KEUPER MIOSPORES FROM WORCESTERSHIRE, ENGLAND

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ABSTRACT. Twenty-six species assigned to eighteen genera are recorded from the Upper and Lower Keuper of Worcestershire. One new infotumma (Brassiiella), one new genus (Bredigera), 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 microflora 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 microflora 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-beded, 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 Yuectites vogesiacus and subsequently Wills (1910) recorded the same species together with Schizoneura paradoxo, Equisitites arenaceus, and 'Volzia heterophylla'. This latter, a supposed male conifer cone, is now reassigned as Mascolostrobus willisi Trowrow (Trowrow 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-beded 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. 856542) 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 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 'alveolit' 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.

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SYSTEMATIC SECTION

Anteturma spirites H. Potonié 1893
Turma trilites (Reinsch 1881) emend. Potonié and Kremp 1954
Subturuca azonotriletes Luber 1935
Infraturma apiculatis (Bennie and Kidston 1886) emend. Potonié 1956
Subinfraturma verrucati Dybova and Jachowicz 1957
Genus verrucosispores (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.

Verrucosispores 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. ×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, 60–102μ in diameter (mean 75μ; forty measured specimens). Amb circular; verrucae low with irregular bases; differentiated contact facets.

*Description.* The spore exine is 3–5μ 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 curvatures (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 µ high and 2-6 µ 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. morulæ 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.

Subinfratrumpa GRANULATI Dybova and Jachowiæ 1957
Genus CYCLOGRANISPORITES Poliæ 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 Conosmunda sporites 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 µ (mean 26 µ, measured on nine specimens), and is further differentiated from C. congestus by the absence of lips.

EXPLANATION OF PLATE 35

All magnifications × 750.
Figs. 1-3. Verrucosispores spp. 1-3; V. contactus sp. nov. Oblique polar views showing the differentiated contact areas and the bifid terminations of the tetrads spores. 1, PF2393. 2, PF2395, 3, PF2392. Holotype. 4-5. V. morulæ Klaus. 4, PF2387. 5, PF2388.
Figs. 6-9. Cyclogranisporites spp. 6. C. oppressus Leschik; PF2386.
Figs. 7-9. C. congestus Leschik, 7. PF2382. 8, PF2396. 9. PF2383.
Figs. 10-11. Saccatoispores radialis Leschik. 10, PF2359, 11, PF2438.
Fig. 12. Aliispores minutissimse sp. nov. Oblique polar view of holotype; PF2424.
Localities of figs. 1-8, 10-11, Lower Keuper, Bromsgrove. Figs. 9, 12, Lower Keuper, Hadley.
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 Bulme (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 49–66μ (mean 59μ, based on nine specimens).

Description. The exine is about 2μ 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 9 μ. Although the shape of these processes may vary (see text-
fig. 3) the cross-section is circular, being 2-3 μ 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 μ apart). *C. longodontis* sp. nov. differs from *C. mesozoicus* Klaus in the
smaller triradiate mark and the larger, more variable sculptural elements.

_Turma_ _aletes_ Ibrahim 1933
_Subturma_ _azonomicites_ (Luber 1935) _emend._ Potonié and Kremp 1954
_Infraturma_ _striataphy_ _infraturma_ _nov._

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

**Genus** _Brodispora_ _gen._ _nov._

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

**Discussion.** These aleule 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 oxida-
tion, and behaves like that of the miospores with which they are associated; the possi-
bility 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 plausable orientation, which is used here in describing
the spore, is set out in text-fig. 4.

**Comparison.** The genera _Chomotritiletes_ (Naum.) ex Naumova 1953 from the Upper
Devonian and _Circuliprtyes_ de Jersey 1962 from the Trias are striate aleule spores,
differing only in the incomplete striae of _Chomotritiletes_ as opposed to the continuous
striations of _Circuliprtyes_. They both differ from _Brodispora_ in being of circular out-
line 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 × 750, unless otherwise stated.

Figs. 1-5. _Conchonotritiletes longodontis_ _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, ×
2,000. 2. PF2516/760271. 3. PF2474. 4-5. PF2476.

Figs. 6-9. _Brodispora striata_ _gen._ _et_ _sp._ _nov._ 7, ×1,500. 6-7, PF2516/850209. 8, PF2516/878267.
9. _Holotype._ PF2478.

Figs. 10-11. _Cameropitris securis_ Leisch. 10, ×1,500. PF2516/780283. 11, PF2447.
All specimens from the Upper Keuper of Longdon.
Diagnosis. Exine thin, outline oval, striae thin and polar areas unsculptured. Size 30–40 μ × 20–34 μ (mean of seventeen specimens, 35 × 28 μ).

Description. The outline in polar view is oval with broadly rounded ends and is smooth except in polar section where the striae are seen in optical section. The striae concentrated in the equatorial area are narrow, only 1–2 μ wide and separated by areas of smooth exine 2–6 μ 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 sacctites Erdtmann 1947
Subturma monosaccites (Chitaley 1951) emend. Potonié and Klaus 1954
Infraturma Aletesacciti Leschik 1955
Genus ENZONALASPORITES Leschik 1955

1955 Vailaspores Leschik, pl. 6, figs. 6-8, 10.

*Type species.* *E. wigens* 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 wigens* Leschik 1955
Plate 37, figs. 8-10

1955 *Enzonalasporites obligans* 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
British specimens are compared with the type species. This differs from *P. latus* 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 tetract 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 succinctisporites 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.


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. augustus 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.

Subtura* disaccites Cookson 1947
Infraturma striatitii 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. Diploxylenoid, spore body circular, proximal cap split by longitudinal laeure into two halves. Proximal cap smooth or micropunctate, overlapping the spore body profile in polar view. Sacchi larger than the spore body and more or less semicircular in outline. Sacchi 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 30×28 μ (means of fifteen measured specimens) while the overall length varies from 48–77 μ. The proximal cap is divided by a laeure passing through the proximal pole but the two halves are never widely separated and are not greatly thickened. The sacchi are large, without a lateral exoexinal connexion, and the thin saccus exine possess a microreticulate 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 *Unanestispores* 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 sacces arrangement comparable

**EXPLANATION OF PLATE 38**

Magnification ×750, unless otherwise stated.

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

Figs. 4–6. *Allispores 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, ×2,000, 10, PF2409, 11, PF2411.


Localities of figs. 1–3, 7–11, Lower Keuper, Bromsgrove. Figs. 4–6, Lower Keuper, Hadley, Figs. 12–13, Upper Keuper, Longdon.
to that in other bisaccate grains then the furrow will be on the proximal face (cf. Johnsonus 1962). The function of this furrow remains problematical. In bisaccate grains of extant plant groups germination is distal from a point between the sacci attachments. Many Palaeozoic bisaccate grains apart from having apparent distal germination also show a tetrads scar on the opposite face. Perhaps the ‘furrow’ of *Ovalipollis* is a monolete tetrads scar, corresponding with a tetragonal tetrads 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 germination furrow, or it has a proximal monolete aperture. Until *Ovalipollis* is found in a tetrads 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 saci.

*Ovalipollis breviformis* Krutzsch 1955

Plate 39, figs. 11-12

1955 *Unaxestisporites moebii* 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 (Kratzsch 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 *Unaxestisporites moebii* Leschik, pl. 8, fig. 9.

1960 *Ovalipollis lunensis* 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 (Kratzsch 1955), the Middle Keuper of Switzerland (Leschik 1955), the Keuper of Poland (Paatsch 1958), the Keuper of the Eastern Alps (Klaus 1960), and the Lower Triassic of Western Canada (Jansonius 1962).

Infraturna DISACCOMONOLETES Klaus 1963

Genus LABISPORITAE Leschik 1956 emend. Klaus 1963

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

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

Infraturna PINOSACCHITI Erdman 1956 emend. Potonié 1958

Genus ALISPORITAE Daugherty 1941

1955 *Scopalisporites* 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 *Scopalsporites toralis* Leschik.

Discussion. In the majority of specimens of this species the sacci are connected laterally by a narrow extinal strip which is never more than a few microns wide in polar view. The sacci 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. *Ellipsennodolithosporites plicatus* Klaus. 1, \( \times 2,500 \), showing the proximal spore body sculpture.

1–2, PF2524.

Figs. 3–4. *Alisporites cf. parasus* de Jersey. 3, PF2466. 4, PF2516/780161.

Fig. 5. *Labisporites grandatus* Leschik. 5, PF2516/885272.

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

Figs. 9–10. *Ovalispores ovalis* Krutetsch. 9, PF2515/735172. 10, PF2442.

Figs. 11–12. *O. breviformis*. 11, PF2515/665700. 12, PF2515/584210.

Fig. 13. Trisaccate grain, PF2462.


Location of figs. 1, 2, 4, 5, 9–12, 14, Upper Keuper, London. Figs. 3, 6, 7, 13, 15, Lower Keuper, Bromsgrove. Figs. 8, 16, 17, Lower Keuper, Hadley.
Alisporites circulicorpus sp. nov.

Plate 39, figs. 6-8; text-fig. 8

Holotype. Plate 39, fig. 8; Slide PF2460. Sample HA 1, Hadley; Lower Keuper.


Description. Spore-body dark coloured and large (51 × 50 μ; 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 46–70 μ (mean 61 μ; measured on fifteen specimens).

Comparison. A. circulicorpus sp. nov. differs from A. opii Daugherty and A. toralis comb. nov. in its spore body/saccus ratio. The general sculpture of A. circulicorpus sp. nov. is similar to that of A. toralis comb. nov. and in some respects to Succhnitosporites grandior Leschik.
Aliisporites cf. parvus de Jersey 1962

Discussion. The distinctive features of this species are the small size (overall length 42-53μ, measured on eight specimens) and the comparatively small sacci. Specimens present in the British Keuper are thus compared with those described as A. parvus by de Jersey (1962) from the Australian Triasie Ipswich Coalfield.

Aliisporites 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. minitusaccus 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. parvis has tapering sacci which are attached distally near to the distal pole.

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.

Infraordina Podocarpoiditi Potonié, Thomson, and Pflug 1950

Genus Platysaccus (Naumova) ex Potonié and Klaus 1954

Genoelectotype. 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 $57-68 \mu$ and the spore body $33 \times 27 \mu$. The
sacculi are large compared with the spore body but are not so markedly diploxytonoid as those observed in the Zechstein.

**Turgut Plicates** (Naumova 1937, 1939) emend. Potonié 1960
Subturgut Monocolpates Iversen and Troels-Smith 1950
Infraturgut Intortes (Naumova 1937) emend. Potonié 1958
Genus Cycadopites (Wodehouse 1933) ex Wilson and Webster 1946

1938 Azoanletes Lubet, p. 154, figs. 10-11.
1939 Subsacculifer Lubet, pl. A, fig. 1.
1953 Gingkoecyadeophytes Smolilovich.
1954 Entylios Naumova ex Potonié and Kremp.
1955 Cycadofur Lubet, figs. 10-11.
1960 Lagenella (Malawinka 1949) Klaus (pars).

_Type species._ *C. follicularti* Wilson and Webster 1946, pl. 1, fig. 7; Tertiary, Montana.

**Discussion.** Malawinka (1949) erected the genus *Lagenella* without designating a type. Klaus (1960) validated the genus and selected *L. cincta* Malawinka as the ‘genotype’. This species is a non-striate form and cannot be separated from *Cycadopites* as used here. However, Klaus includes within *Lagenella* monosulcate striate microspores previously assigned to *Decussatisporites* Leschik 1955. This latter genus is validly established and I prefer to rate the presence or absence of striations as a generic character. *Decussatisporites* is thus used in the original sense of Leschik (1955) and the non-striate forms of *Lagenella*, sensu Klaus, are placed in synonymy with *Cycadopites*.

*Cycadopites subgranulosus* (Couper) comb. nov.
Plate 39, figs. 16-17

1958 *Monosulcites subgranulosus* Couper.

This species, based on British Liassic material (Couper 1958), is found in small numbers in Upper and Lower Keuper samples. It differs from those species described by Jansonius (1962) in the nature of the exinal sculpture.

*Cycadopites acerrimus* (Leschik) comb. nov.
Plate 39, figs. 14-15

1955 *Monocolpoidenites acerrimus* Leschik.

**Discussion.** This common British Keuper species is also known from the Swiss Keuper and similar forms are present in the Canadian Trias (*Cycadopites* sp. R. Jansonius 1962). *C. acerrimus* differs from *C. subgranulosus* comb. nov. in having a smooth exine, from *C. dijkstrae* Jansonius 1962 in the absence of lips and from *C. harti* Jansonius in the lack of ‘drawn out cones’ at the ends of the long axis.

**Genus Camerosporites** Leschik emend.

_Type species._ *C. secatus* Leschik 1955, pl. 5, fig. 11; Keuper, Switzerland.

_Emended diagnosis._ Amb elongate-oval, bilaterally symmetrical. On one face is a thin
elongated exinal area (?) sulcus) surrounded equatorially by large verrucose sculptural elements which may extend on to the opposite face.

Discussion. The genus is rather summarily described by Leschik: '... Nur eine Symmetricalene vorhanden. Kammern verschieden gross.' The sulcus in Camerosporites is often irregular and not clearly defined (unlike the sulcus in Cycadopterites). Nevertheless, there is an elongated thin area which can reasonably be interpreted as a sulcus and for this reason the genus is emended and placed in the Turma (Abteilung) Monocolpates.

Comparison. Camerosporites here emended differs from Thymospora Wilson and Venkatachala 1963 (syn. Verucosporites (Knox) ex Potonié and Kremp 1954) in the more fusiform outline and being monosulcate as opposed to monolete. Hoegiosporis Cookson 1961 from the Australian Cretaceous is similar to Camerosporites in the possession of large verrucate processes but differs in the circular outline and the smaller number of verrucate which, in Cookson's spore, are restricted to the equator. The distinctive sculpture of Camerosporites differentiates it from all other monosulcate grains.

Camerosporites secatus Leschik 1955
Plate 36, figs. 10-11; Plate 38, figs. 12, 13; text-fig. 10

Description. The outline is fusiform 44 x 31 μ (means of nineteen measured specimens) with broadly rounded ends. On one surface (presumed distal) the exine is thin forming an elongated sulcus of which the boundaries are not precisely defined. This sulcus is fairly wide but towards the equator small verrucae appear which rapidly become large at the equator where they appear as flat or rounded-topped protuberances 4-7 μ high and up to 13 μ wide at the base. The large sculptural elements may be confined to this equatorial zone or be present on the other (proximal) face (text-fig. 10b).

Comparison of Assemblages with Those of the British Zeichstein (Upper Permian)

From the range chart (text-fig. 13) it will be seen that very few miospores persist from the older assemblages into the Triassic. Changes in the groups above generic rank can be followed. Text-fig. 11 gives the constituent percentages of supra-generic groups for the Upper Keuper, Lower Keuper, and the Upper Permian. The Permian information has been compiled by averaging all the frequencies observed by the author in samples from Hilton, Westmorland, and Kimberley, Nottinghamshire. (A fuller account of British Upper Permian miospores is given in the next paper in this volume.) It can be
seen that for the bisaccate Striatitii a marked decrease occurs from the Zechstein to the Lower Keuper and that this trend is maintained in the Upper Keuper. Of some six bisaccate striate genera present in the Upper Permian, two are present in the Lower

TEXT-FIG. 11. The percentages (based upon counts of 200 grains) of the various species (A) and selected supra-generic groups (B) in some British Permo-Trias deposits.

Keuper (one of which is restricted to this horizon), while only one genus (Ovalipollis) is present in the Upper Keuper. The reverse of this is seen in the sharp increase in triradiate misospores (i.e. non-cingulate and non-zonate types) in the Lower Keuper and which is also maintained in the Upper Keuper. The sudden increase in the number and species of bisaccate non-striate forms in the Upper Permian (such types being almost absent in the Carboniferous) is sustained in the Trias although many species are
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Text-fig. 13. Chart of the ranges of some British Permian-Triassic spores. For Striatites read Prototodiscosiphon.
different, while monosaccate forms are also more generally abundant than in the Upper Permian. Monosaccate grains, which first appear in Britain in the Permian, also show greater representation both specifically and numerically in the Keuper. Monolete forms (e.g. Lueckisporites), often present in considerable numbers in the Carboniferous, have not been observed in the Permo-Trias of the area studied.

Owing to a lack of knowledge of the natural botanical affinity of many of these types, the changes outlined above, expressed in terms of changes in the macroflora, must be conjectural. It is not clear, for instance, which group or groups of plants is represented by the decline and virtual extinction in Trias times of the bisaccate Striatitii. Bisaccate striate pollen (Lueckisporites s.str.) have been found in the fructification of the conifer Ullmannia frumentaria Goepert, while others (Prototaenioxyalinus s.str.) are closely associated with Glossopteris, a presumed Pteridosperm (Potonie and Schweitzer 1960, Pant and Nautiyal 1960). Further Coniferous groups (as well as possible Cordaites) are represented by monosaccate grains, while diploxylonoid pollen of the Platylococcus habit may have Podocarp affinities. Alisporites-like pollen suggests the presence of Pteridosperms (or possible Conifers) in the assemblages. The absence of cingulate and zonate triradiate types (Densiosporites, Cristatisporites) in the Permo-Trias attests to the decline of some Pteridophyte group (probably the Lycopsidea), but the reappearance of triradiate non-zonate spores in the Trias may represent the re-emergence of other Pteridophyte groups (most probably the Filicales). The steady increase in the type and number of monosaccate pollen is taken to be indicative of the rise of the Cycadophytes, although this type of pollen may be also Pteridospermous (Townrow 1960).

The decrease in the triradiate non-zonate mioospores in the Permian and the great increase in sacate forms is seen as a response to a climatic change towards aridity, to which the seed habit of the Gymnosperms is better adapted than the ‘water dependent’ life cycles of most Pteridophyte groups. The presence or return of such forms in the late Trias is probably correlated with a return to more humid climatic conditions.

COMPARISON WITH PREVIOUSLY DESCRIBED TRIASSIC ASSEMBLAGES

European Trias

The most comprehensive works on Keuper microfloras are those of Leschik (1955) and Klaus (1960). The majority of the species found in the present study can be identified with reference to these two works and many forms are common to all three areas. The most important of these are the presence of Verrucosisporites, Camerosporites, Enzonatisporites, Alisporites, and Ovalipollis. This latter genus appears for the first time generally in the Keuper (but see Taugourdeau-Lantz 1962), and is present in all European Keuper assemblages examined (see also Pautsch 1958, Taugourdeau-Lantz and Jekowsky 1959, Reinhardt 1964). However, several forms recorded by Leschik (1955) and Klaus (1960) are not apparently represented in the present samples, viz. Zebrazisporites, Kraeuselisporites, Decussatissporites, and Aratriisporites.

Australian Trias

Knowledge of Triassic microfloras in Australia is due mainly to de Jersey (1962) on the Ipswich Coalfield (pre-Middle Trias) and Balme (1963) on the Lower Triassic.
Kockatae Shale of Western Australia. Papers by de Jersey (1949) and Taylor (1953) are less useful because of the uneven distribution of nomenclature employed and the absence of photographs. The Kockatae assemblage has little in common with the British assemblages. In some respects (the presence of *Striatis*, *Taeniasporites*, *Crustae- spores*) a Permian nature is present although *Kraeusellisporites*, *Vitreisporites*, *Osmundac- idites*, and *Lycopsidaceidites* emphasize its Mesozoic character. *Ovalipollis*, which appears to be a Northern Hemisphere genus, is absent, as are *Cycadophytes* and *Alisporites*-like bisaccate grains. This latter genus, however, is present in some quantity in the Ipswich Coalfield, associated with *Cycadophytes* (= *Ginkgoceadoxophytes* de Jersey), *Calamospora*, and *Osmundacites*. The most interesting record, however, is that of undisputed *Chordasporites* previously known only from the Alpine Keuper (Klaus 1960) and now recovered from the British Lower Keuper. The presence of this genus and the absence of *Ovalipollis* would suggest a Lower Keuper age for the Ipswich deposits.

**North America**

Jansonius (1962) describes a rich microflora from the Lower Triassic Tood/Grayling Formation of Canada. This differs from the British Keuper assemblages essentially in the presence of a variety of bisaccate stritate grains which perhaps, but not necessarily (Leschik 1955), suggests its Early Triassic age. The appearance of *Ovalipollis*, however, tends to discredit such an assumption and this Canadian assemblage is perhaps most similar to that described by Balme (1963).

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