

KEUPER MIOSPORES FROM WORCESTERSHIRE, ENGLAND

by R. F. A. CLARKE

ABSTRACT. Twenty-six species assigned to eighteen genera are recorded from the Upper and Lower Keuper of Worcestershire. One new infraturma (*Striatapiti*), one new genus (*Brodipora*), and five new species are described. The Zechstein, Lower and Upper Keuper spore assemblages are compared and the macrofloral changes within this period discussed. The present assemblages are compared with previously published Triassic microfloras and a distribution chart for twenty-two genera is given.

THIS paper gives an account of British Keuper miospores which are compared with previously described assemblages, and with the British Zechstein microfloras studied by the author. While plant remains have been known for many years to occur in British Keuper sediments (Murchison and Strickland 1837, Brodie 1856, 1865, Arber 1909, Wills 1910) no account of the microflora has been published. The only previous records of Keuper spores in Britain are Wills (1910) who figures some spores incidentally in the course of a study of the macrofossils, and Chaloner (1962).

Location and geological horizon of samples

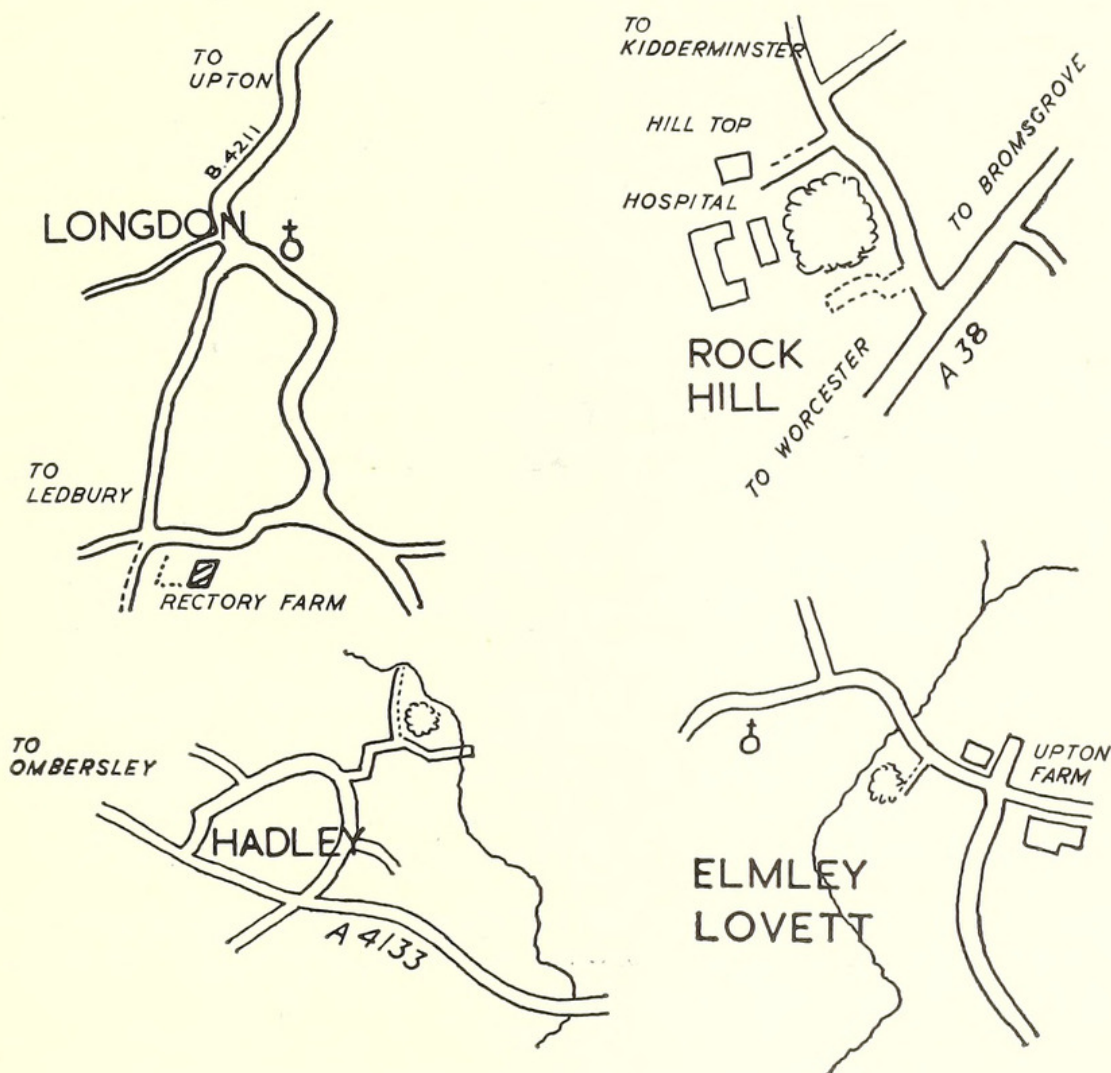
1. Samples BH 1–BH 6 are from the Lower Keuper Sandstone (Waterstones of some authors) exposed in a quarry in the grounds of Bromsgrove Hospital (text-fig. 1). This is the largest of four quarries located on Rock Hill (Murchison and Strickland 1837, Wills 1910), all of which are now disused and in the process of being filled in. The quarry in the hospital grounds exposes the typical false-bedded, coarse-grained sandstone in which are conspicuous lenses of marl ('lifts' of Wills 1910). These are variable in extent both laterally and vertically and probably represent the sites of old water courses or temporary lakes. It is from such lifts that the majority of the best plant remains have been collected. A most conspicuous lens is observed on the north-west face of the quarry and situated about half-way up the sequence where extensive collecting has created a considerable overhang. The spore-bearing samples were collected from these lenses. It is from these quarries on Rock Hill that Arber (1909) recorded *Yuccites vogesiacus* and subsequently Wills (1910) recorded the same species together with *Schizoneura paradoxa*, *Equisitites arenaceus*, and '*Voltzia heterophylla*'. This latter, a supposed male conifer cone, is now reassigned as *Masculostrobus willsi* Townrow (Townrow 1962b).

2. Sample EL 1 is from the Lower Keuper Sandstone of Elmley Lovett, 4 miles west of Bromsgrove (text-fig. 1). This old exposure mentioned by Murchison and Strickland (1837) consists of a track cutting and a small quarry which is very much overgrown, but one side of the track again exposes yellow, coarse-grained, false-bedded sandstone containing numerous plant remains. Sample EL 1 was collected from the marl lens at the base of the sequence where the section is 'shored-up' by bricks.

3. Samples HA 1 and HA 2 are from the Lower Keuper of Hadley Mill (National Grid Ref. 865642) approximately 2 miles west of Droitwich (text-fig. 1). The quarry

is disused and somewhat overgrown but consists of massive false-bedded sandstone which, as at Elmley Lovett, contains plant remains surrounded by 'oxidation rings'. The samples were taken from the more marly lenses as in the previous localities.

4. Sample L 2 is from the Arden Sandstone (Upper Keuper) of a small exposure on the west side of the yard at Rectory Farm, Longdon (Grid Ref. 836354), 3 miles south



TEXT-FIG. 1. Sketch-maps of the localities from which samples have been collected for the present study.

of Upton-upon-Severn. Here medium grained, white weathering sandstone with carbonaceous 'flecks' is seen alternating with more marly layers (Richardson 1905).

5. Sample BR 1 was obtained from the Geological Survey Museum, collected by Brodie. The location is given as Longdon but it is not known if it comes from Rectory Farm.

Sample lithologies. BH 6, Reddish-brown, slightly micaceous marl; plant remains. BH 5, Reddish-brown, non-micaceous mudstone; plant remains. BH 2 and BH 1, Reddish-brown slightly calcareous marl. HA 2, Fine-grained, slightly calcareous, micaceous sandstone. HA 1, Reddish-brown mudstone. EL 1, Reddish-brown marly sandstone. BR 1, Fine-grained laminated marly sandstone; plant remains. L 2, Green and red mudstone.

Maceration technique. (1) Twenty grams of sediment is crushed to less than one millimetre particle size. (2) If calcareous, sample is allowed to stand in dilute 20 per cent. hydrochloric acid, and then brought to the boil. (3) Residue is placed in 40 per cent. cold commercial hydrofluoric acid until no further reduction in bulk takes place (time, 24 hours to 4 days). (4) The 'silica gel' is rejected by adding 20 per cent. hydrochloric acid and centrifuging (5 minutes at 2,500 r.p.m.). (5) If much carbonaceous matter is present, sample is oxidized; 12–15 hours in concentrated nitric acid. (6) Humic acids are neutralized by addition of sodium carbonate solution. (7) Sample is centrifuged, washed, and slightly acidified; a small drop of phenol is added. Where necessary bromoform, diluted with one-fifth acetone per volume, is used to concentrate the spores by floatation, after the sample has been thoroughly dehydrated with acetone.

The slide collection. The majority of spores illustrated are from single spore preparations mounted in glycerine jelly, unstained except where indicated on the slide, and made permanent with a candle-wax surround. Reference to a particular spore in an assemblage slide is made by a circle on the back of the slide. All the preparations are housed in the Geological Survey and Museum, London.

Acknowledgements. I should like to thank Professors S. E. Hollingworth and T. Barnard for the use of laboratory facilities at University College London, and the Geological Survey and Museum for making available Upper Keuper material from Longdon. The present paper formed part of a doctoral thesis of the University of London under the supervision of Dr. W. G. Chaloner to whom the author is greatly indebted for constant advice, helpful discussion, and the critical reading of the manuscript. Finally I wish to express my gratitude for a grant from the Department of Scientific and Industrial Research.

SYSTEMATIC SECTION

Anteturma SPORITES H. Potonié 1893

Turma TRILETES (Reinsch 1881) emend. Potonié and Kremp 1954

Subturma AZONOTRILETES Lubert 1935

Infraturma APICULATI (Bennie and Kidston 1886) emend. Potonié 1956

Subinfraturma VERRUCATI Dybova and Jachowicz 1957

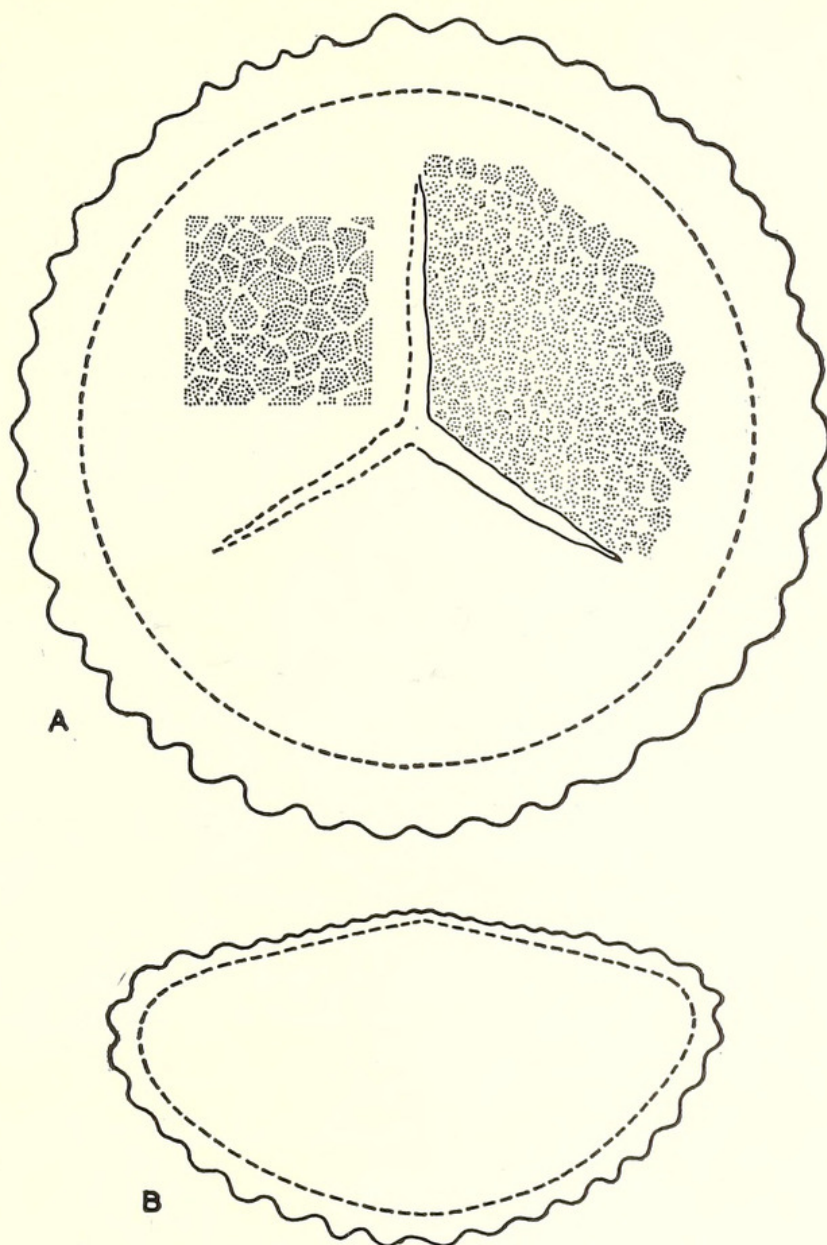
Genus VERRUCOSISPORITES (Ibrahim) emend. Potonié and Kremp 1954

Discussion. The more inclusive emendation of Potonié and Kremp (1954) is used here in preference to the restrictive use advocated by Bhardwaj (1956, p. 125) which I find difficult to apply in the present material.

Verrucosisporites morulae Klaus 1960

Plate 35, figs. 4–5

Discussion. Although the size of the distal verrucae bases varies between 2–5 μ the height remains constant (also commented upon by Klaus 1960, p. 130). In the present specimens the sculpture of the contact faces is less coarse than that covering the remainder of the spore surface. Such a feature is not apparent from the photograph of the holotype and does not appear in the specific diagnosis. The British specimens are here assigned to *V. morulae* on the basis of their size range, size of the verrucae, and exine thickness, together with stratigraphic and geographic considerations. *V. morulae* differs from *V. tumulosus* Leschik 1955 in the higher verrucae; other than this the two species are very similar. *V. morulae* has previously been recorded from the Carnian of the Eastern Alps (Klaus 1960).



TEXT-FIG. 2. *Verrucosisporites contactus* sp. nov. Diagrammatic reconstructions. A, Polar aspect, proximal on the right-hand side showing the differentiated contact areas and the form of the distal verrucae bases on the left-hand side. B, Polar section. $\times 1,000$.

Verrucosisporites contactus sp. nov.

Plate 35, figs. 1–3; text-fig. 2

Holotype. Plate 35, fig. 3. Slide PF2392. Sample BH 6, Bromsgrove Hospital Quarry; Lower Keuper.

Diagnosis. Triradiate, verrucate miospore, $60\text{--}102\mu$ in diameter (mean 75μ ; forty measured specimens). Amb circular; verrucae low with irregular bases; differentiated contact faces.

Description. The spore exine is $3\text{--}5\mu$ thick and the proximal face bears a well-developed

triradiate mark which extends one-half to one-third the spore radius. The commissures are hair-like, unaccompanied by any obvious thickening or elevations (lips), and each arm frequently bifurcates at its extremity (in more than 90 per cent. of the specimens observed). The contact faces are differentiated by their smaller sculptural elements and their limits are often depicted by their darker colour (Pl. 35, figs. 1, 3); no curvaturae (arcuate ridges) are present. The distal surface and that part of the proximal face not occupied by the contact faces possess a sculpture made up of low, flat or round-topped verrucae $1-2\mu$ high and $2-6\mu$ wide at the base; in polar view the bases of the verrucae are rounded, irregular or polygonal. Forty to sixty verrucae may be seen in profile around the equator.

Comparison. *V. contactus* sp. nov. differs from *V. morulae* Klaus in the smaller, more irregular-sized verrucae, the better-defined contact areas, and the bifid terminations of the triradiate mark. These latter two features also serve to differentiate the new species from *V. tumulosus* Leschik 1955.

Subinfraturma GRANULATI Dybova and Jachowicz 1957

Genus CYCLOGRANISPORITES Potonié and Kremp 1954

Cyclogranisporites congestus Leschik 1955

Plate 35, figs. 7-9

Discussion. This species has only previously been recorded from the Middle Keuper of Switzerland (Leschik 1955). The British specimens agree very well with the description given by Leschik except in the larger size of the present specimens, but it is not clear if the measurements given by Leschik represent mean values, or dimensions of the holotype. *C. congestus* is very similar to a form described as *Conosmundasporites othmari* by Klaus (1960) and from the description of the latter it seems possible that *C. othmari* is a badly preserved specimen of *C. congestus*.

Cyclogranisporites oppressus Leschik 1955

Plate 35, fig. 6

Discussion. This locally abundant Lower Keuper species has been previously recorded from the Swiss Keuper (Leschik 1955). It is a very small form between $20-30\mu$ (mean 26μ , measured on nine specimens), and is further differentiated from *C. congestus* by the absence of lips.

EXPLANATION OF PLATE 35

All magnifications $\times 750$.

Figs. 1-5. *Verrucosisporites* spp. 1-3, *V. contactus* sp. nov. Oblique polar views showing the differentiated contact areas and the bifid terminations of the tetrad scar. 1, PF2393. 2, PF2395, 3, PF2392. Holotype. 4-5, *V. morulae* Klaus. 4, PF2387. 5, PF2388.

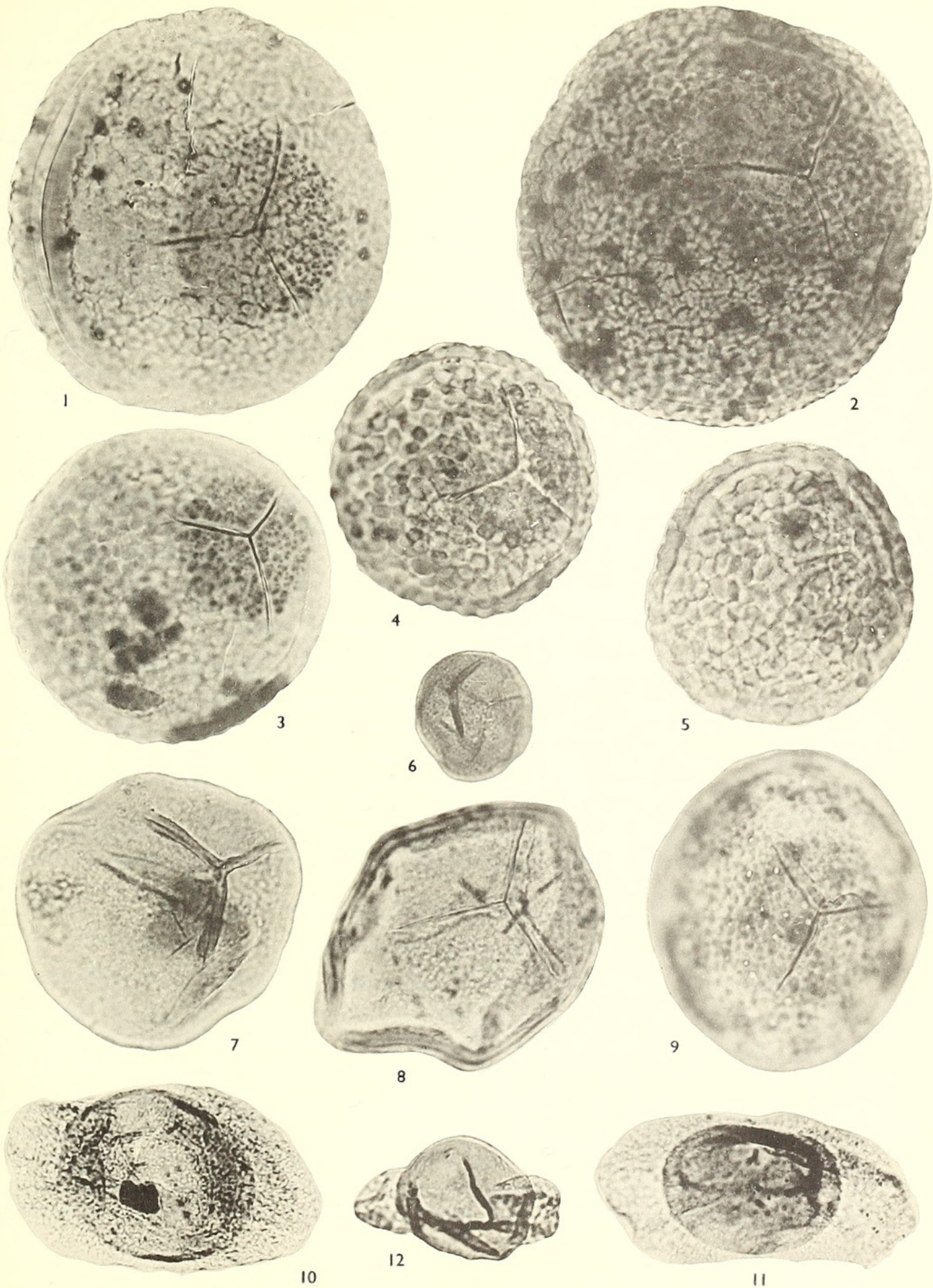
Figs. 6-9. *Cyclogranisporites* spp. 6, *C. oppressus* Leschik; PF2386.

7-9. *C. congestus* Leschik. 7, PF2382. 8, PF2396. 9, PF2383.

Figs. 10-11. *Succinctisporites radialis* Leschik. 10, PF2359. 11, PF2458.

Fig. 12. *Alisporites minutisaccus* sp. nov. Oblique polar view of holotype; PF2424.

Localities of figs. 1-8, 10-11, Lower Keuper, Bromsgrove. Figs. 9, 12, Lower Keuper, Hadley.



CLARKE, Upper Triassic miospores

Subinfraturma NODATI Dybova and Jachowicz 1957
Genus OSMUNDACIDITES Couper 1953

Type species. *O. wellmanii* Couper 1953, pl. 1, fig. 5. Jurassic, New Zealand.

Discussion. The genus was originally described as triradiate although such a feature is often not clearly displayed (e.g. Couper 1958, pl. 16, fig. 4). Forms thought to be assignable to this genus occurring in the British Triassic lack a discernible triradiate mark; such is the case also in the material studied by Klaus (1960). This contrasts curiously with forms described by Balme (1963) from the Australian Trias which are clearly triradiate.

Cyclogranisporites is differentiated from *Osmundacidites* by the presence of closely spaced sculptural elements which can only be described as granae while *Osmundacidites* may also, and commonly does, develop cones, papillae, and sub-baculate processes. On general morphological grounds, however, the two genera would appear to be very similar.

Osmundacidites alpinus Klaus 1960

Plate 37, figs. 13–14

Discussion. The original description of Klaus (1960) constitutes the sole previous record of this species which is differentiated from the type species by being smaller and having smaller sculptural elements.

Subinfraturma BACULATI Dybova and Jachowicz 1957
Genus CONBACULATISPORITES Klaus 1960

Type species. *C. mesozoicus* Klaus 1960, pl. 29, fig. 15. Keuper, Eastern Alps.

Discussion. The cardinal characteristics of this genus are the triangular outline in polar view, the length of the triradiate mark being approximately two-thirds the spore radius and the possession of baculate processes. A miospore form found in the British Upper Keuper satisfies two of the above requirements but has a very small triradiate mark. Rather than create a new monotypic genus the present forms are assigned to *Conbaculatisporites* Klaus (also monotypic). The present genus differs from *Baculatisporites* Thomson and Pflug 1953 only in the triangular polar contour.

Conbaculatisporites longdonensis sp. nov.

Plate 36, figs. 1–5; text-fig. 3

Holotype. Plate 36, fig. 1. Slide PF2475. Sample L 2, Rectory Farm, Longdon; Upper Keuper.

Diagnosis. Triangular baculate miospore. Triradiate mark small; proximal baculae smaller than those borne distally; baculae variable in shape and size; discrete. Overall size 49–66 μ (mean 59 μ , based on nine specimens).

Description. The exine is about 2 μ thick and the small triradiate mark, which on many specimens is not easily seen, is unaccompanied by any form of thickening. The size of this feature is variable but seldom exceeds one-third the spore radius. No contact areas are delimited but the proximal face bears a sculpture of small cones and baculae which increase in size towards the equator and which show their greatest expression distally

where they may be up to 9μ . Although the shape of these processes may vary (see text-fig. 3) the cross-section is circular, being $2-3\mu$ at the base. These baculae are flat-topped, round-topped, occasionally pointed, never bifid at the tips (as in *Raistrickia*) and well separated ($4-5\mu$ apart). *C. longdonensis* sp. nov. differs from *C. mesozoicus* Klaus in the smaller triradiate mark and the larger, more variable sculptural elements.

Turma ALETES Ibrahim 1933

Subturma AZONALETES (Luber 1935) emend. Potonié and Kremp 1954

Infraturma STRIATAPITI infraturma nov.

Diagnosis. This new infraturma is proposed to include all alete miospores showing striations concentrated in the (presumed) equatorial region.

Genus BRODISPORA gen. nov.

Type species. *B. striata* sp. nov.

Diagnosis. Oval striate body. Striations localized in a median zone; remainder of body laevigate.

Discussion. These alete striate bodies are fairly common in the British Upper Keuper. They are presumed to be miospores on the grounds that the wall is resistant to oxidation, and behaves like that of the miospores with which they are associated; the possibility that they might be Acritarchs is lessened by the fact that other planktonic bodies are absent from the samples containing *Brodispora* gen. nov. As there is no tetrad scar and as the grains are always found singly it is impossible to give an indisputable basis for their orientation. The most plausible orientation, which is used here in describing the spore, is set out in text-fig. 4.

Comparison. The genera *Chomotriletes* (Naum.) ex Naumova 1953 from the Upper Devonian and *Circulisporites* de Jersey 1962 from the Trias are striate alete spores, differing only in the incomplete striae of *Chomotriletes* as opposed to the continuous striations of *Circulisporites*. They both differ from *Brodispora* in being of circular outline and developing the striations in such a way that the whole of at least one spore face is covered rather than their being concentrated in the equatorial zone.

Brodispora striata sp. nov.

Plate 36, figs. 6-9; text-fig. 4

Holotype. Plate 36, fig. 9. Slide PF2478. Sample L 2. Rectory Farm, Longdon; Upper Keuper.

EXPLANATION OF PLATE 36

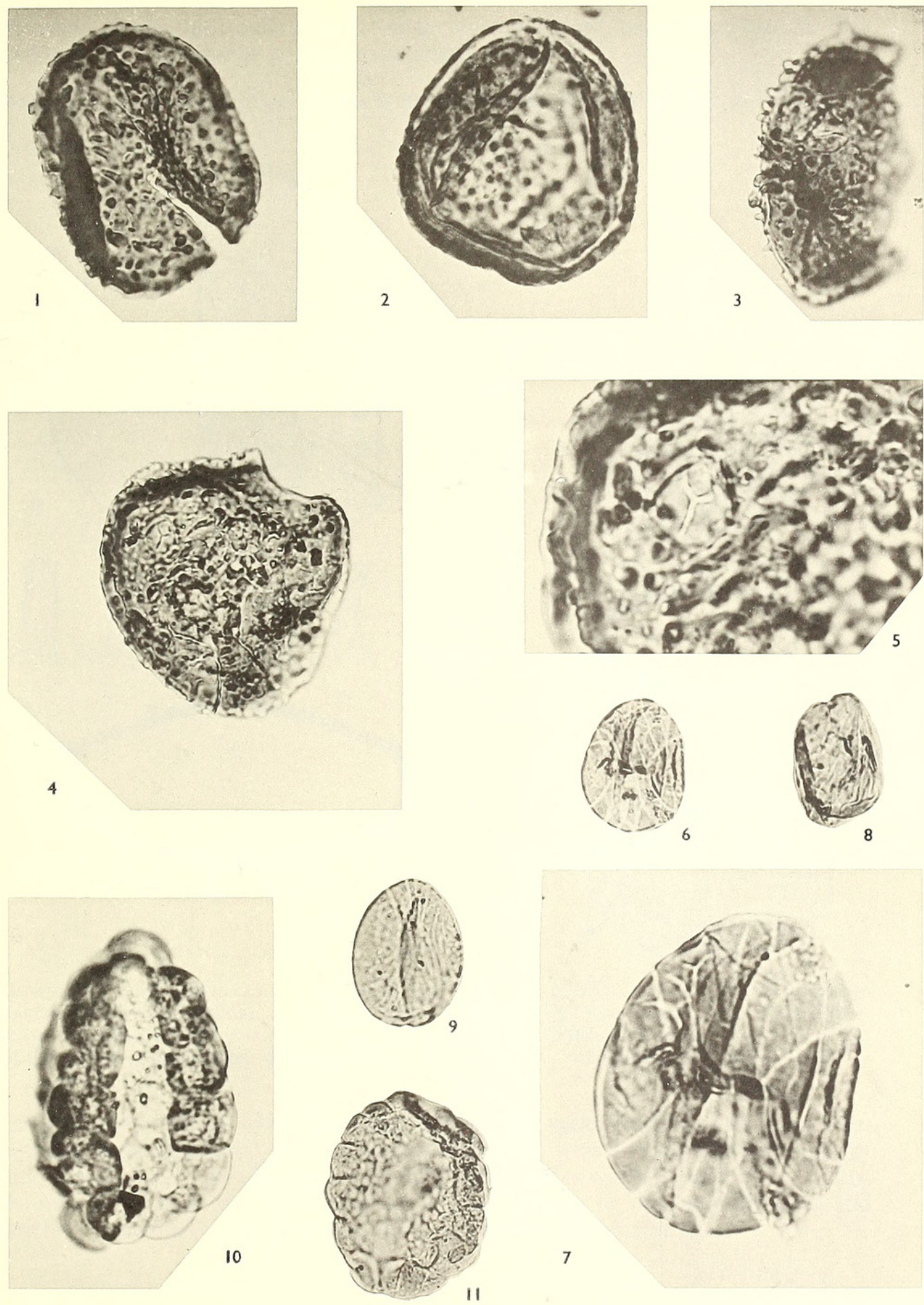
Magnification $\times 750$, unless otherwise stated.

Figs. 1-5. *Conbaculatisporites longdonensis* sp. nov. 1, Holotype, PF2475, showing the distal sculpture. 2-4, Oblique polar aspects of other specimens. 5, Part of 4 showing the small triradiate mark, $\times 2,000$. 2, PF2516/760271. 3, PF2474. 4-5, PF2476.

Figs. 6-9. *Brodispora striata* gen. et sp. nov. 7, $\times 1,500$. 6-7, PF2516/850209. 8, PF2516/878267. 9, Holotype, PF2478.

Figs. 10-11. *Camerosporites secatus* Leschik. 10, $\times 1,500$. PF2516/780283. 11, PF2447.

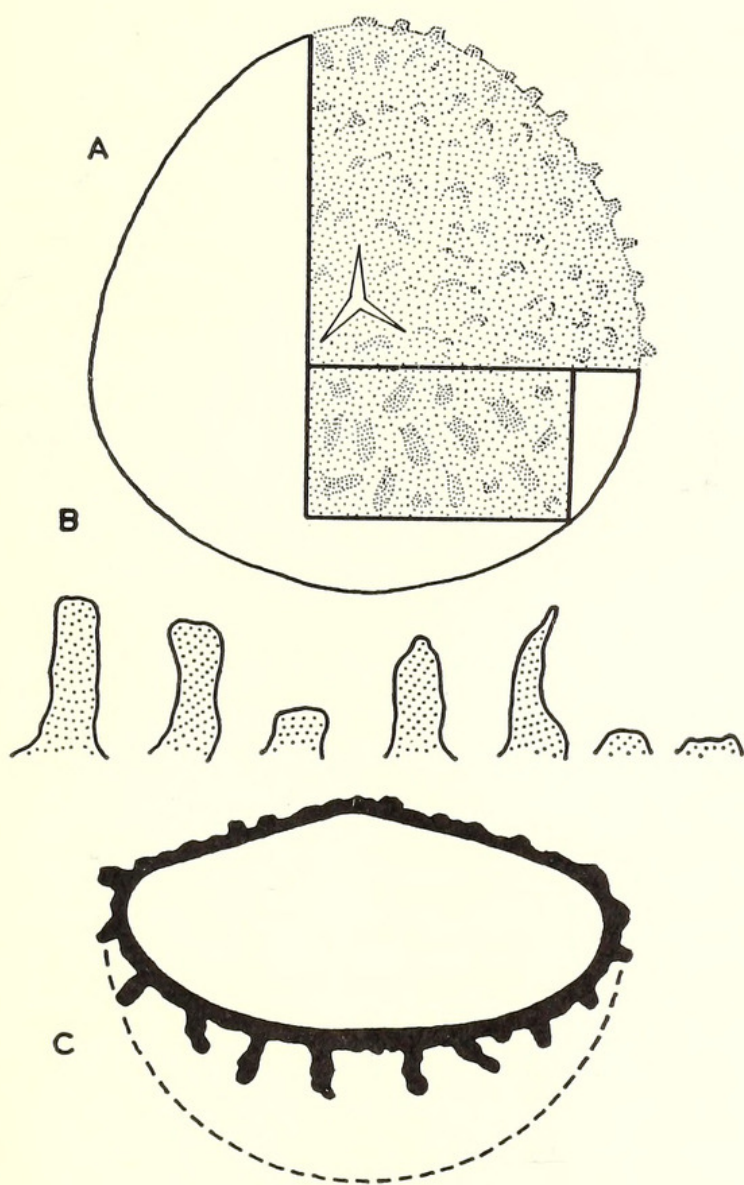
All specimens from the Upper Keuper of Longdon.



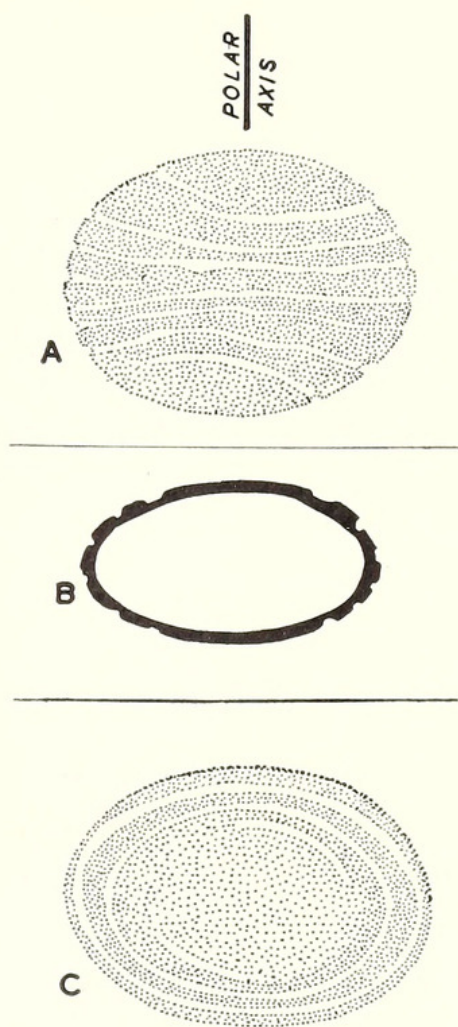
CLARKE, Upper Triassic miospores

Diagnosis. Exine thin, outline oval, striae thin and polar areas unsculptured. Size $30\text{--}40\mu \times 20\text{--}34\mu$ (mean of seventeen specimens, $35 \times 28\mu$).

Description. The outline in polar view is oval with broadly rounded ends and is smooth



TEXT-FIG. 3. *Conbaculatisporites longdonensis* sp. nov. Diagrammatic reconstructions. A, Proximal polar aspect (above) and distal aspect (rectangle). B, Showing variation of the sculptural appendages. C, Polar section. $\times 1,000$.



TEXT-FIG. 4. *Brodispora striata* gen. et sp. nov. Diagrammatic reconstructions. A, Equatorial view. B, Polar section. C, Polar view. $\times 1,000$.

except in polar section where the striae are seen in optical section. The striae concentrated in the equatorial area are narrow, only $1\text{--}2\mu$ wide and separated by areas of smooth exine $2\text{--}6\mu$ wide which in equatorial view appear to widen somewhat terminally. The number of striae is difficult to determine but appears to vary between seven and fourteen; sometimes small transverse striae may connect the major ones.

Anteturma POLLENITES R. Potonié 1931

Turma SACCITES Erdtman 1947

Subturma MONOSACCITES (Chitaley 1951) emend. Potonié and Klaus 1954

Infraturma ALETESACCITI Leschik 1955

Genus ENZONALASPORITES Leschik 1955

1955 *Vallasporites* Leschik, pl. 6, figs. 6–8, 10.

Type species. *E. vigens* Leschik 1955, pl. 5, fig. 24; Keuper, Switzerland.

Discussion. Although it was considered by both Leschik (1955) and Klaus (1960) as a saccate genus I am doubtful whether this is correct. *Enzonalasporites* seen as a flattened object can reasonably be described as having an inner central area surrounded by an outer equatorial feature, but this structure is probably not a saccus. It appears rather, that the exoexine of the proximal face is a series of sinuous ridges which become better developed at the equator without the wall being cavate. However, until the nature of the wall is elucidated the genus is left as originally classified. *Enzonalasporites* differs from *Zonalasporites* Leschik 1955 in its smaller size and the less distinct separation of the equatorial and central areas.

Enzonalasporites vigens Leschik 1955

Plate 37, figs. 8–10

1955 *Enzonalasporites obliquus* Leschik, pl. 5, figs. 23, 25.

Discussion. This species is known from the Keuper of Switzerland (Leschik 1955). *E. tenuis* Leschik is very similar to the present species and may be synonymous with it. Klaus (1960) records *E. tenuis* from the Carnian of the Eastern Alps.

Genus PATINASPORITES (Leschik 1955) emend. Klaus 1960

Type species. *P. densus* Leschik 1955, pl. 16, fig. 11; Keuper, Switzerland.

Discussion. In the emended sense *Patinasporites* differs from *Enzonalasporites* in the greater width of the surrounding equatorial feature, the better development of the sinuous exoexinal ridges (muri), and the generally larger size. *Zonalasporites* is similar to the present genus but differs in the smaller exoexinal muri.

Patinasporites cf. *densus* Leschik 1955

Plate 37, figs. 11–12

Comparison. Leschik's (1955) species is based primarily on size, and on this basis the

EXPLANATION OF PLATE 37

Magnification $\times 750$, unless otherwise stated.

Figs. 1–2. *Accinctisporites lignatus* Leschik. 1, PF2480. 2, PF2497.

Fig. 3. *Succinctisporites grandior* Leschik, PF2526.

Fig. 4. Diploxytonoid grain. *Platysaccus* sp., PF2441.

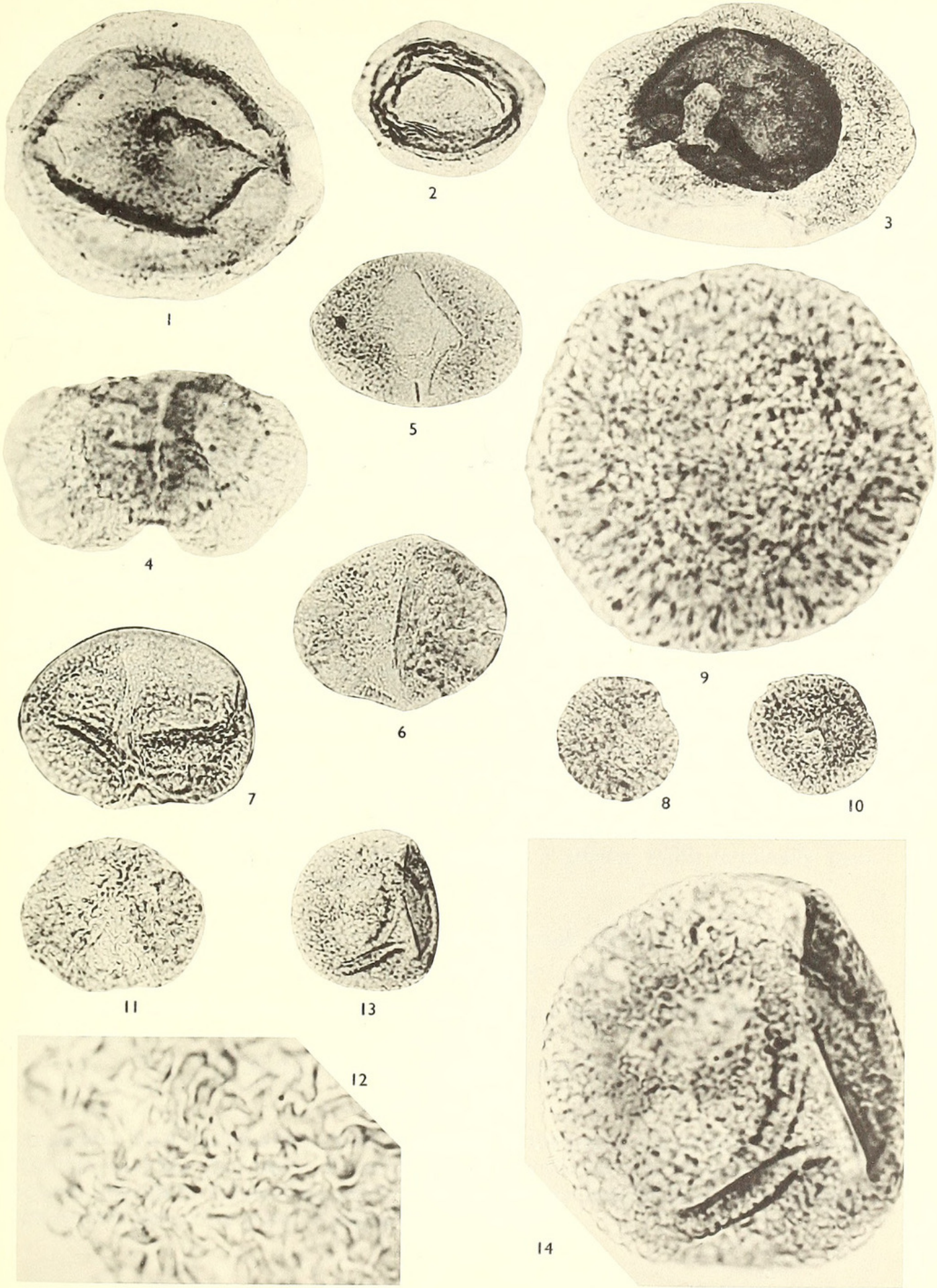
Figs. 5–7. *Klausipollenites devolvens* comb. nov. 5, PF2429. 6, PF2428. 7, PF2426.

Figs. 8–10. *Enzonalasporites vigens* Leschik. 8–9, PF2434. 9, $\times 2,500$. 10, PF2435.

Figs. 11–12. *Patinasporites* cf. *densus* Klaus. 11–12, PF2440. 12, $\times 2,500$.

Figs. 13–14. *Osmundacidites alpinus* Klaus. 13–14, PF2457. 14, $\times 2,000$.

Localities of figs. 1–3, Lower Keuper, Bromsgrove. Figs. 4–14, Upper Keuper, Longdon.



CLARKE, Upper Triassic miospores

British specimens are compared with the type species. This differs from *P. iustus* Klaus 1960 which is larger and has a more clearly defined central area.

Genus ELLIPSOVELATISPORITES Klaus 1960

Type species. *E. plicatus* Klaus 1960, pl. 36, fig. 65; Carnian, Eastern Alps.

Discussion. The diagnostic characteristics of this genus are the elliptical outline and the presence of a coarsely wrinkled velum (saccus?) which completely surrounds the spore body. The conspicuous series of sinuous ridges may be localized on the proximal face of the spore body or be present also as part of the velum sculpture; they frequently show a micropunctuation (Pl. 39, fig. 1). *Ellipsovelatisporites* is most similar to *Vesicaspora* Schemel 1951 from which it differs in the presence of the sinuous muri.

Ellipsovelatisporites plicatus Klaus 1960

Plate 39, figs. 1–2

This species found in the British Upper Keuper has been previously recorded from the Carnian of the Eastern Alps (Klaus 1960).

Genus SUCCINCTISPORITES Leschik 1955

Type species. *S. grandior* Leschik 1955, pl. 7, fig. 12; Keuper, Switzerland.

Discussion. Many of the species originally assigned to this genus are unacceptable (Jansonius 1962, p. 62). The type species and a few other species may be regarded as conforming to the original diagnosis, and the genus, in this sense, is present in the British Trias. Leschik (1955) does not discuss the attachment of the saccus to the spore body except to remark that it is obscure. While this is so it appears from the present material that a thinner exinal area exists over the (presumed distal) polar region. As there is no tetrad scar it is not possible to give a definite orientation but it is considered here that the exine becomes cavate near to the equator and the saccus is regarded as attached to the central body on the distal face (text-fig. 5). *Succinctisporites* differs from *Accinctisporites* Leschik 1955 in having a saccus showing a greater width terminally than laterally, when viewed down the polar axis.

Succinctisporites grandior Leschik 1955

Plate 37, fig. 3; text-fig. 5

This locally abundant Lower Keuper form has been recorded from the Keuper of Switzerland.

Succinctisporites radialis Leschik 1955

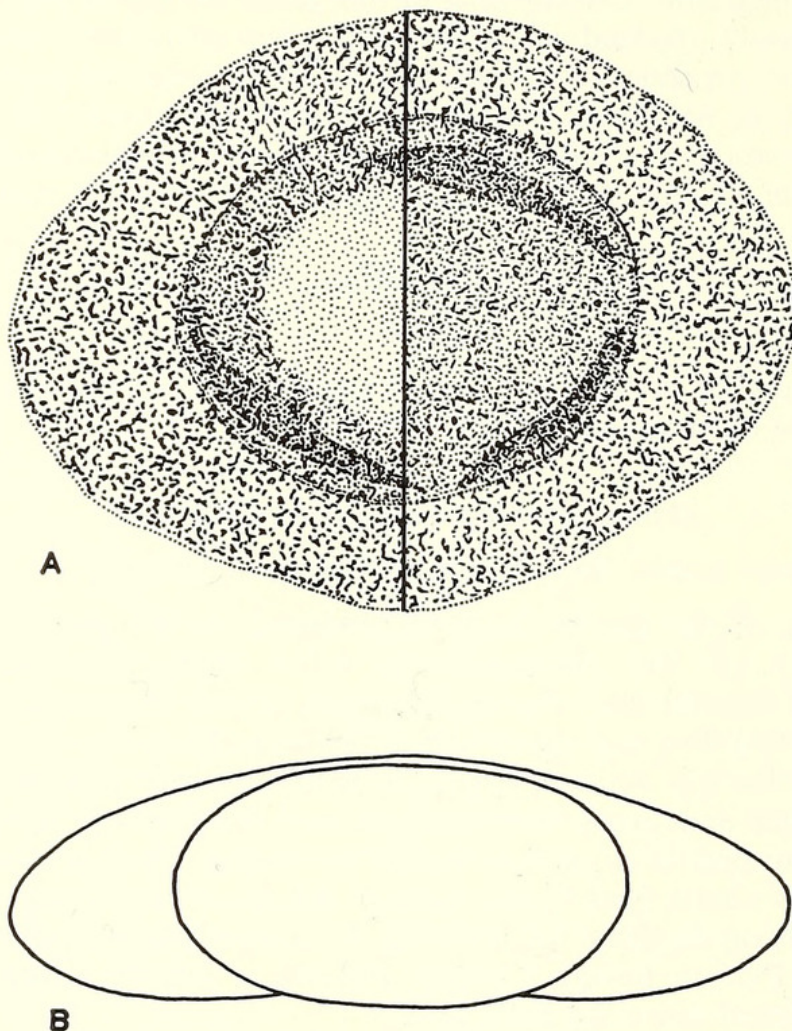
Plate 35, figs. 10–11

Comparison. This species differs from *S. grandior* in the radial alignment of the saccus reticulum, and like that species is known from the Swiss Keuper. In some samples it becomes difficult to differentiate the two species and the specific diagnoses appear to represent extremes of a more or less continuous series.

Genus ACCINCTISPORITES Leschik 1955

Type species. *A. lignatus* Leschik 1955, pl. 6, fig. 17; Keuper, Switzerland.

Discussion. The morphology of this genus is similar to that of *Succinctisporites* Leschik, differing only in the possession of a circular spore body surrounded by a saccus of uniform width.



TEXT-FIG. 5. *Succinctisporites grandior* Leschik. Diagrammatic reconstructions. A, Proximal face (right), distal face (left). B, Polar section. $\times 1,000$.

Accinctisporites lignatus Leschik 1955

Plate 37, figs. 1-2

Discussion. As in *Succinctisporites* the saccus attachment is often obscure but the relationship between the saccus and the spore body is presumed to be similar to that already indicated for *Succinctisporites*. The terse circumscription of Leschik's species makes comparison difficult, but it seems that *A. angustus* Leschik has a wider saccus and that *A. sinuosus* Leschik is separated from the type species by the presence of endoexinal swellings. Both *A. exundatus* Leschik and *A. nexus* Leschik are much larger

forms (90–105 μ). *A. lignatus* has previously been recorded only from the Middle Keuper of Switzerland.

Subturma DISACCITES Cookson 1947

Infraturma STRIATITI Pant 1954

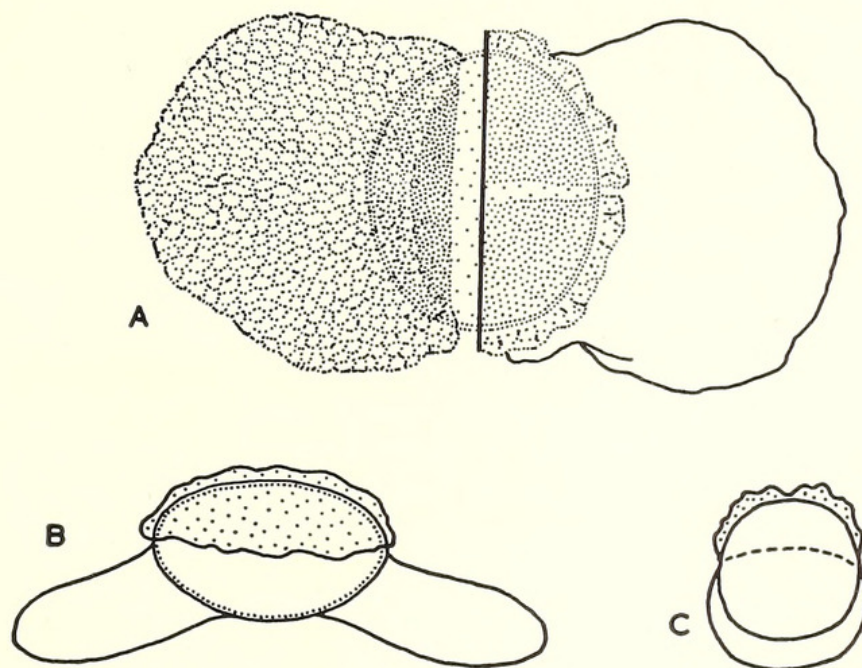
Genus LUECKISPORITES Potonié and Klaus 1954 emend. Klaus 1963

Lueckisporites triassicus sp. nov.

Plate 38, figs. 7–11; text-fig. 6

Holotype. Plate 38, fig. 7. Slide PF2408. Sample BH 6, Bromsgrove Hospital Quarry; Lower Keuper.

Diagnosis. Diploxytonoid, spore body circular, proximal cap split by longitudinal laesure into two halves. Proximal cap smooth or micropunctate, overlapping the spore



TEXT-FIG. 6. *Lueckisporites triassicus* sp. nov. Diagrammatic reconstructions. A, Polar aspect of proximal face showing the divided 'cap' (right), and the distal face (left). B, Equatorial view. C, Terminal polar section. $\times 1,000$.

body profile in polar view. Sacci larger than the spore body and more or less semi-circular in outline. Sacci distally attached near to the pole leaving only a narrow area of thinner exine between the attachments.

Description. This species is common in samples examined from the Lower Keuper, above which it is absent in the area studied. The spore body dimensions are $30 \times 28\mu$ (means of fifteen measured specimens) while the overall length varies from 48–77 μ . The proximal cap is divided by a laesure passing through the proximal pole but the two halves are never widely separated and are not greatly thickened. The sacci are large, without a lateral exoexinal connexion, and the thin saccus exine possesses a micro-reticulate sculpture. The attachments distally are generally straight, extend to the equator and are accompanied by crescent shaped folds (thickenings?); between these

folds is a leptoma but no distinct colpus is developed. The saccus offlap is greater than the overlap on to the spore body.

Comparison. *L. triassicus* sp. nov. differs from the type species in the circular spore body, the finely reticulate saccus sculpture and the presence of folds associated with the distal saccus attachments, and from *L. junior* Klaus and *L. tattooensis* Jansonius in the circular spore body and the greater saccus offlap.

Genus CHORDASPORITES Klaus 1960

Type species. *C. singulichorda* Klaus 1960, pl. 33, fig. 45; Keuper, Eastern Alps.

Discussion. This genus is characterized by the presence of an exinal strand (chorda) developed parallel to the long axis of the grain and passing through the pole (presumed proximal); the chorda is present on that face opposite the convergence of the sacci which is taken to be distal. The shape of the chorda and the irregularity of its development suggests that it is a fold produced by compression. The position of the fold is probably a result of the compression of the cap which is thickest in a line passing through the proximal pole; such a line of thickening may be accompanied on either side by narrow lines of thinner exine. *Chordasporites* differs from *Lueckisporites* s. str. in the presence of a chorda and a generally smoother proximal cap.

Chordasporites singulichorda Klaus 1960

Plate 38, figs. 1–3

Comment. The genus contains only two very similar species. The type species is known only from the present record and that of Klaus (1960). *C. australensis* is an Australian form which differs from *C. singulichorda* in having a thinner spore body, absence of a proximal cap and thinner exinal areas adjacent to the chorda (de Jersey 1962).

Genus OVALIPOLLIS Krutzsch 1955 emend. Klaus 1960

1955 *Unatextisporites* Leschik.

Type species. *O. ovalis* Krutzsch 1955, pl. 1, fig. 2; Lias, Germany.

Discussion. The interesting point about this genus is the interpretation of the position and function of a furrow which is present on one of the spore surfaces and disposed parallel to the long axis of the grain. Krutzsch in the original description makes no reference to proximal and distal faces but Klaus (1960) states that the furrow is on the side opposite the sacci convergence. If *Ovalipollis* has a saccus arrangement comparable

EXPLANATION OF PLATE 38

Magnification $\times 750$, unless otherwise stated.

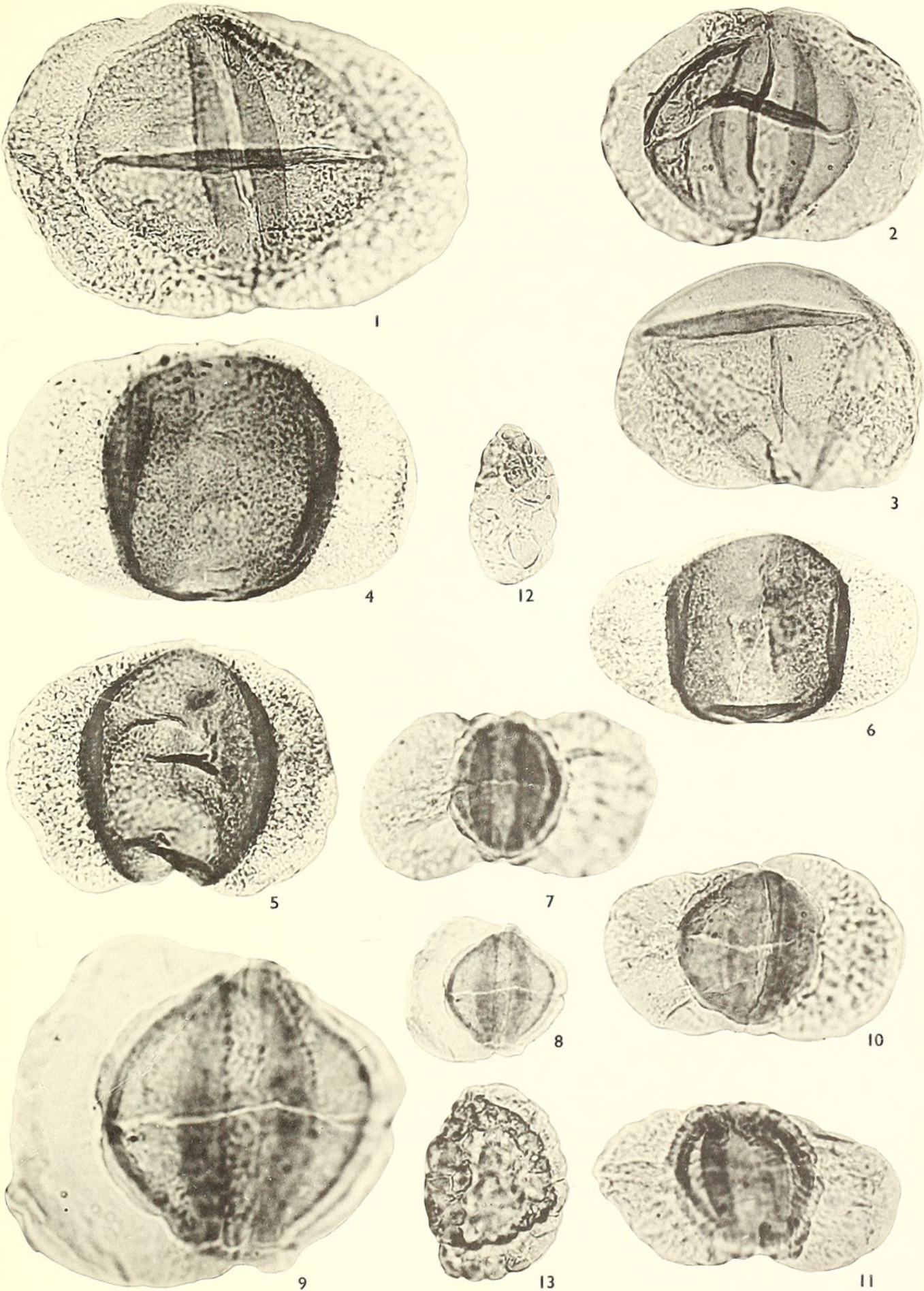
Figs. 1–3. *Chordasporites singulichorda* Klaus. 1, PF2402. 2, PF2401. 3, PF2399.

Figs. 4–6. *Alisporites toralis* comb. nov. 4, PF2418. 5, PF2416. 6, PF2420.

Figs. 7–11. *Lueckisporites triassicus* sp. nov. 7, Polar aspect of holotype, PF2408. 8–9, PF2410. 9, $\times 2,000$. 10, PF2409. 11, PF2411.

Figs. 12–13. *Camerosporites secatus* Leschik. 12, PF2446. 13, PF2448.

Localities of figs. 1–3, 7–11, Lower Keuper, Bromsgrove. Figs. 4–6, Lower Keuper, Hadley. Figs. 12–13, Upper Keuper, Longdon.



CLARKE, Upper Triassic miospores

to that in other bisaccate grains then the furrow will be on the proximal face (cf. Jansonius 1962). The function of this furrow remains problematical. In bisaccate grains of extant plant groups germination is distal from a point between the sacchi attachments. Many Palaeozoic bisaccate grains apart from having apparent distal germination also show a tetrad scar on the opposite face. Perhaps the 'furrow' of *Ovalipollis* is a monolete tetrad scar, corresponding with a tetragonal tetrad arrangement. On this basis then *Ovalipollis* may be considered comparable in its anatomy and orientation to other bisaccate grains in the Permo-Triassic. The 'furrow' is, however, often open at the ends, giving it an elongated 'hour-glass' shape. Either the genus is a monosulcate pollen with a distal germinal furrow, or it has a proximal monolete aperture. Until *Ovalipollis* is found in a tetrad the question of proximal and distal faces will remain unsolved, but for the present purpose it is regarded as a bisaccate pollen with a long monolete mark on the proximal face and distally inclined sacchi.

Ovalipollis breviformis Krutzsch 1955

Plate 39, figs. 11–12

1955 *Unatextisporites mohrensis* Leschik, pl. 8, figs. 7–8.

1960 *Ovalipollis grebeae* Klaus, pl. 35, figs. 52, 55.

Discussion. This species is known from the Rhaeto-Lias of Germany (Krutzsch 1955), the Middle Keuper of Switzerland (Leschik 1955), the Keuper of the Eastern Alps (Klaus 1960), and the Lower Triassic of Western Canada (Jansonius 1962). It differs from *O. ovalis* Krutzsch in the smaller size and more oval outline, and is less fusiform than *O. longiformis* Krutzsch.

Ovalipollis ovalis Krutzsch 1955

Plate 39, figs. 9–10

1955 *Unatextisporites mohri* Leschik, pl. 8, fig. 9.

1960 *Ovalipollis lunsensis* Klaus, pl. 34, figs. 46–49; pl. 37, fig. 67.

Discussion. This species, usually associated with *O. breviformis*, has been previously recorded from the Rhaeto-Lias of Germany (Krutzsch 1955), the Middle Keuper of Switzerland (Leschik 1955), the Keuper of Poland (Pautsch 1958), the Keuper of the Eastern Alps (Klaus 1960), and the Lower Triassic of Western Canada (Jansonius 1962).

Infraturma DISACCIMONOLETES Klaus 1963

Genus LABIISPORITES Leschik 1956 emend. Klaus 1963

Type species. *L. granulatus* Leschik 1956, pl. 22, fig. 11; Zechstein, Neuhoof.

The type species, based on Permian material, persists in small amounts from the British Zechstein through the Keuper (Pl. 39, fig. 5).

Infraturma PINOSACCITI Erdtman 1956 emend. Potonié 1958

Genus ALISPORITES Daugherty 1941

1955 *Scopulisporites* Leschik.

Discussion. The most pertinent comparison of this genus is with *Pityosporites* Seward 1914 emend. Manum 1960. Despite several emendations to both genera there still

exists no satisfactory basis for their separation. To arrive at a solution to this problem would seem almost impossible as the diagnosis of *Pityosporites* is based on a specimen in lateral (equatorial) view while the type of *Alisporites* is orientated in the equatorial plane (polar view). It is therefore not known what *Pityosporites* looks like in polar view. To base a distinction on the degree of saccus inclination distally is difficult unless the attachments both proximally and distally are distinct and the degree of saccus inclination seen in lateral view is often a function of the amount of collapse which has taken place between the saccus attachments. Generic separation based on the presence or absence of a colpus (sulcus) is subjective in that the presence may be a function of maturity and its retention a matter of preservation. This seeming lack of a good basis for their separation confuses the stratigraphic use of the two genera and it may be better to combine them. If this be the case *Pityosporites* has priority as a name. However, *Alisporites* is based upon a specimen in polar view which is well preserved while *Pityosporites* is in lateral view and badly preserved. Because of these latter two shortcomings and the scepticism of some authors as to its type material being pollen at all (Walton 1925, Edwards 1928) *Pityosporites* may be considered a 'confused genus' and abandoned.

Alisporites toralis (Leschik) comb. nov.

Plate 38, figs. 4-6; text-fig. 7

1955 *Scopulisporites toralis* Leschik.

Discussion. In the majority of specimens of this species the sacchi are connected laterally by a narrow exinal strip which is never more than a few microns wide in polar view. The sacchi attachments both proximally and distally are ill defined and a distinct colpus is seldom developed. This species is known from the Swiss Keuper and is a common form in the British Lower Keuper. The species differs from the type species in the shape of the spore body and the less well-defined saccus attachments, and from *A. microreticulatus* Reinhardt 1964 in the shape of the spore body and the less-well-defined 'Keimfurche'.

EXPLANATION OF PLATE 39

Magnification $\times 750$, unless otherwise stated.

Figs. 1-2. *Ellipsovelatisporites plicatus* Klaus. 1, $\times 2,500$, showing the proximal spore body sculpture. 1-2, PF2524.

Figs. 3-4. *Alisporites* cf. *parvus* de Jersey. 3, PF2466. 4, PF2516/780161.

Fig. 5. *Labiisporites granulatus* Leschik. 5, PF2516/885272.

Figs. 6-8. *Alisporites circulicarpus* sp. nov. 6, PF2461. 7, PF2465. 8, Slightly oblique polar view of holotype, PF2460.

Figs. 9-10. *Ovalipollis ovalis* Krutzsch. 9, PF2515/735172. 10, PF2442.

Figs. 11-12. *O. breviformis*. 11, PF2515/665300. 12, PF2515/584210.

Fig. 13. Trisaccate grain, PF2462.

Figs. 14-17. *Cycadopites* spp. 14-15, *C. acerrimus* comb. nov. Distal polar view. 14, PF2516/740332. 15, PF2453. 16-17, *C. subgranulosus* comb. nov. 16-17, PF2449. 17, $\times 2,000$, showing the granulose sculpture.

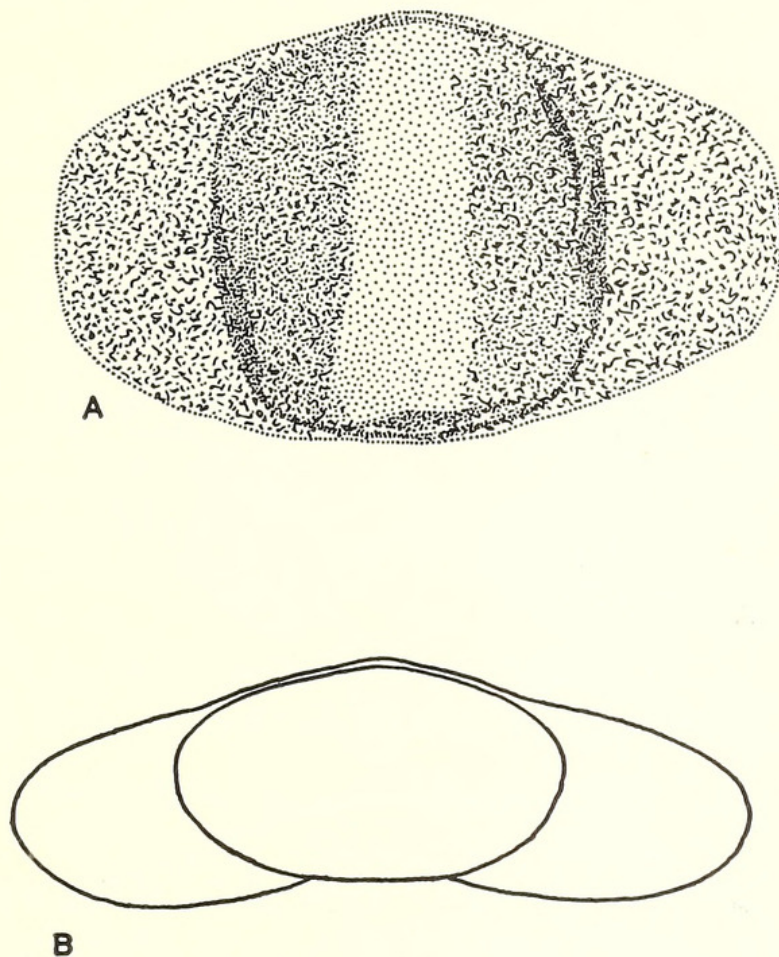
Location of figs. 1, 2, 4, 5, 9-12, 14, Upper Keuper, Longdon. Figs. 3, 6, 7, 13, 15, Lower Keuper, Bromsgrove. Figs. 8, 16, 17, Lower Keuper, Hadley.



CLARKE, Upper Triassic miospores

Alisporites circulicarpus sp. nov.

Plate 39, figs. 6–8; text-fig. 8

Holotype. Plate 39, fig. 8. Slide PF2460. Sample HA 1, Hadley; Lower Keuper.*Diagnosis*. Haploxytonoid. Spore body circular or oval. No tetrad scar visible. Sacci small. Offlap small and crescent shaped.

TEXT-FIG. 7. *Alisporites toralis* comb. nov. Diagrammatic reconstructions. A, Polar view. B, Polar section. $\times 1,000$.

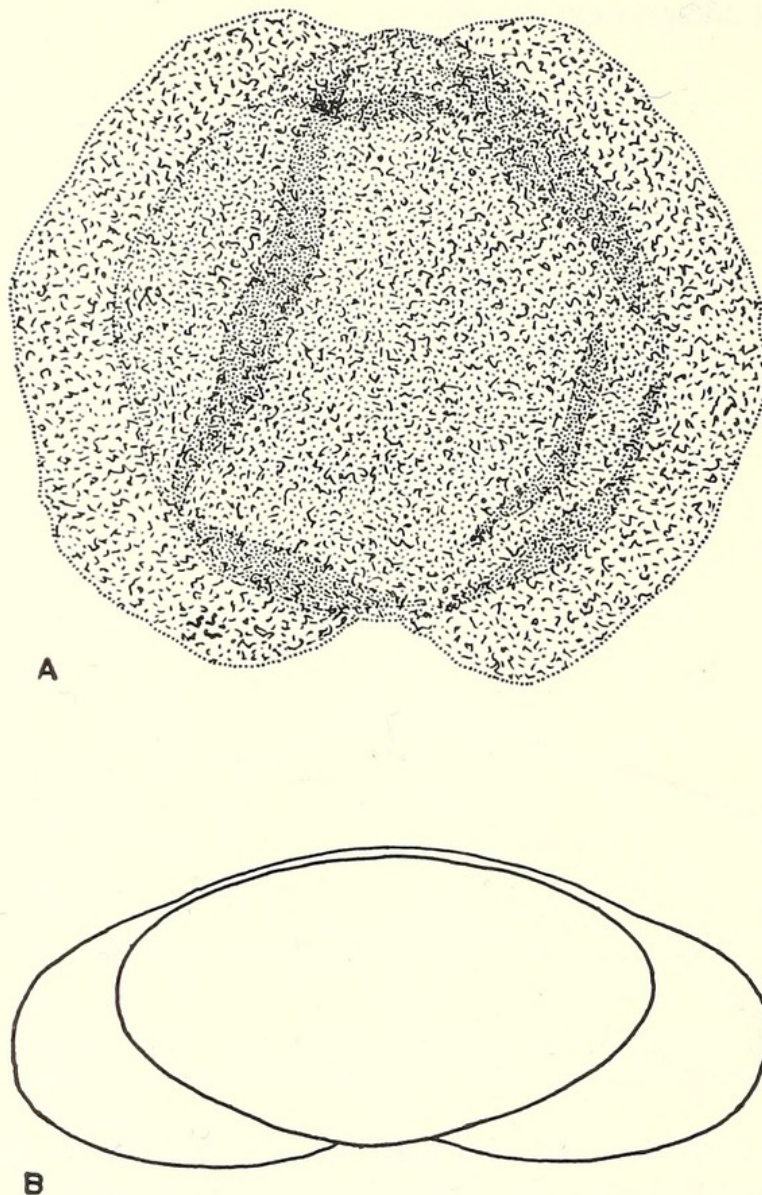
Description. Spore-body dark coloured and large ($51 \times 50 \mu$; means of fifteen measured specimens) compared with the sacci which in polar view show a small offlap terminally. Laterally the sacci may be connected by a thin exoexinal strand, but this is not common. The attachments of the sacci both proximally and distally remain obscure and thus it is not clear at what point the exine becomes cavate. The saccus sculpture is reticulate and a colpus has not been observed between the saccus attachments distally. The overall length is $46\text{--}70 \mu$ (mean 61μ ; measured on fifteen specimens).

Comparison. *A. circulicarpus* sp. nov. differs from *A. opii* Daugherty and *A. toralis* comb. nov. in its spore body/saccus ratio. The general sculpture of *A. circulicarpus* sp. nov. is similar to that of *A. toralis* comb. nov. and in some respects to *Succinctisporites grandior* Leschik.

Alisporites cf. *parvus* de Jersey 1962

Plate 39, figs. 3-4

Discussion. The distinctive features of this species are the small size (overall length 42-53 μ , measured on eight specimens) and the comparatively small sacci. Specimens



TEXT-FIG. 8. *Alisporites circulicarpus* sp. nov. Diagrammatic reconstructions. A, Proximal polar aspect. B, Polar section. $\times 1,000$.

present in the British Keuper are thus compared with those described as *A. parvus* by de Jersey (1962) from the Australian Triassic Ipswich Coalfield.

Alisporites minutisaccus sp. nov.

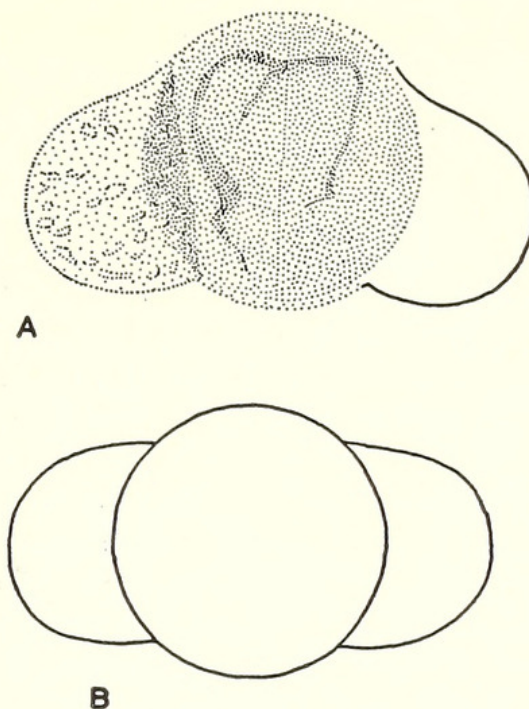
Plate 35, fig. 12; text-fig. 9

Holotype. Plate 35, fig. 12. Slide PF 2424. Sample HA 1, Hadley; Lower Keuper.

Diagnosis. Spore small, body circular; sacci smaller than spore body. Saccus width smaller than spore body width. Saccus attachments terminal; no distinct leptoma.

Description. Spore-body circular, only occasionally oval $31 \times 32 \mu$ (means of ten measured specimens). The spore body proximal face bears a microgranular sculpture and is slightly more densely coloured than the sacci. These latter are small, semicircular in polar outline and their width is considerably less than that of the spore body (i.e. diploxylonoid in the sense of Hart 1960, p. 5). The sacci are discrete and attached terminally although in many instances the attachments are not clearly defined. The saccus sculpture is punctate to microreticulate.

Comparison. *A. minutisaccus* sp. nov. differs from the type species in the much smaller size, and the saccus/spore body ratio. *A. toralis* comb. nov. is a much larger and more coarsely reticulate form and *A. cf. parvus* has tapering sacci which are attached distally near to the distal pole.



TEXT-FIG. 9. *Alisporites minutisaccus* sp. nov.
A, Oblique polar view (based on specimen).
B, Polar profile. $\times 1,000$.

Genus KLAUSIPOLLENITES Jansonius 1962

Type species. *K. (al. Pityosporites) schaubergeri* Potonié and Klaus 1954, pl. 10, fig. 7; Zechstein, Alpine area.

Klausipollenites devolvens (Leschik) comb. nov.

Plate 37, figs. 5–7

1955 *Pityosporites devolvens* Leschik.

Comparison. This species is recorded from the Middle Keuper of Switzerland. It is similar to *K. schaubergeri* (which is observed in small numbers in the present material, see text-fig. 11), but differs in the more prolate form of the spore body, and the less tapering sacci.

Infraturma PODOCARPOIDITI Potonié, Thomson, and Pflug 1950

Genus PLATYSACCUS (Naumova) ex Potonié and Klaus 1954

Genolectotype. *P. papilionis* Potonié and Klaus 1954, pl. 10, fig. 12; Zechstein, Alpine area.

Platysaccus sp.

Plate 37, fig. 4

Description. Non-striate diploxylonoid grains form a rare constituent of the British Upper Keuper assemblages. Such grains have been placed in *Platysaccus*. On three measured specimens the overall length is $57\text{--}68 \mu$ and the spore body $33 \times 27 \mu$. The



Clarke, R F A . 1965. "Keuper miospores from Worcestershire, England."
Palaeontology 8, 294–321.

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