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

K.T. Higgs a,*, V.I. Avkhimovitch b, S. Loboziak c, N. Maziane-Serraj d, M. Stempień-Salek e, M. Streeł d

a Department of Geology, University College Cork, Cork, Ireland  
  b Bel NIGRI, Starborisovsky trakt, 220060 Minsk, Belarus  
  c U.S.T.L., UPRÉSA 8914 du CNRS, Earth Sciences, Villeneuve d'Ascq Cedex, France  
  d Services Associés de Paléontologie, University of Liège, B18 Sart Tilman, B4000 Liège, Belgium  
  e Institute of Geological Sciences, Al. Zwirki I Wigury 93, Warsaw, Poland

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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 tanarne* 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

* Corresponding author. Fax: +353-21-271565.  
E-mail address: k.higgs@ucc.ie (K.T. Higgs)

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 Streeł et al. (1987),
Higgs et al. (1988) and revised by Maziane et al. (1999). Meanwhile in eastern Europe a Famenian 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. Srečel and Loboziak (1996) have indicated that the main reason for these differences is the existence of two major phytogeographic provinces in this area in Famenian 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 Famenian 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 Famenian 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 Famenian successions and zonation schemes.

2. Systematic descriptions

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

Anieturra SPORTES H. Potonié, 1893.
Turra TRILETES (Reinsch) Dettmann, 1963.

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 1

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. Hook Head, Ireland, HK3 ML 1104 US.
8. Hook Head, Ireland, HK3 -331278.
9. Hook Head, Ireland, HK3 ML 1102 US.
10. Hook Head, Ireland, HK3 3301122.
11. Hook Head, Ireland, HK3 ML 1116 US.
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 μm) exoexine (usually less than 2 μm); and (2) forms with a relatively thick (>3 μm) exoexine.

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**PLATE II**

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. Hook Head, Ireland, 75/1411(A) 7651050 GSI.
5. Hook Head, Ireland, F8(E) 4101360 US.
6. Hook Head, Ireland, F8(E) 3971262 US.
7. South Ringabella, Ireland, SR35(A) 3821235 US.
8. Hasselbachtal, Germany, HB18–19(A) 1821075 GSI.
9. Hook Head, Ireland, F8(A) 5211270 US.
10. Starobin B/H, Belarus, 239, 289–293.2 m, L19.
11. Starobin B/H, Belarus, 239, 239 m, Q30/1.
These thicker walled forms are very similar in structure to *Geminispora* Balne 1962, however, assignment to *Geminispora* 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).


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

*Description:* Trilete camerate miospores. Amb convexly triangular. Sutural 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 innsubordinate 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 assignation (Byvscheva, 1985) to the acamerate genus *Cymbosporites*. The synonymy of *Grandispora acuta* and *Grandispora saurota*, as suspected by Playford and McGregor (1993, p. 38), has also been confirmed in the present study. *Grandispora famenensis* (Naumova) Strelt 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 *Sporozonotriletes* cf. *S. uncatus* Hacquebard; Strelt 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 subc-
circular to convexly triangular. Suturæ accompanied by sinuous and flexuous lips up to 6 μm in height, extending almost to the equator, and terminating in curvatæ. 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 subdianaphidus 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 (Ischkenko) Byvscheva, 1985 differs from G. cornuta in being larger in size and in possessing longer slender spines.

**Grandispora distincta** (Naumova) Avkhumovitch 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) Avkhumovitch, pl. 1, 5.

(Combination invalid. ICBN Art. 32.2.)

Description: Trilete camerate miospores. Amb subcircular to convexly triangular with apices slightly pointed. Suturæ accompanied by sinuous lips 3–5 μm in height. Suturæ 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.

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**PLATE IV**

1 and 2. Grandispora fannensis (Naumova) Stee1 1974 var. fannensis.


2. Starobin B/H, Belarus, 239, D40/2.


4. Hook Head, Ireland, HK23, 1661137.

5. Hook Head, Ireland, HK3, 5351124.


7. Beverwe, Ourthe Valley, Belgium, 47/9, 2450/139.

8. Hasselbachal, Germany, HB18. 19, 4751011.


10. Esnou, Ourthe Valley, Belgium, 12/2, L5/5.

11 and 12. Grandispora microaculeata (Kedo) comb. nov.


**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 carinate miospores. Amb subspheroidal and surrounded by convexly triangular. Suturalae usually distinct and accompanied by leuctive labra up to 7 µm in height. Suturalae extend almost to the equator and terminate in curvaturae imperfectae. Exoexine thin but slightly thickened at the equator, up to 2 µm in thickness. Intine distort, 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 intine, and discrete conate and spinose ornament ranging from 1.5 to 2.5 µm in height.

**Comparison:** The specimens described and figured as *Spelaeotriotes 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 intine/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 *Acanthozonotriotes 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) Streeck 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 intine.

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**PLATE V**


5. Pomerania, Poland, G9 1/1, 16/34.
**Grandispora facialis** (Kedo) Avkhimovitch in Avkhimovitch et al. (1988) (Plate II, 10 and 11; Plate III, 1–3).

1957 *Hymenozonotriletes facialis* 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 *Archeozonotriletes flavus* (Kedo) Kedo, pp. 54–55, pl. 13, figs. 9–11.
1976 *Grandispora notensis* Playford; Playford, p. 8, fig. 12, 24–26; pl. 9, figs. 1–3.
1988 *Grandispora facialis* (Kedo) Avkhimovitch in Avkhimovitch et al., p. 172.
1993 *Grandispora flavus* (Kedo) Avkhimovitch, pl. 1, fig. 11.

**Description:** Trilete camerate miospores. Amb convexly triangular. Sutureae accompanied by sinusus and flexuous labra, extending almost to the equator. Intine 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 facialis*, *Hymenozonotriletes flavus* and *Hymenozonotriletes ventosus*. Consequently, they are now included in one species: *Grandispora facialis*.

**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 facialis*. *Grandispora sola* Braithwa 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. facialis*. 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. facialis*. Both types possess three apical papillae. *Grandispora clandesitina* Playford, 1976 has a similar ornamentation but is much smaller in size, and possesses a larger and rather indistinct intine.

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

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

1957 *Archeozonotriletes constrictus* Kedo, pl. 4, fig. 1.
1957 *Archeozonotriletes serenus* Kedo, pl. 3, fig. 25.
1963 *Archeozonotriletes nucositya* Kedo var. *punctatus* Kedo, pl. 7, figs. 177–179.
1963 *Archeozonotriletes deimicus* Kedo var. *punctatus* Kedo, pl. 7, figs. 175, 176.

**PLATE VI**

1–3. *Grandispora minuta* (Kedo) comb. nov.
2. Shestkovitchi B/H, Belarus, 3247/85, CS4/3.
5 and 6. *Grandispora tanarica* sp. nov.
5. LaGombe, Ourthe Valley, Belgium, Go37, 2393/679.
6. Hook Head, Ireland, HK, ML1106 US.
8. *Grandispora tanarica* sp. nov. Hook Head, Ireland, HK27, 235123.
<table>
<thead>
<tr>
<th>TAXA</th>
<th>EXINE FEATURES</th>
<th>ORNAMENT SHAPE/HEIGHT</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Grandispora acuta</em></td>
<td>Exo 1.5-3μ, Int 75-90%</td>
<td>3-10μ</td>
</tr>
<tr>
<td><em>G. cornuta</em></td>
<td>Exo 1.5-2μ, Int 75-90%</td>
<td>5-16μ</td>
</tr>
<tr>
<td><em>G. distincta</em></td>
<td>Exo 4-7.5μ, Int 90%</td>
<td>1-2μ</td>
</tr>
<tr>
<td><em>G. echinata</em></td>
<td>Exo 1-2μ, Int 75-80%</td>
<td>1.5-2.5μ</td>
</tr>
<tr>
<td><em>G. facilis</em></td>
<td>Exo 2-3μ, Int 33-65%</td>
<td>2-3μ</td>
</tr>
<tr>
<td><em>G. famenensis</em></td>
<td>Exo 3-6μ, Int 75-90%</td>
<td>1.5-6μ</td>
</tr>
<tr>
<td><em>G. gracilis</em></td>
<td>Exo 2μ, Int 90%</td>
<td>1-1.5μ</td>
</tr>
<tr>
<td><em>G. lupata</em></td>
<td>Exo 5-10μ, Int 75%</td>
<td>2-3μ</td>
</tr>
<tr>
<td><em>G. micronistata</em></td>
<td>Exo 2-3μ, Int 75%</td>
<td>2-5μ</td>
</tr>
<tr>
<td><em>G. microseta</em></td>
<td>Exo 2μ, Int 75-90%</td>
<td>3-5μ</td>
</tr>
<tr>
<td><em>G. minuta</em></td>
<td>Exo 1.5-3μ, Int 90%</td>
<td>1-1.5μ</td>
</tr>
<tr>
<td><em>G. senticosa</em></td>
<td>Exo 2-3μ, Int 50-90%</td>
<td>5-20μ</td>
</tr>
<tr>
<td><em>G. tamarae</em></td>
<td>Exo 2μ, Int 90%</td>
<td>2-5μ</td>
</tr>
</tbody>
</table>

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

1974 *Grandispora famenensis* (Mnukova) Srecl in Becker et al., p. 26, pl. 19, figs. 9-11. (Combination invalid, ICN Art. 32.2.)
1976 *Archaeozonotriletes consilvis* Kedo var. *asper* Avkhinovich, pl. 2, figs. 1, 2.

Description: Trilete cameratè miospores. Amb convexly triangular. Suturae distinct, accompanied by lips of variable width, straight to sinuous and extending almost to the equator. Curvatura 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 μm 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 intine and broad to bulbous galeae distinguish this species from others of the genus. The variety *famnenensis* 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 famnenensis* var. *famnenensis*. As the latter is an autonym, this new variety epithet does not require authorship.

*Grandispora gracilis* (Kedo) Steevel comb. nov. var. *minuta* Nekriata, 1974 (Plate IV, 3–6).

1974 *Archeocenotriletes famnenensis* 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. Intine 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 famnenensis* var. *famnenensis* is much larger in size and possesses considerably coarser ornament. *Grandispora famnenensis* var. *gracilis* Kedo, 1963 is similar in ornament style but the ornament is more densely distributed.

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


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

1988 *Grandispora echinata* Haquebard; 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. Intine 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 intine which normally shows only weak separation from the exoexine, and an ornament of very small, discrete, wide based coni.

Comparison: *Cymbosporites acanthacus* (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 famnenensis* var. *minuta* is similar but possesses a thicker exoexine and coarser galeate ornament. *Grandispora echinata* is larger in size, possesses a more clearly separated intine and more slender spines and cones.

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

1974 *Archeocenotriletes micranus* 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. Intine conformable with amb, distinct to obscure, only weakly separated from exoexine. Intine 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 thicke exoexine, a relatively large intine and an ornament of prominent cones.

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

### *Grandispora micronulata* (Kedo) Avkhumovitch comb. nov. (Plate IV, 11 and 12).

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

**Description:** Trilette camerate miospores. Amb convexly triangular. Suturale accompanied by flexuous labra up to 8 µm in height. Intine 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 thickly exoexine and predominately conate ornament and are more appropriately assigned to *Grandispora lupata*. 

**Distinguishing features:** This species is characterised by a distinctly separated intine, 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 intine and thinner exoexine. *Hymenozonotriletes echninatus* Naumova, 1953 appears very similar to *G. micronulata*, particularly the specimens figured as *H. echninatus* by Kedo (1957, pl. 3, fig. 4). Future study of this species may show it to be synonymous with *G. micronulata*. *Grandispora echninata* differs in possessing an ornament of smaller cones.

### *Grandispora microseta* (Kedo) Streel comb. nov. (Plate V, 6–11).


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

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

**Description:** Trilette camerate miospores. Suturale often accompanied by prominent labra extending almost to the spore margin. Intine 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) Avkhumovitch comb. nov. (Plate VI, 1–3).


**Description:** Trilette camerate miospores. Amb subcircular to convexly triangular. Suturale simple
straight extending to edge of the intine. Intine 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 matthewi Higgs et al., 1987 appears similar but differs in possessing a coarser and often fused ornament of bulbous based spines. Cynnosporites acanthaeus (Naunova) Obukhovskaya, 1986 is acamere and possesses wider based spines and cones. Grandispora famesensis var. minuta differs in possessing galeate ornament.

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

1956 Acanthozonotriletes senticosus Ishchenko, p. 87, pl. 16, fig. 200.
1957 Spinizonotriletes uncatus Hacquebard, p. 316, pl. 3, figs. 8–10.
1963 Hymnozonotriletes macrostaeus Kedo, p. 68, fig. 150, non 149.
1971 Grandispora uncata (Hacquebard) Playford, p. 49.
1985 Grandispora senticosus (Ishchenko) Byvscheva, p. 145, pl. 29, fig. 8.

Description: Trilete camerate riospores. Amb convexly triangular. Suturale associated with prominent labrata up to 7 μm in width and height, extending almost to the spore margin. Intine distinct to obscure, outline conformable with amb and comprising 1/2 to 4/5 of the spore radius. Intine 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 labrata and possesses much wider based spines.

Grandispora tamarinae Loboziai sp. nov. (Plate VI, 5, 6 and 8).

1967 Dibolisporites sp. Street, pl. 1, fig. 10.
1967 Acinosporites sp. Street, pl. 1, fig. 13.
1975 Grandispora cf. echnuta Hacquebard, 1957; Higgs, p. 399, pl. 4, fig. 12.

Holotype: Plate VI, 6, Sample K, Harlow 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. Suturale associated with prominent labrata extending almost to the equator. Intine 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 tenispina (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 impenetrus (Sennova) Obukhovskaya, 1986 has similar ornament to Grandispora tamarinae 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
In eastern Europe, twelve *Gephyrocapsa* species have been identified in the Famenian sequence of Byelorussia. The stratigraphic ranges of these taxa are shown in Fig. 3, and a trend of suggested first appearances is again evident in the Famenian interval. These *Gephyrocapsa* species are correlated with the most recent *Famennian* zonation scheme, as given by the modifications of Mazurkevich et al. (1983) and Street et al. (1987), together with recent modifications by Papirov et al. (1997), the Middle or Late *C. globulosa* zones are after Dreezen et al. (1992), and the Early *P. variabilis* zone is after Street et al. (1990).
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–Indorrradites explanatus (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–minuta 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
early *marginifera*-late *rhomboidea* conodont zone. In Byelorussia, it first appears at the base of the *bicornta* miospore zone.

- *Grandispora cornuta* first appears at the base of the *Diductites versabilis*-*G. cornuta* (VC0) miospore zone in Belgium, this latter level correlates with the interval between the latest *marginifera* to middle *expansa* conodont zones, and most probably within the *trachytera* conodont zone (Streel and Loboziat, 1996, text-fig. 3). In Byelorussia *G. cornuta* first appears just above the base of the *versabilis-fumensensis* (VF) miospore zone.

- *Grandispora echinata* first appears in Belgium within the *Apiculveruissora verrucosa-Vallutisporites hystricosus* (VH) miospore zone which correlates with the middle or late *expansa* conodont zone 1 in Byelorussia, this species first appears in the upper part of the VF miospore zone. In both regions the appearance of *G. echinata* occurs immediately before the first inception of *Rariospora lepidophyta*.

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