

Systematic study and stratigraphic correlation of the *Grandispora* complex in the Famennian of northwest and eastern Europe

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Abstract

In northwest and eastern Europe different miospore zonation schemes have been erected for the Famennian rocks, and correlation of these has proved problematical. However, in both regions of Europe *Grandispora* taxa are common elements in the respective Famennian spore successions, and it appears these taxa may have important intra-continental correlation potential. In order to assess this potential, a C.I.M.P. working group has undertaken a taxonomic study of the *Grandispora* complex in the Famennian of both regions. Representative material from Belarus, Poland, Germany, Belgium, France and Ireland has been exchanged, and then jointly studied, at four workshop meetings. A consensus of agreement has been reached on the morphological delineation and nomenclature of 13 species of *Grandispora*, and a description of each taxon is presented. One new species *Grandispora tamarae* is erected, and six new generic combinations are proposed. The stratigraphic range of each species in both regions is documented and calibrated with the respective conodont zonation schemes. It can be shown that many of the *Grandispora* species seem to have their first occurrence at similar stratigraphic levels. These new data allow detailed correlations of the Famennian miospore zonation schemes to be proposed. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: biostratigraphy; Europe; Famennian; *Grandispora*; systematics

1. Introduction

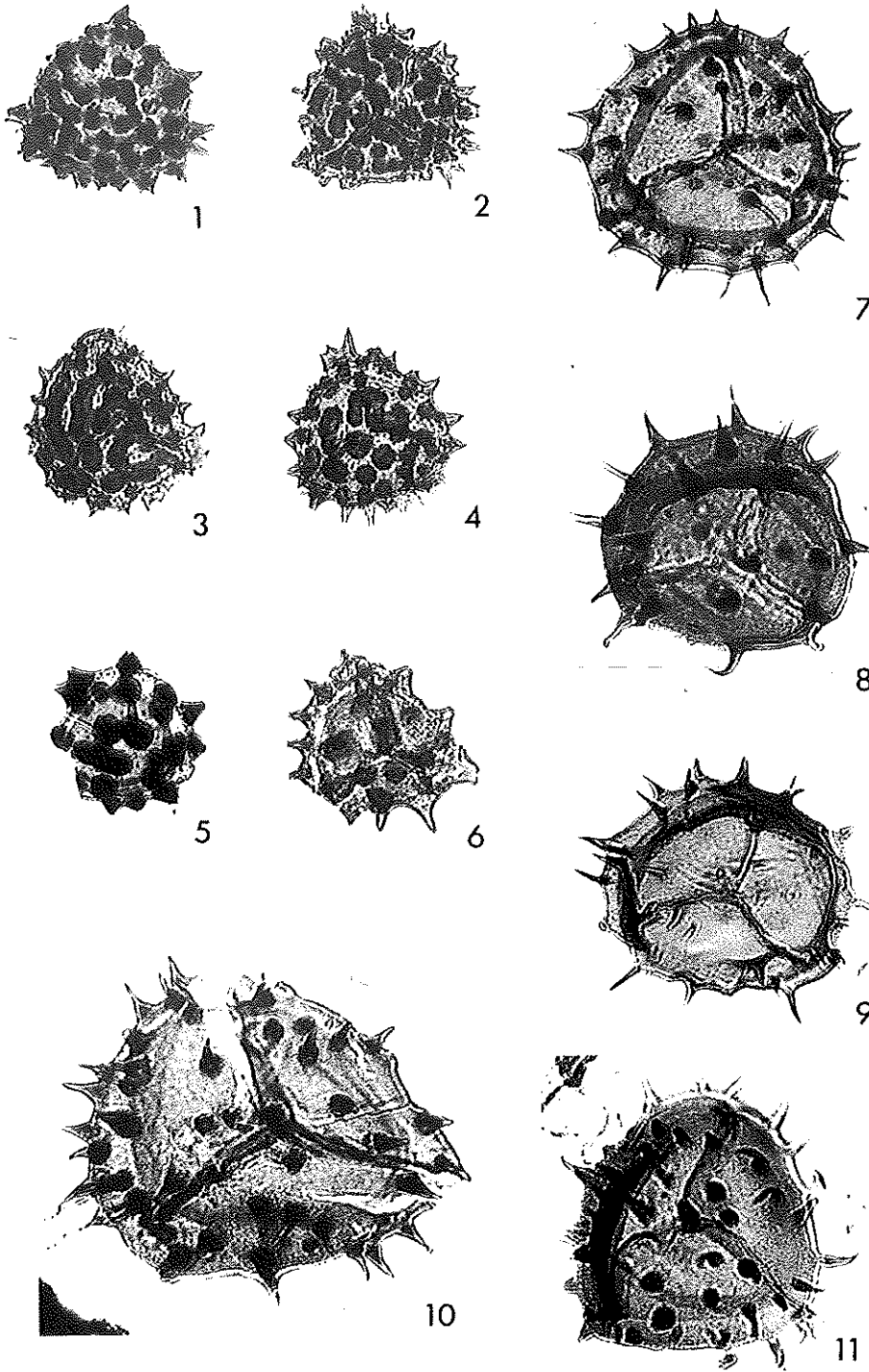
This paper presents the results of the Commission Internationale de Microflore du Paléozoïque (C.I.M.P.) working group study of the *Grandispora* miospore complex occurring in

Famennian strata in selected regions of northwest and eastern Europe. Previous palynological studies of the Famennian in these two areas of Europe have produced two very different miospore zonation schemes. For instance, in northwest Europe the Famennian miospore zonation scheme has been developed from studies in Ireland, Britain, France, Belgium and the western part of Germany, and has been described by Streeel et al. (1987),

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PLATE I



Higgs et al. (1988) and revised by Maziane et al. (1999). Meanwhile in eastern Europe a Famennian miospore zonation scheme has been described by Avkhimovitch (1986, 1993), Avkhimovitch et al. (1989, 1993), mainly from Belarus (Pripyat Depression). There are significant differences between the two miospore zonation schemes, and consequently previous attempts at zonal correlations have proved to be very difficult. Strel and Loboziak (1996) have indicated that the main reason for these differences is the existence of two major phytogeographic provinces in this area in Famennian times, with the western European microfloras being related to a Southern Euramerica–Western Gondwana phytogeographic province and the eastern European microfloras being related to a Northern Euramerica phytogeographic province. It is also clear that the problems caused by these phytogeographic differences have in the past been compounded by the use of different taxonomic, nomenclatural and zonal concepts by eastern and western palynologists.

In both regions of Europe *Grandispora* taxa are common elements in the Famennian spore successions, and many of these taxa have been used as zonal index species in the respective spore zonation schemes. Therefore, the *Grandispora* complex may have important intra-continental correlation potential. In order to assess this potential, a C.I.M.P. working group has undertaken a taxonomic study of the *Grandispora* complexes occurring in the Famennian of both regions. Since 1990, representative material from Belarus, Poland,

Germany, Belgium, France and Ireland has been exchanged and then jointly studied by western and eastern European palynologists at four workshop meetings in Krakow, Lille and Liège (two). A consensus of agreement has been reached on the morphological delineation and nomenclature of 13 species of *Grandispora*. The stratigraphical ranges of these taxa have been determined carefully in each region, which has allowed more accurate and meaningful correlations to be made with the Famennian successions and zonation schemes.

2. Systematic descriptions

The *Grandispora* species studied are formally described in alphabetical order and illustrated in Plates I–VI

Anteturma SPORITES H. Potonié, 1893.

Turma TRILETES (Reinsch) Dettmann, 1963.

Suprasubturma CAMERATITRILETES Neves & Owens, 1966.

Subturma SOLUTITRILETES Neves & Owens, 1966.

Infraturma DECORATI Neves & Owens, 1966.

Genus: Grandispora Hoffmeister et al., 1955 emend McGregor, 1973.

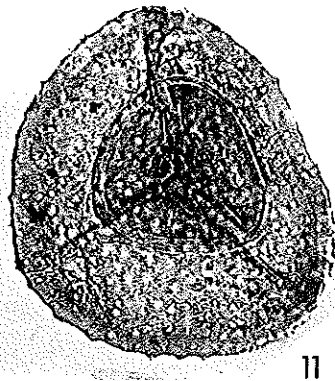
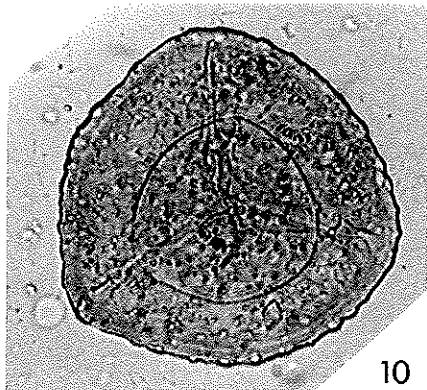
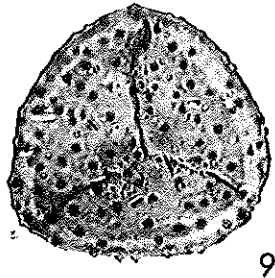
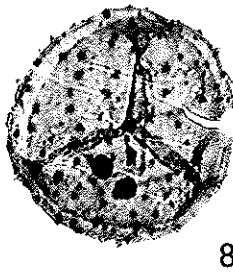
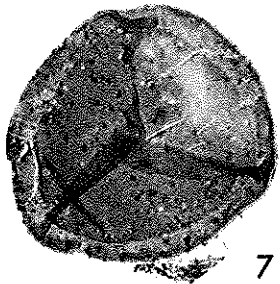
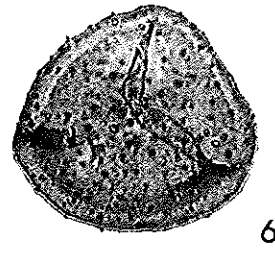
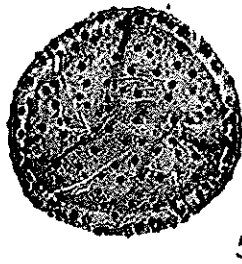
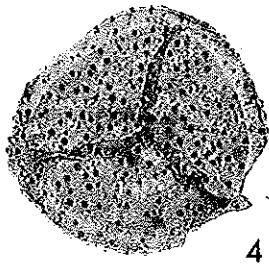
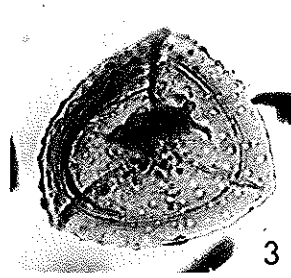
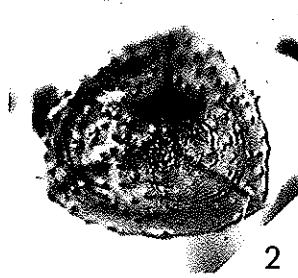
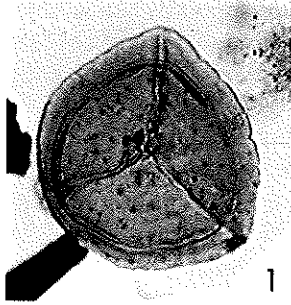
Type: Grandispora spinosa Hoffmeister et al., 1955.

Comments: The authors are in broad agreement with the emended generic diagnosis of McGregor (1973), particularly with reference to the removal of criteria such as: (1) the degree of attachment

PLATE I

- 1–6. *Grandispora acuta* (Kedo) Byvscheva 1980.
 1. North Ringabella, Ireland, NR 49(J) 2571293 US.
 2. South Ringabella, Ireland, SR 23(D) 1721263 US.
 3. South Ringabella, Ireland, SR 23(C) 2721238 US.
 4. South Ringabella, Ireland, SR 23(D) 5841348 US.
 5. South Ringabella, Ireland, SR 23(C) 2721238 US.
 6. South Ringabella, Ireland, SR 23(C) 4031217 US.
- 7–11. *Grandispora cornuta* Higgs 1975.
 7. Hook Head, Ireland, HK3 ML 1104 US.
 8. Hook Head, Ireland, HK3 4331278.
 9. Hook Head, Ireland, HK3 ML 1102 US.
 10. Hook Head, Ireland, HK32 3301122.
 11. Hook Head, Ireland, HK3 ML 1116 US.

PLATE II



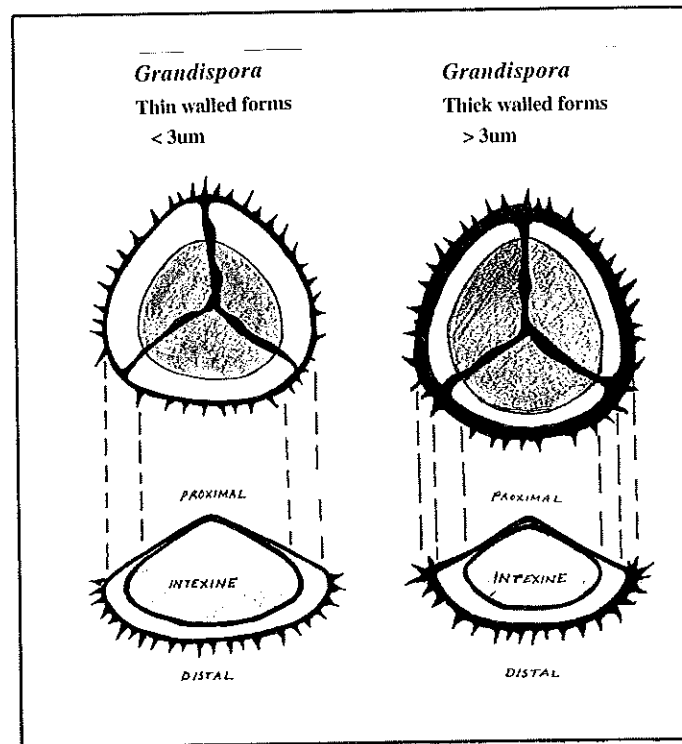


Fig. 1. The two broad morphological groups of *Grandispora* identified in the study.

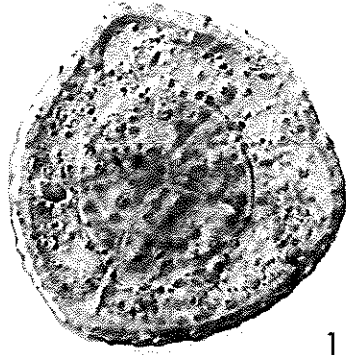
between the intexine/exoexine layers; (2) the extent of the cavity between wall layers, for generic diagnosis. However, the authors concur with the view of Playford (1976) in rejecting the synonymy of *Samarisporites* Richardson 1965 with *Grandispora*, and also the inclusion of forms with bifurcating spines in *Grandispora*.

In the present study, a large number of specimens have been studied and these exhibit wide variability in exoexine thickness. Two broad morphological groupings have been identified (see Fig. 1). These are: (1) forms with a relatively thin ($< 3 \mu\text{m}$) exoexine (usually less than $2 \mu\text{m}$); and (2) forms with a relatively thick ($> 3 \mu\text{m}$) exoexine.

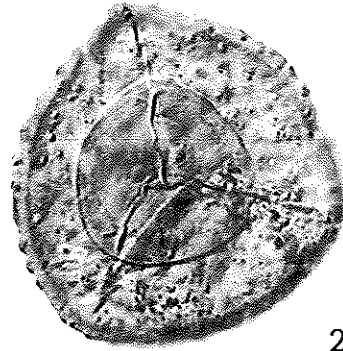
PLATE II

- 1–3. *Grandispora distincta* (Naumova) Avkhimovitch 1993.
 1. Borisov B/H, Belarus, 48/1, 572–577 m, H28/2.
 2. Borisov B/H, Belarus, 48/1, 572–577 m, D27.
 3. Borisov B/H, Belarus, 48/1, 572–577 m, D27.
- 4–9. *Grandispora echinata* Hacquebard 1957.
 4. Hook Head, Ireland, 76/1411(A) 7651050 GSI.
 5. Hook Head, Ireland, H8(E) 4101390 US.
 6. Hook Head, Ireland, H8(E) 3971262 US.
 7. South Ringabella, Ireland, SR35(A) 3821235 US.
 8. Hasselbachtal, Germany, HB18–19(A) 1821075 GSI.
 9. Hook Head, Ireland, H8(A) 5211270 US.
- 10 and 11. *Grandispora facilis* (Kedo) Avkhimovitch 1988.
 10. Starobin B/H, Belarus, 239, 289–293.2 m, L19.
 11. Starobin B/H, Belarus, 239, 239 m, Q30/1.

PLATE III



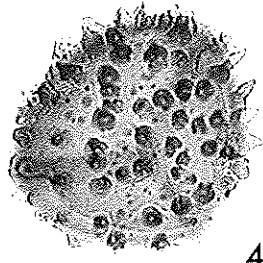
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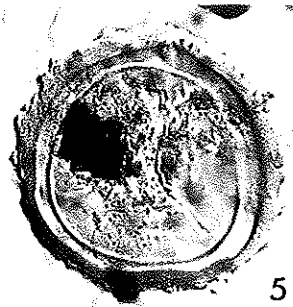
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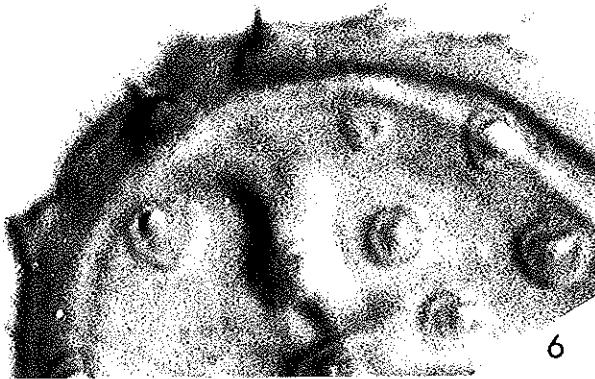
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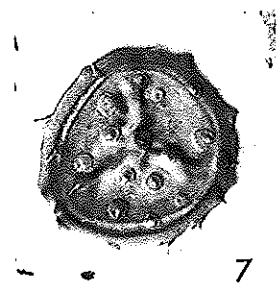
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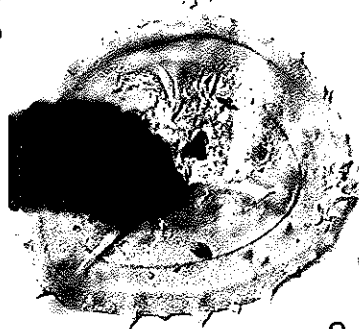
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8



9

These thicker walled forms are very similar in structure to *Geminospora* Balme 1962, however, assignment to *Geminospora* is precluded by Playford's (1983) restated generic diagnosis, which restricted this genus to forms with short (minute) spinae, coni and grana.

The principal morphological criteria adopted in the study to differentiate between the various *Grandispora* species are: (1) exoexine wall thickness; (2) exoexine/intexine ratio; and (3) ornament type, size and distribution. The morphological characteristics of each *Grandispora* species studied are summarised in Fig. 2

Grandispora acuta (Kedo) Byvscheva, 1980 (Plate I, 1–6).

Basionym: *Archaeozonotriletes acutus* Kedo, 1963, Rep. Palaeontol. Stratigr. Byelorussian S.S.R. 4, p. 71, pl. 7, fig. 167.

1980 *Grandispora acuta* (Kedo) Byvscheva, p. 55.

1980 *Asperispora acutus* (Kedo) Van der Zwan, p. 226, pl. 13, figs. 1–5.

1985 *Cymbosporites acutus* (Kedo) Byvscheva, p. 127, pl. 24, fig. 13.

1988 *Spinozonotriletes sawotus* Higgs, Clayton & Keegan, p. 77, text-fig. 28c, pl. 15, figs. 1–3, 7.

1993 *Grandispora sawota* (Higgs, Clayton & Keegan) Playford & McGregor, pp. 38–39, pl. 17, figs. 1–11.

Description: Trilete camerate miospores. Amb convexly triangular. Suturæ distinct and accompanied by flexuous labra, 2–4.5 µm in height, and extending 3/4 or more of the spore radius. Exoexine infragranulate, 1.5–3 µm thick, ornamented equatorially and distally with galeae and insubordinate wide based spines and cones. Elements typically

subcircular in basal outline, 1.5–8 µm in basal diameter, normally 3–10 µm in height, rarely up to 14 µm. Spacing of sculptural elements variable, from densely to widely spaced; discrete to basally coalescent. Intexine laevigate, thin (less than 1 µm), distinct to barely perceptible, conformable with amb and comprising 3/4 to 4/5 of the total spore radius.

Size range: 30–70 µm.

Distinguishing features: This species is distinguished by a relatively thin exoexine and a prominent ornament of bulbous to mammoid based spines.

Remarks and comparison: The camerate nature of this taxon has been confirmed in the present study. Consequently, the authors consider the generic assignment to *Grandispora* made by Byvscheva in 1980 is far more appropriate than her later assignment (Byvscheva, 1985) to the acamerate genus *Cymbosporites*. The synonymy of *Grandispora acuta* and *Grandispora sawota*, as suspected by Playford and McGregor (1993, p. 38), has also been confirmed in the present study. *Grandispora famenensis* (Naumova) Strel comb. nov. var. *famenensis* is similar, but differs in possessing a much thicker exoexinal wall together with shorter and more swollen galeate elements.

Grandispora cornuta Higgs, 1975 (Plate I, 7–11).

1969 *Spinozonotriletes* cf. *S. uncutus* Hacquebard; Strel in Bouckaert et al. (1969, pl. 93, figs. 7, 8).

1975 *Grandispora cornuta* Higgs, pp. 398–399, pl. 4, figs. 4–6.

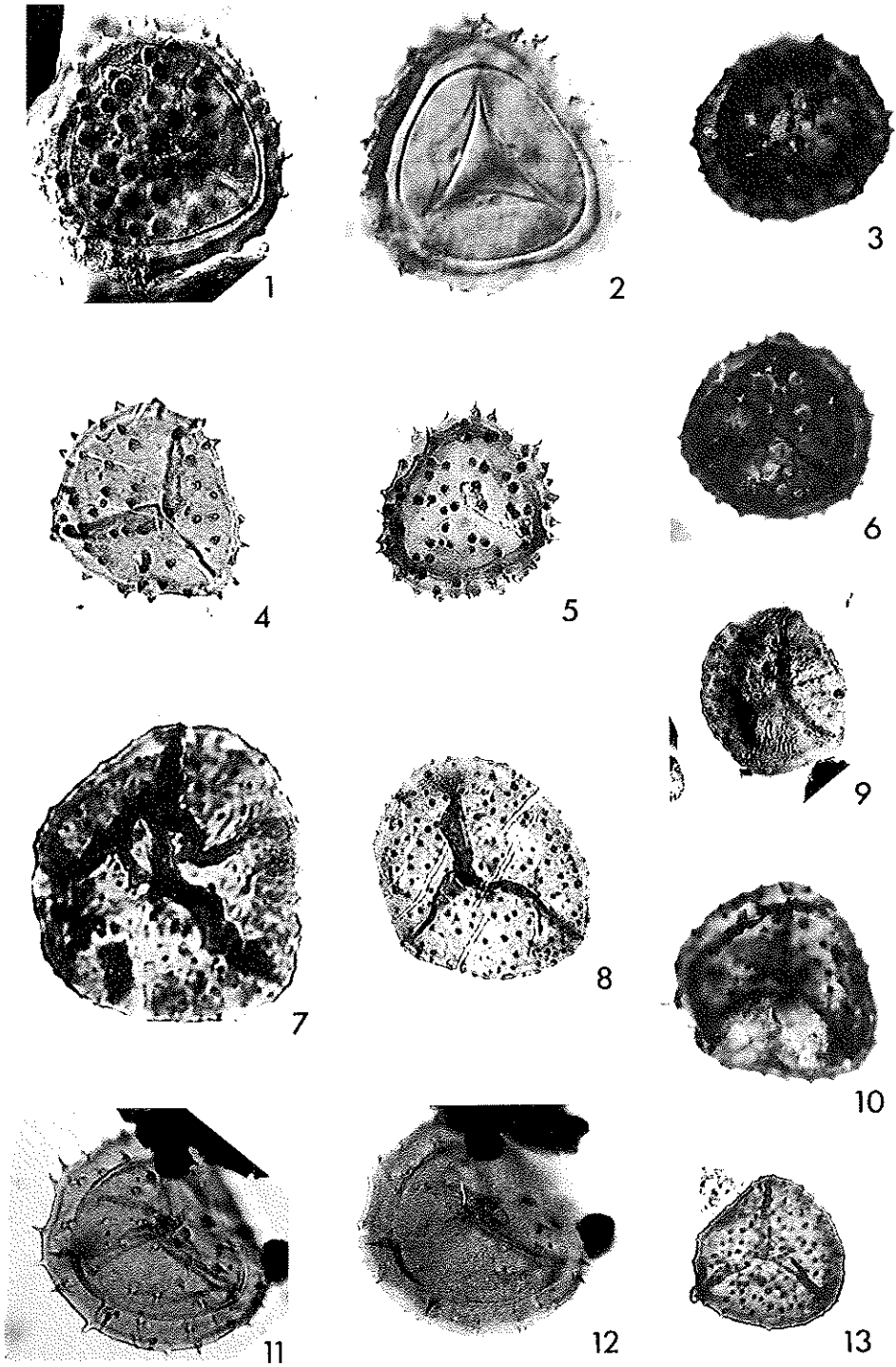
Holotype: Higgs, 1975, pl. 4, fig. 4.

Description: Trilete camerate miospores. Amb sub-

PLATE III

- 1–3. *Grandispora facilis* (Kedo) Avkhimovitch 1988.
 1. Starobin B/H, Belarus, 239, 284–293 m, S30/1.
 2. Starobin B/H, Belarus, 239, 284–293 m, S30/1.
 3. Borisov B/H, Belarus, 48/1, 574–577 m, L28/4.
- 4–9. *Grandispora famenensis* (Naumova) Strel 1974 var. *famenensis*.
 4. Hook Head, Ireland, HK.
 5. Borisov B/H, Belarus, 48/1, 572–577 m, C41/2.
 6. Borisov B/H, Belarus, 48/1, 572–577 m, H47/3.
 7. Borisov B/H, Belarus, 48/1, 572–577 m, H47/3.
 8. Borisov B/H, Belarus, 572–577 m, H47/3.
 9. Borisov B/H, Belarus, 48/1, 572–577 m, F39/1.

PLATE IV



ircular to convexly triangular. Suturae accompanied by sinuous and flexuous lips up to 6 µm in height, extending almost to the equator, and terminating in curvaturae. Intexine distinct to obscure, outline conformable with amb, but often modified by arcuate compression folds along the outer margin. Intexine large, approximately 4/5 of the total spore radius. Exoexine 1.5–2 µm in thickness, ornamented distally and equatorially with prominent spines, 5–16 µm in length. Bases of spines 2–6 µm in width, often swollen or bulbous in shape, tapering uniformly or sharply to pointed and occasionally curved tips. Spines discrete, widely but evenly distributed on the distal surface of the exoexine, with 10–22 spines prominent at the equator.

Size range: 55–84 µm.

Distinguishing features: This species is distinguished by its large, often peripherally folded intexine, a relatively thin exoexine and a prominent ornament of long bulbous based spines.

Comparison: *Grandispora cornuta* appears to be very similar to *Hymenozonotriletes subdiamphidus* Kedo, 1974, however, the spines in *G. cornuta* are more galeate. *Grandispora promiscua* Playford, 1978 also differs in possessing longer and more slender spines on the distal exoexine, together with small cones and spines on the proximal exoexine. *Grandispora senticosa* (Ishchenko) Byvscheva, 1985 differs from *G. cornuta* in being larger in size and in possessing longer slender spines.

Grandispora distincta (Naumova) Avkhimovitch comb. nov. (Plate II, 1–3).

Basionym: *Archaeozonotriletes distinctus* Naumova, 1953, Trudy Inst. geol. Nauk Mosk. 143 (Geol. Surv. 60), pl. 17, fig. 38.

1993 *Grandispora distincta* (Naumova) Avkhimovitch, pl. 1, 5. (Combination invalid, ICBN Art. 32.2.)

Description: Trilete camerate miospores. Amb subcircular to convexly triangular with apices slightly pointed. Suturae accompanied by sinuous lips 3–5 µm in height. Suturae extend almost to the equator. Intexine large forming up to 4/5 of the total spore radius, and weakly separated from the exoexine. Exoexine thickened equatorially, 4–7.5 µm in thickness. Distally and equatorially ornamented with cones 1–1.5 µm in height (rarely 2 µm). Cones discrete and well spaced.

Size range: 55–75 µm.

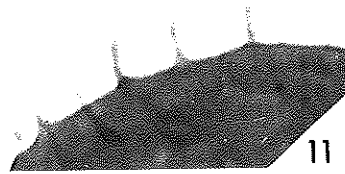
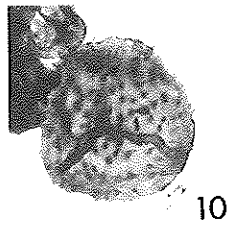
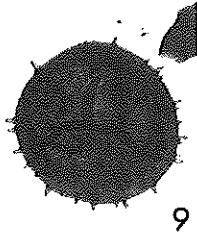
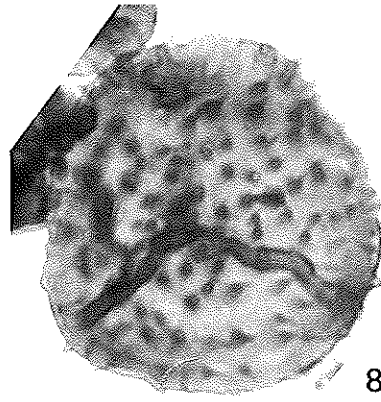
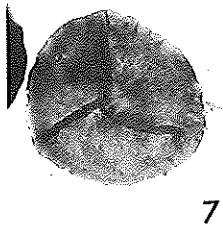
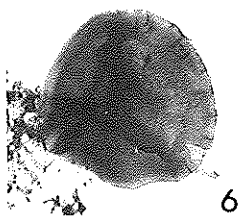
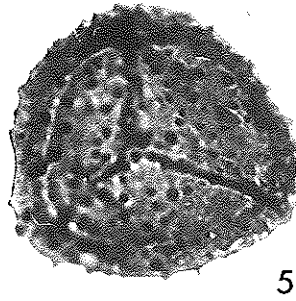
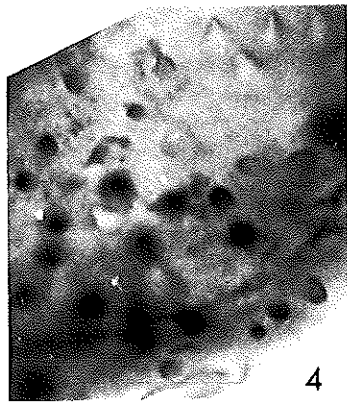
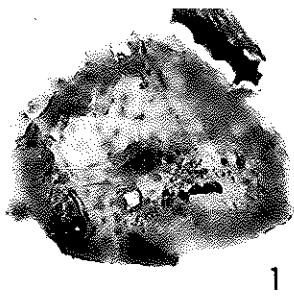
Distinguishing features: This species is distinguished by its thick exoexine, relatively large intexine and small conate ornament.

Comparison: *Archaeozonotriletes microaculeatus* Kedo, 1974 is clearly a closely related form with very similar structure and style of ornament. Its shape is slightly more rounded and there is more separation of the exine layers. Future studies may show this species to be synonymous with *Grandispora distincta*.

PLATE IV

- 1 and 2. *Grandispora famenensis* (Naumova) StreeI 1974 var. *famenensis*.
1. Starobin B/H, Belarus, 239, E53/3.
2. Starobin B/H, Belarus, 239, D40/2.
- 3–6. *Grandispora famenensis* (Naumova) StreeI 1974 var. *minuta* Nekriata 1974.
3. Esneux, Ourthe Valley, Belgium, 11(4), L46/3.
4. Hook Head, Ireland, HK23, 1661137.
5. Hook Head, Ireland, HK5, 5351124.
6. Esneux, Ourthe Valley, Belgium, 11(4), L46/3.
- 7–10. *Grandispora gracilis* (Kedo) StreeI in Becker et al. (1974).
7. Beverire, Ourthe Valley, Belgium, 47/9, 2450/139.
8. Hasselbachtal, Germany, HB18–19, 4751011.
9. Beverie Qu, Ourthe Valley, Belgium, 55, 2444/379.
10. Esneux, Ourthe Valley, Belgium, 12/2, L5/5.
- 11 and 12. *Grandispora micromulata* (Kedo) comb. nov.
11. Borisov B/H, Belarus, 48/1, 572–577, S53/1.
12. Borisov B/H, Belarus, 48/1, 572–577, S53/1.
13. *Grandispora gracilis* (Kedo) StreeI in Becker et al. (1974). Menen B/H, Belgium 201–202, Y4/8.

PLATE V



Grandispora echinata Hacquebard, 1957 (Plate II, 4–9).

1957 *Grandispora echinata* Hacquebard, p. 317, pl. 3, fig. 17.

Holotype: Hacquebard, 1957, pl. 3, fig. 17.

Description: Trilete camerate miospores. Amb subcircular to convexly triangular. Suturæ usually distinct and accompanied by flexuous labra up to 7 µm in height. Suturæ extend almost to the equator and terminate in curvaturæ imperfectæ. Exoexine thin but slightly thickened at the equator, up to 2 µm in thickness. Intexine distinct, outline conformable with amb and forming 3/4 or slightly more of the total spore radius. Ornament of small spines and cones restricted to the distal surface of the exoexine and to the equatorial regions. Spines and cones 1.5–2.5 µm in height, 1–2 µm in basal diameter. Elements discrete, not crowded, 2–6 µm apart.

Size range: 62–93 µm in Hacquebard (1957) and 50–75 µm in Playford (1964) (both in Horton Group).

Comments: The holotype from the early Mississippian Horton Group of Eastern Canada has been refigured (but not redescribed) by McGregor and McCutcheon (1988, text-fig. 4f, pl. 3, fig. 15). They also illustrated the shape and size of the ornament on the holotype (1.5–2.5 µm in basal width and up to 2.5 µm in height).

Distinguishing features: This species is distinguished by the possession of a thin exoexine, a relatively large and clearly defined intexine, and

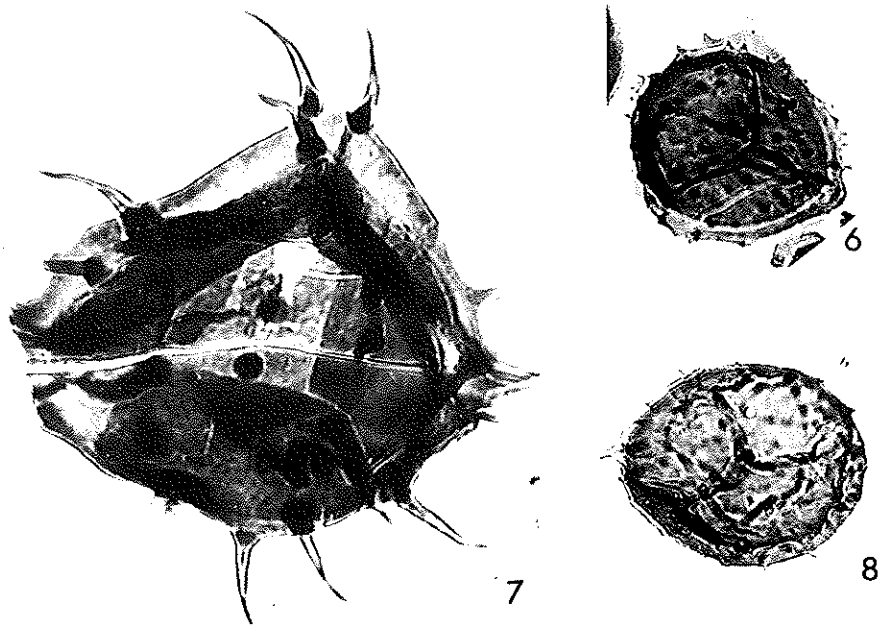
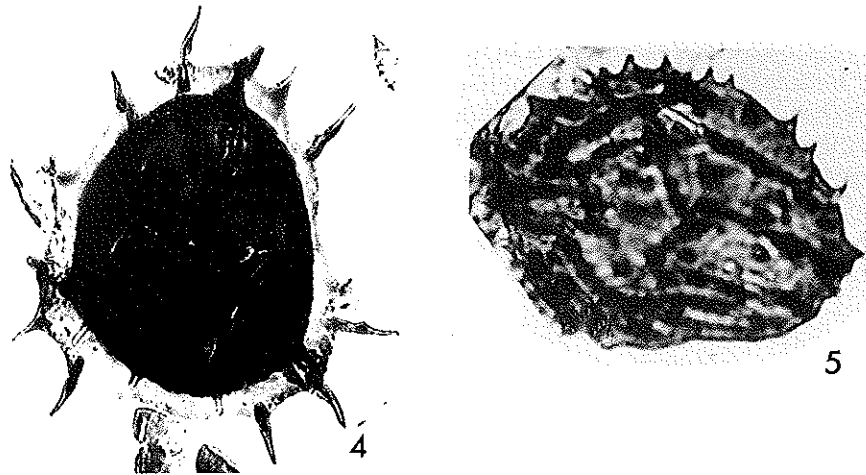
discrete conate and spinose ornament ranging from 1.5 to 2.5 µm in height.

Comparison: The specimens described and figured as *Spelaeotriletes echinatus* by Utting (1987, p. 89, pl. 4, figs. 9–12) from the Viséan Windsor Group of Eastern Canada appear to be slightly different from the type material from the older Horton Group, in that the Windsor Group specimens appear to have a more robust and variable ornament and a thicker and more rigid exoexine. The specimens described as *Grandispora echinata* in Playford and McGregor (1993) from the Bakken Formation of Southern Saskatchewan also differ from the type material in having a larger intexine/exoexine ratio (80/90%) and possessing coarser ornament (up to 4 µm in height). Byvscheva (1985) and Playford and McGregor (1993) have suggested that *Grandispora echinata* may be synonymous with *Acanthozonotriletes spinosus* Ishchenko, 1956, and if this was confirmed then *A. spinosus* would have nomenclatural priority over *G. echinata*. In the present study it has not been possible to determine the morphological relationship between these two taxa. However, we note that if synonymy is proven in the future then taxonomic complications will arise, as the newly created binomen will become a junior homonym of the type species *G. spinosa* Hoffmeister 1955. *G. echinata* differs from *Grandispora gracilis* (Kedo) Strel comb. nov. in having coarser ornament (1.5–2.5 µm in *G. echinata*), it is also larger in size, and possesses a slightly smaller and more distinctly separated intexine.

PLATE V

- 1–5. *Grandispora lupata* Turnau 1975.
1. Gorzyslawr B/H, Belarus, 3183–3201, F2/15.
2. Gorzyslawr B/H, Belarus, 3183–3201, F2/19.
3. Gorzyslawr B/H, Belarus, 3183–3201, F2/19.
4. Gorzyslawr B/H, Belarus, 3183–3201, F2/20, × 1500.
5. Pomerania, Poland, G9 11/1, 16/34.
- 6–11. *Grandispora microseta* (Kedo) Strel in Becker et al. (1974).
6. Menen B/H, Belgium, 201–202, F35/4.
7. Menen B/H, Belgium, 201–202, W1/4.
8. Menen B/H, Belgium, 201–202, F15/4, × 1000.
9. Chera Qu, Belgium, CHE3, 3549/665.
10. Menen B/H, Belgium, 201–202, F15/4.
11. Menen B/H, Belgium, 201–202, F35/4, × 1250.

PLATE VI



Grandispora facilis (Kedo) Avkhimovitch in Avkhimovitch et al. (1988) (Plate II, 10 and 11; Plate III, 1–3).

- 1957 *Hymenozonotriletes facilis* Kedo, p. 24, pl. 3, fig. 2.
 1957 *Hymenozonotriletes flavus* Kedo, p. 22, pl. 2, fig. 12.
 1957 *Hymenozonotriletes ventosus* Kedo, p. 24, pl. 3, fig. 1.
 1974 *Grandispora* sp. A Becker et al., p. 26, pl. 19, figs. 4, 5.
 1971 *Grandispora notensis* Playford, pp. 48–49, pl. 16, figs. 3, 4; pl. 17, fig. 16.
 1974 *Archaeozonotriletes flavus* (Kedo) Kedo, pp. 54–55, pl. 13, figs. 9–11.
 1976 *Grandispora notensis* Playford; Playford, pl. 8, fig. 12, 24–26; pl. 9, figs. 1–3.
 1988 *Grandispora facilis* (Kedo) Avkhimovitch in Avkhimovitch et al., p. 172.
 1993 *Grandispora flavus* (Kedo) Avkhimovitch, pl. 1, fig. 11.

Description: Trilete camerate miospores. Amb convexly triangular. Suturae accompanied by sinuous and flexuous labra, extending almost to the equator. Intexine distinct, outline conformable with amb, forming 1/3 to 2/3 the total spore radius. Exoexine lighter in colour and thickness, equatorially 2–3 µm in thickness. Distal surface of exoexine and equatorial regions ornamented with discrete cones, 1.5–5 µm in height and 1–3 µm in basal diameter. Cones usually well spaced and evenly distributed. Small spines occasionally present.

Size range: 70–85 µm.

Comment: A complete morphological gradation has been observed by Avkhimovitch between the three Russian species *Hymenozonotriletes facilis*, *Hymenozonotriletes flavus* and *Hymenozonotriletes ventosus*. Consequently, they are now included in one species: *Grandispora facilis*.

Distinguishing features: This species is distinguished by its thick exoexine, and relatively small exoexine which bears a well spaced ornament of small cones.

Comparison: The specimens figured by Playford in 1971 (pl. 16, figs. 3, 4; pl. 17, fig. 16) and in 1976 (pl. 8, figs. 12, 24–26; pl. 9, figs. 1–3) as *Grandispora notensis* respectively from the Lower Carboniferous of the Bonaparte Gulf Basin of Western Australia and Northern Territory and the Upper Devonian and Lower Carboniferous of the Canning Basin of Western Australia appear to be identical in morphology to *Grandispora facilis*. *Grandispora sola* Braman and Hills, 1992 from the Frasnian of Northwest Canada is very similar in structure and ornament distribution and differs only in the slightly smaller size (up to 2 µm) of the echinate elements, this species may prove to be synonymous with *G. facilis*. Specimens figured as *Grandispora* sp. A respectively in Becker et al. (1974, pl. 19, figs. 4, 5) and in Van der Zwan (1980, pl. 18, fig. 1) appear to be identical in structure and ornament to *G. facilis*. Both types possess three apical papillae. *Grandispora clandestina* Playford, 1976 has a similar ornamentation but is much smaller in size, and possesses a larger and rather indistinct intexine.

Grandispora famenensis (Naumova) Strel comb. nov. var. *famenensis* (Plate III, 4–9; Plate IV, 1 and 2).

Basionym: *Archaeozonotriletes famenensis* Naumova, 1953, Trudy Inst. geol. Nauk Mosk. 143 (Geol. Surv. 60), p. 117, pl. 17, figs. 31–34.

- 1957 *Archaeozonotriletes consimilis* Kedo, pl. 4, fig. 1.
 1957 *Archaeozonotriletes serenus* Kedo, pl. 3, fig. 25.
 1963 *Archaeozonotriletes macrospinosus* Kedo var. *punctatus* Kedo, pl. 7, figs. 177–179.
 1963 *Archaeozonotriletes devonicus* Kedo var. *punctatus* Kedo, pl. 7, figs. 175, 176.

PLATE VI

- 1–3. *Grandispora minuta* (Kedo) comb. nov.
 1. Shestkovichi B/H, Belarus, 3247/85, C54/3.
 2. Shestkovichi B/H, Belarus, 3247/85, C54/3.
 3. Litkovitchi B/H, Belarus, 505, 302, C56/3.
 4. *Grandispora senticosa* (Ishchenko) Byvscheva, 1985. Hook Head, Ireland, HK2 4521320 US.
 5 and 6. *Grandispora tamarae* sp. nov.
 5. LaGombe, Ourthe Valley, Belgium, Go37, 2393/679.
 6. Hook Head, Ireland, HK, ML1106 US.
 7. *Grandispora senticosa* (Ishchenko) Byvscheva, 1985. Hook Head, Ireland, HK3 4331278 US.
 8. *Grandispora tamarae* sp. nov. Hook Head, Ireland, HK27, 2351233.














TAXA	EXINE FEATURES	ORNAMENT SHAPE/HEIGHT
<i>Grandispora acuta</i>	Exo 1.5-3 μ , Int 75-90%	 3-10 μ
<i>G. cornuta</i>	Exo 1.5-2 μ , Int 75-90%	 6-16 μ
<i>G. distincta</i>	Exo 4-7.5 μ , Int 90%	 1-2 μ
<i>G. echinata</i>	Exo 1-2 μ , Int 75-80%	 1.5-2.5 μ
<i>G. facillis</i>	Exo 2-3 μ , Int 33-66%	 2-3 μ
<i>G. famenensis</i>	Exo 3-6 μ , Int 75-90%	 1.5-6 μ
<i>G. gracilis</i>	Exo 2 μ , Int 90%	 1-1.5 μ
<i>G. lupata</i>	Exo 5-10 μ , Int 75%	 2-3 μ
<i>G. micronulata</i>	Exo 2-3 μ , Int 75%	 2-5 μ
<i>G. microseta</i>	Exo 2 μ , Int 75-90%	 3-5 μ
<i>G. minuta</i>	Exo 1.5-3 μ , Int 90%	 1-1.5 μ
<i>G. senticosa</i>	Exo 2-3 μ , Int 50-90%	 5-20 μ
<i>G. tamarae</i>	Exo 2 μ , Int 90%	 2-5 μ

Fig. 2. Morphological characteristics of each *Grandispora* species studied.

1974 *Grandispora famenensis* (Naumova) Streef in Becker et al., p. 26, pl. 19, figs. 9–11. (Combination invalid, ICBN Art. 32.2.)

1976 *Archaeozonotriletes consimilis* Kedo var. *asper* Avkhimovitch, pl. 2, figs. 1, 2.

Description: Trilete camerate miospores. Amb convexly triangular. Suturae distinct, accompanied by

lips of variable width, straight to sinuous and extending almost to the equator. Curvaturae observed in some specimens. Intexine conformable with amb, large, forming 3/4 to 4/5 of the total spore radius. Intexine usually distinct with a small separation from exoexine. Exoexine thickened equatorially forming a 3–6 μ m thick exoexine wall.

Distal surface of exoexine and equatorial region ornamented with prominent galeae. Elements up to 6 μm in height (typically 4–5 μm); bases broad and swollen, 4–8 μm in width, surmounted by short spinose tips. Elements discrete and uniformly spaced 3–12 μm apart.

Size range: 55–(70)–85 μm .

Distinguishing features: The thick exoexine, distinct intexine and broad to bulbous galeae distinguish this species from others of the genus. The variety *famenensis* is characterised by prominent based galeae 4–6 μm in height.

Comment: No holotype was designated by Naumova (1953), therefore a neotype is proposed here (Plate IV, 2). A number of varieties, e.g. *minuta*, *gracilis* (based on size variations in spore diameter and ornament), have been described for the species by various eastern European palynologists. The creation of these varieties automatically established the taxon *Grandispora famenensis* var. *famenensis*. As the latter is an autonym, this new variety epithet does not require authorship.

Grandispora famenensis (Naumova) Streef comb. nov. var. *minuta* Nekriata, 1974 (Plate IV, 3–6).

1974 *Archaeozonotriletes famenensis* Naumova var. *minutus* Nekriata, p. 91, pl. 25, figs. 3–5.

Holotype: Nekriata, 1974, pl. 25, fig. 5.

Description: Trilete camerate miospores. Amb convexly triangular. Suturae distinct straight accompanied by narrow labra, extending almost to the equator and terminating in curvaturae imperfectae. Exoexine 1.5–3 μm in thickness. Distal surface of exoexine and equatorial regions ornamented with small galeae, 1.5–3 μm in height (typically 2 μm) and 1.5–3 μm in basal width. Galeae broad to bulbous based, normally discrete, rarely fused and well spaced. Intexine distinct to obscure often weakly separated from the exoexine, and comprising 3/4 to 4/5 of the total spore radius.

Size range: 40–60 μm .

Comparison: *Grandispora famenensis* var. *famenensis* is much larger in size and possesses considerably coarser ornament. *Grandispora famenensis* var. *gracilis* Kedo, 1963 is similar in ornament style but the ornament is more densely distributed.

Grandispora gracilis (Kedo) Streef comb. nov. (Plate IV, 7–10, 13).

Basionym: *Archaeozonotriletes gracilis* Kedo, 1957, Rep. Palaeontol. Stratigr. Byelorussian S.S.R. 4, pp. 3–45, pl. 4, fig. 2.

1974 *Grandispora gracilis* (Kedo) Streef in Becker et al., p. 26, pl. 19, figs. 1–3. (Combination invalid, ICBN Art. 32.2.)

1988 *Grandispora echinata* Hacquebard; Avkhimovitch et al., pl. 4, fig. 18.

Description: Trilete camerate miospores. Amb subcircular to convexly triangular. Suturae accompanied by sinuous lips up to 5 μm in height. Intexine large, up to 4/5 of the total spore radius and showing little separation from exoexine. Exoexine up to 2 μm in thickness and ornamented distally with small wide based cones normally 1 μm in height and basal diameter, but occasionally up to 1.5 μm in height. Cones discrete, well spaced and also present on the equator. Arcuate compression folds often developed near the equatorial regions.

Size range: 30–55 μm .

Distinguishing features: This species is distinguished by the possession of a relatively large intexine which normally shows only weak separation from the exoexine, and an ornament of very small, discrete, wide based coni.

Comparison: *Cymbosporites acanthaceus* (Naumova) Obukhovskaya, 1986 has similar ornament but is acamerate. *Grandispora clandestina* Playford, 1976 is similar in size and structure and only appears to differ in possessing slightly larger conate ornament. This species may prove to be a junior synonym of *Grandispora gracilis*. *Grandispora famenensis* var. *minuta* is similar but possesses a thicker exoexine and coarser galeate ornament. *Grandispora echinata* is larger in size, possesses a more clearly separated intexine and more slender spines and cones.

Grandispora lupata Turnau, 1975 (Plate V, 1–5).

1974 *Archaeozonotriletes micronulatus* Kedo, pl. 8, figs. 5, 6, non 4.

1975 *Grandispora lupata* Turnau, pp. 517–518, pl. 6, figs. 1–3.

Holotype: Turnau, 1975, pl. 6, figs. 1, 2.

Description: Trilete camerate miospores. Amb convexly triangular. Suturae accompanied by narrow flexuous labra up to 7 μm in height and extending

to the spore margin. Intexine conformable with amb, distinct to obscure, only weakly separated from exoexine. Intexine forms 3/4 of the total spore radius. Exoexine thickened equatorially to form darkened margin up to 10 µm in thickness. Exoexine ornamented distally and equatorially with cones, 2–3 µm in height, 1.5–2 µm in basal width. Ornament discrete and well spaced, 2–9 µm apart. *Size range*: 64–95 µm.

Distinguishing features: This species is distinguished by possession of a thick exoexine, a relatively large intexine and an ornament of prominent cones.

Comparison: The two figured specimens (but not the holotype) of *Archaeozonotriletes micronulatus* Kedo, 1974, pl. 13, figs. 5, 6 appear to be identical to *Grandispora lupata*. *Grandispora distincta* is similar in structure to *G. lupata* but differs in possessing considerably smaller coni.

Grandispora micronulata (Kedo) Avkhimovitch comb. nov. (Plate IV, 11 and 12).

Basionym: *Archaeozonotriletes micronulatus* Kedo, 1974, Neftianogo Institut (BelNIGRI) Minsk, p. 53, pl. 13, fig. 4, non pl. 8, figs. 5, 6.

Description: Trilete camerate miospores. Amb convexly triangular. Suturæ accompanied by flexuous labra up to 8 µm in height. Intexine distinct and comprising 3/4 of the total spore radius. Outline conformable with amb. Exoexine 2–3 µm in thickness at the equator ornamented distally and equatorially with widely spaced spines. Spines 2–5 µm in height, wide based 1.5–2 µm in basal width, and uniformly tapering to pointed apices.

Size range: 65–75 µm.

Comment: The holotype of *Grandispora micronulata* figured in Kedo (1974, pl. 13, fig. 4) is clearly different in morphology from Kedo's other two figured specimens in pl. 13, figs. 5, 6. These latter two specimens possess a significantly thicker exoexine and predominately conate ornament and are more appropriately assigned to *Grandispora lupata*.

Distinguishing features: This species is characterised by a distinctly separated intexine, prominent labra and well spaced slender spines.

Comparison: *Grandispora upensis* (Kedo) Byvscheva, 1980, a Tournaisian species, has a

similar type of ornament but can be distinguished from *Grandispora micronulata* by its relatively larger and less distinctly separated intexine and thinner exoexine. *Hymenozonotriletes echinulus* Naumova, 1953 appears very similar to *G. micronulata*, particularly the specimens figured as *H. echinulus* by Kedo (1957, pl. 3, fig. 4). Future study of this species may show it to be synonymous with *G. micronulata*. *Grandispora echinata* differs in possessing an ornament of smaller cones.

Grandispora microseta (Kedo) Strel comb. nov. (Plate V, 6–11).

Basionym: *Hymenozonotriletes microsetus* Kedo, 1963, Rep. Palaeontol. Stratigr. Byelorussian S.S.R. 4, p. 64, pl. 5, fig. 129.

1969 *Hymenozonotriletes microsetus* Kedo, pl. 5, 129; Bouckaert et al., pl. 93, fig. 9 non 10.

1974 *Grandispora microseta* (Kedo) Strel in Becker et al., pl. 18, figs. 13–17. (Combination invalid, ICBN Art. 32.2.)

Description: Trilete camerate miospores. Suturæ often accompanied by prominent labra extending almost to the spore margin. Intexine thin (1 µm), poorly discernible, conformable with amb and comprising 3/4 to 4/5 of the spore radius. Exoexine distally ornamented with slender and rather needle-like spines, 3–5 µm in height and 1–1.5 µm in width. Spines discrete, generally 4–6 µm apart.

Size range: 45–55 µm.

Distinguishing features: This species is distinguished by its ornament of discrete slender spines.

Comparison: *Grandispora upensis* is similar but possesses a sparser ornament of wider based tapering spines. *Grandispora* sp. in McGregor and McCutcheon (1988, pl. 1, figs. 2, 4c) has a very similar style of ornament and is closely comparable with *G. microseta*.

Grandispora minuta (Kedo) Avkhimovitch comb. nov. (Plate VI, 1–3).

Basionym: *Archaeozonotriletes minutus* Kedo, 1963, Rep. Palaeontol. Stratigr. Byelorussian S.S.R. 4, p. 71, pl. 7, figs. 165, 166.

1963 *Archaeozonotriletes devonicus* Kedo var. *minor* Kedo, pl. 7, figs. 173, 174.

Description: Trilete camerate miospores. Amb subcircular to convexly triangular. Suturæ simple

straight extending to edge of the intexine. Intexine distinct to obscure, often showing small separation from exoexine and forming 4/5 of the total spore radius. Exoexine thickened equatorially, up to 3 µm, forming a darkened margin. Distal surface of exoexine and equatorial regions ornamented with discrete ornament of small fine cones, 1–1.5 µm in height, less than 1 µm in width.

Size range: 30–45 µm.

Distinguishing features: This species is characterised by its small size, relatively thick exoexine and discrete ornament of very small slender coni.

Comparison: *Cristatisporites matthewsii* Higgs et al., 1988 appears similar but differs in possessing a coarser and often fused ornament of bulbous based spines. *Cymbosporites acanthaceus* (Naumova) Obukhovskaya, 1986 is acamerate and possesses wider based spines and cones. *Grandispora famensis* var. *minuta* differs in possessing galeate ornament.

Grandispora senticosa (Ishchenko) Byvscheva, 1985 (Plate VI, 4 and 7).

- 1956 *Acanthozonotriletes senticosus* Ishchenko, p. 87, pl. 16, fig. 200.
 1957 *Spinozonotriletes uncatatus* Hacquebard, p. 316, pl. 3, figs. 8–10.
 1963 *Hymenozonotriletes macrosetosus* Kedo, p. 68, fig. 150, non 149.
 1971 *Grandispora uncata* (Hacquebard) Playford, p. 49.
 1985 *Grandispora senticosa* (Ishchenko) Byvscheva, p. 145, pl. 29, fig. 8.

Description: Trilete camerate miospores. Amb convexly triangular. Suturæ distinct, bordered by prominent flexuous labra up to 7 µm in width and height, extending almost to the spore margin. Intexine distinct to obscure, outline conformable with amb and comprising 1/2 to 4/5 of the spore radius. Intexine thin, laevigate and occasionally bearing peripheral folds. Exoexine ornamented equatorially and distally with long prominent spines. Spines 5–20 µm in length and 3–7 µm in basal width, normally tapering evenly to pointed and often curved tips. Spines discrete and well spaced, 15–25 elements at equator.

Size range: 70–150 µm.

Comparison: *Grandispora cornuta* is smaller in size and possesses smaller and predominately galeate

ornament. *Grandispora conspicua* (Playford) Playford, 1971 lacks elevated labra and possesses much wider based spines.

Grandispora tamaræ Loboziak sp. nov. (Plate VI, 5, 6 and 8).

- 1967 *Dibolisporites* sp. Strel, pl. 1, fig. 10.
 1967 *Acinosporites* sp. Strel, pl. 1, fig. 13.
 1969 *Spinozonotriletes* cf. *S. tenuispinus* Hacquebard, 1957; Bouckaert et al. (1969) pl. 93, fig. 6.
 1974 *Grandispora* cf. *tenuispina* (Hacquebard) Playford, 1971; Becker et al., p. 26.
 1975 *Grandispora* cf. *echinata* Hacquebard, 1957; Higgs, p. 399, pl. 4, fig. 12.

Holotype: Plate VI, 6, Sample K, Harrylock Formation, Old Red Sandstone, Hook Head, County Wexford, Ireland (after Higgs, 1975, pl. 4, fig. 12).

Repository: Centre for Palynological Studies, University of Sheffield, Catalogue No. ML 1106 K.
Derivatio nominis: In honour of the Russian palynologist Tamara Byvscheva.

Diagnosis: Trilete camerate miospores. Amb convexly triangular. Suturæ associated with prominent labra extending almost to the equator. Intexine thin (1 µm), large, approximately 4/5 of the total spore radius and only narrowly separated from thicker (2 µm) exoexine. Distal ornament of mainly cones and rare spines, 2–5 µm in height and 2–5 µm in basal diameter, typically possessing decurrent sides and sharply pointed tips, often bent over. Elements well spaced (4–10 µm apart) but frequently located on arcuate and concentric folds, often giving a false impression that the elements have merged laterally.

Size range: 48–65 µm.

Comparison: *Grandispora tenuispina* (Hacquebard) Playford, 1971 is much larger in size (103–113 µm), with longer spines (up to 16 µm) which are arranged in concentric rows. *Cristatisporites imperpetuus* (Sennova) Obukhovskaya, 1986 has similar ornament to *Grandispora tamaræ* but the exoexine is extended equatorially into a thin flange, and there is little separation of the exinal layers.

3. Stratigraphic correlation

Nine species of *Grandispora* have been identified in the Famennian spore succession of western

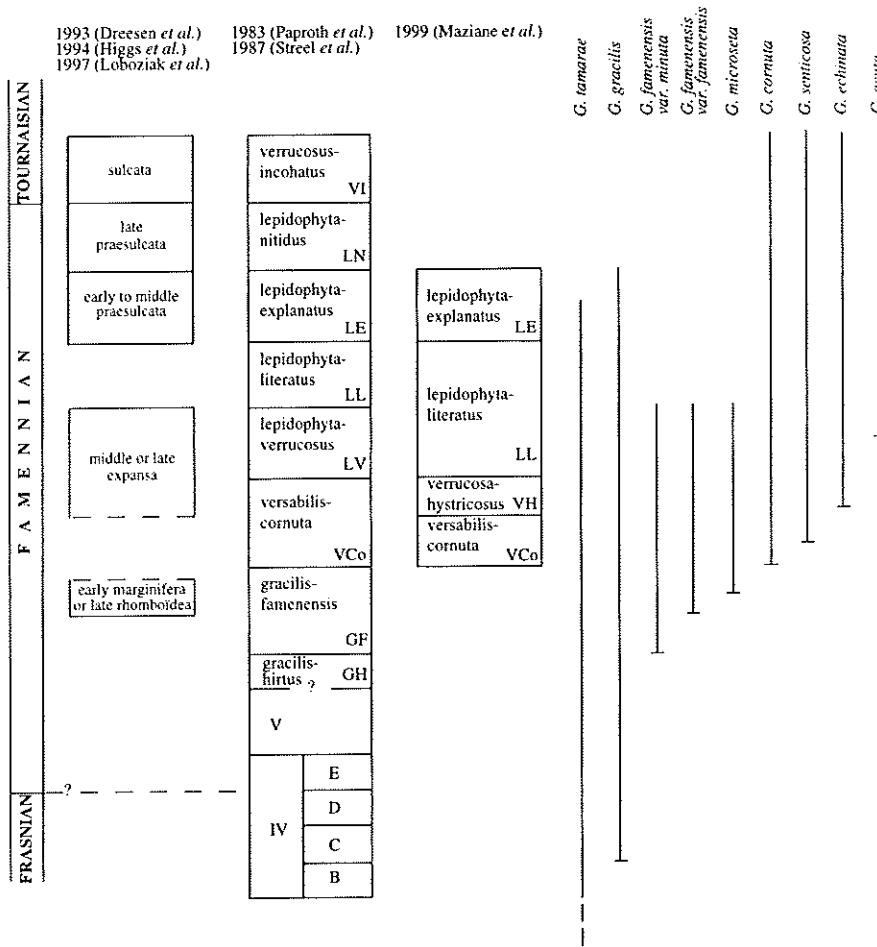


Fig. 3. Stratigraphic ranges of *Grandispora* species in western Europe and a proposed correlation of the miospore zones with the conodont zonation.

Europe. The stratigraphic ranges of these taxa are shown in Fig. 3 and a clear picture of staggered first appearances within the Famennian interval is revealed. These spore ranges are correlated with the spore zonation scheme as described by Paproth et al. (1983) and Streele et al. (1987), together with recent modifications by Maziane et al. (1999) at the level of the LV/LL biozones. Also shown in Fig. 3 is a proposed correlation with the standard conodont zonation. The correlations with the late *rhomboidea* to early *marginifera* zones are after Loboziak et al. (1997), the middle or late *expansa* zones are after Dreesen et al. (1993), and the early *praesulcata* to *sulcata* zones are after Higgs and Streele (1994).

In eastern Europe, twelve *Grandispora* species have been identified in the Famennian sequence of Byelorussia. The stratigraphic ranges of these taxa are shown in Fig. 4 and a trend of staggered first appearances is again evident in the Famennian interval. These *Grandispora* species ranges are correlated with the most recent Famennian miospore zonations in Byelorussia as given by Avkhimovitch (1986) and Avkhimovitch et al. (1988, 1989) with additional data from Avkhimovitch (1993) and Avkhimovitch et al. (1993). Note the modification at the level of the *lebedianensis* zone. Fig. 4 also shows a proposed correlation with the conodont zonation scheme,

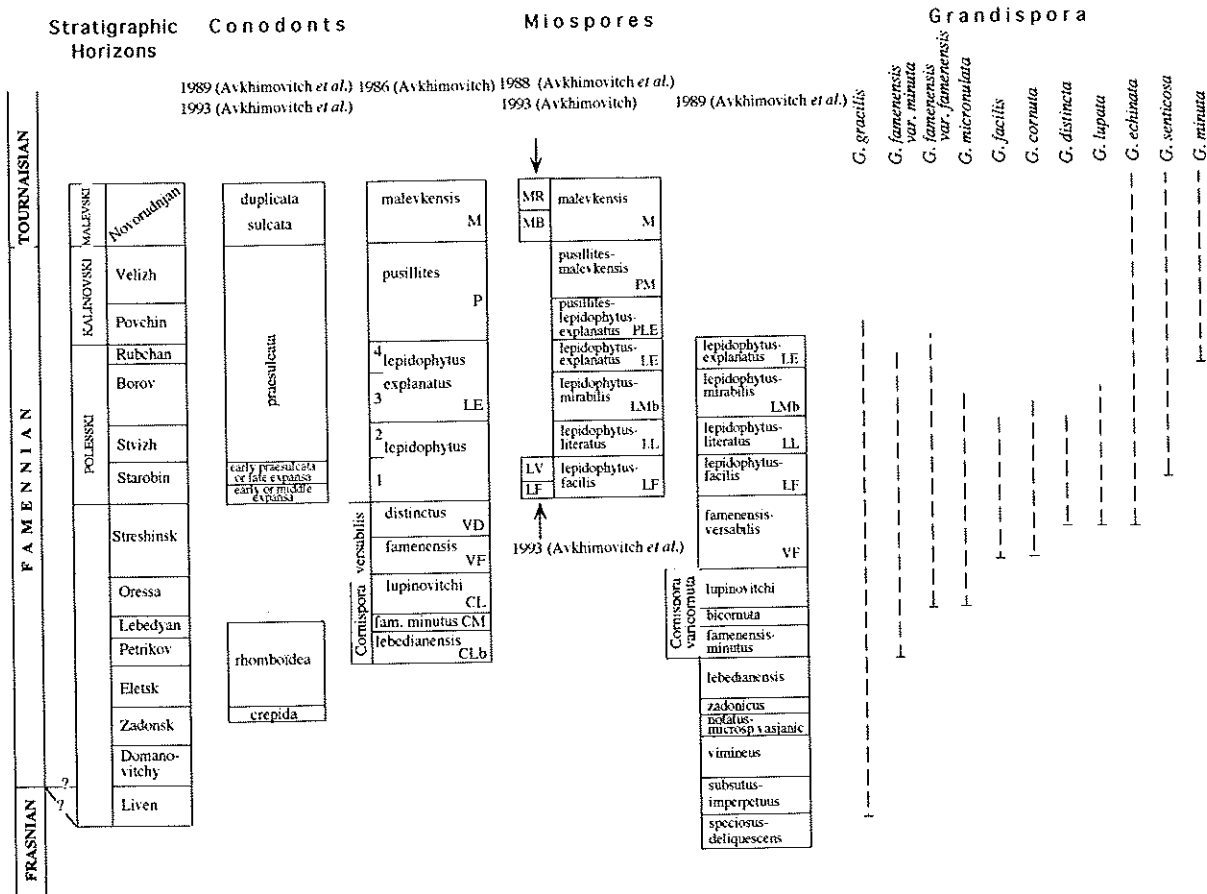


Fig. 4. Stratigraphic ranges of *Grandispora* species in eastern Europe and a proposed correlation of the miospore zones with the conodont zonation.

data from Avkhimovitch et al. (1989, 1993). The stratigraphic horizons shown are as used in the former USSR.

Seven *Grandispora* taxa have been identified that are common to both the Famennian regions, these are: *Grandispora gracilis*, *Grandispora famenensis* var. *minuta*, *Grandispora famenensis* var. *famenensis*, *Grandispora cornuta*, *Grandispora senticosa*, *Grandispora echinata* and *Grandispora acuta*. Fig. 5 shows a plot of the respective ranges of these common taxa within the framework of a best fit correlation of the miospore and conodont zonation schemes. Consequently, five of the *Grandispora* species seem to have their first occurrences almost simultaneously. The only exceptions are *Grandispora senticosa* and *Grandispora acuta*,

which both have slightly older first occurrences in Byelorussia compared with western Europe.

- *Grandispora gracilis* first appears in the late Frasnian in both regions and ranges up into the latest Famennian *Retispora lepidophyta*–*Indotrivradites explanantus* (LE) miospore zone.
- *Grandispora famenensis* var. *minuta* first appears close to the base of the Middle Famennian, in western Europe at the base of the *Grandispora gracilis*–*G. famenensis* (GF) miospore zone and in Byelorussia at the base of the *famenensis*–*minutus* miospore zone corresponding to the upper part of the *rhomboidea* conodont zone.
- *Grandispora famenensis* var. *famenensis* first appears in the middle part of the GF miospore zone in Belgium, where it correlates with the

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