BRITISH PERMIAN SACCATE AND MONOSULCATE MIOSPORES

by R. F. A. CLARKE

ABSTRACT. Thirty-three species belonging to seventeen genera are recorded and described from the British Upper Permian (Zechstein). Six species are considered to be new. Three variants are described for *Lueckisporites virkkiae* Potonié and Klaus 1954 and the diagnosis is emended. The sample localities, brief lithological descriptions, and some spore frequencies are given together with a comparison of the present assemblages with those previously described from other parts of the world. It is concluded that a uniform flora existed throughout the Upper Permian in Great Britain and that this differed little from the Permian vegetation of Western Europe in general.

PREVIOUS work on the miospores of the British Permian is limited to a short publication by Chaloner and Clarke (1962) and the observations of Jansonius (1962). The aim of the present paper therefore is to describe the British Permian microfloral assemblages and to compare these with those previously described from other parts of the world.

Slide collection and maceration technique. The majority of the specimens illustrated in this paper are from single spore mounts. The method of making these and the preparation of the residues from the samples has already been described (Clarke 1965, this volume). The slide collection is housed in the Geological Survey and Museum, London.

Classification and terminology. The system used here to group spores into supra-generic categories is the 'Morphographic Classification' outlined by Potonié and Kremp (1954, 1955, 1956) coupled with subsequent additions (Potonié, 1956, 1958, 1960) and modifications set up by later authors. Some of the less obvious terms employed to describe the morphology of the different spore types are illustrated in text-fig. 1.

Sample localities

1. Hilton, Westmorland. The Hilton Plant Bed is exposed in Hilton Beck, 3 miles east-north-east of Appleby, Westmorland. The junction between the Penrith Sandstone and the Plant Beds is seen in the river bank on the north side at the western end of Ash Bank Wood. Most of the Plant Beds are exposed in the river bluff on the south side of the beck and consist of a series of well-bedded, alternating sandstones and thin pale-grey or olive-green shales (text-fig. 2).

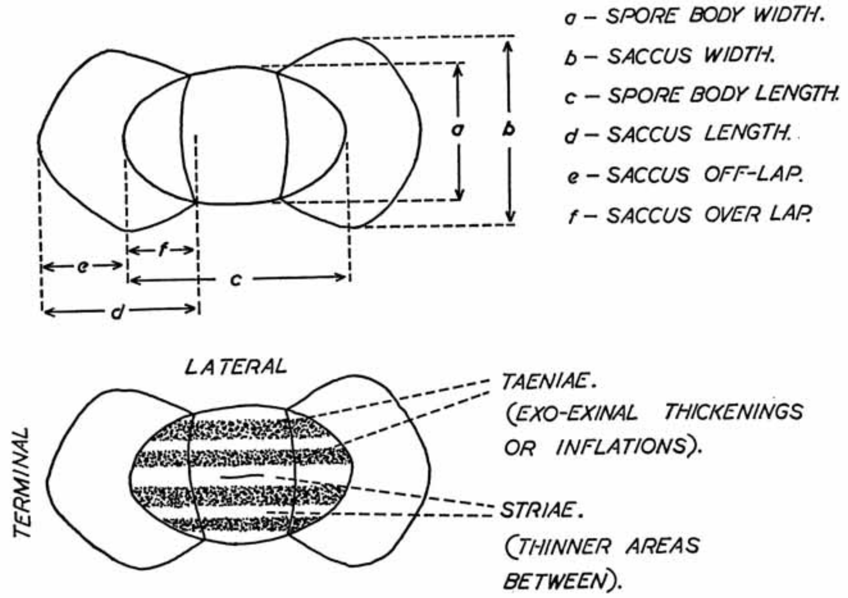
2. Kimberley, Nottinghamshire. A 20-foot section of Lower Permian Marl (= Marl Slate of some authors) is exposed on the south side of the more northerly railway cutting (disused) some 500 yards west of the tunnel at Kimberley, west of Nottingham. At this point a 4-foot-thick Permian breccia overlies, unconformably, Carboniferous Coal Measure Sandstone. This is overlain by the alternating sandstones and shales of the Lower Permian Marl, containing ill-preserved plant remains. The top of the cutting exposes the Lower Magnesian Limestone, which here is arenaceous and gritty, obscuring a clear demarcation between this and the Lower Permian Marl (text-fig. 3).

3. Haughton Hall Boring. Located 4 miles south of East Retford, Nottinghamshire. All Permian samples examined between 987–1,117 feet contain spores.

Acknowledgements. I would like to express my thanks to Professors S. E. Hollingworth and T. Barnard for the use of laboratory facilities at University College, London. The help of Mr. M. A. Calver and the Geological Survey of Great Britain who kindly made available the Haughton Hall Borehole

[Palaeontology, Vol. 8, Part 2, 1965, pp. 322–54, pl. 40–44.]

material and gave permission for the data to be published, and Mrs. H. H. Stoneley who supplied information on the Kimberley section is acknowledged with gratitude. To Dr. J. Jansonius I owe special thanks for allowing me complete freedom with the study of the Hilton Plant Beds after he had already started work on this section himself. The present paper formed part of a larger study of British Permo-Triassic spores, for a doctoral thesis, under the supervision of Dr. W. G. Chaloner to whom I am greatly indebted for immeasurable help and the critical reading of this manuscript. Finally I should like to thank the Department of Scientific and Industrial Research from whom I have been in receipt of a grant.



TEXT-FIG. 1. A generalized bisaccate miospore, in polar view, illustrating various terms used in this paper.

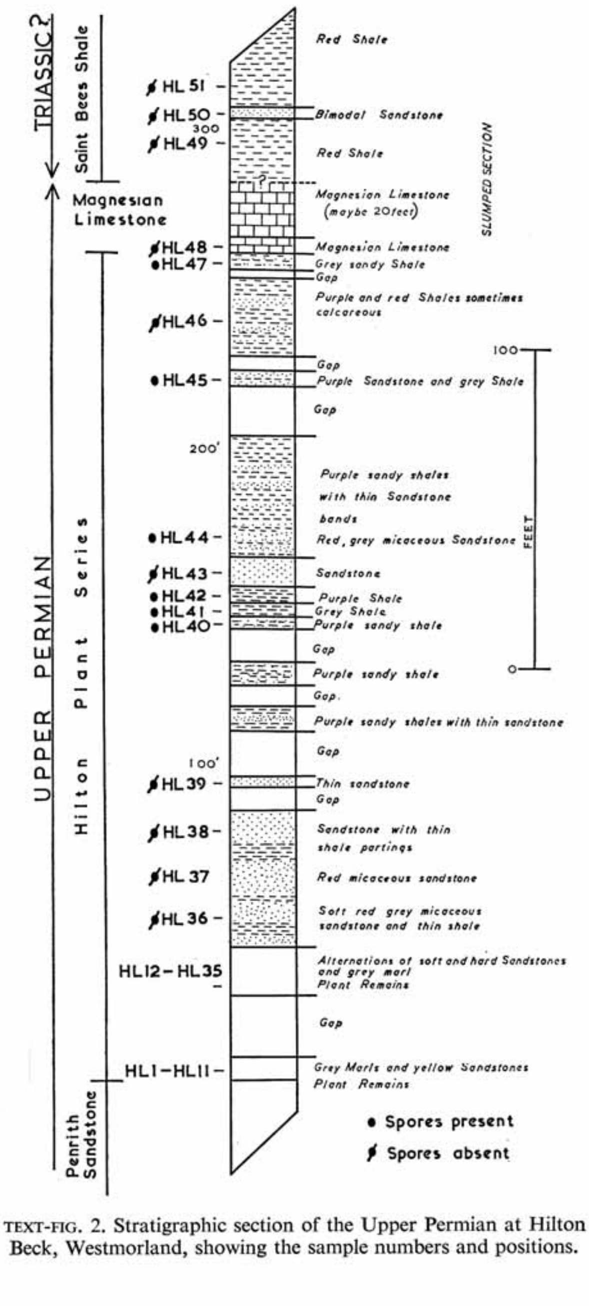
SYSTEMATIC SECTION

Anteturma POLLENITES R. Potonié 1931
Turma SACCITES Erdtman 1947
Subturma MONOSACCITES (Chitaley 1951) Potonié and Klaus 1954
Infraturma VESICULOMONORADITES (Pant) Bhardwaj 1955
Genus POTONIEISPORITES Bhardwaj 1954

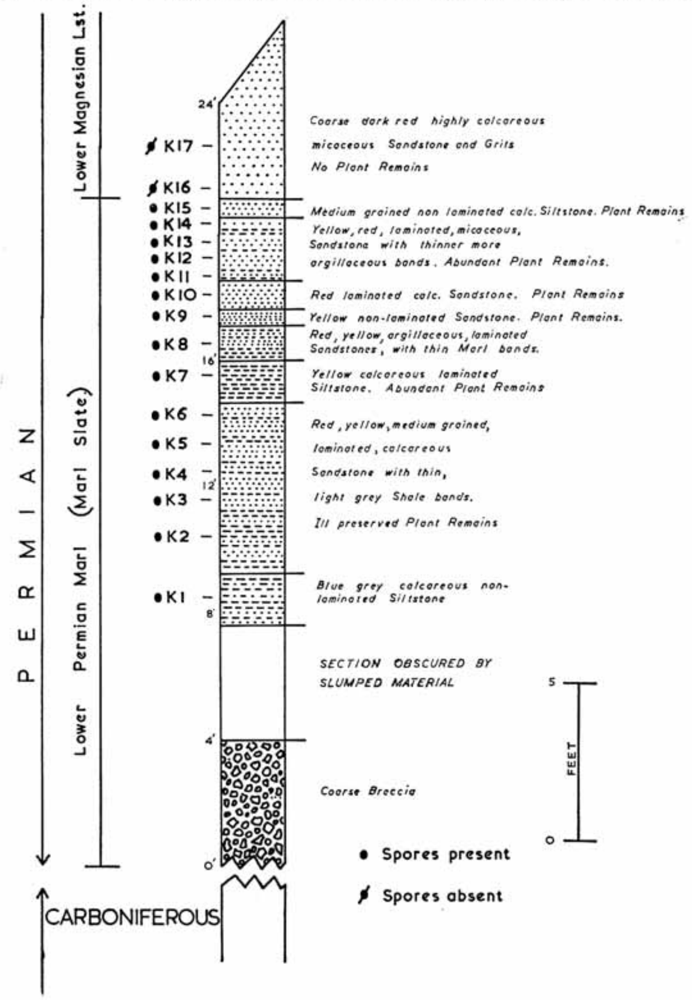
1962 *Hoffmeisterites* Wilson, pl. 3, fig. 4.

Type species. P. novicus Bhardwaj 1954.

Discussion. P. novicus and other species since assigned to the genus all show a series of folds which, broadly speaking, may be resolved into two separate sets. The first is



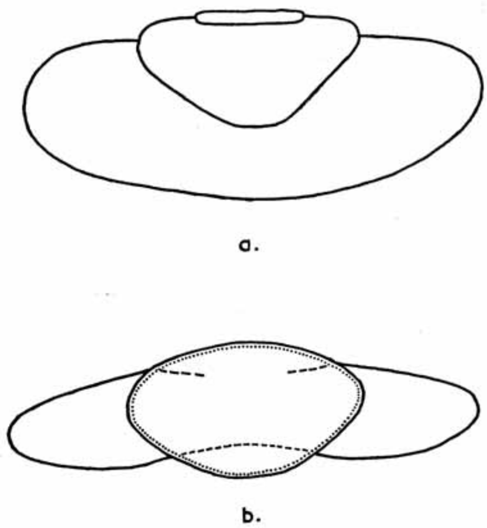
TEXT-FIG. 2. Stratigraphic section of the Upper Permian at Hilton Beck, Westmorland, showing the sample numbers and positions.



TEXT-FIG. 3. Stratigraphic section of the Upper Permian (Lower Permian Marl) at Kimberley, Nottinghamshire, showing the position and number of samples.

a set disposed along the inner margin of the spore body while the second set is situated closer to the polar region and orientated perpendicular to the long axis of the grain. It is the interpretation of the position and function of these folds which has led to certain differences of opinion with respect to the reconstruction of the spore. Bhardwaj (1956) interprets both sets of folds as compression features and regards the saccus as being free (unattached) in the distal region (Bhardwaj 1956, text-fig. 11). A somewhat different view is taken by Potonié and Lele (1961) who suggest that both series of folds are situated distally and form part of a single set which more or less delimits the germinal area. From the present study I accept the latter view and believe that the saccus is attached in the region of these folds (text-fig. 4*b*).

Comparison. Vestigisporites Hart 1960 is a monosaccate, monolete genus which, in polar view, can appear similar to *Potonieisporites* (e.g. *V. methoris* Hart 1960). *Vestigisporites* differs, however, in the less well-developed saccus swelling laterally, which is



TEXT-FIG. 4. Diagrammatic reconstruction of *Potonieisporites* Bhardwaj, in lateral (equatorial view). *a*, The reconstruction of Bhardwaj (1956), showing the saccus unattached (free) over the distal surface. *b*, The present interpretation where the saccus is attached to the spore body in this region.

never as large as that terminally. *Florinites* Schopf, Wilson, and Bentall 1944 has a distal attachment of the saccus, which is free proximally, and also has a triradiate mark. The lateral constriction of the saccus and the characteristically thickened 'sulcus' is sufficient to distinguish *Sahnisporites* Bhardwaj 1954 from *Potonieisporites*.

Potonieisporites novicus Bhardwaj 1954

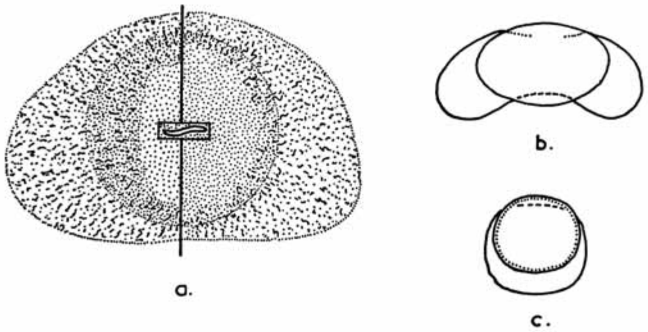
Plate 40, fig. 6, Plate 44, fig. 13; text-fig. 4

Comparison. P. neglectus Potonié and Lele 1961 differs from this species in the polygonal or trapezoid shape of the spore body and the smaller width of the saccus laterally. *P. simplex* Wilson 1962 is a smaller form in which lips are developed around the laesura (commissura of Wilson), while *P. bhardwaji* Remy and Remy 1961 appears to differ in its larger size, absence of a rim separating the saccus edge and the spore body, and a longer monolete mark.

Genus VESTIGISPORITES Balme and Hennelly 1955 emend. Hart 1960

Type species. V. rudis Balme and Hennelly 1955.

Comparison. Vestigisporites differs from *Illinites* (Kosanke) Potonié and Klaus in being an essentially monosaccate genus with the bisaccate construction as the exception, and lacks the variation in the shape of the tetrad scar exhibited by *Illinites*.



TEXT-FIG. 5. *Vestigisporites minutus* sp. nov. *a*, ×1,000 (based on holotype). Polar view showing the monolete mark (in rectangle), the proximal surface on the right-hand side, and the distal surface with 'sulcus' on the left. *b*, Lateral polar section. *c*, Terminal polar section.

Vestigisporites minutus sp. nov.

Plate 40, figs. 7–9; text-fig. 5

Holotype. Plate 40, fig. 7. Slide PF2196. Sample H 12, Hilton Beck, Near Appleby, Westmorland; Upper Permian.

Diagnosis. Small, bilateral, monosaccate miospores. Haploxylonoid. Spore body circular, rarely oval. Exine thin. Monolete. Terminal saccus swelling small compared with spore body; connected laterally by exoexinal strip. Saccus finely infra-reticulate. The saccus attachment distally leaves an elongated oval area free where the exine is thin.

Description. The grains are fossilized giving a preferred orientation flattened in the equatorial plane. The circular spore body is dark coloured and the monolete mark is short, often indistinct and sometimes open. In polar view the saccus completely surrounds the spore body but is not as wide laterally as terminally. One edge of the saccus appears to be attached equatorially and the other edge attached distally. The saccus offlap terminally (text-fig. 1) is slightly greater than the overlap on to the spore body.

Dimensions. (Thirty specimens.) Spore-body length 24(29)31 μ, spore-body width 28(32)35 μ, overall length 42(48)54 μ, overall width 32(35)40 μ.

Comparison. V. minutus sp. nov. is most similar to *V. hennellyi* Hart 1960 but differs in its very much smaller size and darker spore body. A reduction of the lateral saccus extension to give a bisaccate condition has not been observed for *V. minutus* sp. nov.; such a condition exists for *V. hennellyi* (Hart 1960, p. 15).

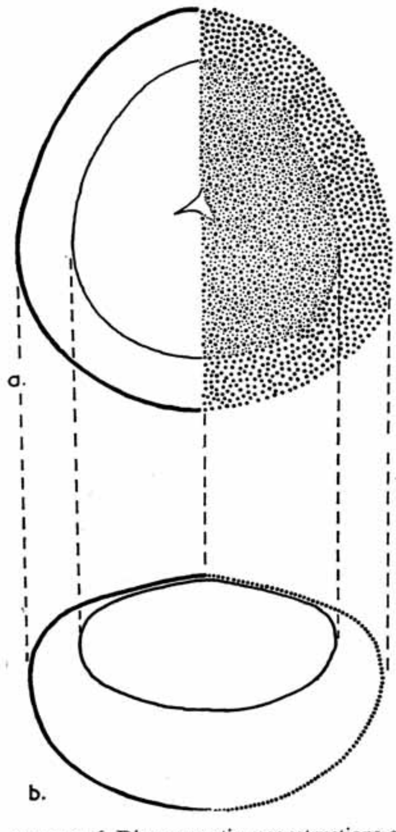
Infraturma TRILETESACCITI Leschik 1955
Genus PERISACCUS Naumova 1953 emend. Klaus 1963

1955 *Simplicesporites* Leschik.

Type species. P. verruculatus Naumova 1953.

Discussion. The genus *Perisaccus* is based on Russian Upper Devonian material and first appears as a *nomen nudum* in Naumova (1937); the genus is validated by Naumova (1953). The emendation of Potonié (1958) describes the spore as monosaccate, without a Y-mark and with an infra-reticulate saccus. A different aspect is given by the subsequent emendation of Klaus (1963) who ascribes to the genus a small Y-mark and a granular saccus sculpture.

Leschik (1955, 1956) describes and figures spores assigned to *Simplicesporites* Leschik which are almost certainly the same generically as those described by Klaus (1963) as *Perisaccus*. Leschik describes *Simplicesporites* as a 'zonate' genus and makes no reference to a Y-mark. However, the British material shows a development of secondary folds which cross the spore body margin without displacing it, and two independent superimposed sets of secondary folds can be seen within the area of the zona. These observations are consistent with a saccate rather than a zonate structure. Such features are clearly seen in Leschik's 1955 pl. 5, fig. 3. The inequality of the zona width described by Leschik for *S. virgatus*, &c., appears to be merely due to the difference in orientation of the grain when fossilized. The triradiate mark is always small and appears often as a triangular tear in the exine. Although not clearly demonstrable it appears that the saccus is attached proximally and is separated from the endexine distally (text-fig. 6).



TEXT-FIG. 6. Diagrammatic reconstructions of *Perisaccus granulosus* comb. nov., ×1,000. *a*, Polar view. *b*, Polar section, showing the relationship of the saccus to the spore body.

Comparison. Perisaccus differs from *Florinites* in the position of the saccus attachment, which is distal in the latter genus. *Endosporites* Wilson and Coe possesses a larger

Y-mark and a limbus which is not present in *Perisaccus*. *Remysporites* Butterworth and Williams 1958 differs also in the larger Y-mark, and its larger overall size. *Nuskoisporites* Potonié and Klaus has the saccus attached both proximally and distally. While Leschik's genera *Accinctisporites*, *Patinasporites*, *Zonalasporites*, and *Succinctisporites* are monosaccate, the attachment of the saccus is not discussed by that author and all are considered to be alete.

Perisaccus granulosus (Leschik 1955) comb. nov.

Plate 42, figs. 10–11; text-fig. 6

1955 *Simplicesporites granulosus* Leschik.
1963 *Perisaccus granulatus* Klaus, pl. 4, fig. 12.

Description. The central body, as seen in polar view, is circular or oval and darker coloured than the saccus. The spore body is smooth, the exine 1 μ thick and there is a small Y-mark, often in the form of a triradiate tear. The Y-mark is less than one-third the spore radius and often open. The saccus is attached to the spore body proximally; the distal surface remaining free. The saccus offlap (width) is less than half the spore body radius, and sculptured with closely packed isodiametric granules 1 μ in diameter.

Dimensions. (Twenty specimens.) Spore-body diameter 35(44)51 μ, saccus width 6(9)13 μ, overall diameter 54(62)72 μ.

Comparison. *P. granulosus* comb. nov. differs from *P. pendens* (Leschik 1955) comb. nov., the latter having a triangular outline, although the spore body is circular. Other than this the two species are closely similar.

Perisaccus laciniatus (Leschik 1955) comb. nov.

Plate 42, fig. 12

Comparison. *P. laciniatus* comb. nov. differs from *P. virgatus* comb. nov. in the lack of spines attached to the granules, and from *P. granulosus* comb. nov. in the larger saccus.

Genus NUSKOISPORITES Potonié and Klaus 1954

1944 *Hymenozonotriletes* Mehta, pl. 1, fig. 1.
1951–2 *Hymenozonotriletes* Mehta; Goswami, pl. 13, fig. 11 (not fig. 10 as stated).
1951–2 (?) *Florinites sp.* Schopf, Wilson, and Bentall; Goswami, pl. 12, fig. 4.

Type species. *N. dulhuntyi* Potonié and Klaus.

Discussion. The diagnosis of Potonié and Klaus (1954) is written broadly around the type species; the genus at that time being monotypic. Some authors regard the presence of a limbus as an essential feature of the genus (Balme and Hennelly 1956*b*, Piérart 1959), while others (e.g. Potonié and Lele 1961) take a broader generic concept.

The saccus in *Nuskoisporites* is attached both proximally and distally leaving a non-cavate area over the proximal and distal poles where the exine (exoexine plus endexine) is thinner. The actual site of saccus attachment is seldom clearly shown and appears to be variable. It thus seems that *Nuskoisporites* may have functioned as a pollen with distal germination thus differing from a monosaccate microspore like *Endosporites*.

Separation of species is based primarily upon the length and form of the Y-mark, the saccus reticulum and the width of the saccus in relation to the spore body radius. Many authors (Virkki 1945, Potonié and Lele 1961, Høeg and Bose 1960) have remarked on the considerable variation within the species recognized.

Nuskoisporites dulhuntyi Potonié and Klaus 1954

Plate 40, figs. 1–2

Discussion. The cardinal characteristics of this species are the short Y-mark, the uniform width of this feature, and the presence of a limbus. *N. rotatus* Balme and Hennelly differs from the present species in the larger spore body, while *N. triangularis* (Mehta) Potonié and Lele 1961 possesses a larger Y-mark and lacks a limbus. *N. crenulatus* Wilson 1962 is a smaller form, without a limbus, and with a crenulate contact edge where the saccus overlaps the spore body. *N. radiatus* Hennelly 1958 lacks a limbus and has a finely infra-reticulate saccus.

Nuskoisporites cf. *rotatus* Balme and Hennelly 1956*b*

Plate 40, fig. 3

Discussion. The present specimens lack a limbus. Balme and Hennelly (1956*b*, p. 245) state that such a feature is only sometimes present and no mention of the limbus is made by Høeg and Bose (1960). *N. rotatus* is characterized by its small saccus width, long Y-mark, and the general absence of a limbus.

Infraturma STRIASACCITI Bhardwaj 1962 (= STRIATORNATI Jansonius 1962)
Genus CRUSTAESPORITES Leschik 1956 emend. Jansonius 1962

1955 *Lueckisporites* Potonié and Klaus; Balme and Hennelly, pl. 4, fig. 44.
1955 *Lueckisporites* Potonié and Klaus; Klaus, pl. 33, fig. 5.
1962 'Multistriate, monosaccate grain', Jizba, pl. 122, fig. 24.

Type species. C. globosus Leschik 1956.

Discussion. Leschik (1955) describes *Crustaesporites* as a trisaccate genus. Jansonius (1962), however, considers the trisaccate appearance to be the result of irregular constriction of a monosaccate miospore. The British material shows considerable variation

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EXPLANATION OF PLATE 40

Magnification ×750 unless otherwise stated.

Figs. 1–3. *Nuskoisporites spp.* 1–2, *N. dulhuntyi* Potonié and Klaus. 1, PF2189. 2, PF2190. 3. *N.* cf. *rotatus* Balme and Hennelly, PF2191.

Figs. 4–5. *Crustaesporites globosus* Leschik. 4, Trisaccate condition, PF2193. 5, Showing the development of four sacci; PF2194.

Fig. 6. *Potonieisporites novicus* Bhardwaj, ×500, PF2202.

Figs. 7–9. *Vestigisporites minutus* sp. nov. 7, Holotype, PF2196. 8, PF2197. 9, PF2198.

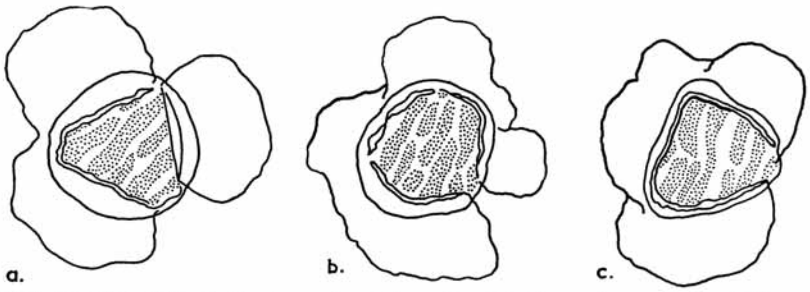
Figs. 10–11. *Falcisporites zapfei* Leschik. 10, PF2318. 11, PF2274.

Fig. 12. *Illinites klausi* sp. nov., holotype, PF2290.

Localities of figs. 1–2, 4–6, 12, Lower Permian Marl, Kimberley. Figs. 7–11, Hilton Plant Bed. Fig. 3, Haughton Hall Boring, Lower Permian Marl, depth 1,095 feet.

between a trisaccate condition and an irregular monosaccate structure (text-fig. 7, Pl. 40, figs. 4–5). While it is perhaps reasonable to consider the original structure as monosaccate, such irregularities of saccus structure have been demonstrated to occur as 'aberrants' of living bisaccate pollen (Van Campo-Duplan 1947, 1950, Van Campo-Duplan and Gaussen 1948, Martin 1961).

The frequency of occurrence of *Crustaesporites* in the present material is less than 1 in 2,000 and it is always associated with bisaccate striate genera. This association is maintained in all other localities from which *Crustaesporites* has been recorded (Europe,



TEXT-FIG. 7. Polar views of *Crustaesporites globosus* Leschik (drawn from specimens) illustrating variation in the outline of the saccus structure. *a*, More or less trisaccate condition. *b* and *c*, Irregular saccus.

Canada, Australia). In number of taeniae and saccus sculpture *Crustaesporites* resembles the bisaccate genus *Protohaploxypinus* most closely and probably represents aberrant spores of this genus. Nevertheless, I consider their recognition as a distinct genus an inevitable consequence of a morphographic treatment.

Crustaesporites globosus Leschik 1956

Plate 40, figs. 4–5

The variation in the shape of the saccus structure, encountered in the present material, is shown in text-fig. 7.

Subturma DISACCITES Cookson 1947
Infraturma STRIATITI Pant 1954
Genus LUECKISPORITES Potonié and Klaus 1954 emend. Klaus 1963

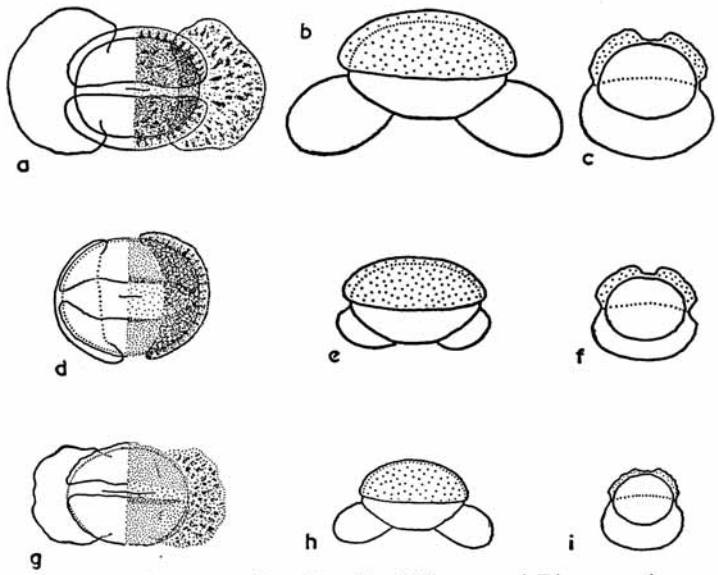
Type species. L. virkkiae Potonié and Klaus 1954.

Lueckisporites virkkiae (Potonié and Klaus 1954) emend.

Plate 43, figs. 3, 6–11; text-fig. 8

1960 *Lueckisporites nyakapendensis* Hart, pl. 1, fig. 12.

Emended diagnosis. Bilateral, bisaccate pollen grains. Sometimes haploxylonoid but typically diploxylonoid in overall outline. Spore body circular or oval where the length exceeds the width. Proximal face possesses a variable thickening (Kalotte of Potonié and Klaus) which is split by a laesura parallel to the long axis of the spore into two, more or less equal, halves. Sculpture is infrapunctate or infrabaculate. A monolete mark may be present. Sacci semicircular or more in outline, well developed and discrete. Sacci offlap may be considerable or non-existent. One saccus edge is attached at the equator; the attachment of the other being variable. Infra-sculpture of anastomosing muri forming a microreticulum or punctation; both types may show a radial pattern developed from the distal saccus roots. The exine is thin.



TEXT-FIG. 8. *Lueckisporites virkkiae* Potonié and Klaus emend. Diagrammatic reconstructions to show the differences between the variants A, B, and C. *a–c*, Variant A. *d–f*, Variant B. *g–i*, Variant C. *a*, *d*, *g*, Proximal polar views. *b*, *e*, *h*, Lateral views. *c*, *f*, *i*, Terminal polar sections.

Discussion. The British Permian has yielded many specimens referable generically to *Lueckisporites* s.str. There is a great variety of extreme forms connected by inter-

EXPLANATION OF PLATE 41

Magnification ×750.

Figs. 1–3. *Protohaploxypinus spp.* 1–2, *P. jacobii* Hart. 1, PF2216. 2, PF2217. 3, *P. microcorpus* comb. nov., PF2218.

Figs. 4, 8. *Taeniaesporites spp.* 4, *T. nubilus* comb. nov., PF2226. 8, *T. bilobus* sp. nov., holotype, PF2221.

Fig. 5. *Labiisporites granulatus* Leschik, PF2272.

Figs. 6–7. *Illinites tectus* comb. nov. 6, PF2287. 7, PF2289.

Figs. 9–10. *Striatopodocarpites fusus* Potonié. 9, PF2222. 10, PF2223.

Localities of figs. 1, 2, 4, 8, 10, Lower Permian Marl, Kimberley. Figs. 3, 6, 7, Haughton Hall Boring, Lower Permian Marl, depth 1,095 feet. Figs. 5, 9, Hilton Plant Bed.

mediates, making the separation of several species impossible. Potonié, who has seen the material here under discussion, agrees that the entire range can be included in *L. virkkiae* (personal communication 1962). For this reason it has been thought desirable to emend the specific diagnosis to include all these forms. Within the species three main extremes can be recognized and these are here referred to as variants A, B, and C (text-fig. 8). At no Permian horizon, so far studied, is one of the variants absent although there may be an assemblage shift in any of these directions. Variant A is characterized by the well-developed proximal thickenings, their distinct separation and well-developed sacci (Pl. 43, figs. 3, 8, 9). This variant is most similar to the holotype and *L. microgranulatus* Klaus 1963. Variant B differs in the less well-developed sacci and the negligible amount of offlap (Pl. 43, figs. 10–11). Variant B is similar to *L. parvus* Klaus 1963. Variant C is recognized by a weakly developed proximal cap and its incomplete separation into two halves and the generally smaller overall size (Pl. 43, figs. 6–7). *L. microgranulatus* (kleinere variante) Klaus 1963 is most similar to variant C.

Genus TAENIAESPORITES Leschik emend. Klaus 1963

1954 *Lueckisporites* Potonié and Klaus (pars).
1955 *Lunatisporites* Leschik, pl. 7, figs. 21–24.
1955 *Succinctisporites* Leschik, pl. 7, figs. 4–5.
1956 *Jugasporites* Leschik (pars).
1958 *Pollenites* Pautsch, pl. 1, fig. 8.
1962 *Lueckisporites* Potonié and Klaus; Grebe and Schweitzer (pars).
1963 *Striatites* Pant; Schaarschmidt (pars).
1963 *Striatites* Pant; Klaus (pars).

Type species. T. kraeuseli Leschik 1955.

Discussion. While I accept the arguments of Klaus (1963) concerning previous uses and emendations of the genus and follow his emendation, I feel that the genus should be broadened to include all bisaccate miospores with four primary taeniae and which are haploxylonoid or diploxylonoid in outline, and not to restrict the genus to those forms showing a wide separation of the central taeniae. This is better considered a specific character.

Comparison. Taeniaesporites differs from *Lueckisporites* s.str. in possessing more than two taeniae, from *Protohaploxypinus* emend. Hart 1964 in having less than six primary taeniae, from *Striatopodocarpites* emend. Hart 1964 in the spore body to saccus ratio, and from Striatoabietites emend. Hart 1964 in the presence of fewer taeniae.

Taeniaesporites noviaulensis Leschik 1956

Plate 42, figs 6–7

1962 *Taeniaesporites novimundi* Jansonius (pars), pl. 13, fig. 25 only.
1962 *Lueckisporites noviaulensis* Grebe and Schweitzer, pl. 5, fig. 7.
1963 *Striatites noviaulensis* Schaarschmidt, pl. 15, figs. 5–7, 9.
1963 *Taeniaesporites ortisei* Klaus, pl. 14, figs. 67–70.

Comparison. T. noviaulensis differs from *T. novimundi* Jansonius in the shape of the spore body, the larger sacci and the coarser infra-reticulum; and from *T. kraeuseli* in the shape of the spore body, form of the taeniae, and the shape and sculpture of the sacci.

Taeniaesporites novimundi Jansonius 1962

Plate 44, figs. 1–2

The British specimens agree well with those described by Jansonius (1962) from the Permo-Triassic of Canada.

Taeniaesporites angulistriatus (Klaus 1963) comb. nov.

Plate 44, figs. 11–12

1963 (May) *Striatites angulistriatus* Klaus, pl. 17, fig. 83.
1963 (August) *Striatites ovalis* Schaarschmidt, pl. 15, figs. 1–4.

Discussion. The most distinctive features of this species are the small size, the narrow distal area between the sacci attachments and the scabrate sculpture of both the taeniae and the sacci. *T. angulistriatus* comb. nov. differs from *T. kraeuseli* Leschik in the shape and sculpture of the sacci, and from other species in its taeniae and saccus sculpture.

Taeniaesporites albertae Jansonius 1962

Plate 44, fig. 5

Discussion. This species is distinguished by its broad, slightly thickened taeniae, and the lack of radial alignment of the saccus sculpture. This species differs from *T. noviaulensis* Leschik and *T. novimundi* Jansonius in the broader taeniae, small sacci and the finer reticulum. *T. kraeuseli* differs in the more embracing sacci giving a narrow distal area.

Taeniaesporites labdacus Klaus 1963

Plate 44, figs. 6–10; text-fig. 9

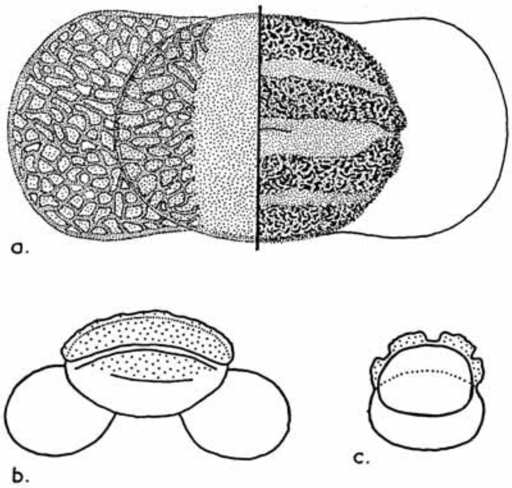
1954 *Lueckisporites sp.* Potonié and Klaus, pl. 10, fig. 2.
1962 *Lueckisporites noviaulensis* Grebe and Schweitzer, pl. 5, fig. 8 (*non* Leschik).

Remarks. This species is characterized by the presence of four taeniae of which the central pair are better developed than the lateral ones, and which may join terminally to form an elevated rectangular area around the proximal pole. A monolete mark is usually present, and thick muri form a coarse infra-reticulum on the sacci.

EXPLANATION OF PLATE 42

Magnifications ×750 unless otherwise stated.
Figs. 1–2. *Striatopodocarpites antiquus* Potonié. 1, PF2438. 2, PF2225.
Figs. 3–5. *Protohaploxypinus chaloneri* sp. nov. 3, PF2211. 4, Holotype, PF2210. 5, PF2212.
Figs. 6–7. *Taeniaesporites noviaulensis* Leschik. 6, PF2230. 7, PF2229.
Figs. 8–9. *Protohaploxypinus* cf. *samoilovichii* Hart. 8, PF2208. 9, PF2209.
Figs. 10–12. *Perisaccus spp.* 10–11, *P. granulosus* comb. nov. 10, PF2204. 11, PF2206. 12, *P. laciniatus* comb. nov., PF2483.
Fig. 13. *Taeniaesporites novimundi* Jansonius showing taeniae sculpture, ×1,500, PF2232.
Localities of figs. 1, 3, 4, 5, 10, 12, Hilton Plant Bed. Remainder from the Lower Permian Marl, Kimberley.

The variation shown by the present material makes it difficult to maintain the difference between this species and *T. alatus* Klaus 1963. The present forms are assigned to *T. labdacus* as this is the first of these two species described by Klaus (1963).



TEXT-FIG. 9. *Taeniaesporites labdacus* Klaus. *a*, Polar view showing the proximal face with the taeniae and monolete mark, on the right, and the distal face on the left (drawn from specimen), ×1,000. *b* and *c*, Diagrammatic reconstructions. *b*, Lateral view. *c*, Terminal polar section.

Taeniaesporites bilobus sp. nov.

Plate 41, fig. 8; text-fig. 10

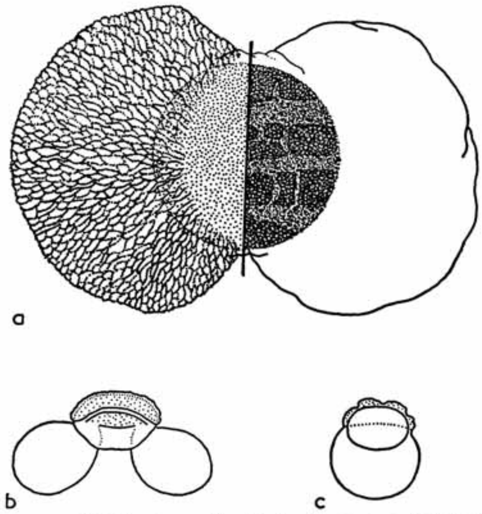
Holotype. Plate 41, fig. 8. Slide PF2221. Sample K 14, Kimberley, Nottinghamshire; Upper Permian (Lower Permian Marl).

Diagnosis. Spore body small, circular, dark coloured, and bearing up to five taeniae. Sacci relatively large and not connected laterally. The saccus sculpture is a medium infra-reticulum with a radial alignment from the saccus roots.

Description. The spore body proximal face is covered by taeniae, more or less parallel-sided, about 5μ wide, and separated by smooth striae. The taeniae are micropunctate and are frequently divided by transverse splits. A monolete mark is sometimes present. The saccus offlap greatly exceeds that of the overlap and the distal saccus attachment is indistinct; the saccus muri are 1–2μ thick.

Dimensions. (Seven specimens.) Spore-body length 27(29)32μ, spore-body width 28(30)33μ, overall length 60(68)79μ.

Comparison. This species differs from other species of the genus in the comparatively larger sacci and the circular spore body.



TEXT-FIG. 10. *Taeniaesporites bilobus* sp. nov. *a*, Polar view showing the arrangement of the proximal taeniae, on the right, and the distal surface on the left (based on the holotype), ×1,000. *b*, and *c*, Diagrammatic reconstructions. *b*, Lateral view. *c*, Terminal polar section.

Taeniaesporites nubilus (Leschik 1956) comb. nov.

Plate 41, fig. 4

1956 *Jugasporites nubilus* Leschik, pl. 21, fig. 14.
1962 *Striatites? nubilus* Jansonius, pl. 14, fig. 20.
1963 *Striatites rarostriatus* Schaarschmidt, pl. 14, fig. 8.

Discussion. This species is characterized by its dumbell shape, thick spore body exine, and the coarse saccus infra-reticulum.

No mention of striations is made in the specific description of *Jugasporites nubilus* by Leschik (1956) but the illustration of the holotype gives the impression that this specimen is striate (see also Jansonius 1962). I accordingly assign it to *Taeniaesporites.*

Comparison. T. nubilus comb. nov. differs from *T. bilobus* sp. nov. in the more oval spore body and the thicker exine, and from the type species in the larger sacci.

Genus PROTOHAPLOXYPINUS Samoilovich emend. Hart 1964

1963 *Striatites* Pant emend. Klaus, pl. 17, figs. 79–82.
1963 *Striatites* Pant; Schaarschmidt, pl. 14, figs. 3–7, pl. 15, figs. 8*a*–8*b*.

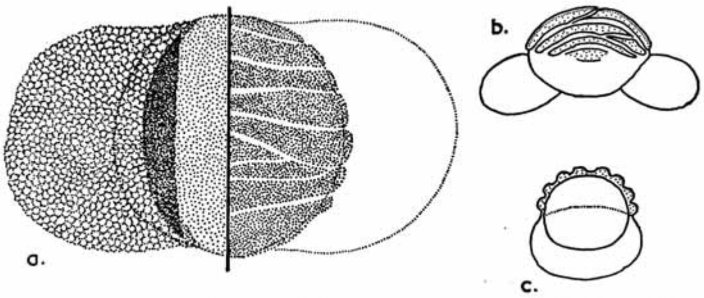
Type species. P. (al. *Pemphygaletes*) *latissimus* Luber and Waltz 1941.

Comparison. *Protohaploxypinus* emend. Hart (1964, p. 1171) differs from *Striatopodocarpites* emend. Hart in being more haploxylonoid and in the more variable form of the spore body. *Lueckisporites* s.str. and *Taeniaesporites* s.str. have fewer taeniae while *Complexisporites* Jizba differs from *Protohaploxypinus* in the presence of a groove surrounding a 'fissured' area on the proximal face. *Striatosaccites* Jizba differs from the present genus in having transverse sexinal strips distally while *Striapollenites* Bhardwaj 1962 has taeniae parallel with the transverse axis (i.e. perpendicular to all the above genera). *Striatoabietites* emend. Hart 1964 differs from *Protohaploxypinus* in showing a distinct angle where the saccus joins the spore body, as seen in polar view.

Protohaploxypinus jacobii Jansonius emend. Hart 1964

Plate 41, figs. 1–2

Remarks. This species is similar to *P. sewardi* (Virkki) Hart 1964, differing only in its larger size, while *P. amplus* (Balme and Hennelly) Hart 1964 has a larger saccus offlap.



TEXT-FIG. 11. *Protohaploxypinus chaloneri* sp. nov. *a*, Showing the form of the proximal taeniae, on the right, and the distal surface on the left-hand side (based on the holotype), ×1,000. *b* and *c*, Diagrammatic reconstructions. *b*, Lateral view. *c*, Terminal polar section.

Protohaploxypinus cf. *samoilovichii* (Jansonius) Hart 1964

Plate 42, figs. 8–9

1963 *Striatites samoilovichii* Jansonius; Schaarschmidt, pl. 14, figs. 3–5.

Remarks. The present forms are identical, except for their smaller size, with those spores described by Jansonius (1962) as *Striatites samoilovichii*.

Dimensions. (Twenty specimens.) Spore-body length 30(36)42μ, spore-body width 36(41)48μ, overall length 60(66)72μ.

Protohaploxypinus chaloneri sp. nov.

Plate 42, figs. 3–5; text-fig. 11

Holotype. Plate 42, fig. 4. Slide PF2210. Sample H 5, Hilton Plant Bed, Westmorland; Upper Permian.

Diagnosis. Spore-body amb circular or subcircular; proximal taeniae 10–12 in number, sometimes anastomosing or interrupted. Sacci well developed and semicircular in outline. Saccus infra-sculpture is a well-defined microreticulum without a radial pattern being developed. Sacci attachments distally show a crescent-shaped thickening which rarely extends to the equator.

Description. In the fossil state the pollen grains are invariably flattened in the equatorial plane and are therefore reconstructed from polar views. The spore body exine is 1–2 μ thick and the taeniae are separated by narrow striae. A monolete mark is not evident although it is occasionally suggested either by the gaping of the more centrally placed taeniae or by an elongated secondary fold in this region. The sacci are discrete and the offlap is equal to the overlap, or somewhat greater. One edge of a saccus is equatorially attached while the other is attached distally, typically midway between the equator and the distal pole.

Dimensions. (Twenty-five specimens.) Spore-body length 30(36)42 μ, spore-body width 30(37)41 μ, overall length 48(57)63 μ.

Comparison. P. minor (Klaus 1963) comb. nov. is most similar to the present species, but differs in the shape of the sacci and the absence of the distal attachment thickenings.

Protohaploxypinus microcorpus (Schaarschmidt 1963) comb. nov.

Plate 41, fig. 3

1963 *Striatites jacobii* Jansonius; Klaus, pl. 17, fig. 79.
1963 *Striatites microcorpus* Schaarschmidt, pl. 14, figs. 6–7.

Remarks. This species, previously known from the Upper Permian of Germany and Austria, shows a large number of taeniae on the proximal face. The number can only be estimated at between ten and twenty, an accurate determination being precluded owing to their crowding and interruption.

Genus STRIATOPODOCARPITES Sedova emend. Hart 1964

1962 *Striatites* Pant; Jizba, pl. 122, figs. 25–30.

Type species. S. tojmensis Sedova 1956.

Discussion. The characteristic features of this genus are the distinctly diploxylonoid outline and the circular spore body with more than five proximal taeniae. The dark colour of the spore body observed in many species of *Striatopodocarpites* tends to

EXPLANATION OF PLATE 43

Magnification ×750 unless otherwise stated.
Figs. 1, 15. *Alisporites nuthallensis* sp. nov. 1, PF2232. 15, Holotype, PF2277.
Fig. 2. *Striatopodocarpites cancellatus* comb. nov., PF2252.
Figs. 3, 8, 9. *Lueckisporites virkkiae* Potonié and Klaus emend., Variant A. 3, Part of 'Kalotte', ×1,500, PF2256. 8, PF2319. 9, PF2257.
Figs. 4–5. *Striatoabietites richteri* Hart. 4, PF2491/720220. 5, PF2487.
Figs. 6–7, 10–11. *L. virkkiae* emend. 6–7, Variant C. 6, PF2259. 7, PF2260. 10–11, Variant B. 10, PF2263. 11, PF2262.
Figs. 12–13. *Platysaccus radialis* comb. nov. 12, PF2486. 13, PF2485.
Fig. 14. *Illinites klausi* sp. nov., PF2291.
Figs. 16–17. *Klausipollenites schaubergeri* Jansonius. 16, PF2266. 17, PF2264.
Localities of figs. 1, 2, 5, 6, 7, 10, 11, 14–17, Lower Permian Marl, Kimberley. Figs. 3, 8, 9, 13, Hilton Plant Bed. Figs. 4, 12, Haughton Hall Boring, Lower Permian Marl, depth 1,095 feet.

obscure the proximal surface features and it is felt that some species of this genus may have been wrongly assigned to *Platysaccus*. It appears that neither Naumova (1937) nor Potonié and Klaus (1954) consider *Platysaccus* as a striate genus, and on this account alone a separation from *Striatopodocarpites* seems meaningful. However, Jansonius (1962) assigns to *Platysaccus* cf. *papilionis* Potonié and Klaus 1954 forms said to have from two to four striations on the proximal face (p. 54 and pl. 12, fig. 19). I prefer to rate the presence or absence of striations as a generic character and to exclude all striate forms from *Platysaccus*.

Comparison. *Striatopodocarpites* differs from *Lueckisporites* s.str. and *Taeniaesporites* s.str. in the greater number of taeniae and the more distinctly diploxylonoid outline. *Rhizomaspora* Wilson 1962 is characterized by having radiating or diverging ribs on the spore body, and *Striatopodocarpites* differs from *Striatoabietites* emend. Hart 1964 in the more circular spore body and the comparatively larger sacci.

Striatopodocarpites fusus (Balme and Hennelly) Potonié 1958

Plate 41, figs. 9–10

Discussion. The cardinal characteristics of this species are the very large sacci, the multistriate spore body and the radially aligned reticulum of the sacci.

The taeniae, six to ten in number, are sometimes divided into irregular 'blocks' by small splits perpendicular to the long axis of the grain. The fine saccus infra-reticulum may be made to appear more coarse by corrosion (Pl. 41, fig. 10).

Striatopodocarpites antiquus (Leschik) Potonié 1958

Plate 42, figs. 1–2

Remarks. A common feature of this species is the small lateral union of the sacci making the pollen monosaccate. This also appears to be the case in the holotype. *S. antiquus* differs from the type species in the greater irregularity of the taeniae and from *S. phaleratus* (Balme and Hennelly) Hart 1964 in the absence of a distal groove bordered by lips. *S. balmei* Sukh Dev 1959 is distinguished by its wider taeniae and a coarser saccus reticulum.

Striatopodocarpites cancellatus (Balme and Hennelly) comb. nov.

Plate 43, fig. 2

1955 *Lueckisporites cancellatus* Balme and Hennelly, pl. 2, figs. 12–15.
1960 *Striatites cancellatus* (Balme and Hennelly) Hart, pl. 7, fig. 10.

Remarks. This species is characterized by the dark spore body, the presence of usually six taeniae and the fine saccus infra-reticulum.

Genus STRIATOABIETITES Sedova emend. Hart 1964

1962 *Illinites* Kosanke; Orlowska-Zwolinska (pars).
1963 *Striatites* Pant; Schaarschmidt (pars).
1963 *Strotersporites* Wilson; Klaus (pars).

Type species. *S. bricki* Sedova 1956.

Discussion. Although valid since 1956 this genus has not been widely used in Western palynological literature due mainly to the limited circulation of Sedova's (1956) publication. This 1956 publication must be regarded as effective although of limited circulation.

Spores assignable to *Striatoabietites* have been described by several authors under *Lueckisporites* and *Striatites*. *Striatoabietites* is characterized by the well-developed sacci which are generally equal in width, although smaller in length, than the striate spore body. The sacci form a distinct angle where they join the spore body, as seen in polar view.

Comparison. The present genus differs from *Striatopodocarpites* in the saccus to spore-body ratio and in being less distinctly diploxylonoid, while *Lueckisporites* s.str. and *Taeniaesporites* s.str. have fewer taeniae (i.e. less than six).

Striatoabietites richteri (Klaus) Hart 1964

Plate 43, figs. 4–5

1955 *Lueckisporites richteri* Klaus, pl. 33, figs. 1–3.
1956 *Taeniaesporites richteri* Leschik, pl. 22, fig. 8.
1958 *Strialites richteri* Potonié, p. 51.
1962 *Illinites striatus* Orlowska-Zwolinska, pl. 3, fig. 3.
1963 *Striatites richteri* Potonié; Schaarschmidt, pl. 13, figs. 21–22; pl. 14, figs. 1–2.
1963 *Strotersporites jansonii* Klaus, pl. 15, figs. 74–75; pl. 16, fig. 78.
1963 *Strotersporites richteri* Klaus, pl. 15, figs. 76–77.

This species, recorded from many Western European and North American localities, is clearly circumscribed in the original description of Klaus (1955).

Genus VITTATINA Luber 1940? ex Potonié 1958

1963 *Striatoluberae* Hart.

Type species. *V. subsaccata* Samoilovich 1953.

Discussion. This genus is attributed to Luber (1940) by Samoilovich (1953) who gives neither a type species nor a generic diagnosis but describes and figures three species of *Vittatina*. The relevant literature (i.e. Luber 1940) is not quoted in Samoilovich's bibliography. I have not seen this work of Luber, nor does it appear to have been seen by other authors subsequent to Samoilovich. The genus was thus invalid until Potonié (1958) gave a short diagnosis and named one species (*Vittatina subsaccata* Samoilovich 1953). Although this was not formally designated the type species by Potonié it may be

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EXPLANATION OF PLATE 44

Magnification ×750 unless otherwise stated.

Figs. 1–2, 5–12. *Taeniaesporites spp*. 1–2, *T. novimundi* Jansonius. 1, PF2234. 2, PF2235. 5, *T. albertae* Jansonius, PF2243. 6–10. *T. labdacus* Klaus. 6, PF2240. 7, PF2244. 8, PF2238. 9, PF2237. 10, PF2236. 11–12. *T. angulistriatus* comb. nov. 11, PF2245. 12, PF2247.

Figs. 3–4. *Illinites delasaucei* Grebe and Schweitzer. 3, PF2279. 4, PF2283.

Fig. 13. *Potonieisporites novicus* Bhardwaj, ×500, PF2203.

Fig. 14. *Labiisporites granulatus* Leschik, PF2270.

Figs. 15–16. *Cycadopites rarus* sp. nov. 15, PF2292. 16, Distal view of holotype, PF2293.

Localities of figs. 5, 11, 12, Hilton Plant Bed. Remainder, Lower Permian Marl, Kimberley.

considered as such since this was the first species used in a valid combination, and the genus becomes valid from that date.

The type species is characterized by the possession of rudimentary sacci. Recently, however, there has been some difference of opinion concerning the limits of the genus. Wilson (1962, p. 24) emends the genus and while accepting *V. subsaccata* as the 'genotype' proposes (p. 25) that the genus be restricted to forms without sacci. Jansonius (1962) makes a similar proposal independently, arguing that the terminal structures, which may be considered as small sacci, might equally well be terminal extensions of the equatorial rim. *Vittatina* is used here for bilateral, multistriate pollen grains which may possess rudimentary sacci and where the distal (? germinal) furrow is at right angles to the proximal taeniae.

Comparison. Vittatina differs from *Protosacculina* emend. Jansonius 1962 in the sacci, where present, being smaller and from *Aumancisporites* emend. Jansonius 1962 in the absence of a transverse distal furrow with thickened margins. Alpern's original description of *Aumancisporites* made no mention of a distal furrow, but on re-examination of Alpern's material Jansonius (1962) emended *Aumancisporites* to include forms which, in other respects, were *Vittatina*-like, and which he considered to have a distal transverse furrow bordered by lips. I think this feature is probably a fold or buckle produced by squashing, and reject his emendation.

Hamiapollenites Wilson (February) 1962 (= *Hamipollenites* of Jansonius (April) 1962) differs from *Vittatina* in the larger size and different shape of the sacci. *Vittatina* differs from the type of pollen previously assigned to *Ephedripites* and *Welwitschiapites* primarily in the absence of a colpus or colpi disposed parallel to the striations.

Vittatina hiltonensis Chaloner and Clarke 1962

See Chaloner and Clarke 1962.

Infraturma DISACCITRILETI Leschik 1955

Genus ILLINITES (Kosanke) emend. Potonié and Kremp 1954

1963 *Limitisporites* Leschik emend. Schaarschmidt.
1963 *Jugasporites* Leschik emend. Klaus.
1963 *Limitisporites* Leschik; Klaus.

Type species. I. unicus Kosanke.

Discussion. The emendation of Potonié and Kremp (1954) emphasizes the inequality of the length of the arms of the tetrad scar, not evident from the original diagnosis of Kosanke (1950). In some Permian bisaccate miospores there exists a gradation from forms possessing a monolete mark (*Limitisporites* Leschik) through forms showing a 'roof-shaped' (= dachformig) split (*Jugasporites* Leschik) to spores possessing a triradiate mark, often with one arm developed to a greater or lesser extent than the other two (*Illinites* Kosanke). Such a gradation of the tetrad scar prompts Grebe (1957) to consider the roof-shaped split as a retrograde or vestigial Y-mark. Such an argument finds a good deal of support from the work of Potonié and Schweitzer (1960) in their study of the pollen of *Ullmannia frumentaria*. Grebe and Schweitzer (1962) accordingly include all the forms discussed above with variable arrangement of the tetrad scar in *Illinites* Kosanke emend. Potonié and Kremp, and this procedure is followed here (see also Klaus 1963, p. 270 footnote).

While it is certain that *Illinites* represents, at least in part, the pollen of *Ullmannia frumentaria* it cannot be assumed that this is the only source plant of *Illinites*, and other closely related or more distantly allied plants or plant groups may have produced spores with a similar variety of the tetrad scar.

Illinites delasaucei (Potonié and Klaus) Grebe and Schweitzer 1962

Plate 44, figs. 3–4

1963 *Limitisporites delasaucei* Schaarschmidt, pl. 11, figs. 14–17.
1963 *Jugasporites delasaucei* Leschik; Klaus, pl. 6, fig. 19.

Remarks. The present forms are well covered by the clear descriptions given by Potonié and Klaus (1954), Klaus (1955), Grebe (1957), Grebe and Schweitzer (1962), and Schaarschmidt (1963). Leschik (1956, p. 132) observes that certain of his specimens assigned to *J. delasaucei* have the sacci connected laterally by an exoexinal strip up to 9 μ wide. The British specimens show this feature to be not greater than 5 μ wide and in the majority of specimens such a feature is not seen.

Illinites tectus (Leschik 1956) comb. nov.

Plate 41, figs. 6–7; text-fig. 12

Remarks. This species shows a less variable tetrad scar than *I. delasaucei*, and further differs in the presence of two 'roughened areas' (thickenings) on either side of the tetrad scar (text-fig. 12).

Illinites klausi sp. nov.

Plate 40, fig. 12, Plate 43, fig. 14; text-fig. 13

Holotype. Plate 40, fig. 12. Slide PF2290. Sample K 14, Kimberley, Nottinghamshire; Upper Permian (Lower Permian Marl = Marl Slate).

Diagnosis. Spore body circular, bearing a small triradiate mark. Sacci small, offlap crescent shaped in polar view.

Description. The spore body is large and dark coloured with exine 2 μ thick. There exists on the proximal face a large triangular area where the exine is thin and within which is a Y-mark (text-fig. 13). The sacci are semicircular or less in outline and the offlap equals the overlap; the greatest width of a saccus, as seen in polar view, is measured along the distal attachment. The saccus infra-sculpture is a fine reticulum.

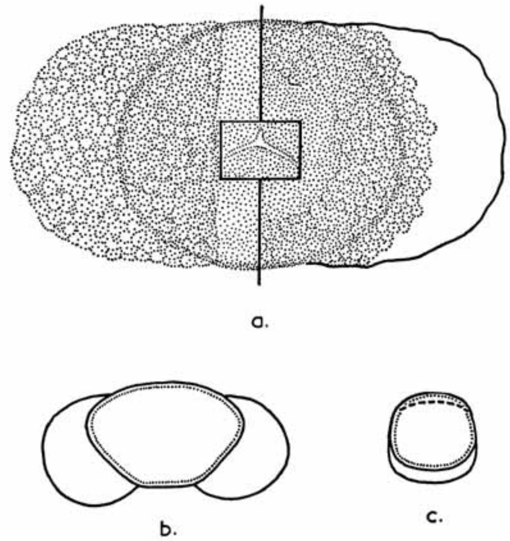
Dimensions. (Sixteen specimens.) Spore-body length 22(27)33 μ, spore-body width 27(32)39 μ, overall length 41(47)50 μ.

Comparison. The present species differs from *I. parvus* Klaus 1963 in the structure of the proximal face of the spore body, and from other species of the genus in the shape of the saccus offlap.

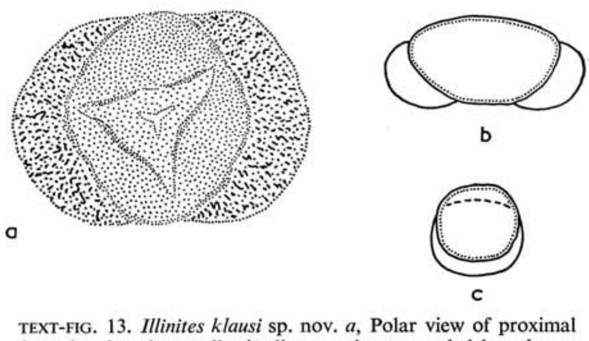
Infraturma DISACCIMONOLETES Klaus 1963
Genus LABIISPORITES Leschik emend. Klaus 1963

Type species L. granulatus Leschik 1956.

Comparison. *Labiisporites* differs from *Illinites* in the absence of a Y-mark and the



TEXT-FIG. 12. *Illinites tectus* comb. nov. *a*, Polar view showing proximal face, on the right, and distal face on the left (drawn from specimen), ×1,000. *b* and *c*, Diagrammatic reconstructions. *b*, Lateral polar section. *c*, Terminal polar section.



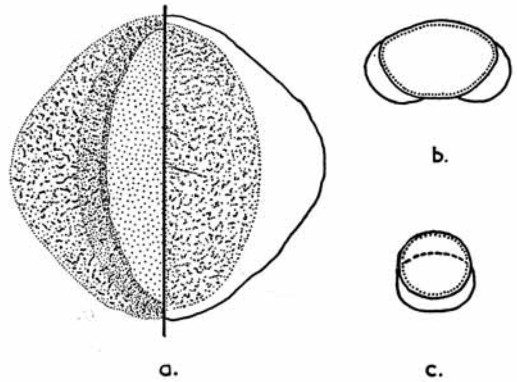
TEXT-FIG. 13. *Illinites klausi* sp. nov. *a*, Polar view of proximal face showing the small triradiate mark surrounded by a larger triangular area (based on holotype), ×1,000. *b* and *c*, Diagrammatic reconstructions. *b*, Lateral polar section. *c*, Terminal polar section.

presence of a distal sulcus. *Alisporites* emend. Nilsson 1958 differs from *Labiisporites* in having a distinct spore body, coarser saccus infra-reticulum and overall larger size.

Labiisporites granulatus Leschik 1956

Plate 41, fig. 5, Plate 44, fig. 14; text-fig. 14

Remarks. This species constitutes a small percentage of the microfloral assemblage in most of the Permian samples studied. There is, however, less variation than observed by Klaus (1963).



TEXT-FIG. 14. *Labiisporites granulatus* Leschik. *a*, Polar view illustrating proximal face with an indistinct monolete mark, on the right, and the distal face on the left (drawn from specimen), ×1,000. *b* and *c*, Diagrammatic reconstructions. *b*, Lateral polar section. *c*, Terminal polar section.

Infraturma DISACCIATRILETI (Leschik 1955) Potonié 1958
Genus KLAUSIPOLLENITES Jansonius 1962

1963 *Falcisporites* Leschik emend. Schaarschmidt (pars).

Type species. K. (al. *Pityosporites*) *schaubergeri* Potonié and Klaus 1954.

Discussion. Manum's (1960) emendation of *Pityosporites* Seward 1914 excluded many species assigned to this genus by Potonié and Klaus (1954). His suggestion that these forms be included in *Jugasporites* Leschik 1956 found little favour and Jansonius (1962) erected the genus *Klausipollenites* to accommodate certain of these miospores excluded from *Pityosporites* by Manum's emendation.

Although *Klausipollenites* is bisaccate there are specimens, which on other grounds cannot be properly excluded from the genus, which show a more or less monosaccate condition. In this case it is difficult to separate the genus from *Vesicaspora* Schemel 1951 (see Jizba 1962).

Comparison. Klausipollenites differs from *Falcisporites* emend. Klaus 1963 in the elongated oval outline and the lack of a distal furrow and from *Alisporites* emend.

Nilsson 1958 in the indistinct spore body of oblate outline and the absence of clear saccus attachments.

Klausipollenites schaubergeri (Potonié and Klaus) Jansonius 1962

Plate 43, figs. 16–17

1963 *Falcisporites schaubergeri* Schaarschmidt, pl. 15, figs. 10–17.

Remarks. This ubiquitous Zechstein form is adequately described in the original description of Potonié and Klaus (1954).

Genus FALCISPORITES Leschik emend. Klaus 1963

Type species. F. (al. *Pityosporites*) *zapfei* Potonié and Klaus 1954.

Discussion. Falcisporites emend. Klaus is characterized by a circular spore body, a distal furrow, and sacci which are not connected laterally. As such the genus is clearly differentiated from *Klausipollenites* but it becomes more difficult to separate *Falcisporites* and *Paravesicaspora* Klaus 1963. This latter genus is said to be characterized by the rhombic-shaped spore body, sacci which embrace laterally, and a distal furrow which is constricted over the distal pole. In the present material and Upper Permian material from Germany (kindly made available by Dr. H. Grebe), which I have examined, I find the distinction between these genera hard to apply. The generally indistinct spore body and the characteristic reticulate sculpture are common to both genera. The overall outline is always oval but the attachment of the sacci may vary between being terminal, leaving a wide zone between the sacci attachments distally, or being more closely attached, leaving a narrow distal zone within which a sulcus may be present. The presence or absence of this last feature may depend on the maturity and preservation of the grain, and the spore-body outline is often obscured by the sculpture. Unless there is stratigraphical significance it may be better not to maintain the two genera. Similarly the spores described by Balme and Hennelly (1955) as *Florinites ovatus* and those by Leschik (1956) as *Sulcatisporites* may be better assigned to *Falcisporites*.

Falcisporites zapfei (Potonié and Klaus) Leschik 1956

Plate 40, figs. 10–11

1954 *Pityosporites zapfei* Potonié and Klaus, pl. 10, figs. 9–10.

Remarks. The variability of this species has already been remarked on (Grebe and Schweitzer 1962, p. 15), and the species is clearly circumscribed in Potonié and Klaus (1954).

Infraturma PINOSACCITI (Erdtman 1945) Potonié 1958

Genus ALISPORITES Daugherty emend. Nilsson 1958

Type species. A. opii Daugherty 1941.

Discussion. Most workers agree that the original diagnosis of Daugherty is too broad. Potonié and Kremp (1956*a*) restrict the genus. Nilsson's (1958) formal emendation (which seems to have been neglected) is not in conflict with this and the genus has been widely accepted in this sense and is so used here, in preference to the much wider concept adopted by Rouse (1959).

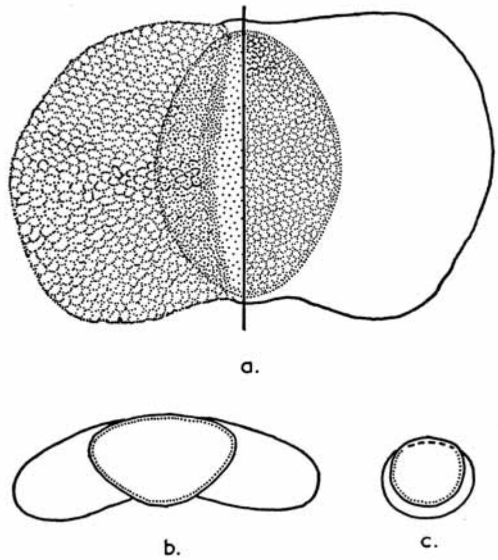
Alisporites differs from *Falcisporites* emend. Klaus in the more distinct prolate spore body.

Alisporites nuthallensis sp. nov.

Plate 43, figs. 1, 15; text-fig. 15

Holotype. Plate 43, fig. 15. Slide PF2277. Sample K 14, Kimberley, Nottinghamshire; Upper Permian (Lower Permian Marl).

Diagnosis. Spore body elliptical where the width exceeds the length, dark coloured, reticulate sculpture. Sacci well developed, joined laterally by a very thin exoexinal strip. Sculpture of sacci medium infra-reticulate.



TEXT-FIG. 15. *Alisporites nuthallensis* sp. nov. *a*, Polar view of proximal face, on the right, and distal face on the left (based on holotype), $\times 1{,}000$. *b* and *c*, Diagrammatic reconstructions. *b*, Lateral polar section. *c*, Terminal polar section.

Description. The outline in polar view is generally oval where the greatest width of the saccus feature is a line drawn over the distal pole at right angles to the long axis of the grain. Occasionally the saccus width is greatest away from the spore body (Pl. 43, fig. 15); in this case the saccus shows a slight indentation at the spore body margin. Distally there is a narrow leptoma delimited by straight or slightly convex saccus attachments. The saccus infra-sculpture is a coarser variation of that seen on the proximal spore body face. The saccus offlap is greater than the overlap.

Dimensions. (Eight specimens.) Spore-body length 30(32)35μ, spore-body width 36(42)44μ, overall length 65(70)74μ.

Discussion. Spore types 74 and 75 of Virkki (1945) appear from illustration and description to be very similar to *A. nuthallensis* sp. nov. As pointed out by Virkki (p. 134) there is close resemblance between these miospores and some pollen of *Caytonanthus* described by Harris (1937).

Infraturma PODOCARPOIDITI Potonié, Thomson, and Thiergart 1950
Genus PLATYSACCUS (Naumova) ex Potonié and Klaus 1954

1955 *Lueckisporites* Potonié and Klaus; Balme and Hennelly, pl. 1, figs. 6–9.
1955 *Cuneatisporites* Leschik.
1962 *Cuneatisporites* Leschik; Bhardwaj, pl. 13, fig. 185.

Genolectotype. *P. papilionis* Potonié and Klaus 1954.

Discussion. This genus is distinguished by its distinct diploxylonoid outline and non-striate spore body. Leschik (1955) erects the genus *Cuneatisporites* for diploxylonoid forms with a 'Keimspalte' (germinal furrow). I cannot see this feature in the illustration of the holotype, which appears to show merely the area of thinner exine between the sacci attachments distally, a feature observed in many bisaccate miospores. Leschik does not compare *Cuneatisporites* with *Platysaccus* and a separation upon the presence of a germinal furrow does not seem justified. *Fimbriaesporites* Leschik 1959 differs from *Platysaccus* in the presence of an exoexinal fringe around the spore body and a transverse split (Leschik 1959, p. 72).

Platysaccus radialis (Leschik 1955) comb. nov.

Plate 43, figs. 12–13

1955 *Cuneatisporites radialis* Leschik, pl. 10, fig. 6.

Description. The spore body is oval where the width exceeds the length. The proximal face is granular or scabrate. The sacci are discrete, three-quarters of a circle in outline, and the offlap is greater than the overlap. One edge of a saccus is attached equatorially while the other is attached near to the distal pole. The distal attachments are accompanied by crescent shaped thickenings (? folds) which usually extend to the equator. A leptoma is present but no colpus is seen within this area. The saccus sculpture is medium reticulate and a radial pattern is developed from the saccus roots.

Dimensions. (Seven specimens.) Spore-body length 20(25)31 μ, spore-body width 32(36)40 μ, saccus width 42(45)50 μ, overall length 56(64)77 μ.

Comparison. *P. radialis* comb. nov. differs from *P. papilionis* in the shape of the spore body and comparatively smaller sacci, while *P. umbrosus* Leschik 1956 possesses an irregular enveloping saccus. *P. leschiki* Hart 1960 is much larger than the present species.

Turma MONOCOLPATES Iversen and Troels-Smith 1950
Subturma INTORTES (Naumova) Potonié 1958
Genus CYCADOPITES (Wodehouse) ex Wilson and Webster 1946

Type species. *C. follicularis* Wilson and Webster 1946.

Comparison. *Cycadopites* differs from *Monosulcites* (Erdtman 1947, Cookson 1947) ex Couper 1953 in the more fusiform outline of the latter, and the dumb-bell shape of the furrow in the former.

Cycadopites rarus sp. nov.

Plate 44, figs. 15–16

Holotype. Plate 44, fig. 16. Slide PF2293. Sample K 14, Kimberley, Nottinghamshire; Upper Permian.

Diagnosis. Outline elliptical; exine thin; large well-defined irregular sulcus extending to the equatorial margin; sculpture finely granular.

Description. The sharp ends of the elliptical outline are 'squared off' where the sulcus is open at this point. The sharply pointed termination (Pl. 44, fig. 15) is formed by the overlap of one side of the sulcus. The sulcus is somewhat irregular and frequently does not show a good dumb-bell shape although in grains where the sulcus is open a closure over the distal polar region is present. Thin lips surround the sulcus which, in normally orientated grains, is approximately one-third the width of the grain at its widest part. Fine closely spaced granules form the sculptural pattern which is uniform over the whole grain.

Dimensions. (Five specimens.) Overall length 66(82)108μ, overall width 28(32)40μ.

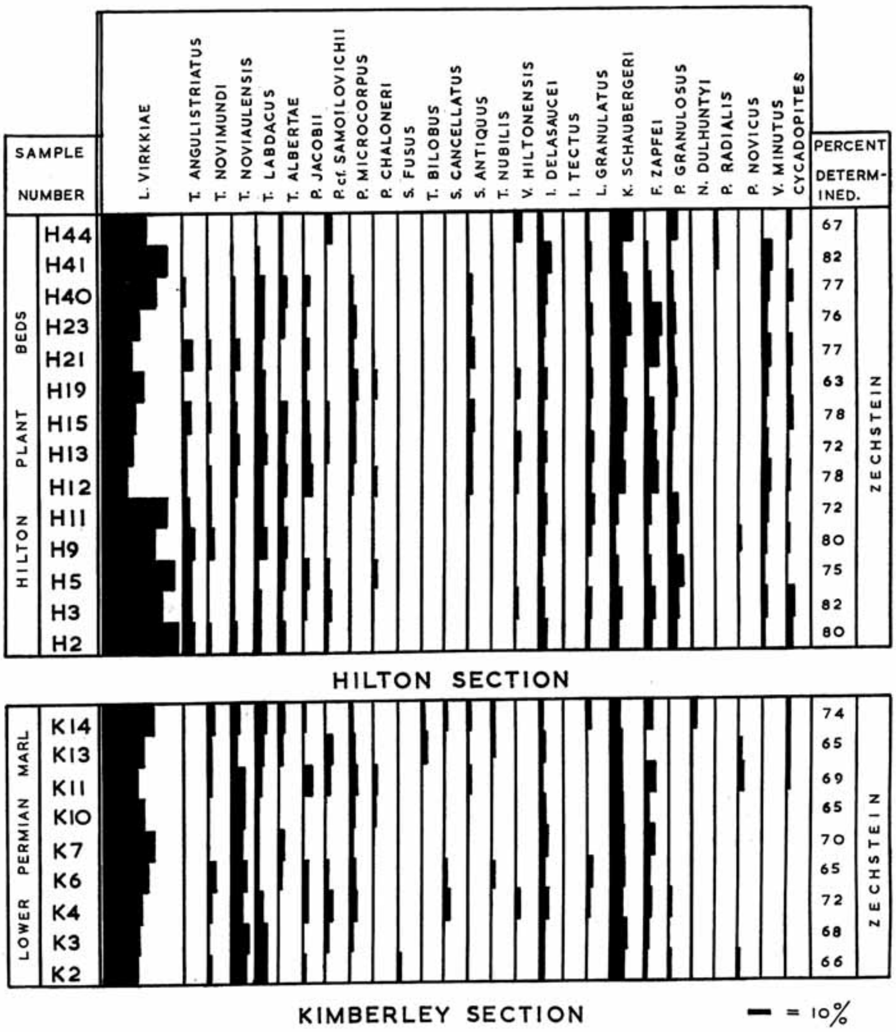
Comparison. *C. rarus* sp. nov. is appreciably larger than any of the monosulcate species described by Jansonius (1962). The closest comparison is made with *Ginkgocycadophytus sp.* Samoilovich 1953 which is very similar.

AN EVALUATION OF THE MICROFLORAL ASSEMBLAGES

Text-fig. 16 shows the distribution and frequencies of the miospores in the two principal sections studied. In all cases the counts are based on 300 spores in each sample, and in each case the percentage determined is given. Those excluded from the total are badly folded, broken, or corroded grains, detached air sacs together with some alete bodies and a few triradiate spores. Of this latter category most are Carboniferous in character and may be reworked; they are not abundant.

The most striking feature of the assemblages is their complete domination by bisaccate forms of which the bisaccate Striatiti constitute the largest part. *Lueckisporites virkkiae* is the dominant species in all the assemblages studied while *Taeniaesporites noviaulensis* and *T. labdacus* are always present. Of the non-striate forms the most common species are *Klausipollenites schaubergeri*, *Falcisporites zapfei*, *Labiisporites granulatus*, and *Illinites delasaucei*. Monosaccate species are represented by *Perisaccus granulosus*, *P. laciniatus*, *Potonieisporites novicus*, *Vestigisporites minutus*, and *Nuskoisporites dulhuntyi*. None of these monosaccate species is common but *V. minutus* occurs frequently in the Hilton section but is curiously absent from the Kimberley section. Monosulcate forms, represented by the single genus *Cycadopites*, constitute a small percentage in most of the samples.

This similarity of the microfloral assemblages is taken to be the product of a uniform vegetation existing during Upper Permian times, and although little can be deduced from the spores concerning the type of vegetational cover, the apparent lack of local masking effects of particular miospore species in individual samples or sections, suggests that the pollen rain had become well mixed. This together with the general saccate character of the grains and the uniformity of the assemblages, despite the varied



TEXT-FIG. 16. Miospore distribution in the Hilton and Kimberley sections.

lithology, suggests that the source vegetation was situated some distance from the area of deposition.

The great increase of saccate forms and the small number of triradiate types in the Permian, as opposed to the Carboniferous, expressed in terms of macrofloral changes, has already been discussed (Clarke 1965*a*). The probable botanical affinities of other spore types is also discussed in that paper. *Vittatina* is considered by some authors to represent the Gnetales. There are, however, both botanical and stratigraphical objections to this and *Vittatina* is probably the pollen of some other Gymnosperm group.

COMPARISON OF THE MICROFLORA WITH OTHER PERMIAN ASSEMBLAGES

The microflora of the Western European Upper Permian is well known. Potonié and Klaus (1954), Klaus (1955, 1963), Leschik (1956), Grebe (1957), Orlowska-Zwolinska (1962), Grebe and Schweitzer (1962), and Schaarschmidt (1963) all describe Upper Permian assemblages. One striking feature of these assemblages is their similarity to each other and to the present assemblages. The ubiquity of *L. virkkiae*, *K. schaubergeri*, *I. delasaucei*, *F. zapfei*, *N. dulhuntyi*, and *S. richteri* is maintained in all the areas, and the frequencies, where plotted (Grebe 1957, Grebe and Schweitzer 1962, Schaarschmidt 1963, Klaus 1963) present a constant pattern suggesting a very uniform composition of the vegetation existing in this region during Upper Permian (Zechstein) times.

Schaarschmidt (1963) separates the Zechstein from the Rotliegende of Germany by the presence, in the former, of *L. virkkiae*, *K. schaubergeri*, *Striatites sp.*, and *S. richteri*. This distinctness of the European Upper Permian microflora, compared with Lower Permian assemblages, is seen with reference to the Autunian of Germany (Remy and Remy 1961) and France (Alpern 1958, Doubinger 1960, 1962). In Western Europe no striate form with well-developed air bladders is recorded before the Upper Permian. There is a singular lack of this pollen in the Autunian which contains a distinctive Carboniferous element associated with an increase in the saccate genera *Florinites*, *Wilsonites*, *Potonieisporites*, *Nuskoisporites*, *Guthorlisporites*, and *Alisporites*. The only striate pollen occurring at this stratigraphic level are *Vittatina*-like forms (*Aumancisporites*, *sensu* Alpern).

Jansonius (1962) describes a microfloral assemblage of Upper Permian to Lower Triassic age from Canada. As with the European Upper Permian the Canadian assemblages are dominated by bisaccate forms of which the bisaccate Striatiti again constitute the most conspicuous part. Similarities extend to the specific level: *S. richteri*, *T. novimundi*, *T. noviaulensis*, *T. albertae*, *T. nubilus*, and *P. jacobii* are common in Britain and Canada. There are, however, important differences; *L. virkkiae*, *K. schaubergeri* (although *K. staplinii* is similar), *F. zapfei*, *I. delasaucei*, and *N. dulhuntyi* are not recorded from Western Canada. Further differences include the absence of *Hamiapollenites* (= *Hamipollenites*) in the British material, and the association, in Canada, of the above forms with *Ovalipollis*, a genus not recorded before the Upper Keuper in Britain.

Permian assemblages are described by Wilson (1962) from the Flowerpot Formation (Guadalupean) and by Jizba (1962) from the American Mid-Continent area (Late Pennsylvanian to Middle Permian in age). Although stratigraphically somewhat older, these American assemblages show certain similarities with those of Britain. Wilson (1962, p. 5) gives the relative percentages of *L. virkkiae*, *Vittatina*, *Potonieisporites*, and *Alisporites*, all of which are present in the British material. However, *Illinites*, *Taeniaesporites*, *Protohaploxypinus*, and *Klausipollenites* are absent in the Flowerpot Formation. The miospore assemblages described by Jizba (1962) from Kansas, Texas, and Oklahoma have, like that from the Flowerpot Formation, in part a European flavour and partly a distinctive element.

The Lower Gondwana (Permo-Carboniferous) of Australia contains a variety of bisaccate striate forms but these are associated with many Carboniferous-like trilete and monolete spores (Dulhunty 1945, Balme and Hennelly 1955, 1956).

The Talchir stage assemblage in India (Virkki 1945, Potonié and Lele 1961) is very similar to that of Australia but in the younger Raniganj stage (Bhardwaj 1962) considerable diversity appears among the bisaccate Striatiti; *Lueckisporites* s.str. is, however, absent.

The Permian assemblages of Tanganyika (Hart 1960) and the Congo (Piérart 1959, Høeg and Bose 1960) are like the Australian Permian microflora.

A comparison with the Antarctic Permian material described by Schopf (1962) is difficult as the preservation of his material is poor. Most of the specimens are assigned to *Accinctisporites* although there is a record of *Striatites* (*Protohaploxypinus*) (Schopf 1962, pl. 2, figs. 5, 12*a*–*b*).

The Russian Permian contains a variety of bisaccate striate forms referable to the genera *Protohaploxypinus*, *Striatopodocarpites*, *Striatoabietites*, and *Striatosaccites*. Forms assignable to *Vittatina* are common and are associated with *Florinites*, *Cycadopites*, bisaccate non-striate and monosaccate types. Trilete spores are present in the Lower Permian.

Thus although bisaccate striate pollen are present in the Permian of all the areas discussed above and although some genera (*Nuskoisporites*, *Cycadopites*) occur in most regions, the British Permian assemblages are most similar to those previously described from Western Europe.

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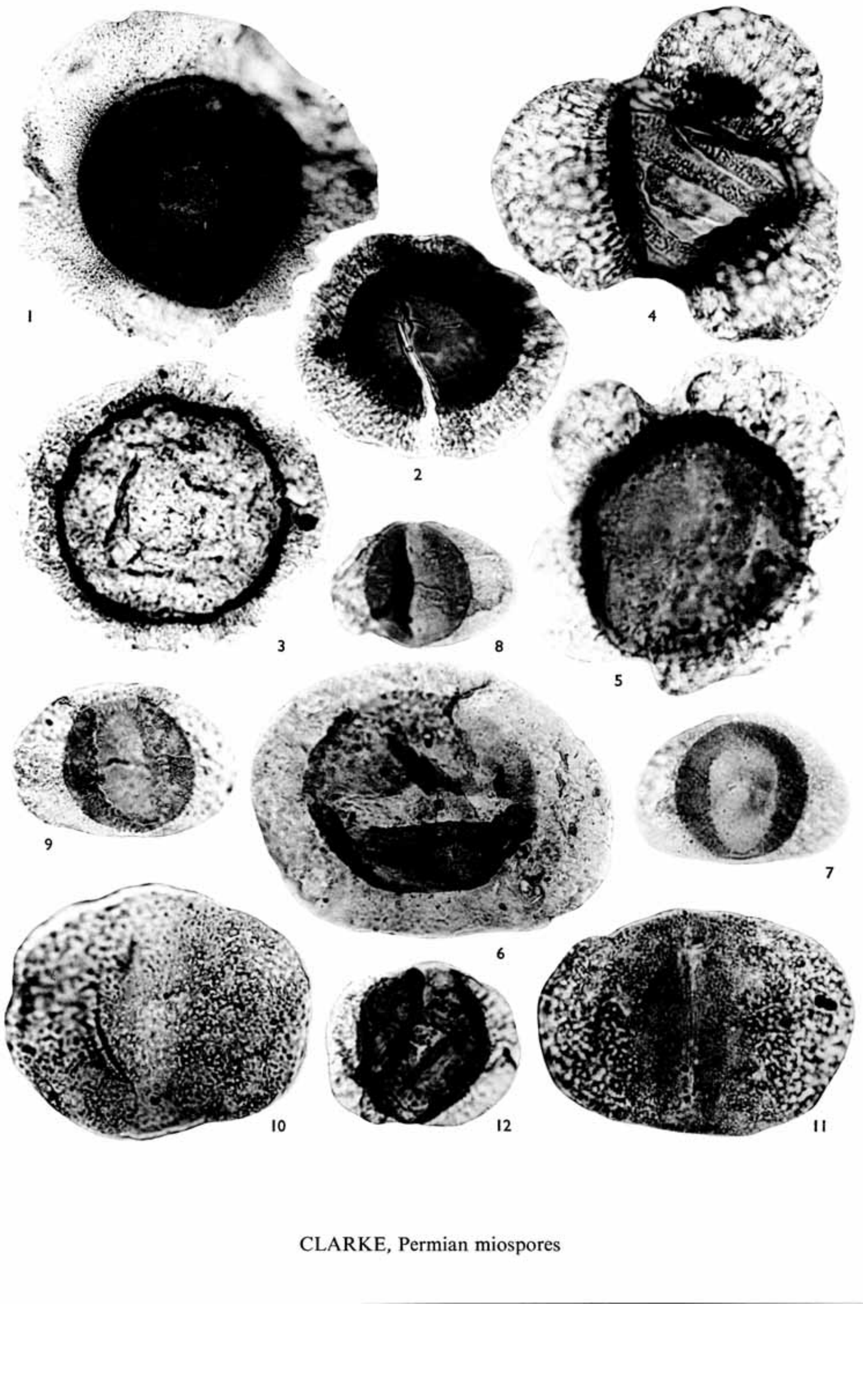
Manuscript received 11 March 1964

APPENDIX

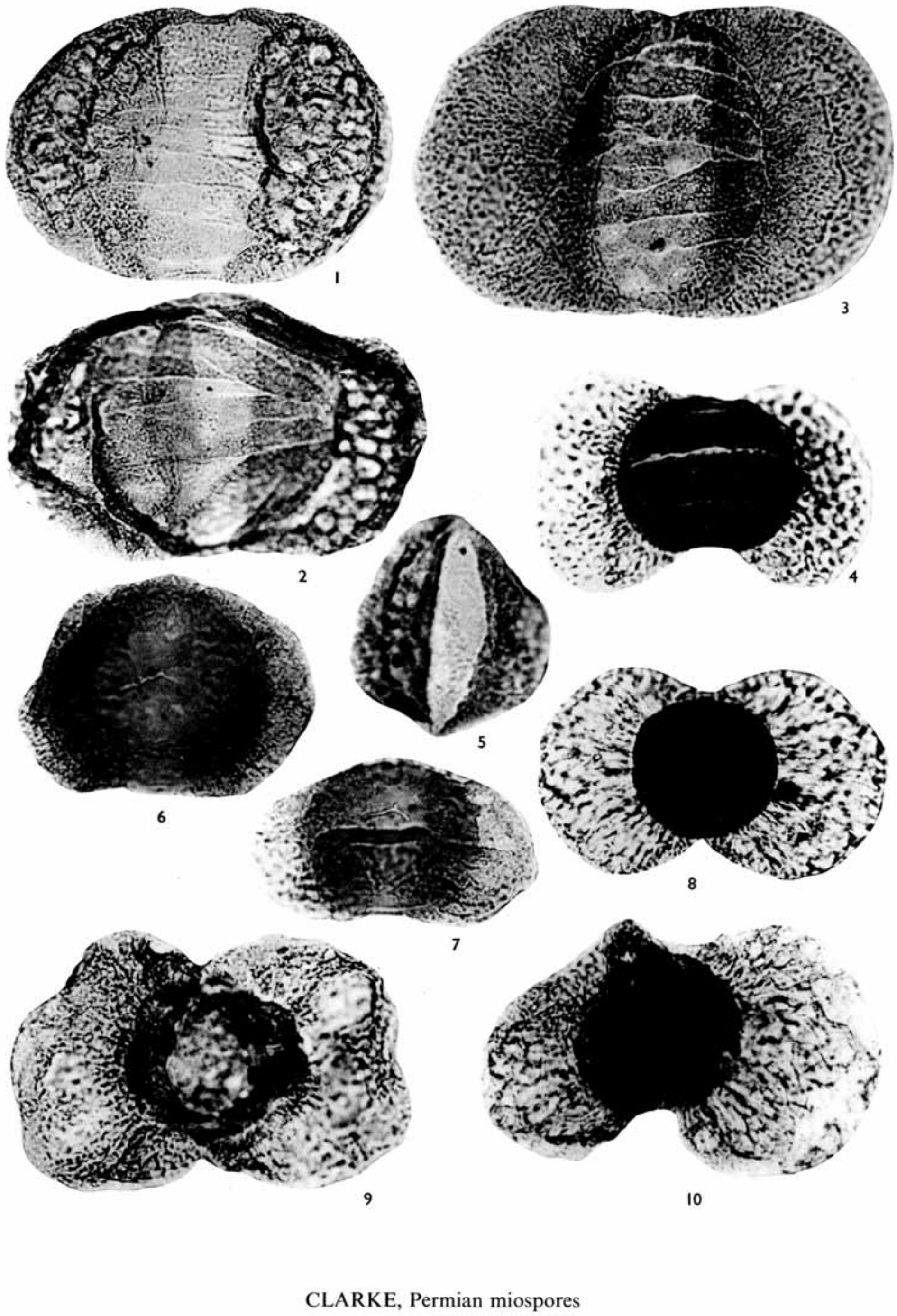
Numbers and lithologies of the better spore-bearing horizons.

Hilton Plant Bed. H44 Red/grey shaley sandstone. H41 Grey non-laminated, non-calcareous shale. H40 Purple sandy non-calcareous shale. H23 Grey sandy, micaceous shale. Plant remains. H21 Grey sandy, micaceous shale. Plant remains. H19 Sandy micaceous shale. H15 Sandy micaceous shale. H13 Green/grey calcareous shale. Plant remains. H12 Green/grey calcareous shale. Plant remains. H11 Green/grey sandy shale. H9 Grey micaceous sandy shale. Plant remains. H5 Grey sandy shale. Plant remains. H3 Grey/green shale. Plant remains. H2 Grey/green sandy shale. Lowest plant horizon.

Kimberley. K14 Calcareous, micaceous, medium-grained shaley sandstone. Plant remains. K13 Micaceous calcareous shale. Plant remains. K10, K11 Laminated calcareous shale. Plant remains. K7 Yellowish/grey calcareous siltstone. Plant remains. K6, K4 Medium-grained calcareous shaley sandstone. Plant remains. K3, K2 Light-grey, calcareous shale.



CLARKE, Permian miospores



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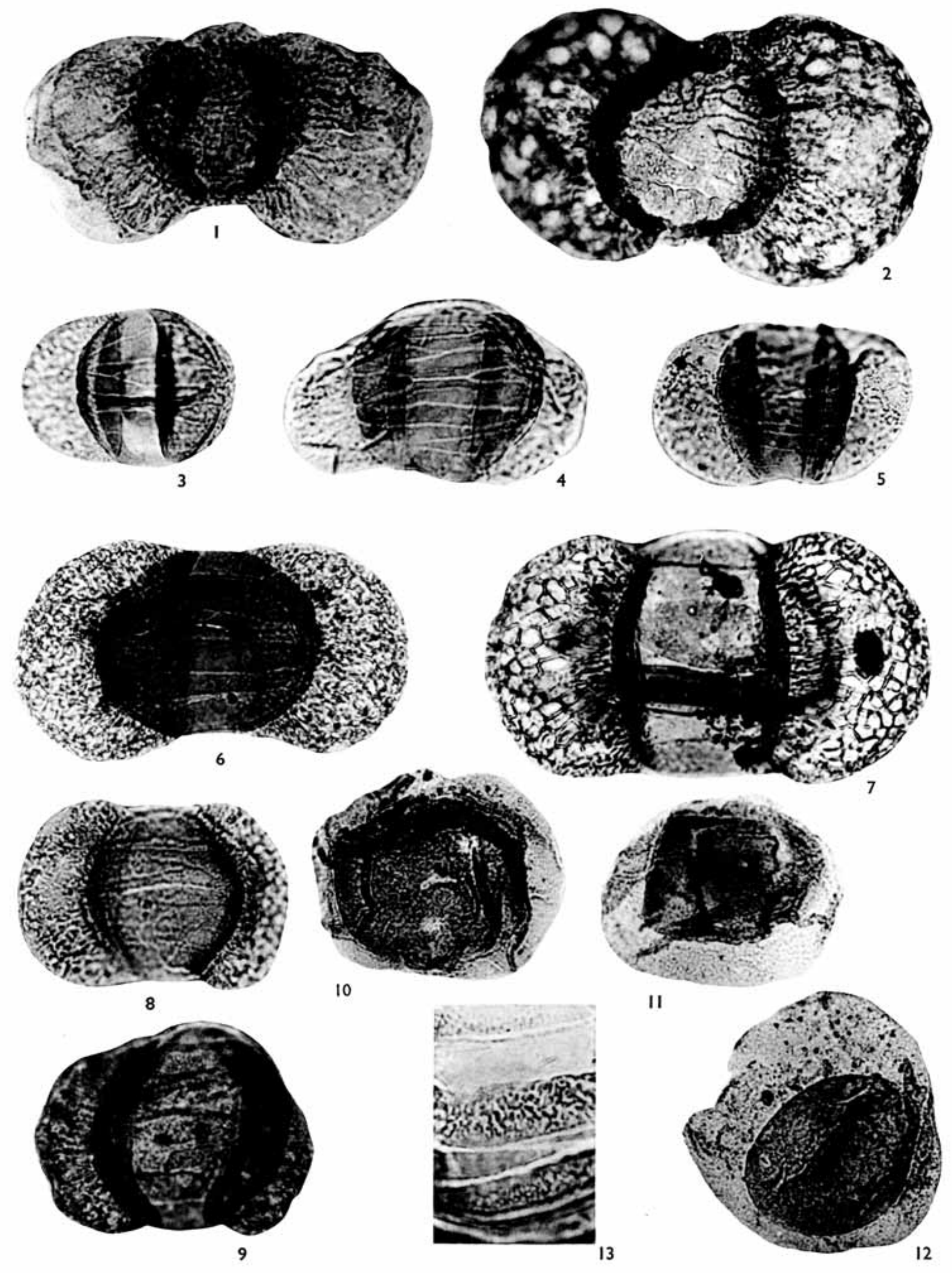

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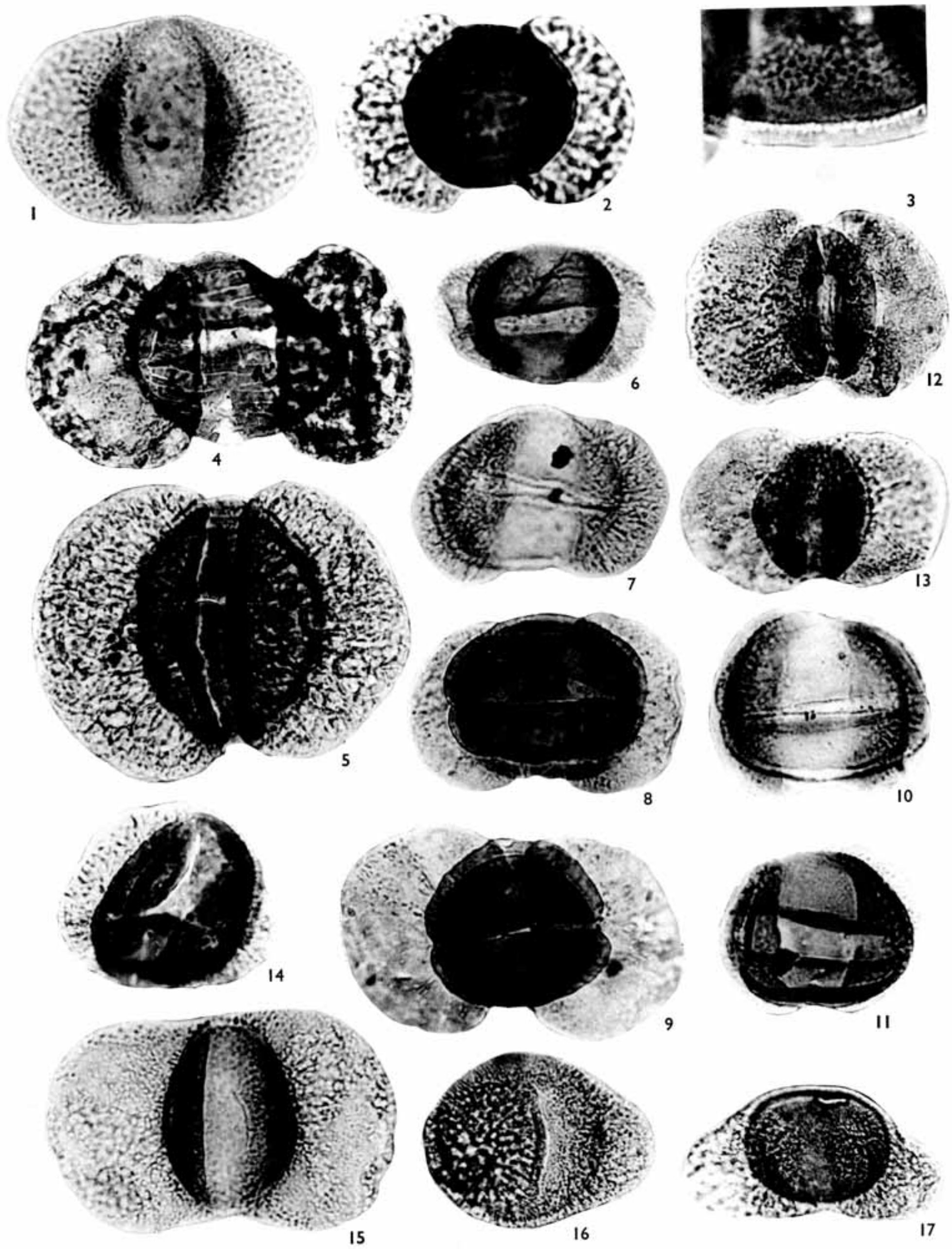

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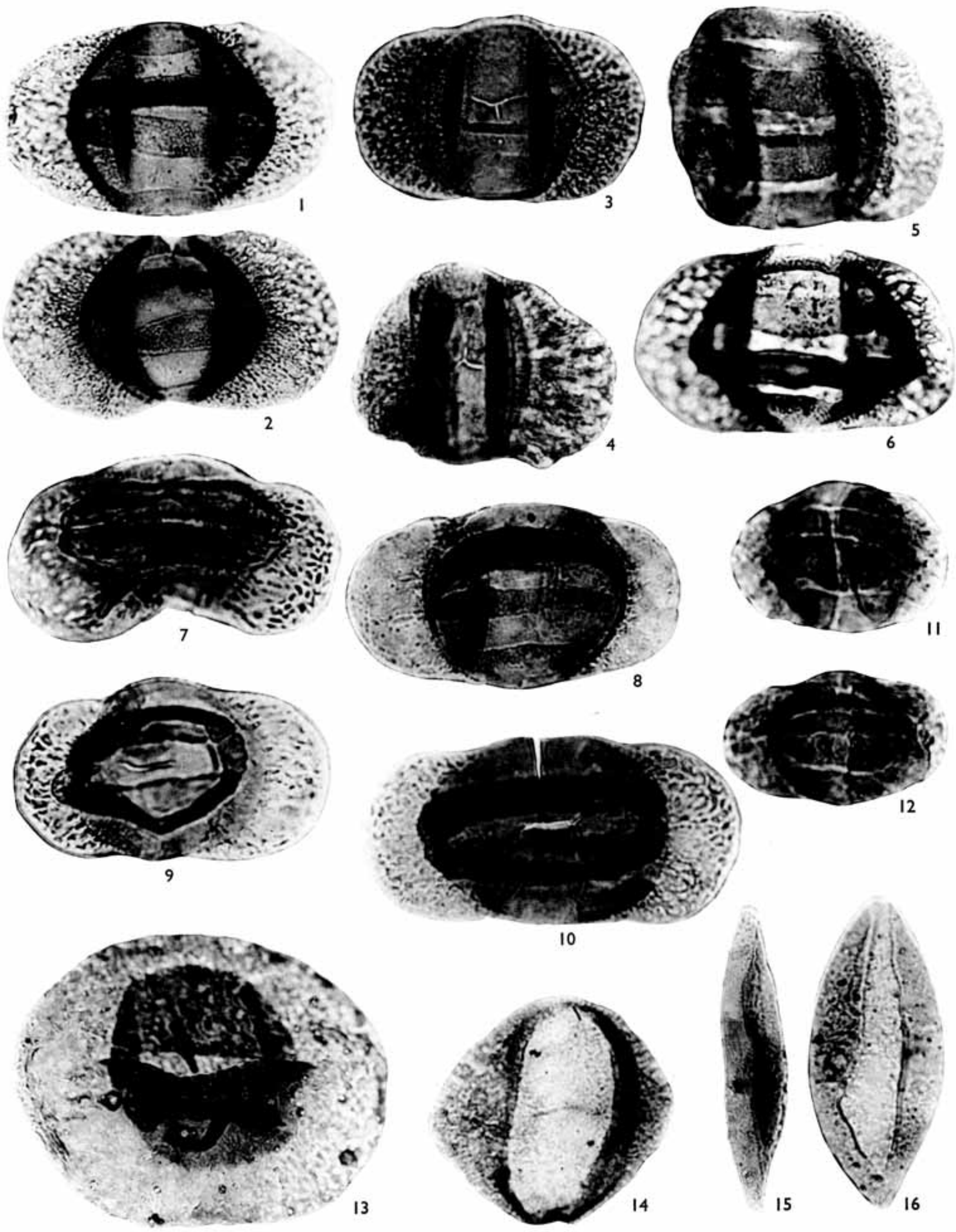

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