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OLIGOCARPIA LINDSAEOIDES (ETTINGSHAUSEN) STUR AND ITS SPORES FROM THE WESTPHALIAN OF CENTRAL BOHEMIA (CZECH REPUBLIC)

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Abstract. Emendation of *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR is suggested based on the study of the holotype and the study of other two specimens from the Kladno-Rakovník and Radnice Basins, (all of Bolsovian age). Measurements of sori and sporangia are given for the first time. Sori are arranged on lateral veins endings on the abaxial side of each pinnule and they are 0.47 mm in diameter. Sporangia of *O. lindsaeoides* are the smallest within the genus. 5 sporangia per sorus are most often. Sporangia are 0.22-0.3mm in diameter, pyriform or rounded, free, short stalked, and annulate. Oblique annulus, consisting of one to two rows of 18 -22 oblong thick-walled cells, is interrupted by a stomium consisting of several thin-walled isodiametric, elongated cells. Trilete, laevigate to scabrate *in situ* spores from 20 to 39 μm in diameter can be correlated with the several dispersed species of *Leiotriletes*. Review of Carboniferous fructifications yielding spores of the *Leiotriletes*-type is given.

■ *Oligocarpia, in situ* spores, Gleicheniaceae, Sermayaceae, Carboniferous, ferns

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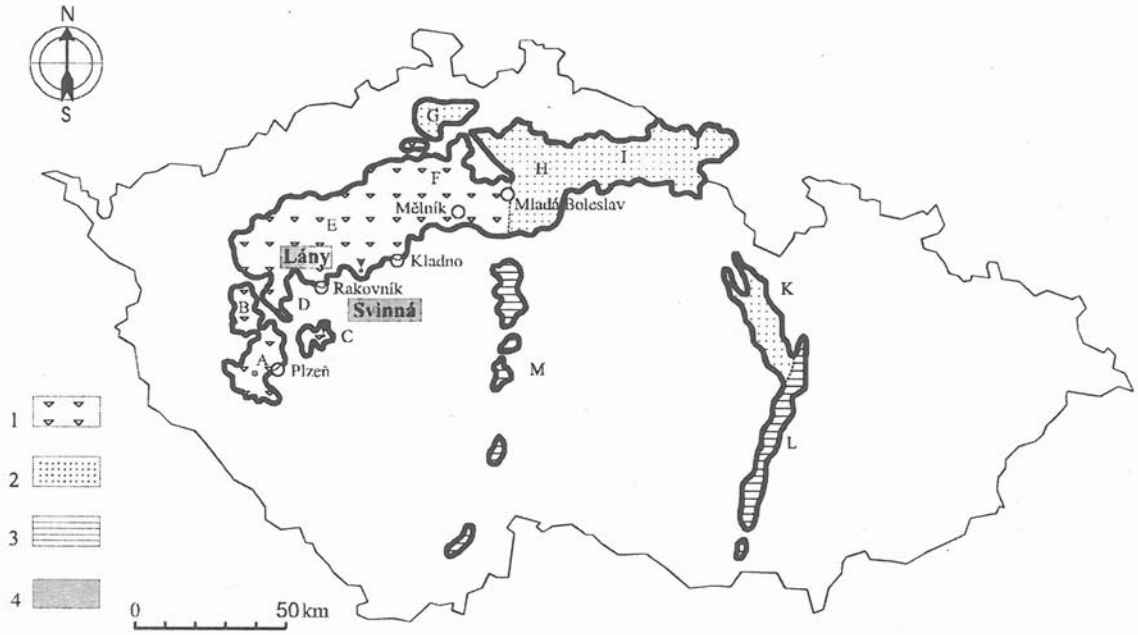
Introduction

Göppert (1841) established the genus *Oligocarpia* GÖPPERT based on a compression specimen consisting of a skeletonized fragment of fertile frond bearing naked sori with annulate sporangia. Type of the genus was chosen as *O. gutbierii* GÖPPERT. Ettingshausen (1854) established *Asplenites lindsaeoides* ETTINGSHAUSEN and *Sacheria asplenioides* ETTINGSHAUSEN. *Asplenites lindsaeoides* was designated on sterile specimens and *Sacheria asplenioides* was designated on fertile specimens. Stur (1877) showed that Ettingsausen's *Asplenites lindsaeoides* and *Sacheria asplenioides* belonged to *Oligocarpia* and placed both species in that genus. Measurements of sori or sporangia were not given either by Ettingshausen (1854) or Stur (1877). Stur (1877), discussing *O. lindsaeoides,* modified the diagnosis by describing the sporangia as free, the annulus as apical and rudimentary, and the sori as composed of 3-5 solitary sporangia arranged in a circle on a punctiform receptacle. Stur (1877) also redefined the generic description of *Oligocarpia.* Stur (1883), studying *O. brongniartii*, modified his generic description from 1877, by describing the sporangia as having dehisced by an apical pore. Later, Stur (1885) revised upward the number of sporangia which may occur in a sorus (text-fig. 2) to a maximum of 17. He also modified his 1883 diagnoses of *O. brogniartii* and *O. pulcherrima* Stur and reviewed the diagnoses of *O. gutbierii* and *O. lindsaeoides.* Lesquereux (1875, 1878) established *O. alabamensis* LESQUEREUX and *O. flagellaris* LESQUEREUX. White (1900) proposed *O. missouriensis* WHITE, Sellard (1908) proposed *O. kansanensis* SELLARD, and Darrah (1938) erected *O. vera* DARRAH. Other treatments of the genus include works by Zeiller (1888), Solms-Laubach (1891), Kidston (1911), Bower (1912), De Pape and Carpentier (1915), Walton (1923) and Darrah (1938). Abbott (1954) revised the genus *Oligocarpia* (O. *gutbierii*, *O. lindsaeoides*, *O. beyrichii* STUR, *O. pulcherrima*, *O. brongniartii*, *O. missouriensis*, *O. vera*) and proposed two new species *O. mixta* ABBOTT and *O. capitata* ABBOTT. Brousmiche (1983) made revision of the original Göppert's diagnosis of the genus *Oligocarpia.* Zodrow and McCandlish (1982) erected *O. bellii* ZODROW from the Carboniferous of Cape Breton Island (Canada).

Material and Method

Specimen No. E1299 is stored in the National Museum in Prague. The Ettingshausen's types (Nos 1854/9/31 and 1854/9/39) are stored in the Geological Survey of Austria in Vienna. Specimen No. E1299 comes from Lány locality (Kladno-Rakovník Basin) (text-fig.1) and it is preserved as a compression in yellow-grey siltstone. Specimens Nos 1854/9/39 (holotype) and 1854/9/31 come from Svinná locality (Radnice Basin) and they are preserved as leaf compressions in yellow tuffaceous sandstone. All three specimens are from the Radnice Member of the Kladno Formation (Carboniferous).

Sporangia were isolated by maceration of the rock with the aid of 35% hydrofluoric acid for 24 hours. Some sporangia with complete annuli were examined under JEOL scanning electron microscope. Samples were macerated in Schulze's



Text-fig. 1. Permo-Carboniferous regions and basins of the Czech Republic (Pešek 1994 supplemented by the authors). 1 - Central and Western Bohemian Upper Palaeozoic Basins: Western Bohemian District: A – Plzeň Basin, B – Manětín Basin, C – Radnice Basin, D – Žihle Basin; Central Bohemian District: E - Kladno-Rakovník Basin, F - Mšeno-Roudnice Basin; 2 - Lugicum Upper Palaeozoic Basins: G - Česká Kamenice Basin, H - Mnichovo Hradiště Basin, I - Krkonoše Piedmont Basin, J - Lower Silesian Basin, K – Orlice, 3 - Furrows: L – Boskovice Graben, M – Blanice Graben; 4 - locality of studied specimen.

solution (nitric acid and potassium chlorate) for 20-30 minutes and washed in distilled water, then treated with 10% potassium hydroxide to remove oxidation products and washed in distilled water again. Sporangia were mounted in glycerine jelly slides. Spores were macerated by nitric acid for 12-24 hours and by KOH by 1-2 hours and washed several times in distilled water.

Systematic part

Order Filicales

Family **Sermayaceae** EGGERT et DELEVORYAS 1967

Oligocarpia GÖPPERT 1841

Type species. *Oligocarpia gutbierii* GÖPPERT 1841.

Emended diagnosis. Fructification of leptosporangiate-type; sori circular, attached on abaxial side of pinnules, placed on endings of lateral veins; sori placed in receptacle, consisting of 3–30 sporangia arranged in concentric circle, sometimes with one sporangium in centre; sporangia pyriform or rounded, stalked, and annulate. Annulus oblique or equatorial consisting of one or two rows of thick-walled cells; elongated dehiscence slit area is directed from apical part of sporangium towards the stalk and consisting of several elongated cells; trilete spores with laevigate, scabrate to microgranulate exine are of the *Leiotriletes-Granulatisporites, Leiotriletes* or *Granulatisporites*-types.

Remarks. Göppert (1841) and Brousmiche (1983) described the annulus of *Oligocarpia* with only one row of thick-walled cells. Our observation shows that annulus in some cases consists of two rows of thick-walled cells.

Oligocarpia lindsaeoides (ETTINGSHAUSEN) STUR

Text-fig. 3; Pl. 1, figs 1-8; Pl. 2, figs 1-6; Pl. 3, figs 1-4, Pl. 4, figs 1-3.

1854 *Asplenites lindsaeoides* ETTINGSHAUSEN, p.42, pl. 20, fig. 4.
1854 *Sacheria asplenioides* ETTINGSHAUSEN, p.40, pl. 20, fig. 1.
1877 *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR, p. 203, text - fig. 32.
1883 *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR, p. 55, fig. 15.
1885 *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR; Stur p. 125, fig. 10.
1963 *Oligocarpia* sp. Němejc, pl. XLIX, figs 1-4.
1998 *Oligocarpia* sp. A *sensu* Bek, p. 163, Tab. 129, figs 4-6.

Holotype. No. 1854/9/39, Pl. 4, figs 2, 3, text-fig. 3 (Ettingshausen 1854, pl. 20, fig. 4), stored in the Geological Survey of Austria (Vienna).

Locus typicus. Svinná near Radnice; Radnice Basin.

Stratum typicum. Upper Carboniferous; Kladno Formation, Radnice Member (Bolsovian age).

Emended diagnosis. Frond tri- or polypinnate, pinnae inserted on a delicate rachis and alternate, open, oval-lanceolate. Main rachis of the frond is slightly S-flexuous, 2 mm wide. Secondary pinnae linear-lanceolate, decurrent. Pinnules of sphenopterid type, 2-5 mm long and 1-3 mm wide. Margin undulate or lobed, lobes undulate to sharply dentate. Secondary and tertiary rachises lax and sub-flexuous. Veins of the pinnules decurrent, slender, and dichotomously branched. Sori are arranged on lateral veins endings. Midvein of pinnules is flexuous. Each sorus consisting of 4-6 sporangia (most frequently 5), occurring on abaxial side of pinnule arranged on

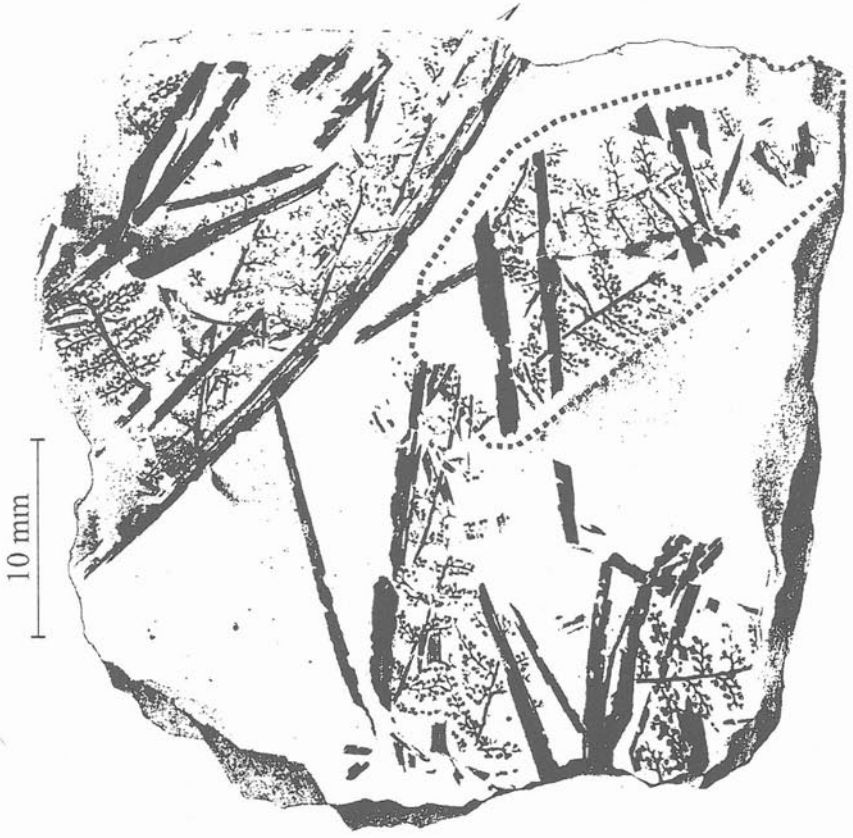
lateral vein endings, 7-9 sorus per pinnule. Sporangia 0.40 mm long, 0.32 mm wide, pyriform or rounded, short stalked, and annulate. Annulus is oblique, consisting of one or sometimes two rows of 18 -22 elongate cells. Trilete spores 20-39 μm in diameter. Rays of trilete mark 3/4 of the radius. Exine 1-2 μm thick, laevigate, irregularly scabrate to microgranulate.

Remarks. In 1854 Ettingshausen defined two species – *Asplenites lindsaeoides* Ettingshausen (1854, pl. 20, fig. 4 – based on the holotype No. 1854/9/39, Pl. 4, figs 2, 3 herein) and *Sacheria asplenioides* Ettingshausen (1854, pl. 20, fig. 1 – based on the holotype No. 1854/9/31, Pl. 4, fig. 1 herein). *A. lindsaeoides* was established on a sterile frond and *S. asplenioides* was established on a fertile frond. Gross morphology of both fronds and their pinnules are clearly similar and there is no reason to distinguish two different species. We suggest to keep the name *Oligocarpia lindsaeoides,* which is currently used for both fertile and sterile specimens as many previous authors did.

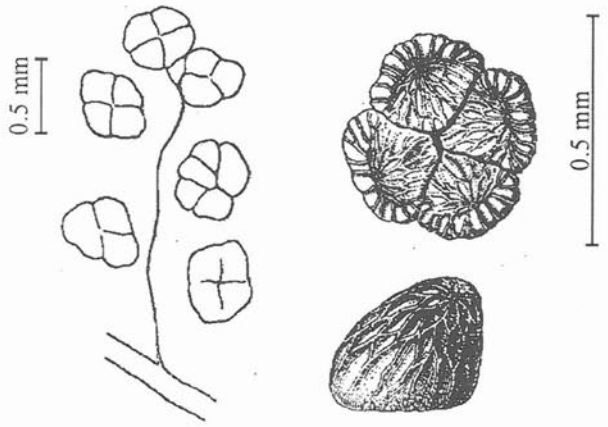
Description. The holotype No 1854/9/39 (Pl. 4, figs 2, 3) shows a frond fragment bearing four secondary pinnae inserted on a main rachis. They are delicate and alternate, open, probably oval-lanceolate. Main rachis of the frond is slightly S-flexuous, 2 mm wide (Pl. 4, fig. 2). Ultimate rachis is inserted on secondary rachis (Pl. 4, fig. 2). The secondary rachis is 1 mm wide and more than 50 mm long. Ultimate pinnae are 20-30 mm long and 10 mm wide, linear-lanceolate (Pl. 4, figs 2, 3). Sterile pinnules are 5 mm long and 3 mm wide. Margin of the pinnules is undulate to lobed with lobes undulate to sharply dentate. Midvein of pinnules is flexuous (Pl. 4, fig. 3). Lateral veins are several times dichotomously branched. There are sterile pinnules only. Besides *O. lindsaeoides* the specimen shows a fragment of *Corynepteris angustissima* (STERNBERG) NĚMEJC.

Specimen No. 1854/9/31 (Pl. 3; Pl. 4, fig. 1) shows two lanceolate secondary pinnae. Outline of pinnules is not clearly seen. The pinnules are decurrent, alternate, 2-2.5 mm long and 1-1.5 mm wide. Midvein of pinnules is flexuous. Lateral veins dichotomise several times. Sori without indusium are located on lateral vein endings. Sorus consists of 4-6 sporangia (most frequently 5). Sporangia are 0.35 mm in diameter, pyriform or rounded, shortly stalked, and annulate (Pl. 3, figs 1,3). Annulus is not clearly seen. Triangular -subtriangular spores are 20 (28) 38 μm in diameter. Rays of trilete mark extending 1/2-2/3 of the radius. Laevigate exine is about 1 μm thick. Sometimes secondary folds of exine occur (Pl. 3, figs 2,4).

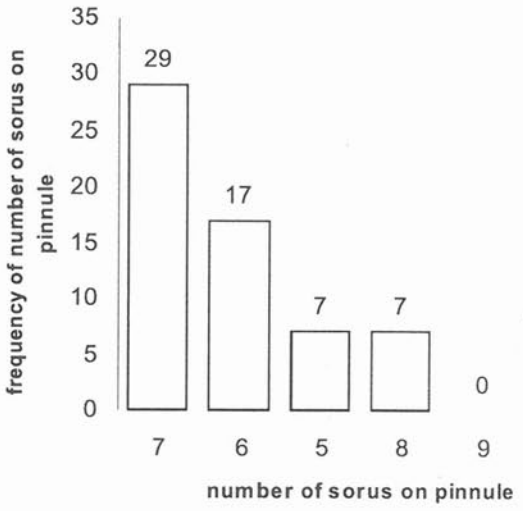
Specimen No. E1299 (Pl. 1, 2) shows tri- or polypinnate frond with a slightly flexuous rachis. Primary pinnae are lanceolate, widest in the middle part, slightly diminished at the base and gradually tapering to the apex (Pl. 1, fig. 2). Secondary pinnae are 20 mm long, lanceolate, widest at the lower third of pinna. The basal pinnae bear 14-30 pinnules. Outline of pinnules is not clearly seen (Pl. 1, fig. 7). They are decurrent, alternate, with blunt to well-rounded apices, 2-3.5 mm long and 1-1.5 mm wide. Midvein of pinnules is flexuous. Lateral veins are not visible. Sori are regularly arranged in one row on entire side of the midvein (Pl. 1, fig. 7). Sori frequently occupy larger part of pinnule surface between midvein and margin, but they are located slightly nearer to the margin than the midvein. Sori without indusium are located on lateral veins endings. Sori



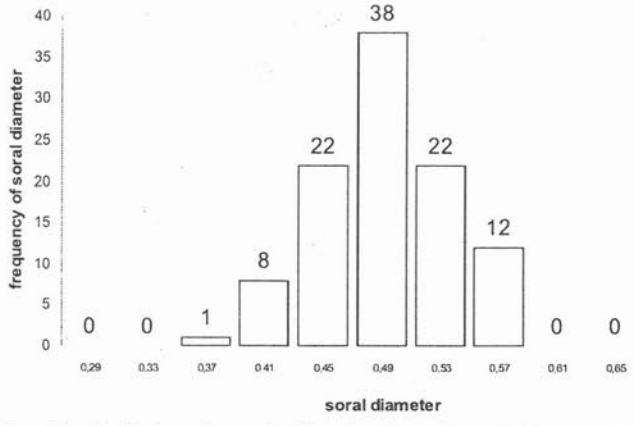
Text-fig. 2. Fertile specimen of *Oligocarpia lindsaeoides* figured by Ettingshausen (1854, Plate 20, fig. 1) as *Sacheria asplenioides*. Original Ettingshausen's specimen (dashed line) is figured in Plate 4, fig. 1(No. 1854/9/31).



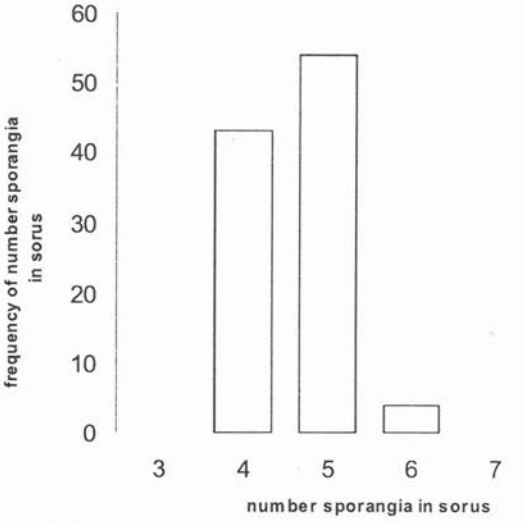
Text-fig. 3. Suggested reconstruction of soral distribution on pinnules (on the left) and sorus with isolated sporangium (on the right) figured by Stur (1885, band XI, p. 128, fig. 19). He did not dispose effective method of maceration of sporangia, thus his reconstruction of sporangia can not be precise.



Text-fig. 4 Chart of sample number of sorus on pinnule in *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR



Text-fig. 5. Chart of sample distribution of soral diameter in *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR

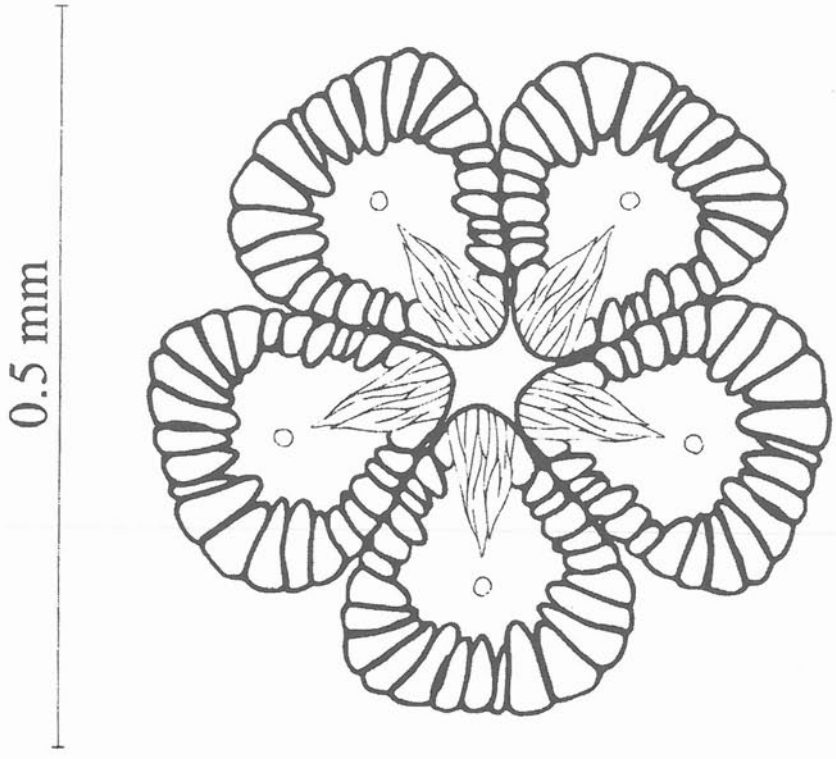


Text-fig. 6. Chart of sample number sporangia in sorus in *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR

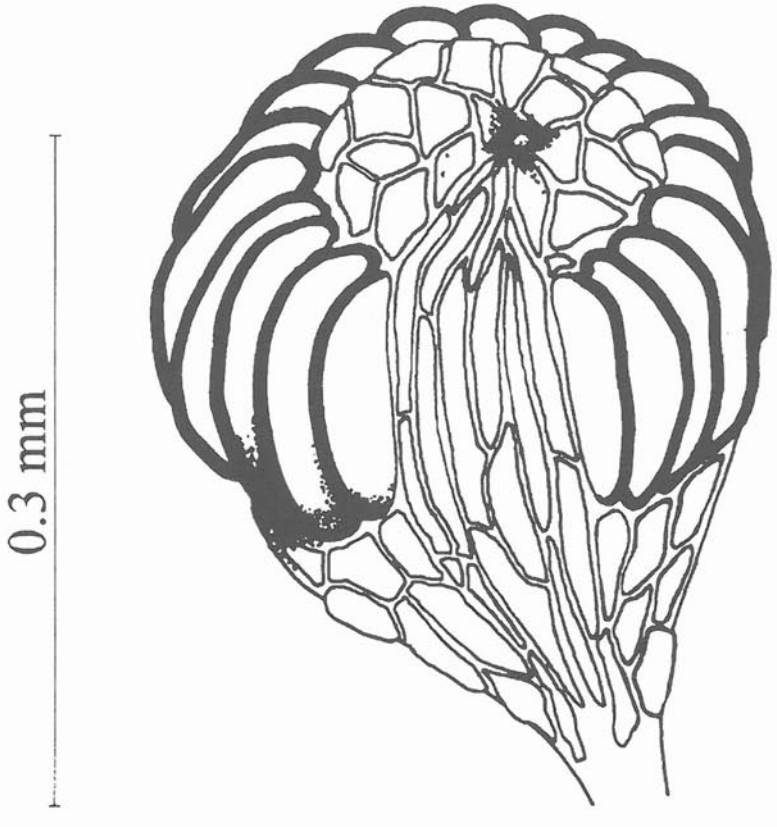
lack centrally located sporangia. 47.5 per cent of pinnules bear 7 sori, 28 per cent bear 6 sori and 24.5 per cent bear 5 and 9 sori (text-fig. 4). Range of soral diameter is from 0.37 to 0.57 mm, depending on the number of sporangia (text-fig. 5). The most frequent soral diameter is 0.50 mm and the mean is 0.47 ± 0.06 mm. The most frequently encountered number of sporangia per sorus is 5 (54 per cent) (Pl. 2, figs 1, 2; text-fig. 7), sometimes 4 (43 per cent) 4 per cent have 6 sporangia (text-figs 67). Sporangia are 0.22-0.3 mm in diameter, pyriform or rounded, shortly stalked, and annulate (text-fig. 8; Pl. 1, figs 1, 5; Pl. 2, figs 3-6). Oblique annulus consisting of one or two rows of 18 -22 oblong thick-walled cells (text-fig. 8; Pl. 1, figs 1, 2; Pl. 2, figs 3, 4, 6) and interrupted by a stomium consisting of several (probably 4-6) thin-walled isodiametric, elongated cells (Pl. 1, fig. 8). Elongated dehiscence slit area is directed from apical part of sporangium towards the stalk and consisting of several elongated, narrow tapering cells (Pl. 1, figs 1, 8; Pl. 2, figs 3, 4). Aperture is seen in the apical area (Pl. 1. figs 1, 5; Pl. 2, figs 3-6) with one very thin-walled cell.

Trilete triangular spores are 20 (32.2) 39 μm in diameter (Pl. 1, figs 3, 4, 6). Rays of trilete mark reach about 1/2–3/4 of the radius. Exine is laevigate, irregularly scabrate, from 1 to 2 μm thick.

Variations. All the spores are closely similar in shape and differ in diameter (Table 1). Difference between extreme values is 19 μm, i.e. 59 per cent of the average. Some spores are developed with an irregular secondary fold of exine (gulaferoid type) and resemble the dispersed species *Leiotriletes gulaferus* POTONIÉ et KREMP. Most of the isolated spores are closely correlable with the dispersed species *Leiotriletes subadnatoides* BHARADWAJ. Spores isolated from Bohemian and Austrian specimens of *Oligocarpia lindsaeoides* have comparable diameter and length of trilete rays. They differ in the thickness of the exine and its sculpture. Bohemian spores are laevigate to scabrate and therefore are closely similar to the dispersed species *Leiotriletes subadnatoides*. Austrian spores are laevigate and are comparable with several dispersed species of *Leiotriletes*, according to the diameter. Table 1



Text-fig. 7. Reconstruction of sorus composed of five mature sporangia with annulus (thick-walled cells) and a dehiscence area consisting of several elongated, narrow cells.



Text-fig. 8. Reconstruction of mature sporangium of *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR with an inclined annulus. An elongated dehiscence slit area is directed from apical part of a sporangium toward to the stalk area and is composed several elongated, narrow cells.

shows selected Carboniferous dispersed species of *Leiotriletes* comparable with these laevigate microspores, although their stratigraphical ranges are different.

Remarks. The hand specimen (No. 1854/9/39) has a different outline than the drawing in Ettinghausen (1854, pl. 20) representing only a part of the original specimen (compare text-fig. 3 and Pl. 4, fig. 1). Nevertheless, its frond is clearly similar in morphology to the figure published by Ettingshausen (1854).

Discussion

a) In situ Leiotriletes

Several spores of the *Leiotriletes*-type have been isolated from numerous Carboniferous fertile fronds (Table 2) of different plant genera and groups. Most of them are closely similar (if indistinguishable) due to very simple morphology. Therefore it is absolutely impossible to distinguish palynologically parent fructifications producing spores of the *Leiotriletes*-type.

Spores produced by several *Oligocarpia* species have exine usually interpreted as laevigate, scabrate to microgranulate (they are classified as *Leiotriletes-Granulatisporites, Leiotriletes* or *Granulatisporites*-types by different authors). These sculptured spores differ from all other similar spores isolated from fructifications of genera like *Renaultia* ZEILLER, *Discopteris* STUR, *Myriotheca* ZEILLER or *Boweria* KIDSTON, which have usually laevigate exine and are compared with *Leiotriletes*.

Spores isolated by Remy and Remy (1957) from *Oligocarpia cliverii* POTONIÉ and *O. gutbierii* have laevigate exine and are closely similar to spores isolated from the type specimen No. 1954/9/31. Spores isolated from specimens named also as *O. gutbierii* by Brousmiche (1983, 1986) possess different spores with microgranulate exine and classified as the *Granulatisporites*-type. It is not probable that both specimens really belong to the identical species. Spores isolated from *Oligocarpia leptophylla* (BUNBURY) GRAUVOGEL-STAMM et DOUBINGER by Grauvogel-Stamm and Doubinger (1975) and all the spores isolated by Brousmiche (1983) from *O.* cf. *leptophylla*, *O. brongniartii* STUR, *O. mixta* (SCHIMPER) ABBOTT and *O.* sp. cf. *O. mixta* are microgranulate and different from those isolated from Bohemian *O. lindsaeoides* and specimens reported by Remy and Remy (1955).

From a palynological point of view there are thus two groups of *Oligocarpia* spores. One is represented by all Brousmiche´s (1975, 1983) specimens with microgranulate spores of the *Granulatisporites*-type and the second group consists of laevigate spores isolated from specimens reported by Remy and Remy (1955), Bek (1998) and herein.

b) Dispersed *Leiotriletes*

The genus *Leiotriletes* was established by Naumova (1937) and emended by Potonié and Kremp (1954) for triangular trilete miospores with convex, straight or concave sides and laevigate, scabrate, infrapunctate and infrareticulate exine. The size of most species vary from 20 to 50 μm. Very similar dispersed miospores are reported from the Silurian to Tertiary of Europe, Asia, Africa, Australia, and America.

More than 100 dispersed Carboniferous *Leiotriletes* species are now recognized. Some species have since been transferred to different taxa like *Waltzispora polita* (HOFFMEISTER, STAPLIN et MALLOY) SMITH et BUTTERWORTH [former *Leiotriletes politus* (HOFFMEISTER, STAPLIN et MALLOY) LOVE], *Granulatisporites adnatoides* (POTONIÉ et KREMP) SMITH et BUTTERWOTH [former *Leiotriletes adnatoides* POTONIÉ et KREMP] and others. Some of them, especially some Russian species, are not of the *Leiotriletes*-type like *L. trivialis* NAUMOVA, *L. platirugosus* (WALTZ) ISCHENKO, *L. vetustus* ISCHENKO, *L. mitis* ISCHENKO and *L. auritus* ISCHENKO.

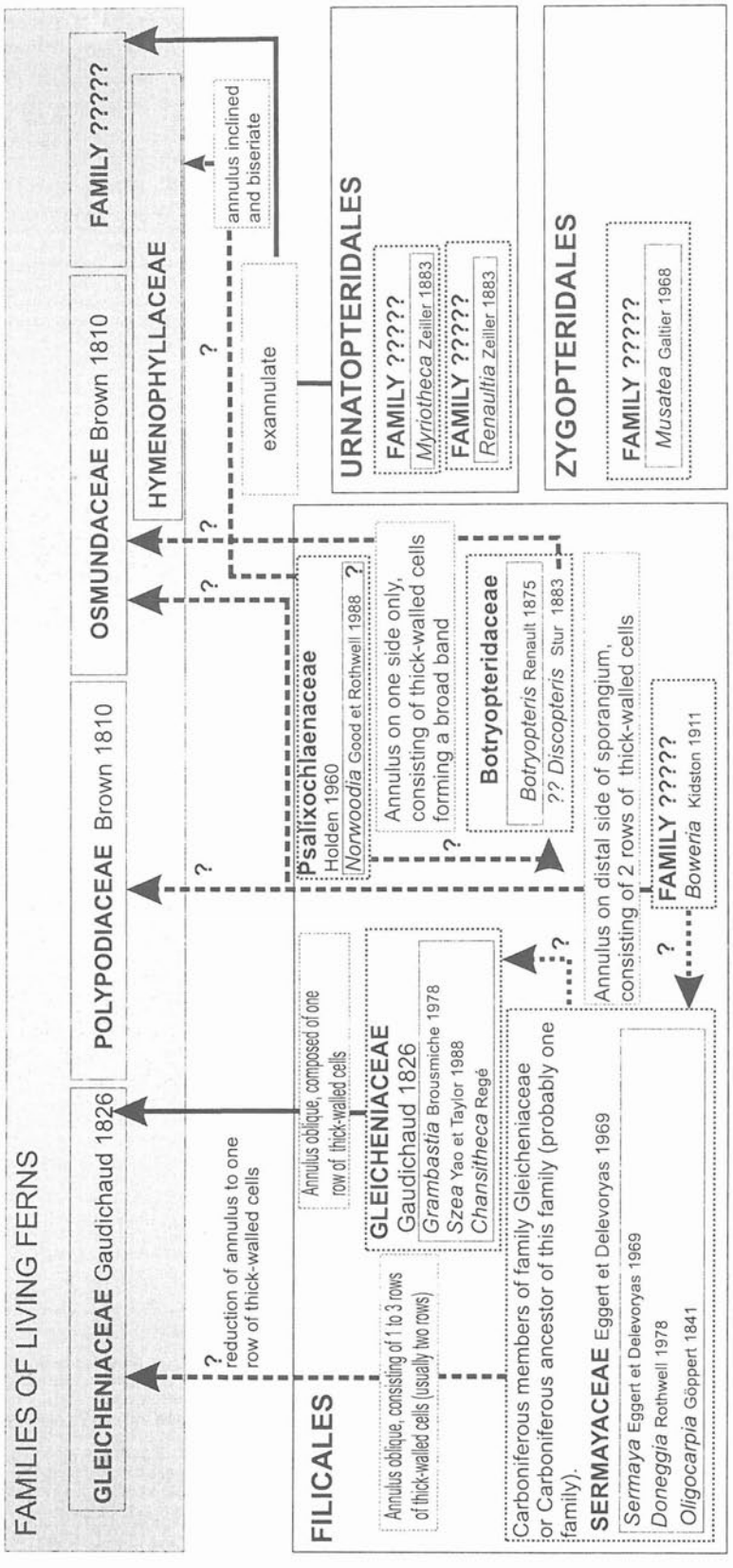
Leiotriletes species represent the morphologically simplest miospores, and are closely similar to each other if not identical. They differ usually only in the shape (from convex to concave sides) and the size. It is highly probable that many dispersed *Leiotriletes* are synonymous, although they may represent different natural (but indistinguishable) species produced by different parent plants of different plant groups. The situation with some Russian miospores of the *Leiotriletes*-type is complicated especially if the descriptions and hand made illustrations are poor. There are several genera with some species closely resembling *Leiotriletes* miospores like *Trachytriletes* NAUMOVA and others but it is impossible to decide if they are or are not of the *Leiotriletes*-type without reexamination of original slides.

c) Comparison with other species of *Oligocarpia* without central sporangia

Oligocarpia lindsaeoides has a special position among other species of the genus. The sorus and sporangia of *O. lindsaeoides* are the smallest from all *Oligocarpia* species. A comparison of soral architecture is given in Table 3. There are three species closely similar in soral and sporangial architecture to *O. lindsaeoides* - *O. capitata*, *O. mixta* and *O. missouriensis*. *O. capitata* has circular sporangia with equatorial annulus, and sori arranged in two rows on either side of midvein, while of *O. lindsaeoides* has pyriform sporangia, with oblique annulus and sori arranged on lateral vein endings. *O. mixta* has a small pyriform sporangia with oblique annulus, like *O. lindsaeoides*. Nevertheless, *O. lindsaeoides* has sori arranged on lateral veins endings, while *O. mixta* has them in clusters near the apex of pinnule lobe. *O. missouriensis* has similar shaped annulus, sporangia and morphology to *O. lindsaeoides*. Nevertheless, *O. missouriensis* sori are arranged in two rows, one on each side of midvein and are 0.6-0.7 mm in diameter, while *O. lindsaeoides* sori are only 0.47 mm in diameter. Stratigraphical ranges of all species of *Oligocarpia* with sori without central sporangia is given in Table 4.

d) Comparison with Sermayaceae

Comparison with other Carboniferous plants producing microspores of the *Leiotriletes*-type is shown on (Table 2). Two genera, *Sermaya* EGGERT et DELEVORYAS and *Doneggia* ROTHWELL are classified as members of the Sermayaceae (Taylor and Taylor 1993) based on morphology and anatomy of petioles, sporangia and spores. We suggest that *Oligocarpia* belongs to the Sermayaceae based on a great similarity of the reproductive organs. Both genera (*Sermaya* and *Doneggia*) were described from petrified specimens, while *Oligocarpia* was described as leaf compressions. *Sermaya* and *Doneggia* are based on detached petioles of the *Anachoropteris*-type that produced alternately arranged pinnae and bluntly lobed sphenopterid pinnules (Taylor 1981). The anatomy of *Oligocarpia* fronds and nature of stems producing



Text-fig. 9. Comparison with Carboniferous plants producing microspores of the *Leiotriletes*-type. This figure shows real or probable relationship of Carboniferous (species see Table 2) and living families. Diagram is based on morphological characters of sporangia according to Stur (1885), Bower (1923, 1926, 1928), Němejc (1962), Brousmiche (1983), Taylor and Taylor (1993), and others.

them is still unknown. *Sermaya, Doneggia* and *Oligocarpia* have annulate sporangia. The annulus is oblique, consisting of two rows of thick-walled cells on the distal face. Dehiscence is evident along a row of thin-walled cells extending medially near the annulus to the area of attachment. When compared with disperse spore taxa, they resemble in the genus *Leiotriletes*. This is another indication of similarity to Sermayaceae. Taylor (1981, p. 265) stated that *Oligocarpia* has been suggested as representing a compressed specimen of *Sermaya*. This comparison made by Taylor (1981) was based on similarities in foliar morphology and the size, shape and structure of the sporangium.

e) Comparison with other taxa producing microspores of the *Leiotriletes*-type (text-fig. 9)

Grambastia BROUSMICHE belongs to ferns closely similar to the Gleicheniaceae. Anatomy of *Grambastia* fronds and the nature of stems that bore them are still unknown. Sporangia are of the same type as in *Sermaya, Doneggia* and *Oligocarpia*, but the annulus has only one row of thick-walled cells. Based on this fact, Brousmiche (1979, 1983) placed this genus in the family Gleicheniaceae. Nevertheless, its exact systematic position is still uncertain. *Oligocarpia* has sori placed on lateral veins, whereas *Grambastia* has sori scattered among lateral veins.

The systematic position of *Boweria* KIDSTON is questionable. Anatomy of *Boweria* fronds is still unknown. The sporangia are isolated and marginal, being attached on the ends of the vein of the pinnule segment. Bower (1926) stated that sporangia of *Boweria* could have been ranked with the Osmundaceae. Němejc (1963) assumed that all the Carboniferous species with an incomplete annulus, which pass as a band across the apex, have a relationship to recent genera *Hemitelia* BROWN and *Cyathea* SMITH. Nevertheless it is clear, based on sporangial wall anatomy, that *Boweria* belongs to proleptosporangiate ferns.

Renaultia ZEILLER and *Myriotheca* ZEILLER were described on fertile fronds from adpression material. Sporangia are exannulate and they opened by an apical porus, while *Oligocarpia* has annulate sporangia. Němejc (1963) stated that both species belong to proleptosporangiate ferns based on sporangial anatomy. Whereas Brousmiche (1983) stated that both genera rather belong to eusporangiate ferns (order Urnatopteridales), because she stated that the sporangial wall consists of more than one-layer of cells.

Discopteris STUR is a generic name used for sterile and fertile pinnules that superficially resemble the pinnules of the sphenopterid type (Taylor 1981). The fertile pinnules of *Discopteris* are characterised by a disk-shape sorus at the end of the midvein consisting of between 50-70 annulate sporangia. Němejc (1963) compared this genus with living member of Osmundaceae based on the character of the sporangium. Taylor (1981) stated that sporangial histology closely resembles a number of ferns, including the genus *Botryopteris* RENAULT (Botryopteridaceae). Brousmiche (1983) and Pfefferkorn (1978) stated that the systematic position of *Discopteris* is still uncertain. It is possible to claim that *Discopteris* occupies a position between eusporangiate and leptosporangiate (proleptosporangiate) ferns.

Norwoodia GOOD et ROTHWELL was described by Good and Rothwell (1988) on compression material. Each sorus is gradate and contains five sessile sporangia borne in a ring. The annulus inclines and is typically biseriate. Taylor and Taylor (1993) stated that the organisation of the fertile parts in this fern is similar to the Carboniferous genus *Psalixochlaena* HOLDEN. Taylor and Taylor (1993) assumed that reproductive parts of *Psalixochlaena* are similar to ferns in the extant family Hymenophyllaceae.

Relationships

Göppert (1841) compared the genus *Oligocarpia* with the recent family Polypodiaceae and Cyatheaceae based on their annulate sporangia. Zeiller (1888) assumed that *Oligocarpia* belongs to the Gleicheniaceae. Bower (1926) stated that the *Oligocarpia* sorus is certainly of the Gleicheniaceous-type, and the sporangia closely resemble those of *Dicranopteris* BERNH, but it is questionable whether the annulus consisted of a single row of cells. According to Bower (1926), only in more recent geological times is clear proof of the Gleicheniaceae forthcoming.

Němejc (1963) stated that *Oligocarpia* may have been related to the family *Gleicheniaceae*, nevertheless he noticed that the annulus is composed (except in *O. vera*) of mostly two sometimes three annular rows of thick-walled cells. In the Gleicheniaceae the sporangium is stalked and exhibits a single row of annulus cells (Bower 1926).

It is possible to observe a great similarity in the sporangia of *Sermaya*, *Doneggia* and the compression genus *Grambastia*. *Grambastia* has an annulus composed of one row of thick-walled cells. According to Brousmiche (1983) *Grambastia* belongs to Gleicheniaceae. However she did not describe the morphology of the stem, which according to Bower (1926), is important for the definite identification of the family. *Sermaya* and *Doneggia* have an annulus composed of two rows of thick-walled cells, as also seen in *Oligocarpia*. *Oligocarpia* are often compared with family Gleicheniaceae (Bower 1926, Němejc 1963, Abbott 1954, Brousmiche 1983). Abbott (1954) stated that family Gleicheniaceae consists of five genera, three living (*Gleichenia* SMITH, *Stromatopteris* METTENIUS and

Table 1. List of dispersed *Leiotriletes* microspores comparable with microspores isolated from *Oligocarpia lindsaeoides*.

Dispersed *Leiotriletes*	Size (μm)	Dispersed *Leiotriletes*	Size (μm)
Leiotriletes adnatoides Potonié and Kremp	30-40	*Leiotriletes marginalis* McGregor	33-54
L. adnatus (Kosanke) Potonié and Kremp	30-40	*L. minutus* (Knox) Potonié and Kremp	25-28
L. asthanensis Singh	35-45	*L. notatus* Hacquebard	37-54
L. confertus McGregor	35-55	*L. parvus* Guennel	16-28
L. gracilis (Imgrund) Imgrund	24-30	*L. rarus* Singh	25-35
L. gulaferus Potonié and Kremp	30-70	*L. sphaerotriangulus* (Loose) Potonié and Kremp	37-60
L. magnificus Singh	22-33	*L. subadnatoides* Bharadwaj	24-29

Platyzoma BERNH) and two fossil (*Gleichenites* and *Oligocarpia*). Furthermore, she regarded the sporangia as having undergone little change in form from the Palaeozoic to the present day, and that the Palaeozoic fern genus *Oligocarpia* can readily be included in the Gleicheniaceae. However, some authors (Eggert and Delevoryas 1967, Rothwell 1978) have suggested transferring *Oligocarpia* to the Sermayaceae (a Carboniferous family of ferns) closely related to recent Gleicheniaceae based on their general morphology, stem anatomy, and reproduction organs. Taylor (1981) stated that althou-

Table 2. Some Carboniferous fructifications produced microspores of the *Leiotriletes*-type.

Parent fructifications	Size of microspores(μm)	Classification	References
Oligocarpia brongniartii Stur	35-36	*Leiotriletes-Apiculatisporis*	Brousmiche 1983
O. gutbierii Göppert	20-35	*Leiotriletes gulaferus* Potonié et Kremp, *Leiotriletes-Granulatisporites*	Remy and Remy 1957, Brousmiche 1983
O. cliverii H. Potonié	30-35	*L. sphaerotriangulus* (Loose) Potonié et Kremp, *L. levis* (Kosanke) Potonié et Kremp	Remy and Remy 1957
O. leptophylla (Bunbury) Grauvogel-Stamm et Doubinger, *O.* cf. *leptophylla*	32-49	*Granulatisporites parvus* (Ibrahim) Potonié et Kremp	Grauvogel-Stamm and Doubinger 1975
O. mixta (Schimper) Abbott	31	*Leiotriletes* spp.	Abbott 1954
O. sp. cf. *O. mixta* (Schimper) Abbott	21-26	*Leiotriletes-Granulatisporites*	Brousmiche 1983
O. sp. A *sensu* Bek (= *O. lindsaeoides* Ettingshausen)	20-39	*L. subadnatoides* Bharadwaj	Bek 1998
Renaultia sp. *sensu* Remy et Remy	25	*Leiotriletes* spp.	Remy and Remy 1957
Renaultia germanica (Potonié) Kidston	27-33	*Leiotriletes* spp.	Brousmiche 1986
?N. gen. et sp. aus dem Saarkarbon *sensu* Remy et Remy	30-35	*Leiotriletes gulaferus* Potonié et Kremp	Remy and Remy 1957
Discopteris occidentalis Gothan	15-23	*Leiotriletes* spp.	Brousmiche 1986
D. karwinensis Stur	21-57	*L. parvus* Ibrahim	Balme 1995
D. karwinensis Stur	21-57	*Punctatisporites-Leiotriletes-Granulatisporites*	Brousmiche 1983
D. schumannii Stur	40-45	*Leiotriletes* spp.	Brousmiche 1986
D. opulenta Danzé	36-61	*Leiotriletes* spp.	Brousmiche 1979
Grambastia goldenbergii (Andrae) Brousmiche	24-42	*Leiotriletes* spp.	Brousmiche 1986
Myriotheca sp. cf. *M. scaberrima* (Lesquereux) Sellards		*Leiotriletes* spp. (immature)	Balme 1995
Musatea duplex (Williamson) Chaphekar et Alvin	37-52	*Leiotriletes-Punctatisporites*	Chaphekar and Alvin 1972
Musatea duplex (Williamson) Chaphekar et Alvin	37-52	*Leiotriletes-Punctatisporites*	Balme 1995
Doneggia complura Rothwell		*Leiotriletes* spp.	Rothwell 1978, Taylor 1981
Doneggia complura Rothwell		*L. levis* (Kosanke) Potonié et Kremp	Balme 1995
Norwoodia angustum Good and Rothwell	16-25	*Leiotriletes* spp.	Rothwell 1976
Sermaya biseriata Eggert et Delevoryas		*Leiotriletes* spp.	Eggert and Delevoryas 1967
Sermaya biseriata Eggert et Delevoryas		*Leiotriletes gulaferus* Potonié et Kremp	Balme 1995
Boweria schatzlarensis (Stur) Kidston	32-58	*Leiotriletes gulaferus* Potonié et Kremp	Brousmiche 1983
Boweria schatzlarensis (Stur) Kidston	32-58	*Granulatisporites granulatus* Ibrahim	Balme 1995
Renaultia crepinii (H. Potonié) Kidston		*Leiotriletes* spp.	Brousmiche 1983, 1986

Table 3 Comparison of soral architecture of *O. lindsaeoides* with that of some other *Oligocarpia* species with sori without central sporangia. (according to Zodrow 1982; modified by authors).

	O. gutbierii	*O. missouriensis*	*O. capitata*	*O. mixta*	*O. vera*	*O. permiana*	*O. bellii*	*O. lindsaeoides*
sporangium								
diameter	0.3 mm	0.3 -0.35 mm	0.3-0.35 mm	0.3 mm	0.35-0.4 mm	max. 0.55 mm	0.3-0.37 mm	0.22-0.3 mm
Shape	sub-spherical	pyriform	circular	pyriform	pyriform	pyriform	pyriform	pyriform
number common	4-5	4-7 5	3-6	4-6 5	4-6 4	2-8	3-6 4	4-6 5
annulus	12 -16 elongate cells, oblique	21 elongate cells, oblique	20-22 oblong cells, equatorial	20-21 elongate cells, oblique	19 elongate cells, oblique	biseriate	15 elongate cells, oblique	18-22 elongate cells, oblique
Sorus								
diameter	0.63 mm	0.6-0.7 mm	0.6-0.7 mm	?	0.64	?	0.65	0.47
distribution	1-2 rows, 1 is common about midvein	2 rows, 1 on each side of midvein	2 rows on either side of midvein	clustered near apex of pinnule lobe	1 row on either side of midvein	?	scattered, not in apical parts of pinnules	lateral veins endidngs

Table 4. Stratigraphical range of Carboniferous species of *Oligocarpia* (species with sori without central sporangia).

	CARBONIFEROUS											PERMIAN
	LOWER		UPPER									
	TOUR.	VIS.	NAMURIAN			WESTPHALIAN				STEPHANIAN		
			A	B	C	A	B	C	D	A	B	C	
O. lindsaeoides													
O. mixta													
O. gutbierii													
O. missouriensis													
O. capitata													
O. vera													
O. permiana													
O. bellii													

gh dehiscence and sporangial shape are similar in the two families (Sermayaceae and Gleicheniaceae), the anatomy of the frond is markedly different.

Yao and Taylor (1988) stated that no Paleozoic ferns possessing the typical gleicheniaceous protostelic and pseudodichotomous branching of the frond are known at the present time. Yao and Taylor (1988) described *Szea sinensis* YAO et TAYLOR as a Paleozoic member of the Gleicheniaceae. They stated that the structure of the sporangia strongly suggests that *Szea, Oligocarpia* and *Chansitheca* share fertile characteristics with the other members of the Gleicheniaceae. Nevertheless we suggest that *Oligocarpia* belongs rather to Sermayaceae based on fact that *Oligocarpia* possess an annulus two rows of thick-walled cells.

Conclusions

The Carboniferous species *Oligocarpia lindsaeoides* probably belongs to the family Sermayaceae. *Oligocarpia* has sporangia with one or two rows of the thick-walled cells and correspond with *Sermaya*. *Sermaya, Doneggia* and *Oligocarpia* are closely related genera based on similarities in foliar morphology and the size, shape and structure of the sporangium. Nevertheless *Oligocarpia lindsaeoides* indicates several points of similarities to the members of the recent family Gleicheniaceae. There are three species closely similar in soral and sporangial architecture to *O. lindsaeoides* - *O. capitata*, *O. mixta* and *O. missouriensis*. Nevertheless, the sporangia of *Oligocarpia lindsaeoides* are the smallest of all other species of the genus, and their sporangia are positioned on lateral vein endings, in contrast to the other species of *Oligocarpia*.

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Explanations to the plates

PLATE 1

Oligocarpia lindsaeoides (ETTINGSHAUSEN) STUR, Lány, Kladno-Rakovník Basin, E1299

1. Detail of sporangia showing the annulus composes of thick-walled cells, polygonal cells of distal end of the sporangia and aperture in the apical area of sporangia; SEM, × 400.
2. Fragment of a pinna; × 1.

3-4, 6. Microspores correlated with the dispersed species *Leiotriletes subadnatoides* BHARADWAJ; All × 500.

5. Two sporangia composing part of sorus; SEM, × 200.
7. Detail of pinnules with sori. Sporangia produced 2 rows, 1 on each side of midvein; × 15.
8. Detail of an elongated dehiscence slit area directed from apical part of a sporangium toward to the stalk area composes of several elongated, narrow cells with tapering; SEM, × 200.

PLATE 2

Oligocarpia lindsaeoides (ETTINGSHAUSEN) STUR, Lány, Kladno-Rakovník Basin, E1299

1-2. Sori consisting of five annulate sporangia; × 100.
3. Isolated sporangium with oblique annulus built of 18-22 oblong thick-walled cells, interrupted by a stomium consisting of several thin-walled isodiametric, elongated cells. Note an aperture in the apical area of sporangia; SEM, × 250.
4. Sporangium with oblique annulus consisting of probably one row of 18-22 oblong thick-walled cells, interrupted by a stomium with several thin-walled isodiametric, elongated cells; SEM, × 400.
5. Sorus composed of four annulate sporangia; SEM, × 200.
6. Isolated sporangium with oblique annulus, consisting of 18-22 oblong thick-walled cells showing an aperture in the apical area of sporangia; SEM, × 250.

PLATE 3

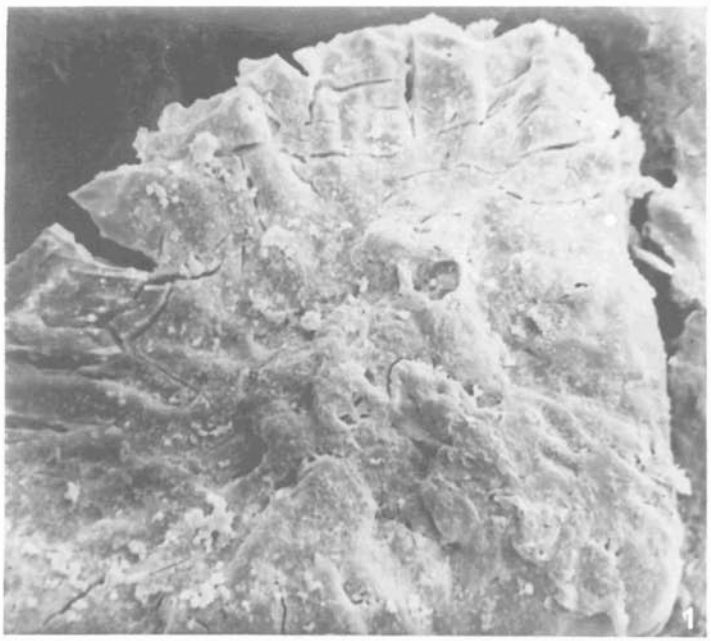
Sporangia and spores of *Oligocarpia lindsaeoides* (ETTINGSHAUSEN) STUR, Svinná locality, Radnice Basin, No 1854/9/31

1. Two sporangia filled with microspores of *Leiotriletes*-type; SEM, ´270.
2. Microspores of *Leiotriletes*-type, proximal surface with open trilete mark; SEM ´, 2500.
3. Sporangium filled with microspores of *Leiotriletes*-type; SEM, ´600.
4. Microspores of *Leiotriletes*-type, proximal surface with open trilete mark; SEM ´2200.

PLATE 4

Oligocarpia lindsaeoides (ETTINGSHAUSEN) STUR, Svinná, Radnice Basin.

1. Holotype of *Sacheria asplenioides* ETTINGSHAUSEN (compare with Text-fig. 3 of this paper), No. 1854/9/31, stored in the Geological Survey of Austria (Vienna), × 2.
2. Holotype of *Oligocarpia lindsaeoides* No. 1854/9/39, showing sterile fragment; on the same slab with a sterile fragment of *Corynepteris angustissima* (STERNBERG) Němejc, × 1.
3. Secondary pinnae with sphenopterid pinnules in detail, (No. 1854/9/39), × 2.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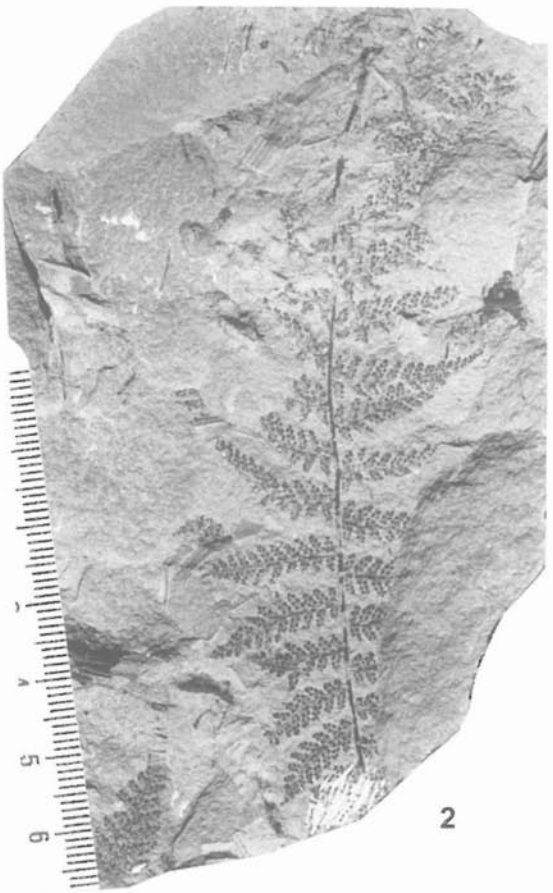
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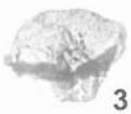
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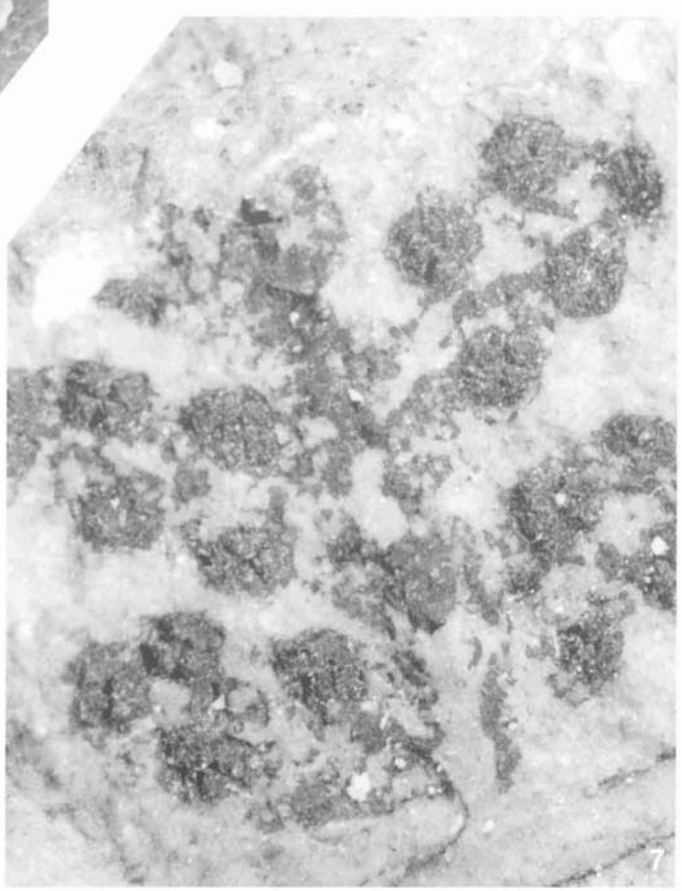
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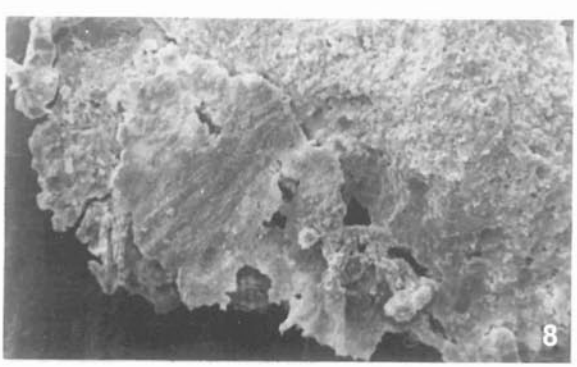
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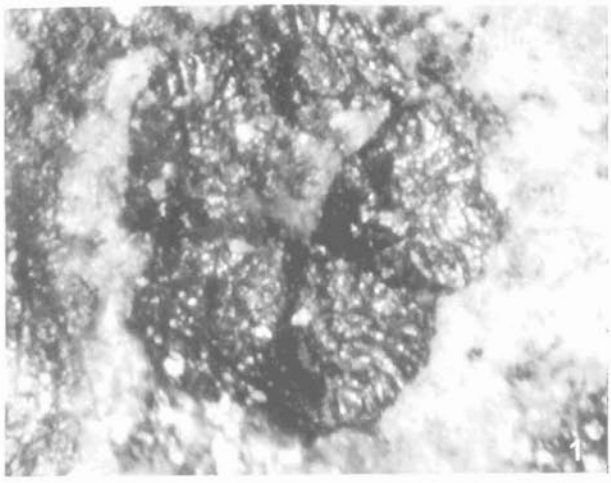
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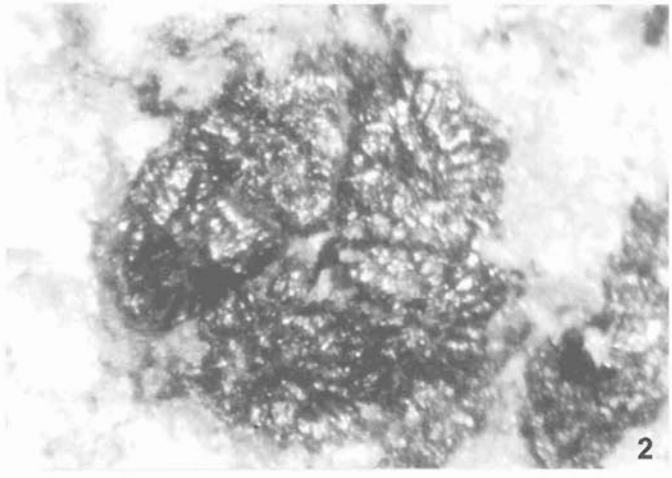
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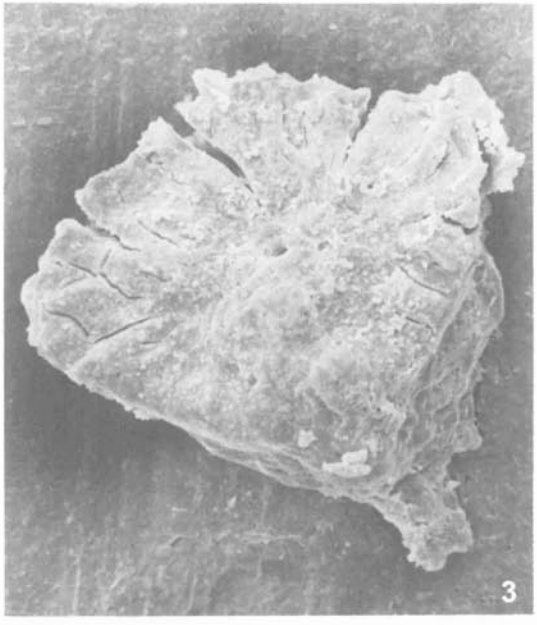
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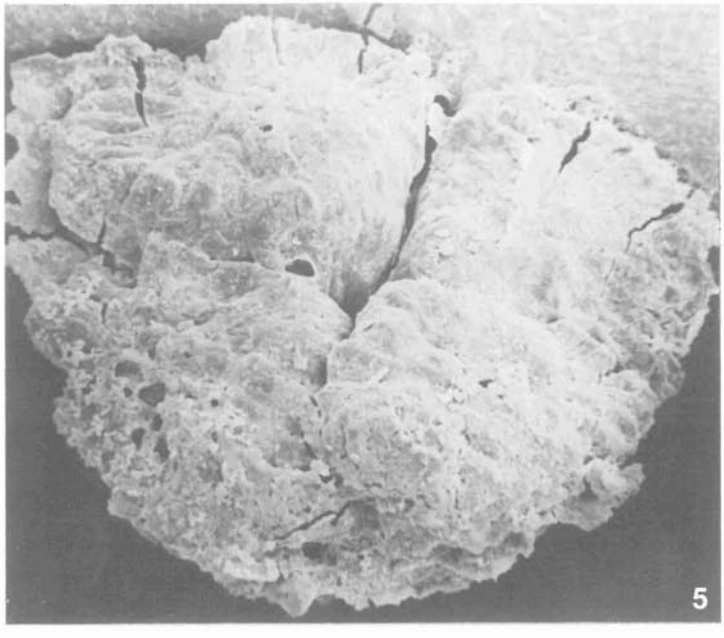
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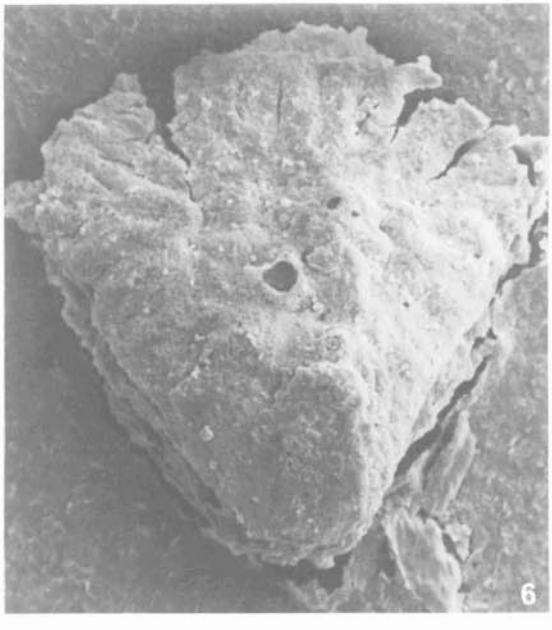
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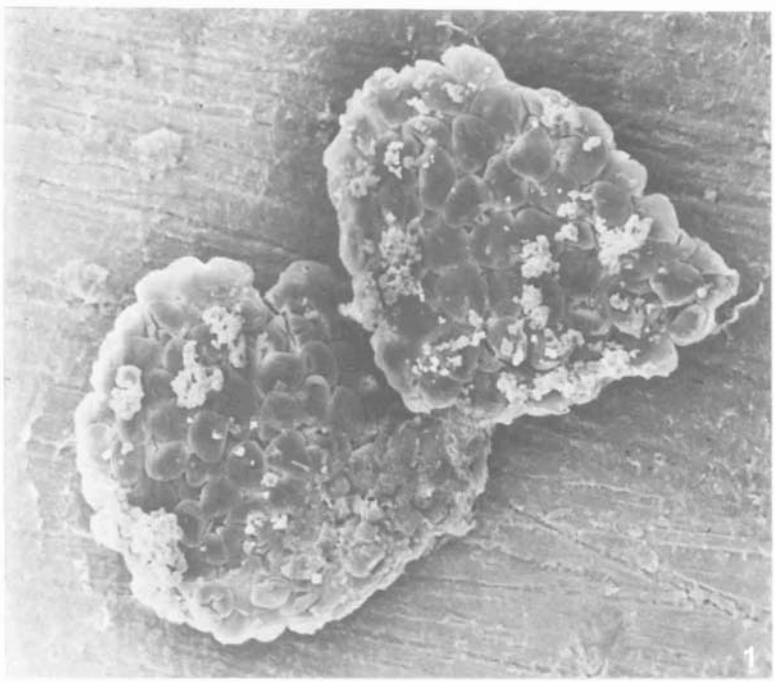
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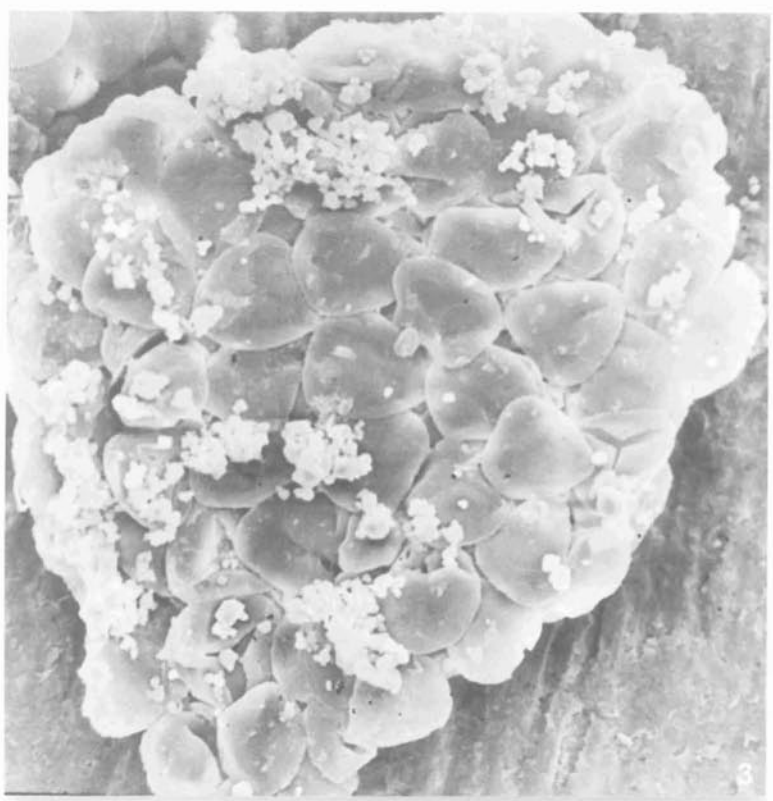
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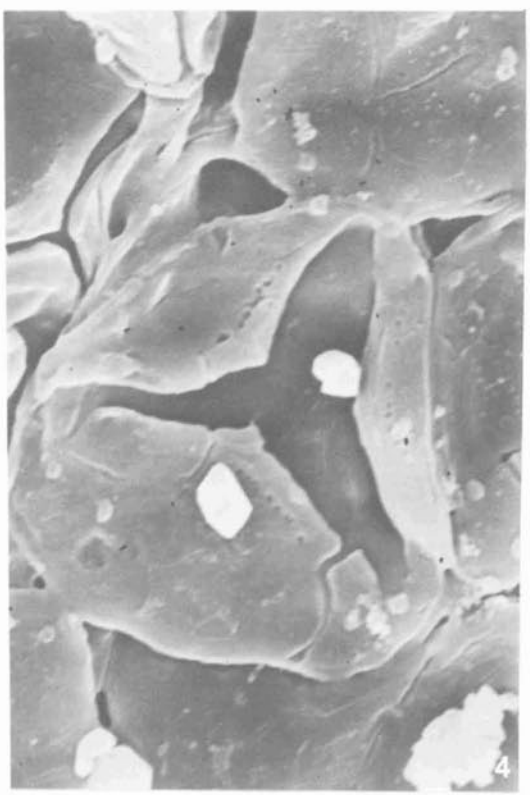
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