FURTHER INTERPRETATION OF *EUCOMMIIDITES* ERDTMAN 1948

by N. F. HUGHES

ABSTRACT. A new interpretation is given of the genus *Eucommiidites* and further illustration of the type species *E. troedssonii*. *E. delcourtii* sp. nov. is erected for pollen observed in the micropyle and pollen chamber of a new Lower Cretaceous seed *Spermatites pettensis* sp. nov., which is also described. This new evidence is all believed to support the gymnospermous origin of *Eucommiidites*.

THE finding of pollen of the *Eucommiidites* type in the micropyle and pollen chamber of a dispersed Lower Cretaceous seed has led to a reassessment of the nature and distribution of this unusual type of pollen grain.

The importance of the Jurassic pollen grain species *Eucommiidites troedssonii* Erdtman has been widely discussed, e.g. Scott *et al.* (1960), Harris (1960*b*), Hughes (1961), because it was originally described by Erdtman (1948) as tricolpate. The pressure to find Jurassic angiosperms has been such that in spite of various attributions of this species to a gymnospermous origin, the suspicion remains that Erdtman may have been right. Some further interpretation is attempted here and a restated diagnosis is given in neutral terms which are better used at least until the grain has been seen in its tetrad.

The specimens discussed below were collected by the author and are deposited in the Sedgwick Museum, Cambridge, numbers K2277–84.

SYSTEMATIC DESCRIPTION AND DISCUSSION

Anteturma POLLENITES R. Potonié 1931
Turma PLICATES (Naumova) Potonié 1960
Subturma PRAECOLPATES Potonié and Kremp 1954
Genus EUCOMMIIDITES Erdtman emend.

1948 Erdtman G., *Geol. Foren. Forh.*, **70**, 267.
1958 Couper R. A., *Palaeontographica*, **103B**, 160.

Restated diagnosis. Pollen grains with oval equatorial outline in usual viewing position. On one face, which is flat, is a long furrow with rounded ends, parallel with the long axis; in the unexpanded condition, the margins of this furrow may close over it in the middle. The opposite face, which is more convex, bears a ring-furrow near the margin, separating the larger part of the face (zonisulcate condition of Erdtman 1952). Ring-furrow exine thin; ring may be incomplete at the ends in the long axis. Pollen wall with thin inner layer and thicker less refractive outer layer.

Generic name. Rouse (1959) preferred *Trifossapollenites* Rouse 1957 on grounds of priority over Couper's final removal of *Tricolpites* from the name in 1958. Rouse's view is not accepted because although Erdtman (1948) used the name *Eucommiidites* only as 'nomen typicum concretum' rather than as a genus, his meaning was perfectly clear in

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using *Tricolpites* as a 'nomen typicum abstractum', which could be taken as a higher grouping; the information given by Erdtman was also adequate in other respects. *T.* (*Eucommiidites*) had appeared several times in European literature before 1957. It is only fair to point out that Rouse (1959) did not actually make the change which he advocated. Finally, if Rouse's name is reconsidered, it will also be necessary to assess the validity of *Protoquercus agdjakendensis* of Bolkhovitina (1953) which may well represent the same pollen. The classification of this genus adopted by Potonié (1960, p. 88) is considered to be flexible and appropriate.

Type species. E. troedssonii Erdtman 1948.

Eucommiidites troedssonii Erdtman

Plate 37, figs. 1–16; text-figs. 1A–F

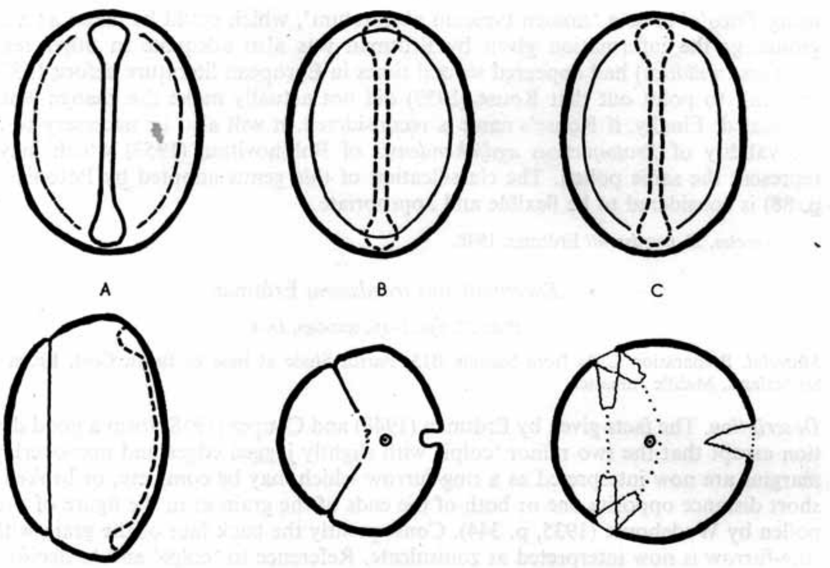
Material. Preparation C104 from Sample B13, Parrot Shale at base of Brora Coal, Brora Mine, Sutherland. Middle Jurassic.

Description. The facts given by Erdtman (1948) and Couper (1958) form a good description except that the two minor 'colpi' with slightly jagged edges and non-overlapping margins are now interpreted as a ring-furrow which may be complete, or broken for a short distance opposite one or both of the ends of the grain as in the figure of *Castalia* pollen by Wodehouse (1935, p. 344). Consequently the back face of the grain with this ring-furrow is now interpreted as zonisulcate. Reference to 'colpi' and to decisions on orientation (mention of poles) should be omitted until evidence is conclusive; the legend of fig. 1*f* in Hughes and Couper (1958) is in error in this respect.

Discussion. The probable orientation of these pollen grains is uncertain because if they are compared with *Classopollis* Pflug which has these structures (description of Couper 1958, p. 157), the ring-furrow must be distal. Their time range is similar to that of *Classopollis* and they sometimes occur in the same samples. On the other hand, the main long furrow is very similar to the single furrow of cycad pollen, which is interpreted in recent material also as distal, i.e. anatreme (Erdtman 1960); cycad pollen is frequently found in the same samples as *Eucommiidites*.

As indicated in Pl. 37, figs. 7–14, in which the grain lies obliquely, the ring-furrow is believed to have been complete. In the more usual view, Pl. 37, figs. 1–5, the minor furrows curve inwards of course but are not seen to join; this may be because the ring is frequently incomplete, or because it passes from view behind the widened and folded end of the long furrow. The holotype (Erdtman 1948, fig. 15) subsequently designated by Nilsson (1958) presents this view. The end views (Pl. 37, figs. 15–16), which are in all cases rare (Couper 1958), give a little cause for disquiet over my interpretation as it is not easy to separate the two distinct kinds of furrow in this view; in fig. 15 the main long furrow is on the right side and in fig. 16 it is upper right. It would seem that this difficulty is increased by the fact that these two grains were inflated before compression in the sediment (nearly circular in optical section), which reduces the contrast normally seen between the furrows. Possibly only inflated grains had any real chance of being preserved in this orientation.

It is clear that the remarks of both Simpson (1937) and Pflug (1953) lend some support to my interpretation. Simpson (as mentioned in Hughes and Couper 1958)



TEXT-FIG. 1. Diagrammatic views of the pollen grain *Eucommiidites troedssonii* Erdtman. A, Front view showing main furrow and ring-furrow (broken line—behind). B, Back view showing complete ring-furrow. C, Back view showing ring-furrow incomplete at the ends. D, Lateral view showing ring-furrow, difference in convexity of faces and position of main furrows, E, End view (theoretical) with ring-furrow, possibly incomplete, and main furrow unexpanded. F, Grain in end view position but with main furrow (right) expanded, consequently circular in optical section, and ring-furrow. This grain is slightly inclined (top to left) to show ring-furrow more clearly and to compare with Plate 37, fig. 15.

EXPLANATION OF PLATE 37

Magnification of all figures ×1,000.

Figs. 1–16, *Eucommiidites troedssonii* Erdtman; sample B13, Brora Coal, Middle Jurassic. 1, Back view; prep. C104/1, 46.0 117.2 OR. 2, Back view; prep. C104/3, 44.2 118.2 OR. 3, Front view; prep. C104/1, 39.3 120.7 OR. Figs. 4–5, Front view; prep. C104/3, 50.1 126.6 OR. 4, High focus. 5, Lower focus. 6, Front view, specimen obliquely compressed; prep. C104/3, 43.0 114.9 OR. 7, Oblique back view, high focus, showing ring-furrow partly open; prep. C104/1, 36.9 108.2 OR. 8, Slightly oblique front view, showing ring-furrow passing round end of main furrow; prep. C104/1, 35.2 126.2 OR. Figs. 9–10, Slightly oblique back view, showing ring-furrow complete at one end. 9, Prep. C104/1, 53.1 108.2 OR. 10, prep. C104/3, 38.7 127.3 OR. Figs. 11–14, Oblique views showing nature of ring-furrow. 11, Prep. C104/1, 37.8 108.9 OR. 12, Prep. C104/3, 43.2 123.7 OR. 13, Prep. C 104/3, 50.7 120.9 OR. 14, Prep. C104/3, 47.8 109.9 OR. Figs. 15–16, End views; prep. C104/1. 15, Inflated specimen, main furrow right, cf. text-fig. 1*f*; 37.8 108.9 OR. 16, Partly inflated specimen, main furrow—upper right; 51.8 124.1 OR.

Figs. 17–18, *Eucommiidites minor* Groot and Penny. 17, Front view, Hauterivian specimen, sample WM 1618/6; prep. M834/1, 49 122 OR. 18, Front view, Barremian specimen, sample WM 1333/10; prep. BP569/3, 48.1 127.8 OR.

obviously saw *Eucommiidites* in the Bora Coal and this led him to discuss and figure pollen of recent Nympheaceae which has an 'opercular' structure, and even to stress the bilateral symmetry in recent *Nelumbium*; unfortunately the fossils he actually figured were of an entirely different type (Hughes and Couper 1958). Without agreeing with Pflug's diagnosis (1953, p. 91) of *Classopollis*, it is worth noting that he regarded *Eucommiidites* as similar to it.

Comparison. Erdtman's original comparison (1948) with pollen of *Eucommia ulmoides* Oliv. has been restudied on material from a tree in the Botanic Garden, Cambridge. As noted by Couper (1958 p. 164), the *Eucommia* pollen (see also Erdtman 1952) has slight pores (tricolporate) and the iregularities of the colpi do not include development of a single cycad-like furrow. *Cercidiphyllum* pollen, which also has colpi of irregular length, has true angiosperm colpate symmetry and is even less like *Eucommiidites*. Pollen of the Nympheaceae, although similar in gross morphology, differs markedly in exine stratification. Such comparison with recent pollen certainly assists in morphologic interpretation, but does not seem likely to result in determination of affinities.

Among fossils the specimens of Delcourt and Sprumont (1956) differ from the holotype and are discussed separately below. The figured specimens of Pons (1956), Delcourt and Sprumont (1957), Oszast (1957), and Nilsson (1958) belong to *E. troedssonii* and also some of those figured by Thiergart (1949), Reissinger (1950), and Kuyl *et al.* (1955); in these latter cases, however, it appears that another undescribed type may be represented by some of the figures. *Trifossapollenites ellipticus* Rouse 1957, of Senonian age, may well prove to be a distinct species, similar to some of the figures of Kuyl *et al.* (1955, pl. 6, figs. 1–6). *T. rugosa* (*sic*) Rouse 1959 is not at all clearly distinguished by its author from *T. ellipticus*. The figures of Oszast show well the ring-furrow interpretation difficulty, which has been discussed above.

Attribution. Kuyl *et al.* (1955) suggest the Chlamydospermales, and Pons (1956) does so quite separately, without quoting any earlier references or opinions on this fossil. Palynological evidence of the widespread existence of plants similar to the Chlamydospermales in Mesozoic times is accumulating; no progress has yet been made, however, with macrofossil identification of the group. In this connexion I regret the placing of fossil pollen species in extant genera such as *Ephedra* (Scott 1960), which is likely to be a hindrance to understanding, if not actually contrary to the Rules of Nomenclature (Potonié 1960, p. 21). If there was a Mesozoic group at all, it is unlikely that its members will prove to be close in affinity to the three surviving relict genera; as has been shown many times with other groups, the evidence of a single organ is quite insufficient. I see no hope of clear understanding of Mesozoic and earlier plant evolution, while such practices are aimed at focusing attention on so-called long-ranging minor taxa; a complete change of attitude is necessary.

Eucommiidites delcourtii sp. nov.

Plate 38, figs. 3, 4, and 7

Diagnosis. Small species of *Eucommiidites* Erdtman emend. Exine of back face with small shallow pits of two sizes, both less than 1 μ in diameter; remainder of exine laevigate, thickness 1–1½ μ.

Dimensions. Length 16–23 μ (mean 19 μ); breadth 12–20 μ (mean 15 μ); twenty-five specimens.

Holotype. Preparation 357A, 42.8 111.8 OR (specimen at outer end of micropyle). One other specimen adjacent to the holotype and six others clearly visible in the pollen chamber are necessary as paratypes.

Locus typicus. Loc. H48B, Ashdown Sands, Lower Cretaceous; Cliff End, Hastings.

Description. Holotype, 21 × 17 μ, is seen in opercular view; the seven paratypes supplement this. These specimens have only been subjected to a short dispersal treatment (to free the seeds from matrix) in boiling water with sodium carbonate; their size is less likely, therefore, to have been increased by swelling, as may well be the case in all mentioned (dispersed) specimens of *E. troedssonii* and *E. minor*.

Comparison. *E. delcourtii* differs from the other two species in size and/or sculpture; it has been observed in the micropyles and pollen chambers of four seeds from the same locality.

Eucommiidites minor Groot and Penny 1960

Plate 37, figs. 17–18

Description. Small species of *Eucommiidites* Erdtman emend. which is nearly circular in equatorial outline and was perhaps nearly spherical. Psilate exine, 1½–2 μ thick. As noted by Delcourt and Sprumont (1956, p. 378) the shape causes oblique and 'end' views to be more frequent than in *E. troedssonii*.

Occurrence. Dispersed pollen in Wealden facies in England from Hauterivian to probably Aptian.

Dimensions. Diameter 18–25 μ.

Discussion. While I may be held partly responsible for the naming of this species, of which I have good material, Groot and Penny (1960) are entirely responsible for the holotype. *E. troedssonii* var. *baldurnensis* of Delcourt and Sprumont (1956) is very likely to be the same as the English material, but I do not elevate or advocate elevating the varietal name because although the drawings are most informative, the photographs could not serve for holotype illustrations. Although the Groot and Penny diagnosis is very tentative and their photograph none too clear, there seems to be no useful purpose in erecting another species for the English material at present. The size range given for *E. troedssonii* from Féron-Glageon by Delcourt and Sprumont (1959) suggests the presence of *E. minor*.

Benettiteae-pollenites lucifer Thiergart 1949 included some small grains originally, and Delcourt and Sprumont (1956) use the name (with drawings only) for some very small grains (13 μ) from Baudour. Thiergart (1949) gave eight separate figures (Trias to

EXPLANATION OF PLATE 38

Figs. 1–7, *Spermatites pettensis* sp. nov., *Eucommiidites delcourtii* sp. nov. Figs. 1–2, *S. pettensis*, Holotype. 1, Apical part, × 190. 2, whole ovule, × 45. Figs. 3–4, *E. delcourtii*, enlarged from fig. 1. 3, Holotype (above) and paratype, attached to tip of micropyle, × 1,200. 4, Paratypes in pollen chamber, × 1200. 5, *S. pettensis*, pollen chamber; prep. 357B, 37.8 114.6 OR, × 500. Figs. 6–7, *S. pettensis*; prep. 357, 43.3 119.6 OR. 6, base of micropyle × 500. 7, *E. delcourtii* pollen in micropyle, × 1200. *Photographs by Miss M. E. Dettman.*

Cretaceous) but six are not usable, and it seems likely that the others refer to larger material perhaps conspecific (if identifiable) with *E. troedssonii*. There seems to be no reason to use this name for the small grains.

DISPERSED 'SEEDS', INCERTAE SEDIS

Form-genus SPERMATITES Miner

Discussion. Miner did not designate a type-species and the taxon is best treated as a form-genus with no such designation (cf. Andrews 1955, p. 7). This generic attribution is preferred for the present material as it refers to seeds (or parts of seeds) as seen after maceration, in transmitted light. There is undoubtedly overlap with the earlier form-genus *Carpolithes* Schlotheim, which, however, is better retained for unmacerated compressions. The species discussed here will clearly be reallocated when it is better understood.

Spermatites pettensis sp. nov.

Plate 38, figs. 1, 2, 5, and 6

Diagnosis. Compressed ovule of generally oval shape with thick nucellar cuticle, which is lightly punctate (punctae $< 1\ \mu$). Pollen chamber well developed. Inner integument cuticle thin with longitudinal cellular markings, continued into a protruding micropylar tube of about one-quarter the length of the nucellar cuticle. Pollen of *Eucommiidites pettensis* in micropyle and pollen chamber.

Dimensions. Length of nucellar cuticle 750 μ (six specimens), maximum width 540 μ; length of micropyle observed to 240 μ.

Holotype. Preparation 357A, 43.3 112.3 OR (Pl. 38, figs. 1, 2).

Locus typicus. Sample H48B, Ashdown Sands, Lower Cretaceous; Cliff End, Hastings.

Description. Holotype 860 $\mu \times 560\ \mu$; 200 μ length of micropyle seen. Nucellar cuticle observed to be punctate at base, thickness $1\frac{1}{2}\ \mu$ or more; large pollen chamber 70 μ high by 100 μ long at apex. Dark rough area of cuticle on one face, 70–100 μ in diameter, about one-third of the length above the base. Upper half or more of nucellar cuticle covered by thin ($\frac{1}{2}\ \mu$) inner cuticle of the integument with elongated cell pattern arranged longitudinally; micropyle with slight irregular folding of cuticle, 30 μ wide increasing to pollen chamber at base. Seven grains of *E. delcourtii* in the pollen chamber, seven more tightly compressed in the upper part of the micropyle and two (one the holotype of *E. delcourtii*) entangled in the slightly torn open end of the micropyle.

Five other specimens, 357/1, 357/2, 357B/1, 357B/2, and 326, show different grades of preservation. Three show pollen in the micropyle and/or the pollen chamber. Two specimens 357B2 and 326 show a dark patch on one face above the base as does the holotype. In these and in 357/1 there is evidence of compression of an original asymmetrical body and the dark patch is probably in the chalazal area although there is no opening. In 357/1 the main cuticle apparently bears isodiametric cell markings overall, but this is a corrosion effect from natural maceration. With such a small number of specimens the state of both development and preservation is bound to differ; further investigation is in hand.

Comparison. These specimens fit the diagnosis of *Spermatites* Miner sufficiently well to be included, but they differ from all of the seven species described by Miner (1935) and the three unnamed species of Schemel (1950) in the presence of the micropylar tube. Pant and Nautiyal (1960) describe three new genera of similar type with pollen chamber and long micropyle (one is short) but disaccate pollen is included in the diagnosis, the sizes are much greater, a chalazal hole is described in each case and they are probably of Permian (Lower Gondwana) age. Thomas and Harris (1960) describe some cycadean seeds and associated pollen from the Yorkshire Middle Jurassic but the present material is clearly distinct. There is no close resemblance to the *Caytonia* seed or pollen of Harris (1960*a*).

Attribution. Speculation on the origin of these gymnospermous ovules is perhaps not yet profitable. The pollen can only be said to resemble that of Cycadophytes, Ginkgoales, and perhaps Chlamydospermales. The probable lack of chalazal opening seems to eliminate Cycadophytes and to suggest Coniferales which, however, do not fit on pollen and other details such as the pollen chamber. There does not appear to be any typical 'megaspore cuticle' (Harris 1954, 1960*a*) and hence Cycads, Ginkgoales, and Conifers are unlikely. The seeds differ in many respects from those of the Caytoniales (Harris 1960*a*) and therefore the Chlamydospermales become the most likely group; they at least have a conspicuous pollen chamber formed just prior to pollenation and a single true integument greatly elongated as a micropylar tube (*Ephedra*). The pollen of the three living genera does not closely resemble *Eucommiidites*, but if several recent indications (Scott 1960) are correct there may have been in the Mesozoic a fairly large Chlamydosperm-like group of which the living genera are mere chance survivors. Some angiosperm seeds possess some of the cuticle characters mentioned but no cases are sufficiently similar to cite.

GENERAL CONCLUSION

In caution, mention should be made of the description by Sahni (1915) of some Recent *Ginkgo* ovules with three types of foreign pollen within the micropyle and pollen chamber; some of the grains had even germinated.

In the present case the pollen (more than twenty-five grains) was all of the same species (*E. delcourtii*). Assuming it to belong to the same unknown plant as the 'seed', the evidence presented clearly indicates a gymnospermous origin for *Eucommiidites* Erdtman, thus strengthening the case presented (Hughes 1961) for angiosperm history beginning in mid-lower Cretaceous time.

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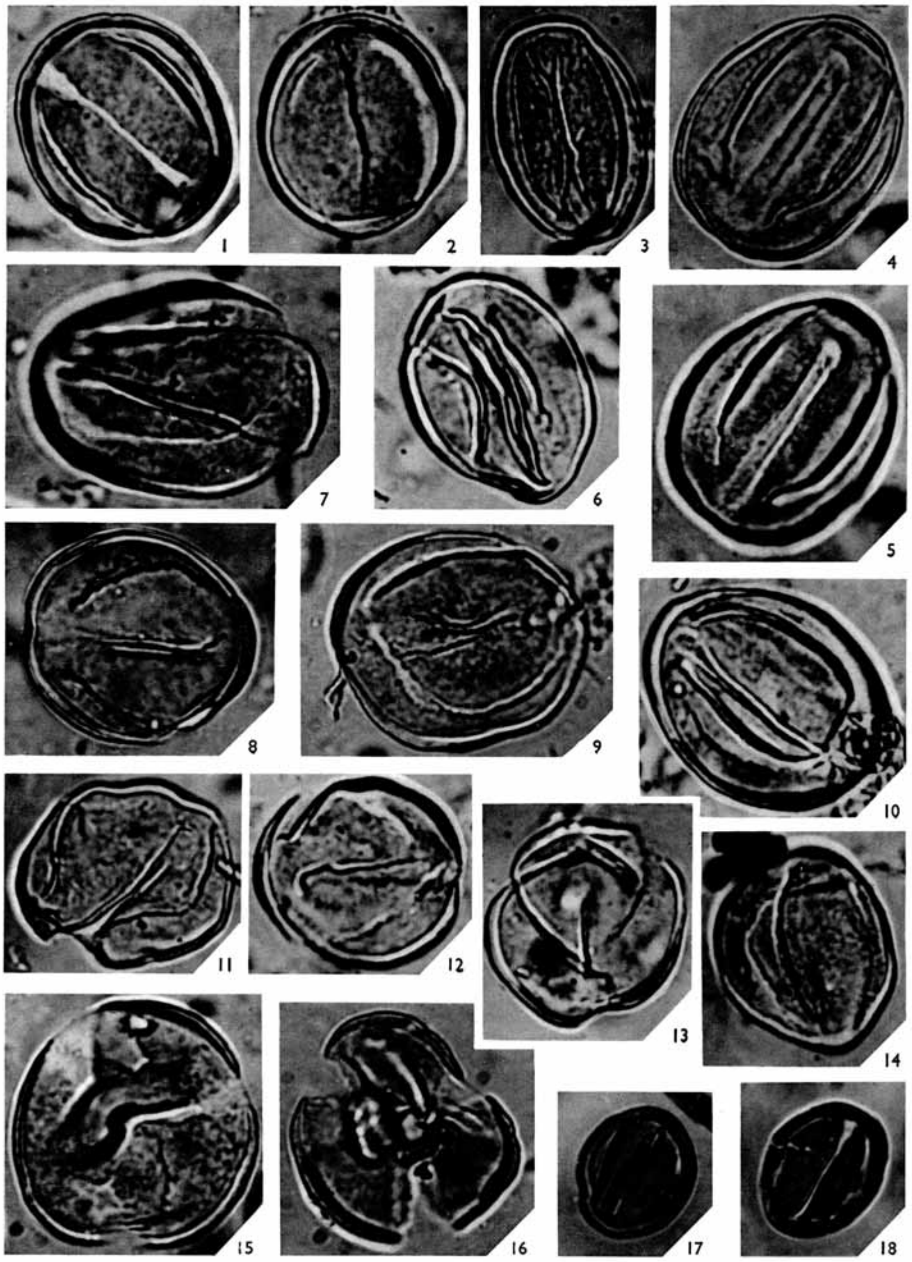
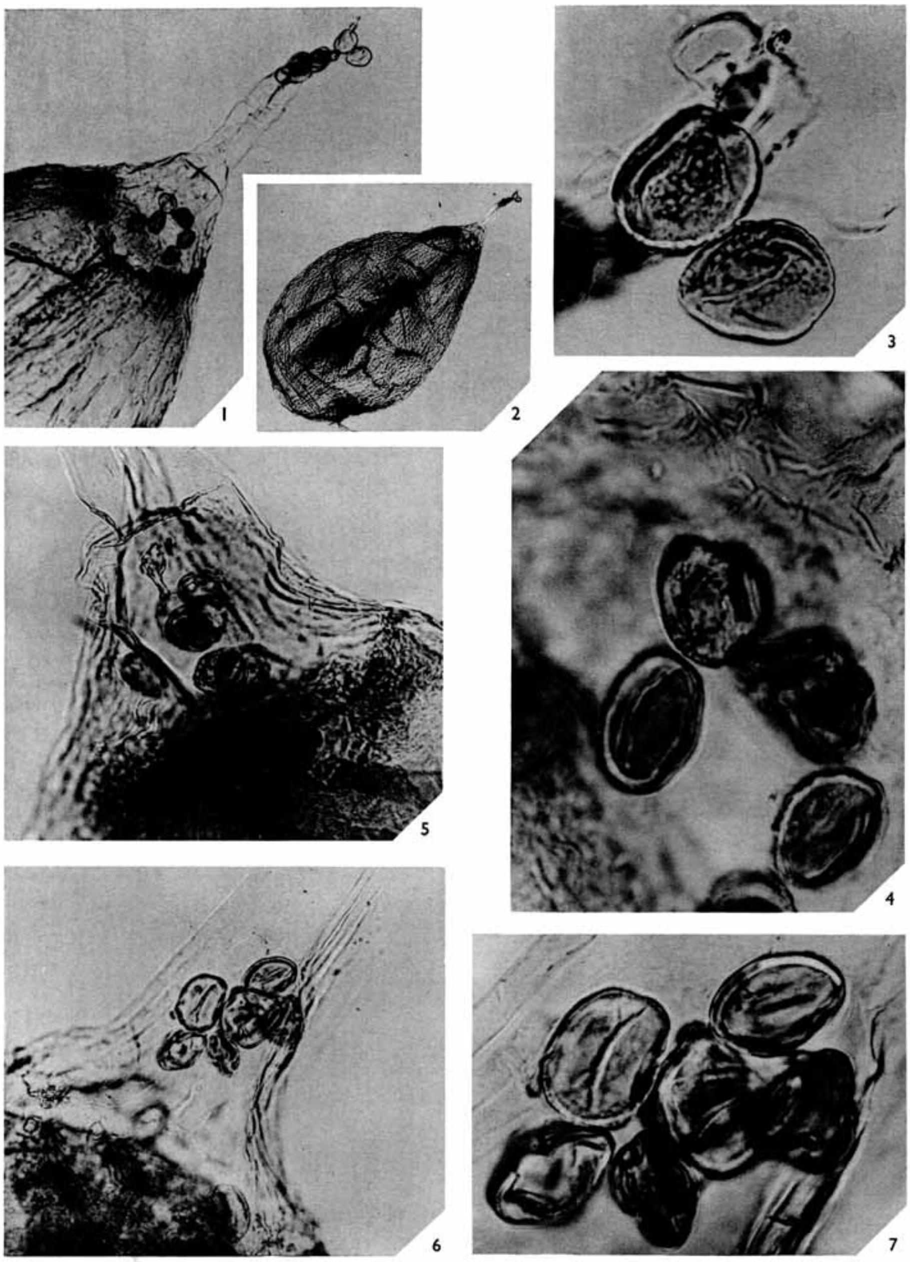


HUGHES, Jurassic and Cretaceous pollen



HUGHES, Cretaceous seeds and pollen