Microspinosporites, a new genus of Palaeozoic pseudosaccate miospores of flemingitalean affinity

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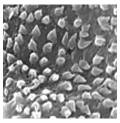

Pennsylvanian microspinate/spinate mio- and microspores are formerly assigned to cingulate species of *Lycospora* (Schopf *et al.*), which were described by Potonié & Kremp. In the present paper, from the three existing species of distally microspinate miospores of this type [*L. granulata* Kosanke, *L. orbicula* (Potonié & Kremp) Smith & Butterworth and *L. chaloneri* Scott & Hemsley] two of them, *L. orbicula* and *L. chaloneri* are assigned to new pseudosaccate miospore genus *Microspinosporites* gen. nov. Miospores of this genus are characterized by inner body and distal and proximal microspinae/spinae, except for the contact area. A cingulum is not developed. The fructifications that produced *Microspinosporites* were bisporangiate cones of the genera *Flemingites* Carruthers and probably *Moscvostrobus* Naugolnykh & Orlova, and were born on arborescent lycopsids of the genus *Paralycopodites* (Moorey & Moorey) DiMichele. The morphology of *Microspinosporites* is similar to that of *e.g.*, *Geminospora* (Balme) Playford and some other pseudosaccate miospore genera. • Key words: *Microspinosporites, Lycospora*, *Flemingites,* Pennsylvanian, Carboniferous.

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The miospore genus *Lycospora* (Schopf *et al*.) Potonié & Kremp is one of the most abundant and most often recorded Carboniferous miospore genera (*e.g.* Smith 1962, Smith & Butterworth 1967, Somers *et al*. 1972, Bek 2012). The genus was established by Schopf *et al*. (1944) and emended by Potonié & Kremp (1954) and Somers *et al*. (1972). The first records of *Lycospora* concern its *in situ* occurrences from mono- and bisporangiate cones of the *Lepidostrobus* and *Flemingites*-types (Hooker 1848, Carruthers 1865, Schimper 1870). Also the stratigraphically oldest records of *Lycospora* from the Upper Devonian of China are *in situ* from cones of arborescent lycopsids (Wang *et al*. 2003a, b). The stratigraphically youngest occurrences of *Lycospora* are from Permian strata both as *in situ* (Rayner 1986) and dispersed spores (Brugman *et al*. 1985, Gao 1985, Górecka & Górecka-Nowak 1999, Lucas *et al.* 2006). The second emendation of the genus published by Somers *et al*. (1972) is important because several species were excluded from the genus. Many holotypes of *Lycospora* species were described, figured and synonymised to four main species, *Lycospora pusilla* (Ibrahim) Potonié & Kremp, *L. noctuina* Butterworth & Williams, *L. orbicula* (Potonié & Kremp) Smith & Butterworth and *L. rotunda* Bharadwaj. The latest research of *in situ Lycospora* had been published especially from the Pennsylvanian of the Czech Republic (Bek & Opluštil 1998, 2004, 2006; Opluštil & Bek 2009). Criteria for a new division of *Lycospora* were suggested by Bek (2012) who divided *Lycospora* into six morphological groups, reporting seventy-one *in situ* records of *Lycospora*, proposed twenty-nine valid species and excluded sixty-three species from the genus. The main aim of this paper is the separation of one group of non-cingulate pseudosaccate miospores with densely microspinate/spinate sculpture on the distal and proximal surfaces (except for contact area), which were produced by bisporangiate cones of the *Flemingites*-type.

Material and methods

Spores are classified according to the system of dispersed spores suggested by Potonié & Kremp (1954, 1955) and improved by Dettmann (1963) and Smith & Butterworth (1967). The terms used for the description of the morphology, including the sculptural elements follows the classification of Punt *et al*. (2007). The species determinations are based only on these original diagnoses, and not on the interpretations of subsequent authors. *In situ* microspores macerated by the author and isolated from cones of the genus *Flemingites* Carruthers are stored in the Geological Institute, Academy of Sciences, v.v.i., Prague, Czech Republic. Dispersed miospores macerated by J. Drábková from the Ovčín locality, Radnice Basin, Czech Republic are stored in the Czech Geological Survey, Prague, Czech Republic.

A NIKON Eclipse 80i microscope was used for the study of the spores. *In situ* spores were recovered by dissolving small portions (separated from the cone specimens with a mounted needle) of cones in nitric acid (40 per cent) for 24–48 hours and KOH (5 per cent) for 20 minutes. Most spores were mounted in glycerine jelly for direct microscopic examination. Some spores were sputter-coated with gold for examination with a Cameca SX100 SEM. Dispersed miospores were macerated using nitric acid (40 per cent) for 12–24 hours and neutralised by KOH (5 per cent) for 10 minutes. The specimen with cones of *Flemingites lycopoditis* Feistmantel (No. 3536) from the Krčelák locality, Lubná, Rako Mine, Kladno-Rakovník Basin (Bolsovian) is stored in the National Museum, Prague, Czech Republic.

Systematic position of cingulate *Lycospora*

Lycospora miospores have been described as having equatorial structure usually named as a flange. Some palynologists interpreted this term as cingulum, some others as cingulum and zona. Morphological heterogeneity of the genus was recognised by Bharadwaj (1957) and Piérart (1964) who distinguished four types of *Lycospora*, Rotunda, Bizonaria and Microcingulata for cingulizonate and Lycospora for cingulate species. Smith & Butterworth (1967, pp. 245–247) recognised two morphological types of *Lycospora*, *L. pusilla* and *L. pellucida* (Wicher) Schopf *et al*., based on histograms of ratios of cingulum (and zona) width to spore radius. Also Thomas (1970), Thomas & Dytko (1980) and Brack-Hanes & Thomas (1983) recognised two main morphologically different types of *Lycospora*, cingulate and cingulizonate based on studies of *in situ* spores.

Bek (2012) recognised two groups of cingulate and four groups of cingulizonate *Lycospora* species. Cingulate *Lycospora* species were divided into morphologically different types that were produced by different parent cone and plant species (Bek & Opluštil 2004, Opluštil & Bek 2009, Bek 2012). The first type (*Lycospora micropapillata* Group) is represented by miospores with a microgranulate to microverrucate sculpture of both surfaces with a higher number of elements on the distal surface. Dispersed species of this group, *Lycospora parva* Kosanke, *L. rugosa* Schemel, *L. tripapillata* Ravn, *L. micropapillata*, *L. pusilla*, *L. rugulosa* Butterworth & Spinner and *L. granianellatus* Staplin were usually produced by the longest and most robust monosporangiate cones of *Lepidostrobus* Brongniart, which could be more than one meter long and about twenty centimeters wide (Bek & Opluštil 2004, Bek 2012). The second morphological type of cingulate *Lycospora* (*Lycospora granulata* Group) is different, because this group is typical for its densely microspinate/spinate distal surface and laevigate, or sometimes microgranulate/microverrucate proximal surface. Only three dispersed species, *L. granulata* Kosanke, *L. orbicula* and *L. chaloneri* Scott & Hemsley were attributed to this group by Bek (2012). Miospores of the *Lycospora micropapillata* Group were produced by monosporangiate cones of the *Lepidostrobus*-type born on arborescent lycopsids of genera *Lepidodendron* Sternberg and *Lepidophloios* Sternberg, but spores of the *Lycospora granulata* Group were produced by bisporangiate *Flemingites* cones which belong to the arborescent lycopsid genus *Paralycopodites* (Morey & Morey) DiMichele.

Morphological differences and different parent cones and plants are the reason for erection of a new miospore genus *Microspinosporites* gen. nov. for pseudosaccate, distally and proximally (except for laevigate contact area) microspinate miospores produced by the cone genera *Flemingites* and probably *Moscvostrobus* Naugolnykh & Orlova (Bek 2012). Another morphological difference is the separation of an inner body, *i.e.* pseudosaccate character. Such a separation is not developed in all other species of *Lycospora*.

Dispersed microspinate *Lycospora*

The firstly erected dispersed species of this type, *Lycospora granulata* was established by Kosanke (1950, p. 45) for miospores with coarsely granulate exine and a small equatorial ridge. The diagnosis is poor (*e.g.* with no recognition of the sculpture of proximal and distal surfaces) and without mentioning the character and dimension of the equatorial structure. The holotype (Kosanke 1950, pl. 10, fig. 6) possesses a dark undulate ring delimiting the proximal surface. From the diagnosis, description and illustration is not clear if this structure is a cingulum or a prominent curvaturae, although it resembles a cingulum-like structure.

The second species of this group, *Lycospora orbicula* is described with (emendation given by Smith & Butterworth 1967, p. 249) an indistinct very narrow cingulum that is less than 1 μm in width and less than one-tenth of the radius. *L. orbicula* is not a typical species of the genus in that the cingulum is weakly developed. Potonié & Kremp (1955, p. 63, pl. 13, fig. 179) and Smith & Butterworth (1967, p. 249) defined *L. orbicula* for miospores with a denticulate margin, a finely granulate exine, and ornament lacking or reduced on the proximal surface. It is important, that in the diagnosis the cingulum is stated to be indistinct, very narrow and less than 1 μm in width. In the description of *L. orbicula*, Smith & Butterworth (1967, p. 249) described the cingulum as apparent only in slightly oblique compression and mentioned the occurrence of curvaturae. In fact, it is questionable if a cingulum can be less than 1 μm wide because the width of the cingulum is usually more than 2 μm (see Felix 1954; Willard 1989a, b; Bek & Opluštil 2004, 2006; Bek 2012). Microspinae are less than 1 μm long being of the same dimension as the equatorial structure.

The last dispersed species of this group, *L. chaloneri*, is known only *in situ* from cones *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas. This species possesses an equatorial structure 2–4 μm wide. Scott & Hemsley (1993, p. 37) interpreted this structure as cingulum and zona. Specimens illustrated by Scott & Hemsley (1993, text-fig. 5B–G) and Hemsley *et al*. (1996, fig. 6; Fig. 1O herein) showing a prominent laevigate proximal contact area and microspinate/spinate remaining proximal portion and distal surface. It is important to realise that the proximal surface is sculptured except for contact area. We do not know any specimen of *Lycospora* with positive sculpture of cingulum or zona (Somers *et al*. 1972; Coquel 1972; Courvoisier & Phillips 1975; Brack-Hanes & Thomas 1983; Thomas 1988; Willard 1989a, b; Bek & Opluštil 1998, 2004, 2006; Bek 2012). Also the prominent microspinae/spinae (or other positive sculpture elements) visible on the margin of spores are not seen on the margins of other *Lycospora* species. The photomicrographs in light microscopy of Scott & Hemsley (1993, text-fig. 5C–F) are important in showing a narrow dark inner ring represented curvaturae, followed by narrow light middle ring and very narrow outer dark ring consists of microspinae/spinae. The contact area does not cover the whole proximal surface and no cingulum is seen. Hemsley *et al*. (1996, fig. 6; Fig. 1O herein) illustrated (SEM) the proximal surface of an *in situ* specimen of *L. chaloneri* where it is possible to see the sculptureless contact area, a sculptureless narrow inner ring (seen as a light middle ring using light microscopy) and a prominent outer ring of microspinae (seen as a dark sculptured outer ring on the margin).

Smith & Butterworth (1967) illustrated dispersed *L. orbicula* with prominent inner body (Smith & Butterworth 1967, pl. 20, fig. 19) and without cingulum (Smith & Butterworth 1967, pl. 20, figs 16–18). Ravn (1986, pl. 18, figs 3, 4; Fig. 1D herein) illustrated dispersed *L. orbicula* with a microspinate margin and a prominent inner body. A cingulum, however, is not seen. *Lycospora granulata* published by Ravn (1986, pl. 18, figs 12–14) probably has a cingulum. It seems, that these miospores have microgranulate proximal surfaces. The specimen on Ravn's (1986) pl. 18, fig. 13 shows a relatively wide equatorial structure.

In situ microspinate *Lycospora*

Lycospora-producing cones have been referred to the genera *Lepidostrobus* and *Flemingites* (Balme 1995). Some *Lepidostrobus* cones were mono-, some others bisporangiate. Brack-Hanes & Thomas (1983) studied the holotype of the type species, *Lepidostrobus ornatus* Brongniart, which yielded only cingulizonate *Lycospora* microspores. Therefore, the genus *Lepidostrobus* was re-defined for microsporangiate cones with cingulizonate and some of cingulate *Lycospora* microspores. Bisporangiate cones producing *Lagenicula*/*Lagenoisporites* megaspores and microspinate cingulate *Lycospora* microspores were assigned to the genus *Flemingites* by Brack-Hanes & Thomas (1983).

Hoskins & Cross (1940) mentioned the occurrence of microspores from bisporangiate cones of *Lepidostrobus aristatus* Hoskins & Cross and *Flemingites bartletii* (Arnold) Brack-Hanes & Thomas, but due to poor drawings (Hoskins & Cross 1940, H, C, figs 15–18) it is not possible to be sure about the precise classification of these microspores.

Moore (1946) described and illustrated microspores isolated from bisporangiate cones *Lepidostrobus comosus* Lindley & Hutton and *L.* cf. *squarossus*. The problem is, that Moore (1946) gave very poor descriptions and measurements of the spores, illustrated several hypothetic stages of maturity of microspores (combination of cingulate and cingulizonate forms with different sculptures) and therefore it is not possible to be sure about precise classification of these microspores.

Chaloner (1953) described microspores from bisporangiate cones *Flemingites russelianus* (Binney) Brack-Hanes & Thomas, *F. olryi* (Zeiller) Brack-Hanes & Thomas and *F. dubius* Binney (synonymous to *Flemingites gracilis* Carruthers). All of them are very similar and Chaloner (1953) mentioned that an equatorial structure is not present, or only very slightly. It is possible to see on Chaloner's illustrations (1953, text-figs 8, 17 and 23), that microspores of all the three cone species have prominent contact areas which only cover the majority of the proximal surface and that a cingulum is not developed.

Felix (1954) is probably the first, who published photomicrographs of *in situ* microspinate microspores of this type isolated from bisporangiate cones *Flemingites diversus* (Felix) Brack-Hanes & Thomas and stressed their finely granulate (probably microspinate) sculpture. However the photomicrographs (Felix 1954, pl. 14, figs 14, 15; pl. 15, fig. 16) are very poor and it is difficult to be sure about the precise classification of these microspores.

The study published by Balbach (1966) is important as she macerated *in situ* microspores from coal-balls specimens of *F. diversus*, described the occurrence of an inner body as an internal membrane and (Balbach 1966, p. 337) mentioned a ridge, that is not easily discernible and appears to be absent in about half of the spores. Very important is Balbach's (1966) remark, that a ridge is formed primarily by an extension of the distal wall with the proximal surface sloping down over it. It means, that the slightly darker ring in the equatorial region cannot be a cingulum (Fig. 1). Balbach (1966) was the first to show a lateral section of microspores of this type (Balbach 1966, pl. 2, fig. 4). It is possible to see an inner body and a different thickness of the distal and proximal exine (although Balbach did not give any measurements). It is also seen well, that there is no thickening/cingulum or zona in the equatorial region. The absence of the cingulum is also demonstrated by Balbach on pl. 2, fig. 2 (Fig. 1B herein), where the inner body is delimited by curvaturae. Microspores isolated by Balbach (1966) from *Lepidostrobus* sp. U also may correspond with those isolated from *F. diversus*, but there is not enough information to be sure about their precise classification.

Hagemann (1966) described distally microspinate microspores from a compression cone of *Lepidostrobus* sp. A with a prominent inner body (Hagemann 1966, taf. 1, figs 6, 8) and microspinate margin. Hagemann (1966, taf. 1, figs 14, 15) also showed a lateral view of compressed microspores where no equatorial thickening can be seen.

Permineralized bisporangiate cones of *Flemingites schopfii* (Brack) Brack-Hanes & Thomas yielded distally rugulo-papillate microspores (Brack 1970). The arrangement of cone anatomy is identical with that of *Lepidostrobus oldhamius* Williamson except for the bisporangiate character. In contrast, a photomicrograph of Taylor *et al.* (2009) shows *Lycospora* with a sculptured proximal surface. Brack (1970) compared the *in situ* megaspores with the species *Lagenicula rugosa* (Loose) Arnold, but Taylor *et al.* (2009) assigned them to the morphologically different genus *Valvisisporites* (Ibrahim) Potonié & Kremp, *i.e.* megaspores produced by sub-arborescent lycopsid genera *Polysporia* Newberry and *Chaloneria* Pigg & Rothwell. Its identical anatomy with the monosporangiate (Courvoisier & Phillips 1975, Willard 1989a) cone *Lepidostrobus oldhamius* is unusual as is the spore's sculptured proximal surface, because almost all other *in situ* microspores isolated from bisporangiate cones of the *Flemingites*-type possess a laevigate proximal hemisphere.

Courvoisier & Phillips (1975) studied *in situ* microspores isolated from the permineralized cones *Lepidostrobus oldhamius* and *Flemingites diversus*. Microspores macerated from *L. oldhamius* are of two types. The first type (specimens 27, 35 and 42 in Courvoisier & Phillips 1975, pl. 1, figs 1–15) possesses a wider equatorial structure, probably consisting of a cingulum and a zona (Courvoisier & Phillips 1975, pl. 1, figs 3, 5, 9). Their distal surfaces are densely microspinate while their proximal surfaces are slightly microspinate (Courvoisier & Phillips 1975, pl. 1, figs 4, 7, 8, 10) or nearly laevigate (Courvoisier & Phillips 1975, pl. 1, fig. 11). The second type of *L. oldhamius* microspores are different (specimens 38 and 113 in Courvoisier & Phillips 1975, pl. 1, figs 12–17). Both surfaces are microspinate with lower number of sculpture elements on the proximal surface. No cingulum is seen on photomicrographs published by Courvoisier & Phillips (1975). These microspores may resemble *L. granulata*, although Courvoisier & Phillips (1975) assigned all *L. oldhamius* microspores to the dispersed miospore species *Lycospora subjuga* Bharadwaj, a typical cingulizonate species.

Microspores isolated (specimens 41 and 114 in Courvoisier & Phillips 1975) from *Flemingites diversus* are without a cingulum as stated by Courvoisier & Phillips (1975, p. 52). The equatorial structure is described as a false ridge. The distal surface is densely microspinate, the proximal surfaces are laevigate and the margins microspinate (Courvoisier & Phillips 1975, pl. 2, fig. 8).

Brack-Hanes & Thomas (1983) in their revision of genera *Lepidostrobus* and *Flemingites* mentioned *in situ* microspores from bisporangiate cone *Flemingites gracilis*, which are of the *Microspinosporites*-type.

Willard (1989a) named *in situ* microspores macerated from the permineralized cones *Lepidostrobus oldhamius* as *Lycospora granulata*. These cingulate microspores have granulate sculpture on both surfaces with a lower number of sculpture elements on the proximal hemisphere (Willard 1989a, figs 4, 7). The equatorial structure is unusualy wide (from 2.2 to 6.8 μm). Generally, they are similar to some *in situ* microspores isolated by Courvoisier & Phillips (1975, specimens 27, 35 and 42) from some specimens of *L. oldhamius.*

Bek (1998) and Bek & Opluštil (1998) described *in situ* microspores (Fig. 1G, L, N) of this type from bisporangite cones *Flemingites lycopoditis* and mentioned, that cingulum is hardly distinct". Opluštil & Bek (2009) isolated microspores of the *Lycospora orbicula*-type from *Flemingites* cf. *russelianus.*

Systematics

Anteturma Sporites H. Potonié, 1893
Turma Triletes (Reinsch) Dettmann, 1963
Suprasubturma Pseudosaccitriletes Richardson, 1965
Infraturma Monopseudosacciti Smith & Butterworth, 1967

Genus *Microspinosporites* gen. nov.

Type species. – Microspinosporites orbiculus (Potonié & Kremp) comb. nov. emend.

Derivation of the name. – According to the typicallly densely microspinate sculpture of the distal and a part of the proximal surface.

Table 1. Measurements of *in situ* and dispersed mio- and microspores of *Microspinosporites* gen. nov. and their stratigraphical ranges.

Dispersed *Microspinosporites*				
Dispersed species	Diameter (µm)	Width of equatorial structure (µm)	Stratigraphic level of holotype	
Microspinosporites orbiculus	26 × 27	Not measured	Bolsovian	
Microspinosporites chaloneri	13.5–25.5	2–4	Asbian	
In situ Microspinoporites				
Parent plant	Diameter (µm)	Width of equatorial structure (µm)	Stratigraphic level	Reference
Lepidostrobus lycopoditis	22–33	2–2.2	Bolsovian	Bek (1998), Bek & Opluštil (1998)
Lepidostrobus diversus	17–27	Not measured	Asturian	Balbach (1966)
Lepidostrobus diversus	19-26	1.2	Asturian	Felix (1954)
Lepidostrobus diversus	20–27	1–1.5	Carbondale	Courvoisier & Phillips (1975)
Lepidostrobus oldhamius (in part)	20–31	1.5	Carbondale	Courvoisier & Phillips (1975)
Flemingites dubius	18–21	Not measured	Duckmantian	Chaloner (1953)
Flemingites olryi	19–34	Not measured	Duckmantian	Chaloner (1953)
Flemingites russelianus	20–34	Not measured	Duckmantian	Chaloner (1953)
Lepidostrobus sp. A	29–31	Not measured	Duckmantian	Hagemann (1966)
Lepidostrobus bartletti	20	Not measured		Felix (1954)
Flemingites schopfii	20–30	2	Langsettian	Brack (1970)
Lepidostrobus sp. U	Not measured	Not measured	Asturian	Balbach (1966)
Lepidostrobus comosus	20–40	Not measured	Asbian	Moore (1946)
Lepidostrobus cf. *squarrosus*	Not measured	Not measured	Asturian	Moore (1946)
Moscvostrobus mirabile	20–25	2–4	Serpukhovian	Naugolnykh & Orlova (2006)
Flemingites gracilis	18–21	2–3	Duckmantian	Brack-Hanes & Thomas (1983)
Flemingites scotii	20	2–4	Viséan	Scott & Hemsley (1993), Hemsley *et al.* (1996)
Lepidostrobus aristatus	26–29	Not measured	Langsettian	Hoskins & Cross (1940)
Flemingites cf. *russelianus*	26–37	1–2	Westphalian	Opluštil & Bek (2009)

Diagnosis. – Trilete pseudosaccate miospores. Circular to subcircular amb. Rays of trilete mark equal to the diameter of the inner body. The equatorial margin finely microspinate to spinate. Proximal surface microspinate to spinate except for laevigate contact area. Distal surface densely microspinate to spinate. Inner body laevigate. Exine is thicker on the distal than on the proximal hemisphere.

Microspinosporites chaloneri (Scott & Hemsley) comb. nov. emend.
Figure 1B, O

1993 *Lycospora chaloneri* Scott & Hemsley, p. 37, text-fig. 5.

Holotype. – BMNH V. 63848, Natural History Museum, London, UK.

Type locality. – Pettycur Fife, Scotland, UK.

Stratigraphic level. – Asbian.

Emended diagnosis. – Pseudosaccate trilete miospores, 13.5–25 µm in diameter. Amb roundly triangular. Rays of trilete mark equal to the diameter of the inner body. Proximal surface microspinate and spinate except for laevigate contact area. Distal surface with spinae and microspinae. Microspinate outer part of the proximal surface 2–4 µm wide.

Microspinosporites orbiculus **(Potonié & Kremp) comb. nov. emend.**
Figure 1C–E, I, J, L, N

1955 *Cyclogranisporites orbiculus* Potonié & Kremp, p. 63, pl. 13, figs 179–183.
1967 *Lycospora orbicula* (Potonié & Kremp) Smith & Butterworth, p. 249, pl. 20, figs 16–19.

Holotype. – Potonié & Kremp, 1955, pl. 13, fig. 179. Preparation 607/2, KT 16.6 110.0.

Type locality. – Baldur Seam, Brassert Colliery, Ruhr Coalfield, Germany.

Stratigraphic level. – Lower Bolsovian.

Emended diagnosis. – Pseudosaccate trilete miospores, 20–35 μm in diameter. Amb circular to oval, margin microspinate. Laesurae simple, equal to the radius of the inner body, sometimes indistinct. Distal surface microspinate, proximal surface microspinate except for laevigate contact area. Distal exine thicker than exine of the proximal surface. Curvaturae sometimes developed. Contact area from three-quaters to the whole radius. Narrow folds commonly occur.

Remarks. – *M. orbiculus* is slightly larger (20–35 μm) than *M. chaloneri* (13.5–25 μm). Another difference is, that the contact area of *M. chaloneri* is more developed and more prominent. The sculpture elements of *M. chaloneri* are generally longer (microspinae and spinae) than those of *M. orbiculus* (only microspinae).

Conclusions

Microspinosporites belong to the group of pseudosaccate genera, especially with *Grandispora* (Hoffmeister *et al.*) McGregor, *Geminospora* (Balme) Playford, *Leiozonotriletes* Hacquebard, *Spelaeotriletes* Neves & Owens. The suprasubturma Pseudosaccititriletes was proposed for: "Trilete spores with a well-developed cavity separating any two layers of the exine and which do not have, in addition, a solid flange. The exine may have a sculpture, infrastructure or both." For discussion and comparison with similar taxa see Richardson (1965, pp. 584, 585).

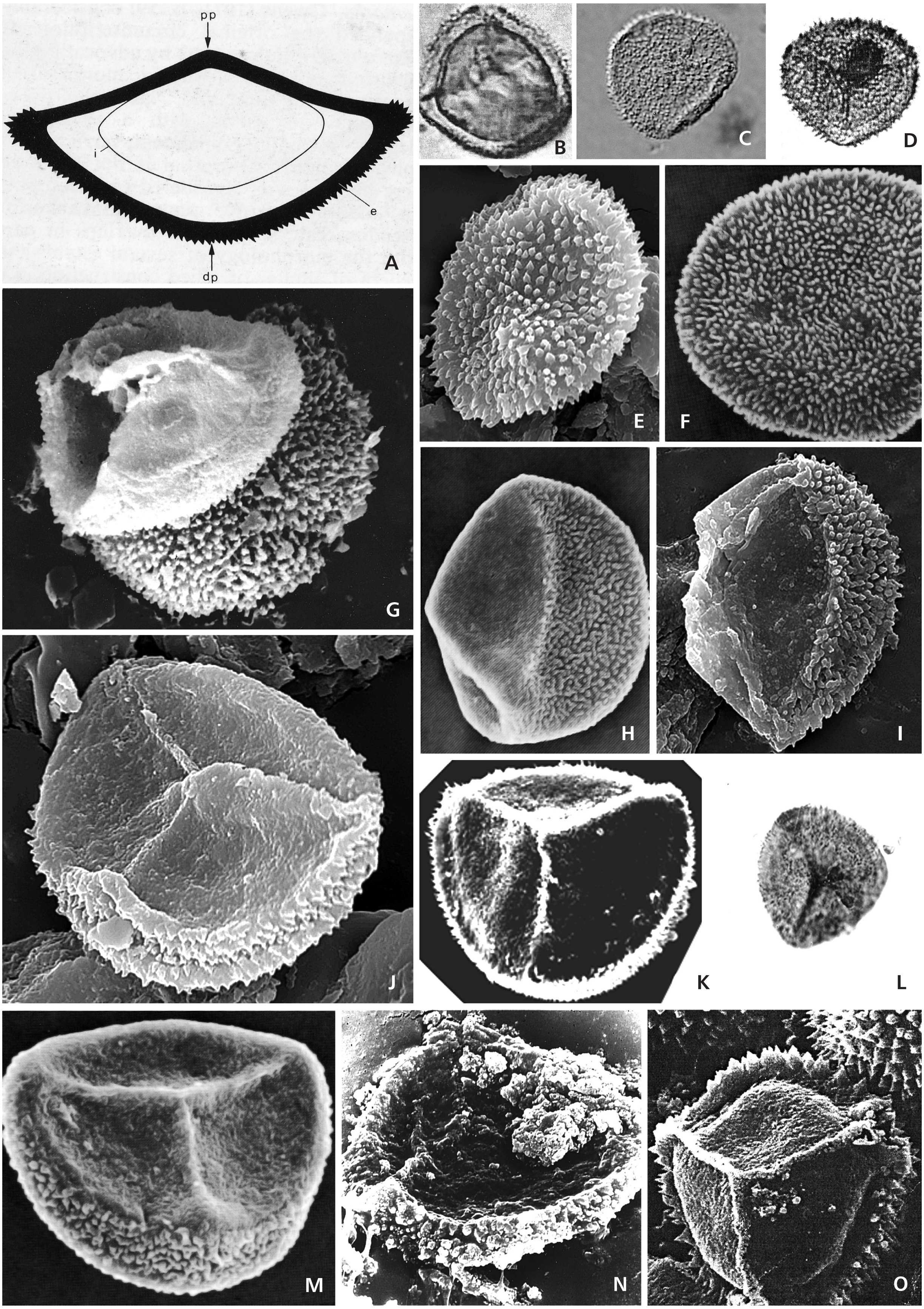
The most similar are some species of the genera *Leiozonotriletes, Geminospora* and *Grandispora*. All these genera are characteristic by central body outline, which are not always distinct and are often not comformable with the equatorial outline which has a variable sculpture.

It seems that there are two types of microspinate/spinate and microgranulate mio- and microspores formerly assigned to the dispersed genus *Lycospora*, *i.e.* *L. granulata*, *L. orbicula* and *L. chaloneri*. *Lycospora granulata* probably possesses a narrow cingulum and the sculpture of proximal and distal surfaces is microgranulate and still represents the group of cingulate miospores *sensu* Bek (2012). *Lycospora orbicula* and *L. chaloneri* are pseudosaccate (Fig. 1A) with a densely microspinate/spinate distal surface, microspinate/spinate proximal surface except for the laevigate contact area and without cingulum. Both species are referred to the new genus *Microspinosporites*.

In situ microspores isolated from *Lepidostrobus oldhamius* (associated with *Lepidophloios hallii* Evers) by Willard (1989a) and Courvoisier & Phillips (1975, in part) are cingulate with microspinate/microgranulate proximal and distal surfaces and probably correspond to the dispersed miospore species *L. granulata*.

In situ microspores isolated from bisporangiate cones *F. diversus* (Felix 1954, Courvoisier & Phillips 1975), *F. russelianus*, *F. olryi*, *F. dubius* (Chaloner 1953), *L.* sp. A (Hagemann 1966), *Flemingites schopfii* (Brack 1970),

Figure 1. A – diagrammatic polar section of *Geminospora lemurata* Balme which corresponds to a section of the genus *Microspinosporites* gen. nov. Legend: pp – proximal pole; dp – distal pole; i – intexine; e – exoexine. From Playford (1983), fig. 5. • B – *in situ Microspinosporites chaloneri* (Scott & Hemsley) comb. nov. emend. isolated from *Flemingites scotii* Jongmans. Notice the prominent inner body and the absence of a cingulum. From Balbach (1966), pl. 2, fig. 2. × 1000. • C – microspinate distal surface of dispersed *Microspinosporites orbiculus* (Potonié & Kremp) comb. nov. emend. from the Ovčín locality, Radnice Basin, Czech Republic. × 1000. • D – proximal view of dispersed *Microspinosporites orbiculus* (Potonié & Kremp) comb. nov. emend. Notice the inner body and the microspinate outer margin. From Ravn (1986), pl. 18, fig. 4. × 1000. • E – microspinate distal surface of *Microspinosporites orbiculus* (Potonié & Kremp) comb. nov. emend. from the Ovčín locality, Radnice Basin, Czech Republic. SEM, × 2000. • F – microspinate distal surface of *Geminospora lemurata* Balme. From Playford (1963), fig. 9B. SEM, × 1200. • G – *Microspinosporites orbiculus* (Potonié & Kremp) comb. nov. emend. *in situ* microspores isolated from *Flemingites lycopoditis* Feistmantel (No. 3536), Krčelák locality, Lubná, Rako Mine, Kladno-Rakovník Basin (Bolsovian). Notice the microspinate sculpture of the distal surface (right) and the sculpture of the proximal surface. The laevigate contact area makes about two-thirds of the radius, proximal surface (left) except for contact area is densely microspinate. SEM, × 2000. • H – semi-lateral view on dispersed *Geminospora lemurata* Balme. Notice the laevigate proximal surface (left) and the densely microspinate part of the distal hemisphere (right). From Playford (1963), fig. 6C. SEM, × 1000. • I – semi-lateral view of dispersed *Microspinosporites orbiculus* (Potonié & Kremp) comb. nov. emend. from the Ovčín locality, Radnice Basin, Czech Republic. Notice the laevigate proximal surface (left) and the densely microspinate part of the distal hemisphere (right). SEM, × 2000. • J – semi-lateral view of dispersed *Microspinosporites orbiculus* (Potonié & Kremp) comb. nov. emend. from the Ovčín locality, Radnice Basin, Czech Republic. Notice the laevigate proximal surface (upper) and the densely microspinate part of the distal hemisphere (lower). SEM, × 2000. • K – proximal surface on *in situ Geminospora lemurata* Balme, isolated from *Bisporangiostrobus harissii* Chitaley & McGregor. Notice the laevigate proximal surface and the microspinate/spinate margin. SEM, × 1000. • L – proximal view of *in situ Microspinosporites orbiculus* (Potonié & Kremp) comb. nov. emend. isolated from *Flemingites lycopoditis* Feistmantel (No. 3536), Krčelák locality, Lubná, Rako Mine, Kladno-Rakovník Basin (Bolsovian), × 2000. • M – semi-lateral view on dispersed *Geminospora lemurata* Balme. Notice the laevigate proximal surface and the densely microspinate part of the distal hemisphere. From Playford (1963), fig. 6F. SEM, × 1000. • N – semi-lateral view of *in situ Microspinosporites orbiculus* (Potonié & Kremp) comb. nov. emend. isolated from *Flemingites lycopoditis* Feistmantel (No. 3536), Krčelák locality, Lubná, Rako Mine, Kladno-Rakovník Basin (Bolsovian). Notice the laevigate proximal surface and the densely microspinate part of the distal hemisphere. SEM, × 2000. • O – proximal surface of *Microspinosporites chaloneri* (Scott & Hemsley) comb. nov. emend. Notice the laevigate contact area, which makes about three-quarters of the radius, the developed labrum and the microspinate part of the proximal surface. From Hemsley *et al.* (1993), fig. 6. SEM, × 2000.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F. gracilis (Brack-Hanes & Thomas 1983), *F. lycopoditis* (Bek & Opluštil 1998) and *F.* cf. *russelianus* (Opluštil & Bek 2009) are pseudosaccate, with microspinate distal and proximal surfaces except for the contact area and have no cingulum. All of them correspond to the new miospore genus *Microspinosporites*.

It seems, that some other pseudosaccate miospore genera, *e.g*. *Geminospora, Grandispora* and *Leiozonotriletes* have similar morphology to *Microspinosporites*. Playford (1983, pp. 312–316) in emendation of generic diagnosis of *Geminospora* mentioned the occurrence of curvaturae, a contact area occupying most or the whole proximal surface. The same type of sculpture elements on the distal surface and the same sculpture on the proximal surface is developed and the inner body can occupy 60 to 98 per cent of spore cavity. *Geminospora* usually possesses a thicker exine and a larger diameter. Specimens of *Geminospora* show a more prominent dark ring on the margin due to the thickness of exine (from 1.5 to 7 μm), which may resemble a cingulum (*e.g*. Chitaley & McGregor 1989, pl. 10, figs 7–12), but, in fact, this represented a prominent curvaturae delimitating the contact area. SEM photomicrographs of dispersed (*e.g.* Playford 1983, figs 6–9; Fig. 1F, H, M) and *in situ Geminospora* (Chitaley & McGregor 1989, Fig. 1K herein) are morphologically very similar (sometimes even identical) to mio- and microspores of *Microspinosporites*. Distal surfaces of both genera (Fig. 1E, F) are the same, lateral views (Fig. 1H, I) are closely similar as well as proximal sculptures (Fig. 1G, J, K, M–O).

Microspinosporites-producing cones belong to the bisporangiate genera *Flemingites* and probably *Moscvostrobus,* born on arborescent lycopsids of the *Paralycopodites*-type.

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