acutely pointed at their extremities. A slight thickening of the exine is visible at the margins of the colpi. The ectosexine forms a reticulum in which the meshes are irregular in shape, 1–3 μ in diameter. The sexine tends to detach and stand away from the grain in compressed specimens.

Dimensions. Polar diameter 21–23 μ, equatorial diameter 18–21 μ (3 specimens only).

Remarks and comparisons. This grain does not resemble any previously described Cretaceous form, but its rarity precludes its designation as a new species. Brenner (1963, p. 91, pl. 38, figs. 6–7) referred tricolpate forms with a coarse reticulum to *Retitricolpites*

georgensis Brenner, but that species is larger than the English form and has a finer, more closely appressed reticulum. Large reticulate forms from the Patapsco Formation were assigned to *R. geranioides* (Couper) by Brenner (pl. 38, fig. 8; pl. 39, fig. 1), a species originally described from the Miocene of New Zealand. This form, in addition to being much larger than the British species, has a more complex reticulum.

Distribution. From Sample F312 only, Lulworth Cove, Upper Albian.

Tricolpites sp. 2

Plate 81, figs. 23, 24

Description. Grains tricolpate, oval in equatorial view, trilobate and radially symmetrical in polar view. Colpi simple, margins smooth, extremities pointed. Exine baculate, bacula expanded at their extremities and fused to form a microreticulum of mesh diameter 0·5–1·0 μ. Sexine approximately 0·8–1·0 μ thick, i.e. about twice as thick as nexine.

Dimensions. Polar diameter 21–27 μ, equatorial diameter 18–24 μ (5 specimens).

Comparison. The grains described above are fairly close to those designated *Tricolpopollenites virgeus* Groot, Penny, and Groot. Brenner (1963, p. 92, pl. 39, figs. 4, 5) reassigned the species to *Retitricolpites* although the specimens described by Brenner possess a finer reticulum than that described by the original authors.

Distribution. On the basis of five specimens distributional records are only provisional. The chief interest of the grain lies in the fact that it appears to be the earliest occurrence of tricolpate grains encountered during this study. It has been recorded only from Leighton Buzzard, in the uppermost sample from the Woburn Sands (Sample F270) and in one sample from the overlying Gault. The first occurrence is thus in the Lower Albian. Associated with the tricolpate grains are well-preserved specimens of *Clavatipollenites rotundus*.

EXPLANATION OF PLATE 81

All figures at magnification ×1,000, unless otherwise stated.

Figs. 1–22. *Tricolpites albiensis* sp. nov. All specimens are from Sample F312, Upper Greensand, Lulworth Cove, Dorset: Upper Albian. 1, F312/4; 49·8, 90·8; equatorial focus. 2–4, F312/4; 46·8, 90·0; Holotype, grain slightly oblique. 2, High focus showing microreticulum. 3, Focus on pole showing colpi almost meeting. 4, The same, ×2,000. 5–7, F312/5; 37·0, 99·7. 5, Equatorial focus. 6, Higher focus approaching pole. 7, Equatorial focus showing bacula, ×2,000. 8, 9, F312/4; 43·6, 96·4; specimen torn along one colpus. 8, Near equatorial focus. 9, High focus. 10, 11, F312/5; 20·0, 102·0. 10. High focus close to pole. 11, Equatorial focus. 12, 13, F312/5; 24·9, 95·0. 12. Equatorial focus. 13, High focus on polar area. 14, 15, F312/5; 33·0, 93·1; equatorial view. 14, Deep focus on two colpi. 15, High focus on one colpus, microreticulum distinct. 16, 17, F312/5; 29·2, 93·2; obliquely orientated specimen. 16, High focus showing two colpi. 17, Median focus showing exine stratification. 18, 19, F312/4; 34·9, 89·4; polar view. 18, High focus. 19, Equatorial focus. 20, F312/5; 33·8, 98·4; equatorial view, median focus. 21, 22, F312/3; 41·0, 90·4; equatorial view. 21, High focus on one colpus. 22, Deep focus on two colpi, exine stratification visible.

Figs. 23, 24. *Tricolpites* sp. 2. F270/6; 58·8, 93·8; Munday's Hill, Leighton Buzzard; Albian. 23, Focus close to equator. 24, Higher focus close to pole.

Figs. 25, 26. *Tricolpites* sp. 1. F312/3; 47·1, 91·5; Lulworth Cove; Upper Albian. 25, High focus showing one of the colpi and the coarse reticulum. 26, Deep focus on reverse face of grain.

SUMMARY AND CONCLUSIONS

Tricolpate pollen grains of undisputed angiospermous origin first appear in England in sediments of Middle Albian age (apart from one known occurrence in what is probably the Lower Albian). They do not become abundant enough for formal description until the Upper Albian. Their appearance is pre-dated, in the Aptian or slightly earlier, by monosulcate grains referable to the genus *Clavatipollenites*. Grains belonging to this genus possess a tectate exine which suggests that they have an angiospermous affinity, although other features of the grains are more gymnospermous in nature.

Although the Lower Greensand (Aptian and Lower Albian) has been intensively studied palynologically, it has not yielded any recognizable angiosperm pollens. This is of interest since it was allegedly from this formation that Stopes (1912, 1915) described petrefactions of angiosperm woods of an advanced type. These fossils have frequently been cited as indicating a long, pre-Cretaceous history of development for the angiosperms as a whole. The absence of recognizable angiosperm pollen from the formation is difficult to reconcile with the presence of highly evolved woods.

The early angiosperm grains which appear in the overlying formation are of simple form, tricolpate, with a microreticulate sexine. The grains are all notably small, not exceeding 20 μ in diameter. Their general lack of specialization and small size is shared by late Lower Cretaceous angiosperm grains recorded from other parts of the globe, notably from North America. This apparent lack of specialization in the earliest angiosperm grains does not readily fit in with the idea of a long pre-Cretaceous history for the group. Rather, grain morphology in the observed earliest occurrences of angiosperm grains is more compatible with the view of an early Cretaceous origin (see Hughes 1961).

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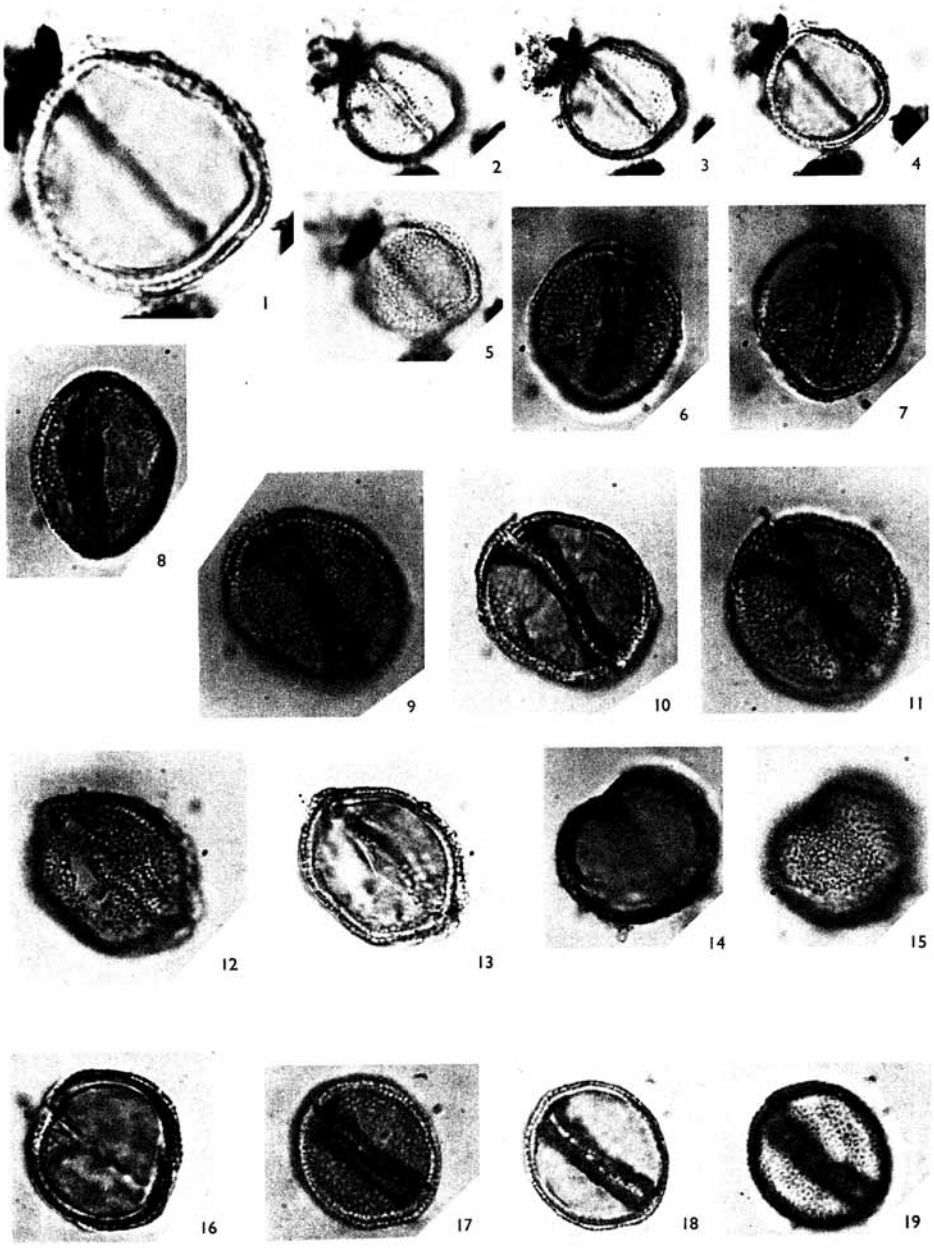
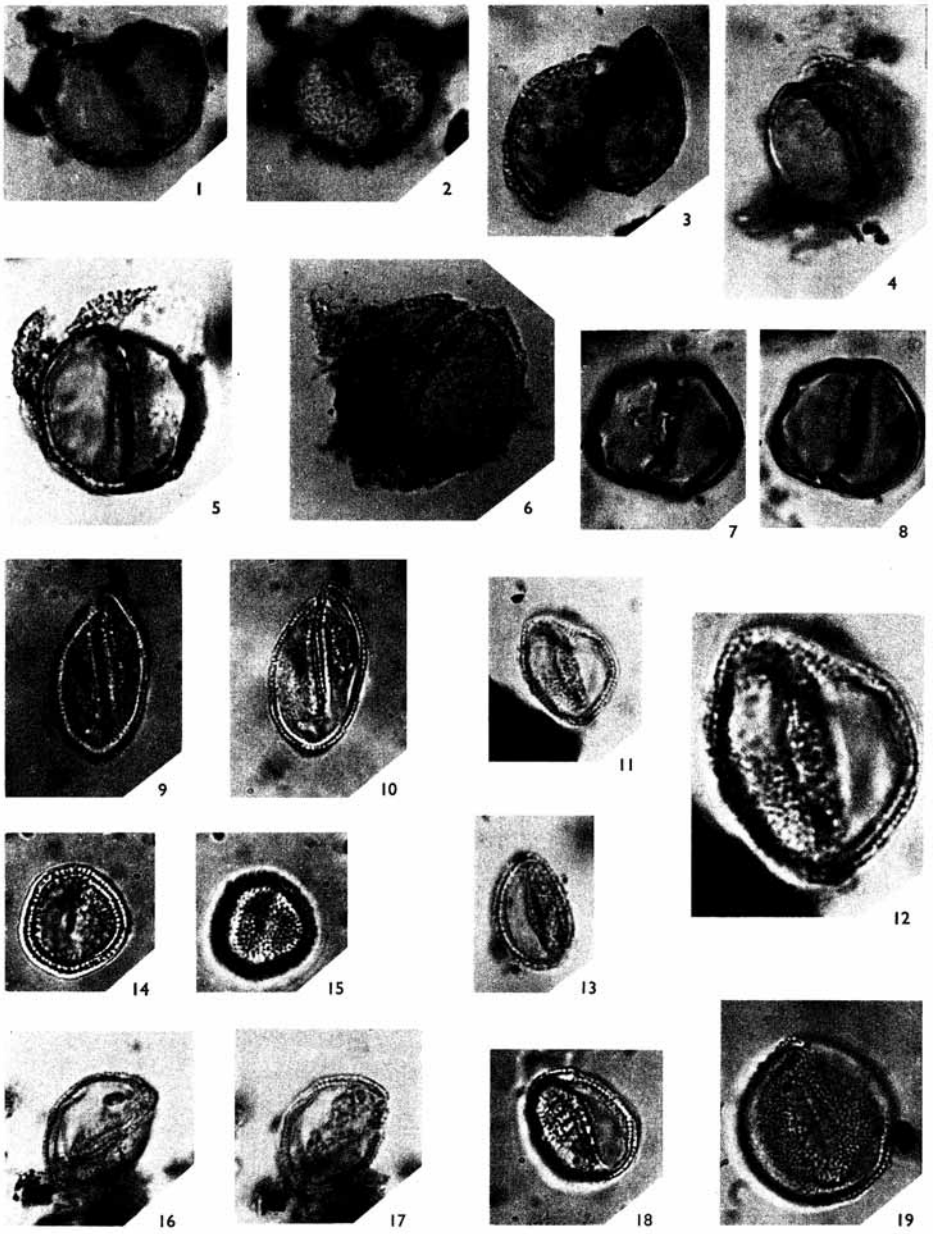
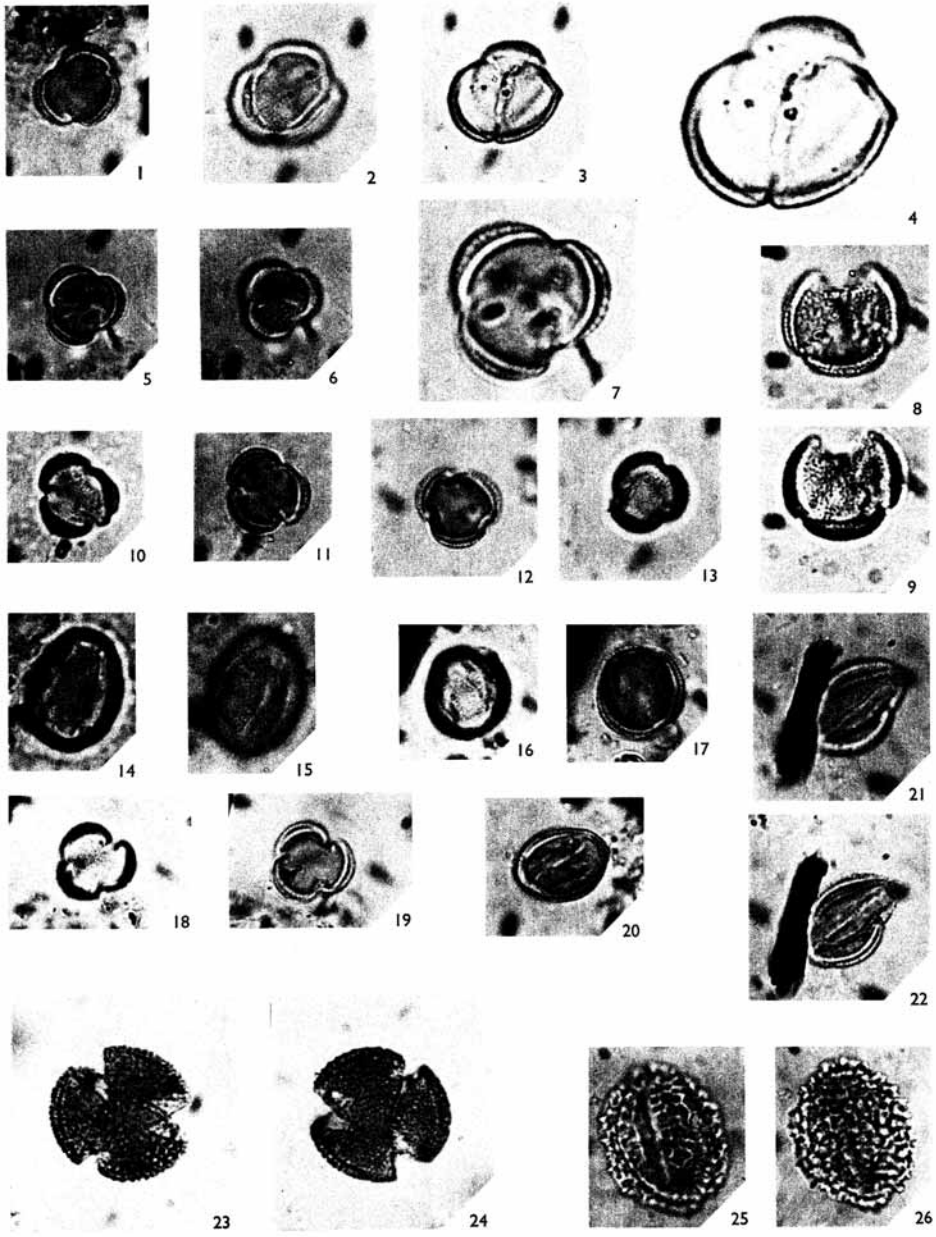


KEMP, Mid-Albian pollen



KEMP, Albian and Barremian pollen



KEMP, Albian pollen