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Miospore assemblages from the Silurian–Devonian boundary, in borehole A1-61, Ghadamis Basin, Libya

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Abstract

Well preserved and diversified miospore assemblages have been recorded from a relatively continuous sequence in borehole A1-61 which spans the Silurian–Devonian boundary in the northwestern part of the Ghadamis Basin, Libya. The sequence is represented by early Devonian Lochkovian beds of the Tadrart Formation that transgress onto the Silurian Ludlow-Pridoli beds of the upper part of the 'Alternances Argilo-gréseuses' Formation. The present work demonstrates a succession of miospore assemblages from closely sampled layers that have been stratigraphically dated as Ludlow–middle Pridoli and early Lochkovian by chitinozoans and acritarchs. Over 80 species of cryptospores and trilete spores have been identified. Modified detailed morphological interpretations are given. The miospore assemblages are correlated with miospore zonation schemes established for the type sequences of the Welsh Borderland, and those previously described from Libya. Early occurrences of some species as *Streelispora newportensis* on the western Gondwana plate, are put forward by comparison with the Old Red Sandstone continent. Phytogeographic and palaeobotanic implications based on these observations are discussed.

Keywords: Miospores; palynology; Silurian; Devonian; palaeogeography; biostratigraphy

1. Introduction

The almost complete Palaeozoic subsurface section in western Libya, ranging in age from Cambrian to late Carboniferous, is of primary importance for the understanding of the early development of miospores of primitive land plants during Palaeozoic time important in this part of the megacontinent Gondwana. For a long time, palynology together with faunal and palaeobotanical data have been applied in petroleum exploration to determine a stratigraphic framework of subsurface Palaeozoic rocks in Libya. However, most of the pioneering work undertaken in this area remained unpublished. Recent investigations carried out on this material, under the impulse of D. Massa, allow to review the resolution of various fossil taxa in the Lower Palaeozoic biostratigraphy of the northern Gondwanan domain. Today, palynological data are integrated together (chitinozoans, acritarchs and miospores). Nonetheless, additional work is still required to be done before standard schemes of palynostratigraphy can be proposed and applied to international correlation. This especially concerns the production of detailed monographs on well age constrained and stratigraphically continuous deposits.

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This article focuses on the detailed description of miospore assemblages from the Upper Silurian and the Silurian–Devonian boundary in the subsurface succession of the Ghadamis Basin, northwest Libya. This work is part of a programme of international collaboration, with Dr. A. Le Hérissé (University of Brest) and Dr. F. Paris (University of Rennes), concerning the study of diversification dynamics of marine and continental palynomorphs and the influence of global changes on their evolution during the Silurian and Lower Devonian on the north Gondwanan margin.

2. Regional geological setting and material

Silurian–Devonian boundary strata are present in western Libya within the Ghadamis Basin in the north and the Mourzouk Basin in the south. The succession is known from a great number of petroleum boreholes. The Lower Devonian is also known from outcrops in the Fazzan area. We refer to Massa (1988) and to Weyant and Massa (1991) for a thorough review of the lithology and Palaeozoic stratigraphy of Libya.

In the north of the Ghadamis Basin where the A1-61 borehole has been drilled, sedimentation is continuous from the Silurian to the Devonian (Fig. 1). In ascending order, the Silurian succession comprises the 'Formation des Argiles Principales' (equivalent of the Tanezzuft Formation in the Mourzouk Basin, Massa and Jaeger, 1971), and by the 'Formation des Alternances Argilo gréseuses' (equivalent of the Acacus Formation). The total thickness of both formations is over 1100 m for the Ludlow and the Pridoli section. They are overlain by the coarse sandstone of the Tadrart Formation, Lochkovian in age.

Samples studied for this paper (Fig. 2) were obtained from the cores C22 to C12 of the A1-61 borehole and they represent 500 m of sediments from the upper part of the Alternances Argilo-gréseuses and the lower part of the Tadrart Formation.

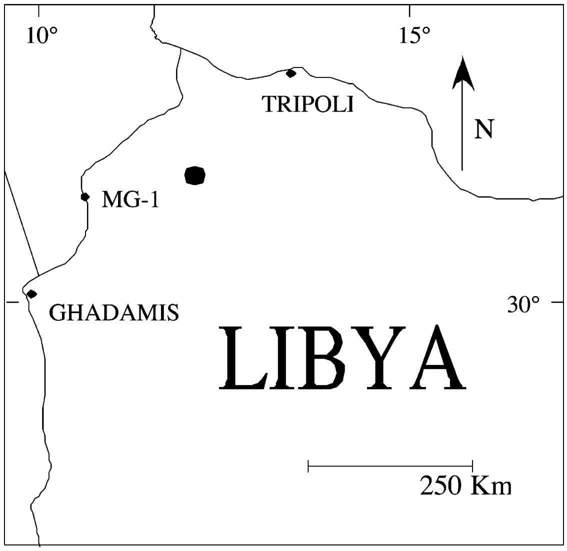


Fig. 1. Schematic map of Libya showing the location of the A1-61 borehole.

Below is a summary of biostratigraphic information provided by chitinozoans from this interval (Jaglin and Paris, 2002):

2040 to 2042.80 m – *Eisenachitina bohemica* biozone – early Lochkovian

2125.10 to 2180.80 m – *Margachitina elegans* with abundant *Pseudoclathrochina carmenchui* – middle Pridoli

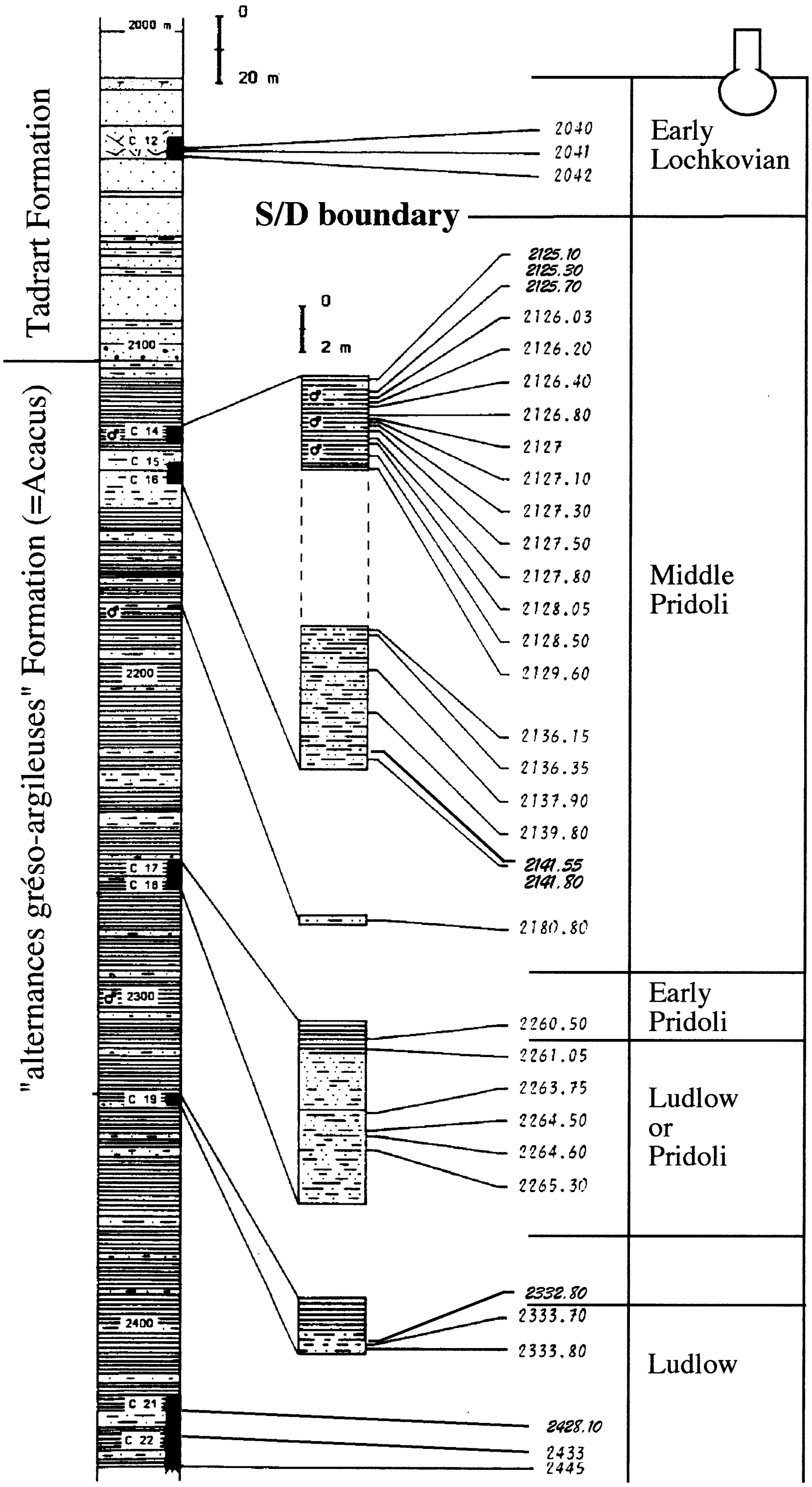
2260.50 m – *Urnochitina urna* and abundant *Pterochitina perivelata* – early Pridoli

2261.05 to 2265.30 m – ? – late Ludlow or Pridoli

2333.70 to 2333.80 m – abundant *Plectochitina carminae* – Ludlow

Several publications and unpublished theses have made reference to acritarchs, cryptospores, and trilete spores from the same stratigraphical interval in the A1-61 borehole (Al-Ameri, 1980; Buret, 1990; Buret and Moreau-Benoit, 1986; Richardson et al., 1981; Streel et al., 1990). However, none of these have given an exhaustive description of the assemblages and their precise distribution around the Silurian–Devonian transition.

Fig. 2. Lithostratigraphic log of the A1-61 borehole (after Massa, 1988), showing the positions of the miospore samples and the stratigraphic ages provided by chitinozoans (Jaglin and Paris, 2002). S/D = Silurian–Devonian.


2000 m
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20 m
Tadrart Formation
"alternances gréso-argileuses" Formation (=Acacus)
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2100
C 14
C 15
C 16
2200
C 17
C 18
2300
C 19
2400
C 21
C 22
0
2 m
2040
2041
2042
S/D boundary
2125.10
2125.30
2125.70
2126.03
2126.20
2126.40
2126.80
2127
2127.10
2127.30
2127.50
2127.80
2128.05
2128.50
2129.60
2136.15
2136.35
2137.90
2139.80
2141.55
2141.80
2180.80
2260.50
2261.05
2263.75
2264.50
2264.60
2265.30
2332.80
2333.70
2333.80
2428.10
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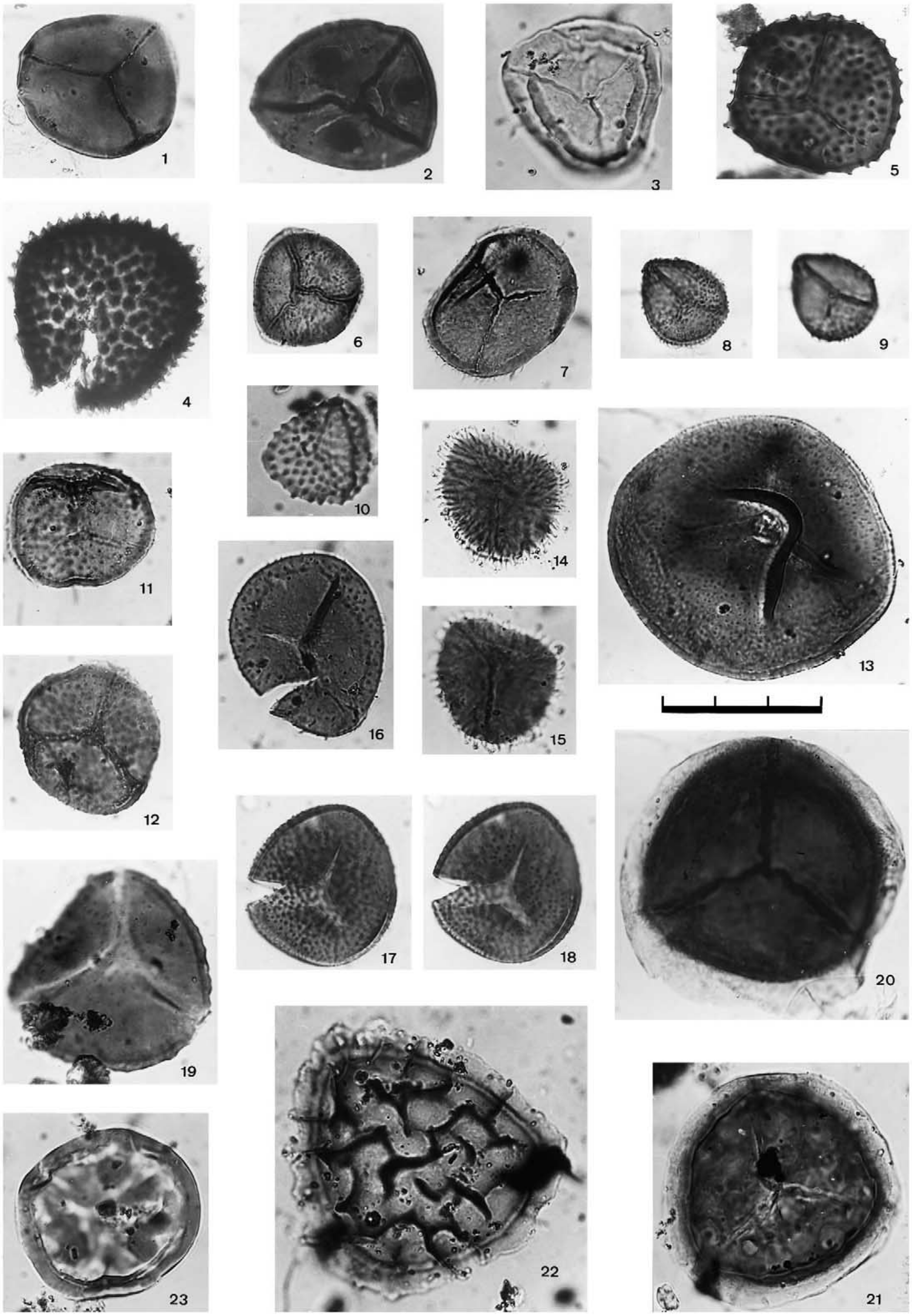
2445
Early Lochkovian
Middle Pridoli
Early Pridoli
Ludlow or Pridoli
Ludlow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3. Systematic palynology

Despite few specimens have been observed, many species have been identified. Because of this small number of specimens recorded, the new forms are described in open nomenclature.
Remark: the miospore term includes cryptospores and trilete spores as recommended in Steemans (2000).

3.1. Trilete spores

Genus *Aneurospora* Streel 1964 emend. Richardson et al. 1982

Aneurospora cf. *A. bollandensis* Steemans 1989 (Plate I, 5)

Synonymy and references:

cf. 1989 *Aneurospora bollandensis* Steemans, p. 96, pl. 20: 14–19.

Plate I. Each figured palynomorph is located by samples, slide number and England Finder coordinates. The scale bar illustrates a length of 30 μm. Figured material from slides numbered L 19..., 20..., 21..., 24... and 35... is housed in the Paleontological Collections of the University of Liège. The other specimens are housed in the Paleontological Collections of the University of Brest.

1: *Ambitisporites avitus/dilutus morphon* Steemans et al., 1996.
2141.55 m, L 35629, R46/2.
2: *Ambitisporites tripapillatus* Moreau-Benoit, 1976.
2126.30 m, L 35632, E34/0.
3: *Amicosporites miserabilis* Cramer, 1966.
2433 m, L CA70, E41/2.
4: *Aneurospora geikiei* Wellman and Richardson, 1996.
2128.05 m, L CA35, E41/3.
5: *Aneurospora* cf. *A. bollandensis* Steemans, 1989.
2125.30 m, L 35623, J42/1.
6: *Aneurospora* sp. 1.
2141.55 m, L 35629, L37/2.
7: *Aneurospora* sp. 2.
2141.55 m, L 35622, H37/0.
8–9: *Aneurospora* sp. 3.
2125.30 m, L 19187, P38/0.
10: *Aneurospora* sp. 5.
2265.30 m, L CA61B, N44/0.
11–12: *Aneurospora* sp. 4.
11: 2141.55 m, L 35629, Q33/4.
12: 2141.55 m, L 19189, G52/3.
13: *Apiculiretusispora perfecta* Steemans, 1989.
2263.75 m, L CA56B, C32/0.
14–15: *Apiculiretusispora synorea* Richardson and Lister, 1969.
2333.80 m, L CA67A, N33/2.
16: *Apiculiretusispora* cf. *A. spicula* Richardson and Lister, 1969.
2041 m, L 35627, R49/4.
17–18: *Apiculiretusispora* sp. 1.
2042.80 m, L 35630, F38/0.
19: *Apiculiretusispora* sp. 2.
2128.50 m, L CA38, F38/0.
20–21: *Breconisporites simplex* Wellman, 1993.
20: 2125.30 m, L 35631, R51/2.
21: 2141.80 m, L CA46, V41/1.
22: *Chelinospora cassicula* Richardson and Lister, 1969.
2041 m, L CA9, L38/4.
23: *Chelinospora obscura* Burgess and Richardson, 1995.
2433 m, L CA70A, Q32/0.

Description: Amb circular with more or less thickened curvaturae, up to 3 μm wide. Trilete mark distinct, sutures simple, up to 2 μm in combined width, straight, extending to inner margin of the equatorial thickness. Contact area laevigate. There is a distinct circular papilla in the centre of each interradial area, 6 μm wide. The distal and equatorial exine is covered by flat, sometimes expanded, topped coni, 1 μm high and 1–2 μm wide, 2–3 μm apart.
Dimension: 31–33 μm (two specimens).
Occurrence: 2125.30, 2141.55 m.
Comparison: Spores essentially comparable with *Aneurospora bollandensis* Steemans 1989 but without a triangular thickened area beyond the sutures.

Aneurospora sp. 1 (Plate I, 6)

Description: Amb triangular to rounded triangular with more or less thickened curvaturae, up to 1.5 μm wide (sometimes indistinct). Trilete mark distinct. Sutures simple or accompanied by folds, up to 2 μm in combined width, straight or sinuous, extending to inner margin of the equatorial thickness. Contact area laevigate. Distal and equatorial area covered with closely spaced hair-like ornament and slender sharply pointed spines, less than 1 μm high.
Dimensions: 18–(22.5)–23.5 μm (nine specimens).
Occurrence: 2125.30, 2126.20, 2129.60, 2141.55, 2180, 2261.05, 2332.80, 2333.70, 2264.50 m.
Comparison: *Aneurospora* sp. A *in* Wellman (1993) is very similar but is ornamented with coni and micrograna.

Aneurospora sp. 2 (Plate I, 7)

Description: Amb subcircular. Equatorial thickening 1.5 μm wide. Trilete mark distinct. Sutures accompanied by lips or folds, up to 1 μm in combined width, extending almost to the spore margin. Exine laevigate in contact areas, distally and equatorially sculptured with irregular hair-like ornament 2 μm high, up to 0.5 μm wide. Distal exine seems to be infragranulate.
Dimensions: 29–29.5 μm (2 specimens).
Occurrence: 2125.03, 2141.55 m.
Comparison: *Aneurospora* sp. 1 has shorter sculpture and is not infragranulate distally. *Aneurospora hispidica* Wellman and Richardson 1996 is ornamented on the proximal face.

Aneurospora sp. 3 (Plate I, 8–9)

Description: Amb rounded triangular to subcircular. Trilete mark distinct. Sutures reach the inner margin of equatorial thickening, simple or accompanied by folds, 1 μm in combined width. Equatorial thickening 1–1.5 μm wide, faintly defined in some specimens. Contact areas smooth. Distal and equatorial areas covered with closely spaced, fine capitate elements, less than 1 μm high, about 0.5 μm apart.
Dimensions: 16.5–19.5–21.5 μm (three specimens).
Occurrence: 2125.30, 2141.55 m.
Comparison: The capitate ornament distinguishes these specimens from other species of *Aneurospora*.

Aneurospora sp. 4 (Plate I, 11–12)

Description: Amb circular to subcircular. Trilete mark merging with equatorial crassitude, simple or with lips, up to 1 μm in combined width. Curvaturae evident on some specimens, forming an equatorial crassitude, 1–2 μm wide. Curvaturae may be invaginated toward the proximal pole, opposite the ends of the trilete rays. Exine may be slightly darkened at the proximal pole. Contact areas smooth. Distally and equatorially sculptured with two different kinds of elements, coni (0.5–1.5 μm high, up to 1 μm wide, 1–2 μm apart) and minute grana, closely spaced and uniformly distributed.
Dimensions: 18–34 μm (10 specimens).
Occurrence: 2125.30, 2125.70, 2126.80, 2136.35, 2141.55 m.
Comparison: The minute grana distinguish that species from other *Aneurospora*.

Aneurospora sp. 5 (Plate I, 10)

Description: Amb rounded triangular. Trilete rays extend nearly to the equator. Sutures accompanied by fine lips, less than 1 μm in combined

width. Faintly defined equatorial thickening formed by curvaturae, about 1.5 μm wide. Proximal face smooth. Distal and equatorial sculpture consists of coni, 1–1.5 μm wide, 1 μm high, and 1 μm apart.
Dimensions: 20 μm.
Occurrence: 2265.30 m.
Comparison: *Aneurospora* sp. A *in* Wellman 1993 has smaller ornament.

Genus *Apiculiretusispora* (Streel 1964) Streel 1967

Apiculiretusispora cf. *A. spicula* Richardson and Lister 1969 (Plate I, 16)

Synonymy and references:

cf. 1969 *Apiculiretusispora spicula* Richardson and Lister, p. 220, pl. 38: 3–4.

Description: Amb subcircular. Exine thin, 0.5 μm. Trilete mark distinct, accompanied by folds, up to 2 μm in combined width. Sutures 2/3 spore radius. Contact areas distinct, smooth, delimited by fine curvaturae perfectae. Outside the contact areas exine sculptured with sharply pointed spines, 0.5 μm high, up to 0.5 μm wide. Elements sparsely and irregularly disposed, 1–3 μm apart.
Dimensions: 33.5 μm.
Occurrence: 2041 m.
Comparison: *Apiculiretusispora spicula* Richardson and Lister has longer spines, 1–2 μm high.

Apiculiretusispora sp. 1 (Plate I, 17–18)

Description: Amb subcircular. Trilete mark with straight and gaping sutures, 2/3 spore radius, surrounded by a thickened triangular area in the apical region. Curvaturae indistinct. Exine 1 μm thick. Proximal surface ornamented with sparse little grana (<0.5 μm). Distal and equatorial areas ornamented with slender sharply pointed spines or coni, 0.5 μm high, up to 0.5 μm wide, and 0.5–1 μm apart.
Dimensions: 30 μm.
Occurrence: 2042.80 m.

Apiculiretusispora sp. 2 (Plate I, 19)

Description: Amb rounded triangular. Exine 1 μm thick. Trilete mark distinct, sutures accompanied by folds. Sutural length cannot be determined. Contact areas bordered by curvaturae which nearly equal equatorial border. Exine equatorially and distally sculptured by minute grana and coni, 0.5 μm high, up to 1 μm wide. Ornament sparsely and irregularly distributed.
Dimensions: 36 μm.
Occurrence: 2128.50 m.

Genus *Chelinospora* Allen 1965

Chelinospora sp. 1 (Plate II, 2)

Description: Amb subcircular to subtriangular with rounded apices. Proximal surface thin and laevigate, sometimes bordered by curved folds. Trilete mark distinct, sutures reach or nearly reach the equator and accompanied by slightly sinuous lips, 0.5–2 μm in combined width. Exine equatorially and distally relatively thick or patinate. Thickness at equator 2.5–4.5 μm. Patina resembling foveae due to the low, wide and convolute muri. Foveae subcircular to elongate, 1–4 μm in diameter, 1–4.5 μm apart.
Dimensions: 24.5, 25.5, 29, 31.5 μm (four specimens).
Occurrence: 2141.55, 2263.75 m.
Comparison: The foveolate sculpture characterises this *Chelinospora*.

Chelinospora sp. 2 (Plate II, 3)

Description: Amb rounded triangular. Trilete mark distinct with straight sutures which extend to inner edge of the crassitude. Contact areas thin, laevigate, delimited by concentric folds. Exine equatorially and distally patinate, thickness at equator 2–2.5 μm, with foveolate sculpture. Foveae subcircular 1 μm in maximum diameter, up to 0.5 μm high, 0.5–1 μm apart.
Dimensions: 22 μm.
Occurrence: 2041 m.
Comparison: Distinguished from *Chelinospora* sp. 1 by the delicate foveolate patina.

Chelinospora? sp. 3 (Plate II, 4)

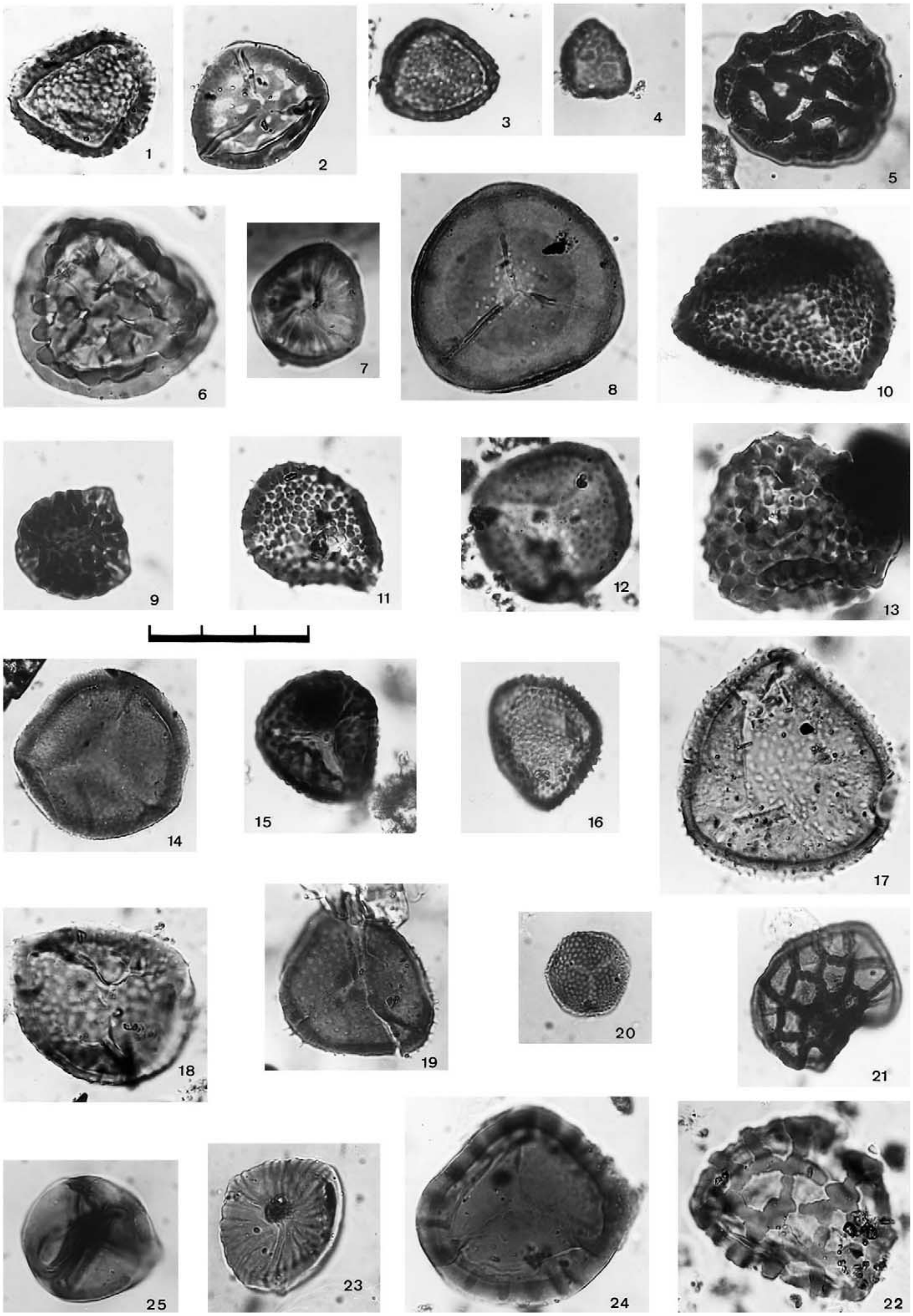
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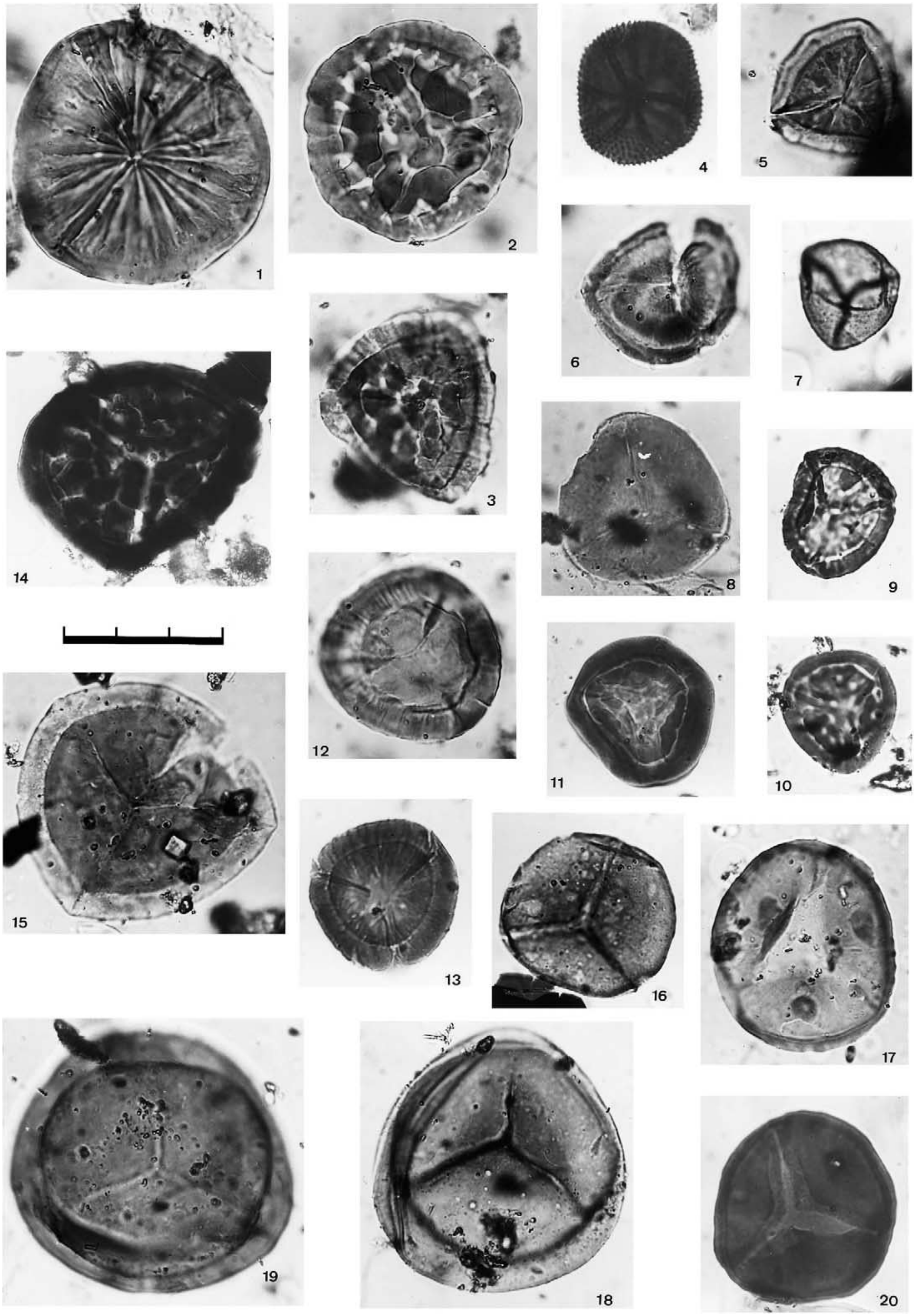
Plate II.

1:	*Chelinospora* sp. A *in* Richardson and Ioannides 1973. 2180 m, L 35623, N46/0.
2:	*Chelinospora* sp. 1. 2263.75 m, L CA56B, J28/0.
3:	*Chelinospora* sp. 2. 2041 m, L 35621, M31/2.
4:	*Chelinospora* sp. 3. 2128.50 m, L CA38, F48/0.
5:	*Clivosispora reticulata* Rodriguez, 1978. 2141.55 m, L 35622, M38/3.
6:	*Clivosispora verrucata* var. *convoluta* McGregor and Camfield, 1986. 2433 m, L CA67A, M44/4.
7:	*Concentricosisporites agradabilis* Rodriguez, 1978. 2141.55 m, L 35629, Q41/2.
8:	*Concentricosisporites sagittarius* Rodriguez, 1983. 2125.30 m, L 35623, K36/3.
9:	*Convolutispora* sp. 2126.20, L 19188, P41/4.
10:	*Cymbosporites dittonensis* Richardson and Lister, 1969. 2125.30 m, L 35631, E54/1.
11:	*Cymbosporites multiconus* Steemans, 1989. 2264.60 m, L CA59B, E38/1.
12:	*Cymbosporites paulus* McGregor and Camfield, 1976. 2127.70 m, L CA14, V37/4.
13:	*Cymbosporites verrucosus* Richardson and Lister, 1969. 2264.50 m, L CA58B, R38/0.
14:	*Cymbosporites* cf. *catillus in* Richardson and Lister 1969. 2141.55, L 19189, T39/2.
15:	*Cymbosporites paulus? in* Wellman 1993. 2126.80 m, L CA24, T31/0.
16:	*Cymbosporites sp. A in* Richardson and Ioannides 1973. 2126.20 m, L 35632, T40/0.
17:	?*Cymbosporites* sp. 1. 2333.80 m, L CA63A, N38/4.
18:	*Cymbosporites* sp. 2. 2332.80 m, L CA64A, R37/2.
19:	*Dibolisporites* sp. 2125.30 m, L 19187, M46/0.
20:	*Dictyotriletes gorgoneus* Cramer, 1967. 2041 m, L 19186, F45/1.
21–22:	*Dictyotriletes* sp. 21: 2126.2 m, L 19188, M53/0. 22: 2433 m, L CA69A, V40/4.
23:	*Emphanisporites neglectus* Vigran, 1964. 2141.55 m, L 35622, K57/0.
24:	*Emphanisporites protophanus* Richardson and Ioannides, 1973. 2264.5 m, L CA57B, G42/2.
25:	*Tetrahedraletes medinensis* Strother and Traverse, 1979. 2141.55 m, L 35629, Q41/0.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Description: Amb triangular. Proximal surface absent. Exine equatorially and distally relatively thick, thickness at equator 1–2 µm, with low convolute and anastomosing muri, 1 µm wide, less than 0.5 µm high, 1 µm apart.
Dimensions: 14.5 µm.
Occurrence: 2128.50 m.
Comparison: Because of the absence of the proximal surface, the attribution to a trilete spore is questionable.

Genus *Convolutispora* Hoffmeister, Staplin and Malloy, 1955

Convolutispora sp. (Plate II, 9)

Description: Amb subtriangular. Trilete mark distinct, bordered by narrow lips. Sutures nearly reach the equator. Exine about 1 µm thick, ornamented on the distal surface with closely spaced, convoluted muri, 1–1.5 µm wide and up

Plate III.

1:	*Emphanisporites rotatus* McGregor, 1973. 2433 m, L CA70A, E27/0.
2–3:	*Emphanisporites splendens* Richardson and Ioannides, 1973. 2: 2433 m, L CA70A, Q55/3. 3: 2433 m, L CA69A, J26/1.
4:	*Emphanisporites* cf. *E. decoratus* Allen, 1965. 2125.30 m, L 19187, N41/0.
5:	*Emphanisporites* sp. C *in* Richardson and Ioannides 1973. 2265.30 m, L CA62B, J34/0.
6:	*Emphanisporites* sp. 2265.30 m, L CA62B, P31/4.
7:	*Granulatisporites* sp. 1. 2125.30 m, L 19187, K43/1.
8:	*Granulatisporites* sp. 2. 2265.30 m, L CA60A, Y41/4.
9:	*Iberoespora cantabrica* Cramer and Diez, 1975. 2125.30 m, L 35623, Q51/4.
10:	*Iberoespora noninspissatosa* Steemans, 1989. 2125.70 m, L CA14, F47/1.
11:	*Iberoespora* sp. 1. 2141.55 m, L 19189, J43/2.
12–13:	*Iberoespora* sp. 2. 12: 2433 m, L CA69B, G37/0. 13: 2041 m, L 35628, H35/2.
14:	*Lophozonotriletes? poecilomorphus* Richardson and Ioannides, 1973. 2127.50 m, L CA32, R43/0.
15:	*Perotriletes laevigatus* Steemans, 1989. 2141.80 m, L CA46, N35/4.
16:	*Retusotriletes abundo* Rodriguez, 1978. 2125.30 m, L 19187, P30/0.
17:	*Retusotriletes maculatus* McGregor and Camfield, 1976. 2125.10 m, L CA13, Q34/4.
18:	*Retusotriletes triangulatus* Streel, 1976. 2141.80 m, L CA46, T41/2.
19:	*Retusotriletes* sp. B *in* Richardson and Ioannides 1973. 2445.75 m, L CA72B, J53/0.
20:	*Retusotriletes* sp. 1. 2125.30 m, L 19187, N44/3.

to 6 µm long, enclosing circular pits and small channels.
Dimensions: 22 µm.
Occurrence: 2126.20 m.
Comparison: *Convolutispora* sp. B Tekbali 1987 is larger and has prominent lips.

Genus *Cymbosporites* Allen 1965

Cymbosporites? sp. 1 (Plate II, 17)

Description: Amb subtriangular. Proximal surface absent. Exine equatorially and distally patinate. Thickness at equator 3.5–5 µm. Patina irregularly covered with rounded or blunted coni or grana, 1 µm high, 1 µm or less wide, and 1–2 µm apart.
Dimension: 46 µm (two specimens).
Occurrence: 2333.80 m.
Comparison: *Cymbosporites proteus* McGregor and Camfield 1976 is more regularly ornamented.

Cymbosporites sp. 2 (Plate II, 18)

Description: Amb rounded triangular. Trilete mark distinct. Sutures extending to inner margin of the equatorial thickening, sinuous, accompanied by lips, up to 2 µm in combined width. Exine proximally thin, smooth, equatorially and distally relatively thick. Thickness at equator 2–3.5 µm. Patina ornamented with slender spines, less than 0.5 µm wide, 1.5 µm high, and 1 µm apart.
Dimensions: 39 µm.
Occurrence: 2332.80 m.

Genus *Dibolisporites* Richardson 1965

Dibolisporites sp. (Plate II, 19)

Description: Amb rounded triangular to subcircular with an equatorial thickening, 1–3 µm wide. Trilete mark nearly equal to spore radius, sutures simple or accompanied by lips or folds, up to 1 µm in combined width. Contact areas smooth. Exine outside contact areas bears a variable biform sculpture, of setae, spines, and coni that taper to slender stems, topped by blunt, spatulate or bifurcate elements; length, 1–1.5 µm, width of bases up to 1 µm, and 1–3 µm apart.
Dimensions: 29–30.5 µm (five specimens).
Occurrence: 2125.30–2127 m.
Genus *Dictyotriletes* (Naumova 1937) Potonié and Kremp 1954

Dictyotriletes sp. (Plate II, 21–22)

Description: Amb subcircular to broadly subtriangular. Trilete mark, where seen, extending nearly the whole length of spore radius. Sutures simple, straight. Proximal exine laevigate. Distal sculpture consists of muri, very variable in width and height which form a delicate or a broad reticulum. Muri appear to be formed of coalescent verrucae, 2–4.5 µm wide, up to 4 µm high. Lumina of reticulum are also of variable form and dimensions, from polygonal to irregular and from 4 to 9 µm in diameter.
Dimensions: 30–34.5–39 µm (four specimens).
Occurrence: 2126.20–2129.6–2333.80–2433 m.
Comparison: *Dictyotriletes* sp. A *in* Tekbali and Wood (1991) and *Synorisporites* spp. *in* Wellman and Richardson (1996) appear similar but there are no descriptions of these species.

Spore type A *in* Richardson and Ioannides (1973) has a distal sculpture described as a pattern of openings of variable form and dimensions, according to the preservation.

Genus *Emphanisporites* McGregor 1961

Emphanisporites cf. *E. decoratus* Allen 1965 (Plate III, 4)

cf. 1965 *Emphanisporites decoratus* Allen, p. 708, pl. 97: 15–18

Description: Amb subcircular. Sutures extend 3/4 spore radius, accompanied by lips or folds 2 µm in combined width. Contact surface laevigate, bearing radial muri, low, 2 µm wide near the equator, tapering toward proximal pole. Sculpture of proximo-equatorial and distal regions consist of coni, spines and some biform elements (conus topped by a minuscule spine), 0.5 µm wide, 0.5–1 µm high, and 0.5 µm apart. All elements are polygonal in plan view.
Dimensions: 27 µm.
Occurrence: 2125.30 m.
Comparison: *Emphanisporites decoratus* Allen

1965 is larger with rounded ornament in plan view. *Emphanisporites novellus* McGregor and Camfield 1976 bears grana or coni with rounded tips. *Emphanisporites* sp. A *in* Wellman and Richardson (1996) has shorter proximal ribs and rounded ornamentation in plan view on the distal face.

Emphanisporites sp. (Plate III, 6)

Description: Amb subtriangular with an equatorial crassitude, 3.5–4.5 µm wide. Trilete mark distinct, length equal to the spore radius. Sutures straight, simple or accompanied by lips, 1 µm in combined width. Distal surface smooth. Proximal face ornamented with low and thin, radially oriented muri, 0.5 µm wide, less than 1 µm apart. An annular thickening, 3–4 µm width is centrally located on the distal face, enclosing a subtriangular to subcircular flat thickening at the distal pole. This thickening has a width of 10–15% of the equatorial diameter.
Dimensions: 32–33.5 µm (two specimens).
Occurrence: 2265.30–2433 m.
Comparison: The proximal radial muri distinguish this species from *Amicosporites miserabilis* Cramer 1966. *Emphanisporites annulatus* McGregor 1961 is ornamented by coarse radial ribs on the proximal face and lack the thickening at the distal pole.

Genus *Iberoespora* Cramer and Diez 1975

Iberoespora sp. 1 (Plate III, 11)

Description: Trilete cingulate miospore with a subtriangular nearly circular amb. A furrow, 1 µm wide, on the distal surface borders the internal edge of the cingulum, up to 5.5 µm wide. Sutures simple, and extend to about 1/2 of the cingulum. Inspissations are developed at the edges of the interradial areas, up to 5.5 µm in width. Distally the exine is ornamented with low convolute verrucae, 2–3 µm wide.
Dimensions: 28 µm.
Occurrence: 2141.55 m.
Comparison: *Iberoespora glabella* Cramer and Diez 1975 has lips and apparently shorter inspissations.

Iberoespora sp. 2 (Plate III, 12–13)

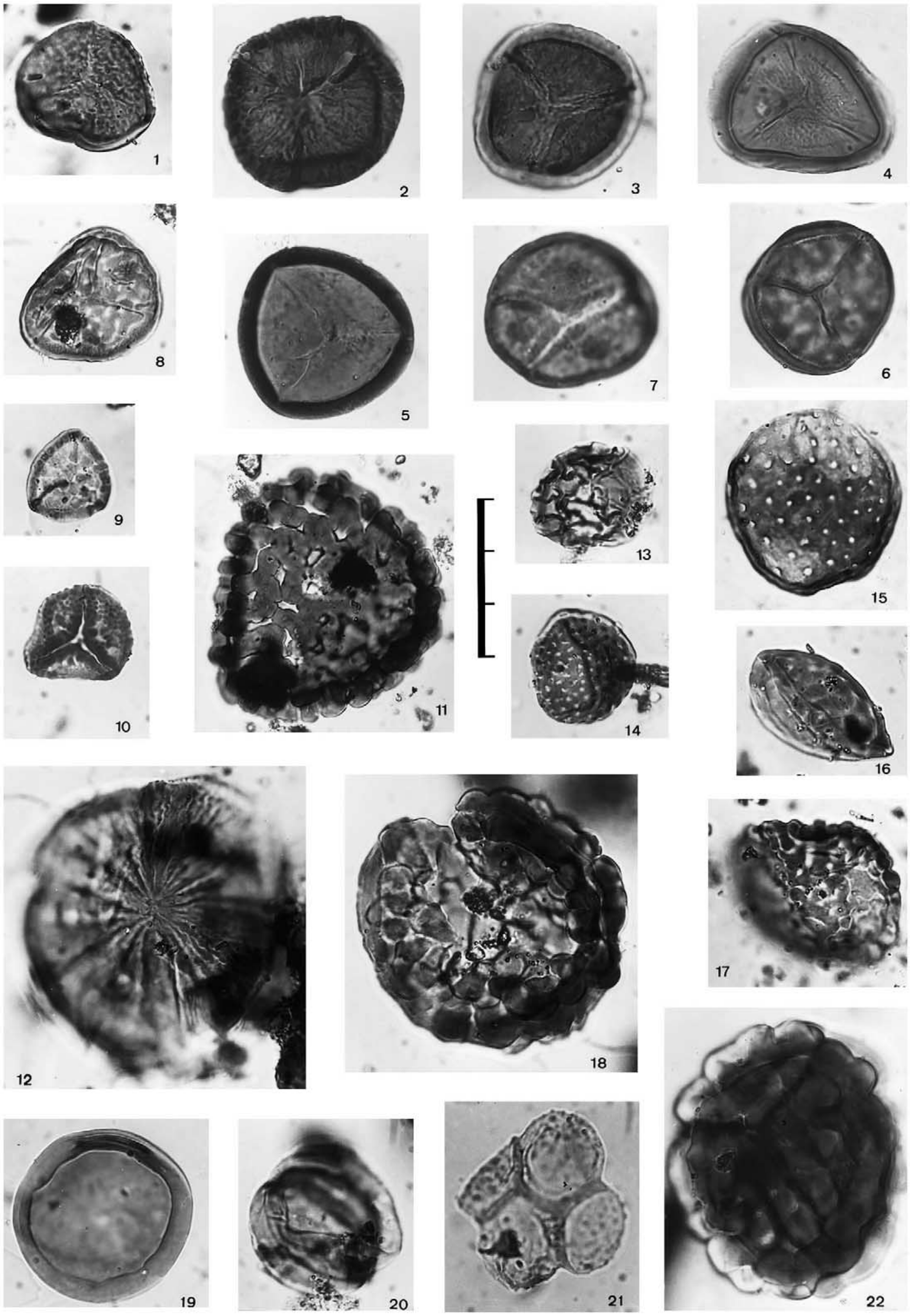
Description: Trilete cingulate miospore with rounded triangular to subcircular amb. Cingulum 4.5–5 µm wide, about 15% of the spore diameter. A more or less distinct furrow on the distal surface borders the internal edge of the cingulum. The furrow is straight to slightly sinuous, up to 2 µm wide. Sutures straight, 5/6 spore radius, simple or accompanied by lips, up to 1 µm in combined width. Distal surface smooth. Cingulum ornamented with low, narrow and slightly sinuous radially oriented muri, less than 1 µm wide, and 1 µm apart. Muri can extend over proximal surface.
Dimensions: 29–34.5 µm (two specimens).
Occurrence: 2041–2433 m.
Comparison: It differs from other species of this genus by the radial muri of the cingulum and proximal face.

Genus *Scylaspora* Burgess and Richardson, 1995

Basionym: *Scylaspora scripta* Burgess and Richardson 1995, late Wenlock to early Pridoli cryptospores and miospores from south and southwest Wales, Great Britain. Palaeontographica Abt. B, 236, pp. 17–18, pl. 7: 5–9.
Generic comments: On the base of the diagnosis from respectively Dufka (1995) and Burgess and Richardson (1995), the genera *Scylaspora* and *Rugosisporites* are identical. Therefore, the genus *Scylaspora* is a junior synonymy of the genus *Rugosisporites* as the former was published a few months after (April and July). The type species of *Rugosisporites* was stated illegally in the original publication (1995). Hence the genus is not valid, Jansonius et al. (1998) corrected this error. Therefore, the name *Rugosisporites* has only been validly published by Jansonius et al. (1998). As *Scylaspora* has been legally published in 1995, this genus name has priority.

Scylaspora chartulata (McGregor and Narbonne) Rubinstein and Steemans, comb. nov. (Plate IV, 2)

Basionym: *Retusotriletes chartulatus* McGregor and Narbonne, 1979, Can. J. Earth Sci. 15, pp. 1301–1302.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Synonymy and references:

1973 *Emphanisporites*? sp. D *in* Richardson and Ioannides, p. 276, pl. 3: 9.
1974 *Emphanisporites* sp. *in* McGregor (1973), pl. 1: 7.
1978 *Retusotriletes chartulatus* McGregor and Narbonne (1978), pp. 1301–1302, pl. 1: 10–12.
1991 Trilete miospore type 1 *in* Burgess and Richardson (1991), p. 618, fig. 3A–C.
1995 *Scylaspora scripta* Burgess and Richardson, pp. 17–18, pl. 7: 5–9.
1995 Trilete miospore type 1 Burgess and Richardson, *in* Steemans, pl. I: 3–4.
1995 *Rugosisporites* cf. *chartulatus* Dufka, pp. 71–72, pl. 2: 9–14.

Genus *Stenozonotriletes* (Naumova 1953) Potonié 1958

Plate IV.

1:	*Scylasporas downiei* Burgess and Richardson, 1995. 2433 m, L CA69B, O39/1.
2:	*Scylaspora chartulata* (McGregor and Narbonne) Rubinstein and Steemans, comb. nov. 2126.2 m, L 35632, V44/0.
3:	*Stellatispora inframurinata* var. *cambrensis* Burgess and Richardson, 1995. 2141.55 m, L 35622, N49/0.
4:	*Stellatispora inframurinata* var. *inframurinata* Burgess and Richardson, 1995. 2263.75 m, L CA56B, G41/3.
5:	cf. *?Stenozontriletes furtivus* McGregor and Camfield, 1976. 2263.75 m, L CA56B, U42/2.
6:	*Synorisporites? libycus* Richardson and Ioannides, 1973. 2125.30 m, L 19187, N48/4.
7:	*Synorisporites papillensis* McGregor, 1973. 2125.30 m, L 35631, T42/0.
8:	*Chelinospora retorrida* Turnau, 1986. 2263.75 m, L CA56B, F28/0.
9:	*Synorisporites verrucatus* Richardson and Lister, 1969. 2141.55 m, L 35622, M36.
10:	*Synorisporites* sp. 2141.55 m, L 35629, H40/1.
11:	Spore type A. 2433 m, L CA69A, G30/3.
12:	*Artemopyra robusta* Wellman and Richardson, 1996 2433 m, L CA70A, M53/4.
13:	*?Rugosphaera tuscarorensis* Strother and Traverse, 1979. 2433 m, L CA69B, O40/0.
14:	*Confossuspora reniforma* Strother, 1995. 2445.7 m, L CA71A, H42/0.
15:	*Confossuspora* sp. 2126.20 m, L 35632, F53/1.
16:	*Hispanaediscus verrucatus* Cramer emend. Burgess and Richardson, 1991. 2265.30 m, L CA61A, V47/3.
17:	*Hispanaediscus lamontii* Wellman, 1993. 2433 m, L CA72B, W41/1.
18:	cf. *Hispanaediscus wenlockensis* Wellman, 1993. 2433 m, L CA70A, V47/4.
19:	*Laevolancis divellomedium* Burgess and Richardson, 1991. 2141.55 m, L 35629, U42/0.
20:	*Pseudodyadospora petasus* Wellman and Ricardson, 1993. 2433 m, L CA70A, V52/0.
21:	*Quadrisporites variabilis* Cramer and Diez, 1972. 2141.55 m, L 35629, V34/0.
22:	Tetrad sp. 2264.5 m, L CA58B, X42/2.

cf. ?*Stenozonotriletes furtivus* Allen 1965 sensu McGregor and Camfield 1976 (Plate IV, 5)

Synonymy and references:

cf. 1976 ?*Stenozonotriletes furtivus* Allen, *in* McGregor and Camfield (1976), p. 27, pl. 4: 7, 8, 11–12.
cf. 1983 ?*Stenozonotriletes furtivus* Allen, *in* Le Hérissé (1983), p. 76, pl. 8: 4–5.
cf. 1990 ?*Stenozonotriletes furtivus* Allen, *in* Buret, p. 74, pl. 6: 12.

Description: Amb subtriangular. Sutures simple, straight, reaching the inner margin of the cingulum. Exine laevigate. Cingulum 3.5 μm wide in the interradial areas and 2 μm wide in the radial areas. Cingulum delimits a triangular proximal surface.
Dimensions: 34 μm.
Occurrence: 2263.75 m.
Comparison: ?*Stenozonotriletes furtivus* (Allen) McGregor and Camfield 1976 has a larger cingulum.

Genus *Synorisporites* Richardson and Lister 1969

Synorisporites sp. (Plate IV, 10)

Description: Amb subtriangular with rounded apices. Equatorial crassitude 1.5–2 μm in width. Trilete mark distinct, with slightly sinuous sutures which extend to the equator and are accompanied by low and broad lips, 4–4.5 μm in combined width. Contact surfaces ornamented with a few irregularly shaped verrucae, 1.5–3 μm in diameter and less than 1 μm in height. The verrucae appear to join near the trilete mark to form the lips. Distal surface ornamented with verrucae, pointed or blunted coni, 0.5–1 μm wide, up to 1 μm high. Ornament rounded to irregular in plan, closely spaced and occasionally coalescent.
Dimensions: 21.5 μm.
Occurrence: 2141.55 m.
Comparison: The way the coalescent verrucae form broad lips distinguish *Synorisporites* sp. from other species of *Synorisporites*.

3.2. Cryptospores

Genus *Confossuspora* Strother 1991

Confossuspora sp. (Plate IV, 15)

Description: Cryptospore with subcircular amb. Proximal hilum thin, outlined by a concentric fold. Exine at the equator and distally foveolate. Foveae circular or subcircular, uniformly distributed, 1–1.5 μm in diameter, up to 1.5 μm deep at equator, and 2–3 μm apart.
Dimensions: 34.5 μm.
Occurrence: 2126.20 m.
Comparison: *Confossuspora reniforma* Strother 1991 has foveae irregular in shape size and distribution.

Genus *Hispanaediscus* Cramer emend. Burgess and Richardson 1991

cf. *Hispanaediscus wenlockensis* Burgess and Richardson 1991 (Plate IV, 18)

Synonymy and references:

cf. 1991 *Hispanaediscus wenlockensis* Burgess and Richardson, p. 611, pl. 1: 4–9.

Description: Cryptospore with subcircular amb. Proximal hilum thin and generally destroyed. Exine distally ornamented with prominent verrucae, with rounded or polygonal bases, and rounded top. 4–9 μm in width, and 2–3 μm in height.
Dimensions: 47–58 μm (four specimens).
Occurrence: 2428.10–2433–2445.75 m.
Comparisons: *Hispanaediscus wenlockensis* Burgess and Richardson 1991 is smaller and has proximal radial muri.

3.3. Incertae Sedis

Tetrad type 1 (Plate IV, 22)

Description: Tetrads of closely adherent spores with murornate sculpture. Proximal surface not seen. Distal exine sculptured with rounded, densely spaced, convolute and anastomosing muri, 5–5.5 μm wide, up to 7 μm high at equator and rounded verrucae, about 5.5 μm wide. The muri appear to be composed of coalescent verrucae.

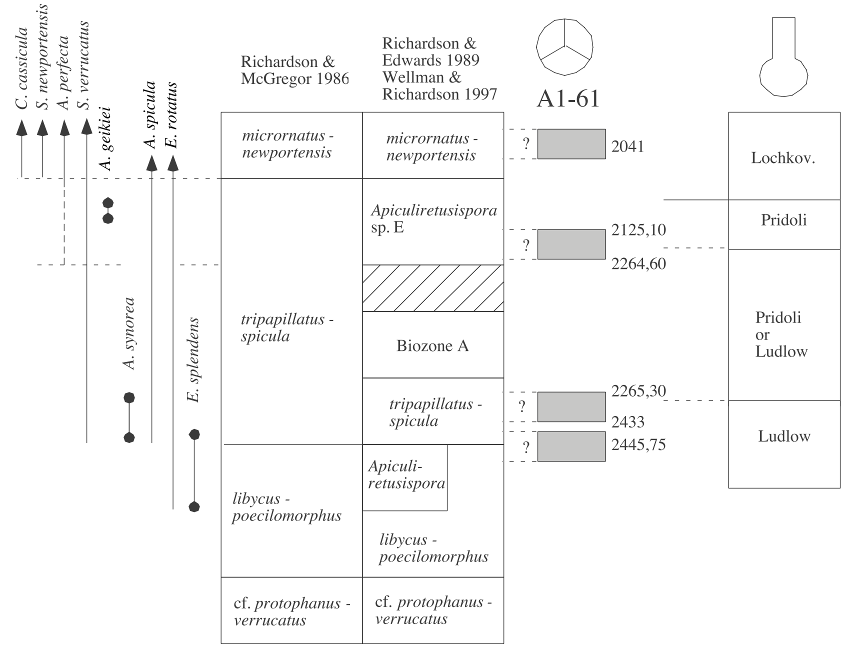

Fig. 3. Miospore biostratigraphy around the Silurian–Devonian boundary, showing the range of some important miospore species and the stratigraphic position of the samples in the A1-61 borehole.

Dimensions: Maximum diameter 46–52–74 μm. Minimum diameter 42.5–47–69.5 μm (three specimens).
Occurrence: 2264.50–2445.75 m

4. Biostratigraphy

4.1. Historic

Miospore biostratigraphy of the late Ludlow to early Devonian is poorly documented. Eight major publications has been used: Burgess and Richardson, 1995; Richardson and Edwards, 1989; Richardson and Ioannides, 1973; Richardson and Lister, 1969; Richardson and McGregor, 1986; Rodriguez, 1983; Steemans, 1989; Wellman and Richardson, 1996.

Three assemblage biozones have been defined in the late Silurian and in the earliest Lower Devonian by Richardson and McGregor (1986). In ascending stratigraphic order there are (Fig. 3): *Synorisporites libycus–?Lophozonotriletes poecilomorphus*, *Synorisporites tripapillatus–Apiculiretusispora spicula* and *Emphanisporites micrornatus–Streelispora newportensis* biozones.

In addition to the nominal species, the *tripapillatus–spicula* biozone of the British and Libyan sequences (C1-34 and B2-34 boreholes) contains the following characteristic species: *Emphanisporites splendens*, *Amicosporites miserabilis* (= *A. splendidus*, see Cramer and Diez, 1975, p. 336), and *Synorisporites verrucatus*. However, *A. miserabilis* is also known in the underlying *libycus–poecilomorphus* biozone (Richardson et al., 1981; Steemans et al., 1996). The first occurrence of tripapillate species is considered to be an important feature of the biozone. However, tripapillate forms have been found in the early Ludlow from the D1-61 borehole of Libya, close to the A1-61, as demonstrated by independent stratigraphic data (Buret, 1990). Rare tripapillate species have also been observed in Ludlow samples from Götland (Steemans, 1995).

Based on study of the same Libyan material published by Richardson and Ioannides (1973), Richardson and Edwards (1989) recognised a new *Apiculiretusispora* subbiozone in the upper part of the *libycus–poecilomorphus* biozone, below the *tripapillatus–spicula* biozone. Consequently, *Emphanisporites splendens* is present only in the *Apiculiretusispora* subbiozone of the C1-34 borehole, although this species was characteristic of the *tripapillatus–spicula* biozone (Richardson and McGregor, 1986). Therefore, if *E. splendens* is still considered a characteristic species of the *tripapillatus–spicula* biozone, then the *Apiculiretusispora* subbiozone has to be a subdivision of this biozone, and not of the underlying *libycus–poecilomorphus* one.

The *libycus–poecilomorphus* biozone was recently subdivided in four subzones in the British Isles (Burgess and Richardson, 1995). In ascending order, there are: *Chelinospora obscura*, *Stellatispora inframurinata* var. *cambrensis*, *Apiculiretusispora? asperata* and *S. inframurinata* var. *inframurinata* subzones. Above this last subzone, the *tripapillatus–spicula* biozone is overlain by biozone A and biozone *Apiculiretusispora* sp. E, both separated by a considerable gap (Richardson and Edwards, 1989; Wellman and Richardson, 1996). The *micrornatus–newportensis* or MN biozone succeeds these biozones (Richardson and McGregor, 1986; Steemans, 1989).

Biozone A, characterised by the incoming of alete cryptospores with a thin proximal surface and distal rugulate sculpture (Richardson and Edwards, 1989), is known only from the type area of the Downton Group. No zonal index species names have been assigned to this biozone.

Apiculiretusispora sp. E which characterises the overlying biozone has not been formally described yet. But on the basis of figured specimens, *Apiculiretusispora* sp. E (Richardson et al., 1981) appears to be a possible synonym of *Apiculiretusispora perfecta* (Steemans, 1989).

The base of the *micrornatus–newportensis* biozone extends from the early Lochkovian of Old Red Sandstone sections, however, does not include the earliest Lochkovian (Richardson et al., 1981; Steemans, 1982; Steemans, 1989).

No independent biostratigraphic data can accurately determine the stratigraphic position of biozones A and *Apiculiretusispora* sp. E. However, both range from the early Pridoli to the earliest Lochkovian.

The base of the *tripapillatus–spicula* biozone is correlated with the Ludlow–Pridoli boundary (Richardson and McGregor, 1986; Burgess and Richardson, 1995; Wellman and Richardson, 1996). Nonetheless, this stratigraphic correlation has yet to be supported by independent biostratigraphic data.

Graptolite species characteristic of the Wenlock–Ludlow boundary have been reported around the base of the *libycus–poecilomorphus* biozone in Libya (Richardson and Ioannides, 1973).

4.2. Biostratigraphic results

More than 80 miospore species have been observed in the studied samples (Fig. 4). The ranges of selected species of biostratigraphic significance are shown on Fig. 5, together with the biozonation established by Richardson and Edwards (1989), Wellman and Richardson (1996). The oldest sample (2445.75 m) in the A1-61 borehole contains, amongst other species, *Emphanisporites splendens* (= *Emphanisporites pseudoerraticus* Richardson and Ioannides, 1973) which is known in the *Apiculiretusispora* subbiozone (Richardson and Edwards, 1989) and in the biozones III–V from Spain (Rodriguez, 1983). In this study, the first occurrence of *Synorisporites tripapillatus* places the base of the *tripapillatus–spicula* biozone of Richardson and McGregor (1986) at the base of the biozone IV of Rodriguez. Therefore, *E. splendens* is extended into the early *tripapillatus–spicula* biozone. This situation has not been observed in the Libyan borehole C1-34, however, there is a gap of about 40 m in the critical part of the sequence (Richardson and Ioannides, 1973).

In addition, *Emphanisporites rotatus* is also present in the oldest sample (2445.75 m). Notably, this species also occurs in the *Apiculiretusispora* subbiozone in the C1-34 borehole (Richardson and Ioannides, 1973). Therefore, the presence of *E. rotatus* and *Emphanisporites splendens* indicates the base of the studied sequence is no older than the *Apiculiretusispora* subbiozone.

The overlying level (sample 2433 m) contains

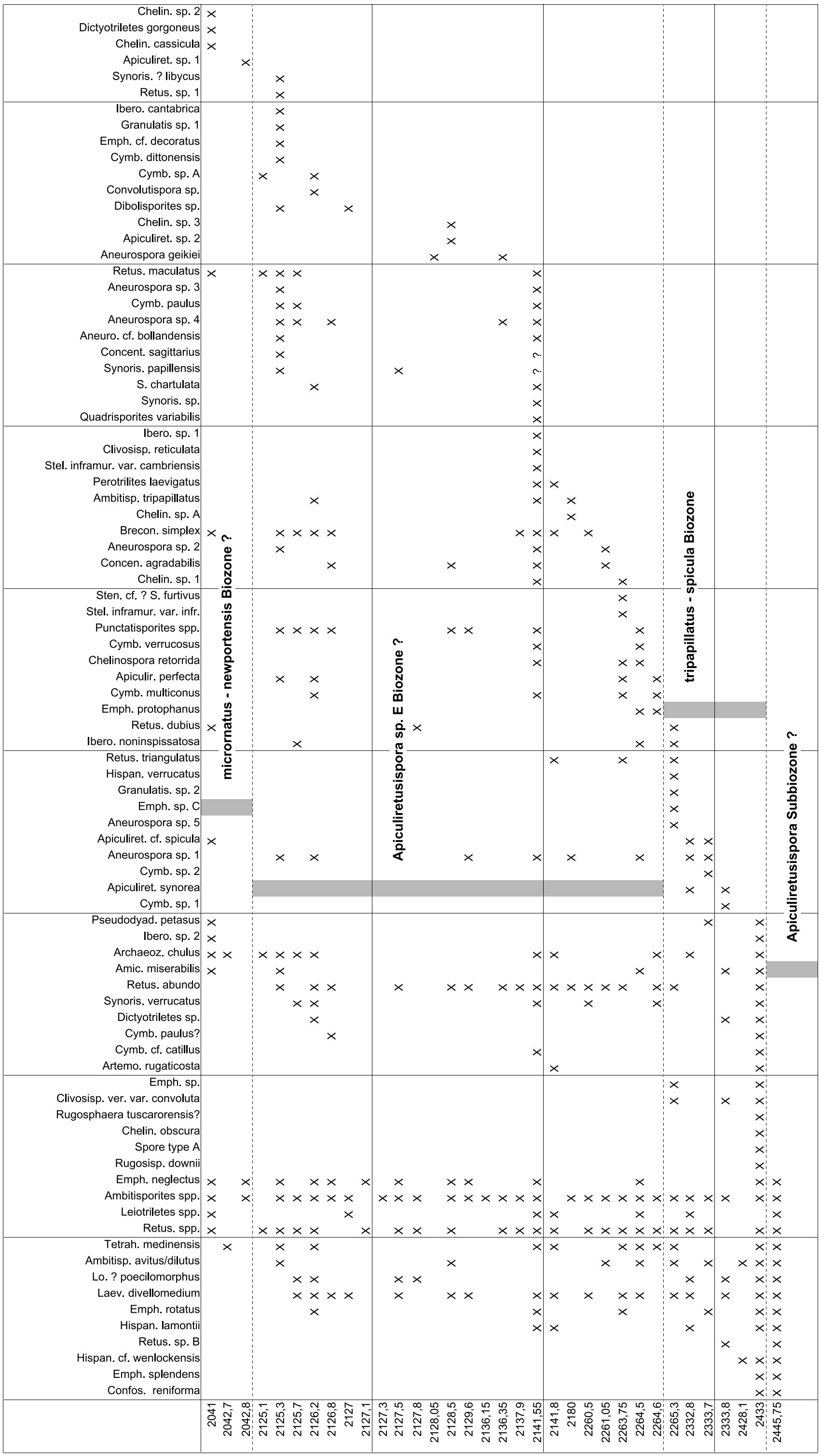

Fig. 4. Stratigraphic occurrence of miospore taxa recorded in all samples in borehole A1-61.

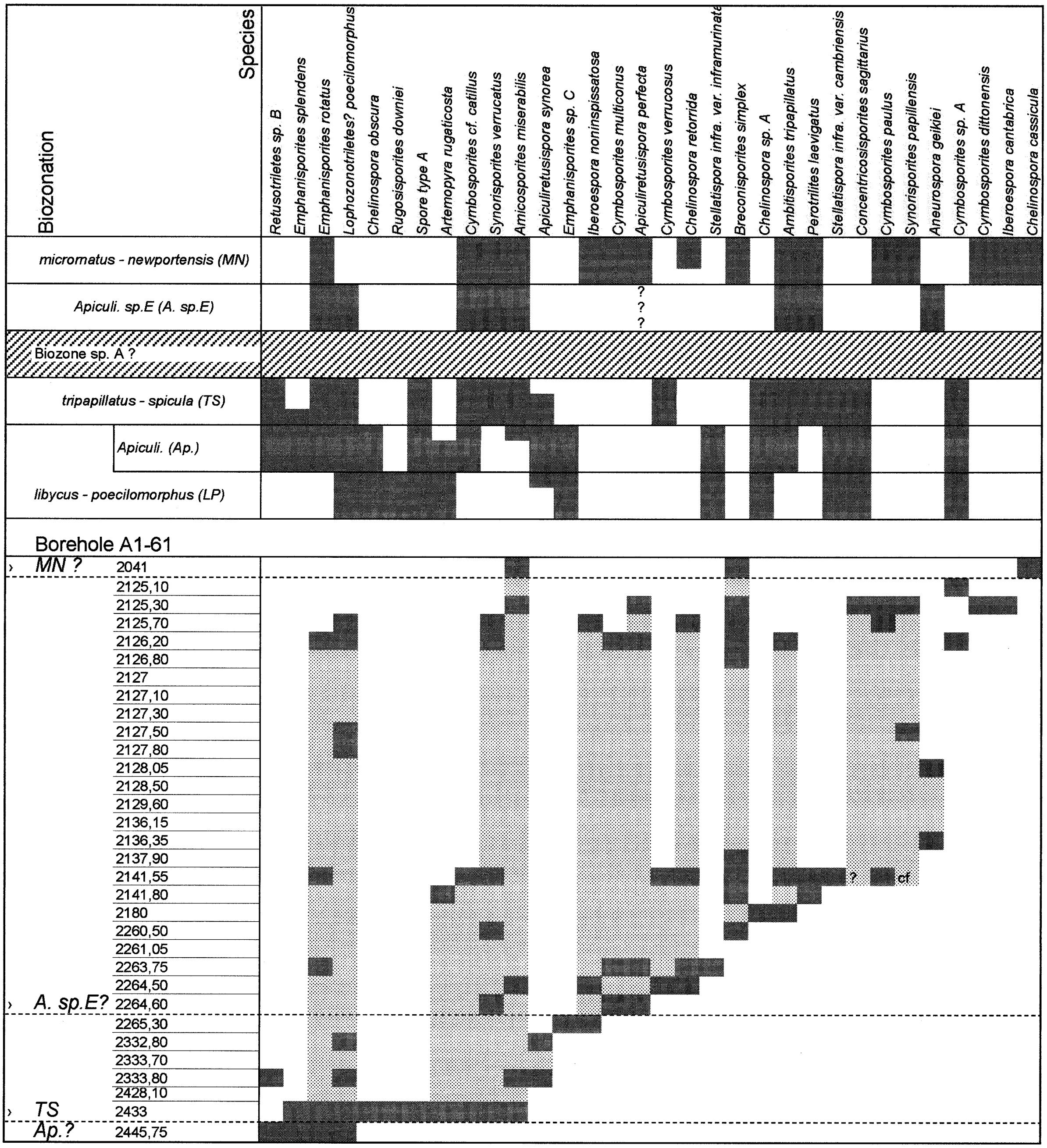

Fig. 5. Stratigraphic distribution and miospore biozonation of selected miospore species in borehole A1-61, with the published biostratigraphic range of these miospores.

Synorisporites verrucatus, which is unknown below the *tripapillatus–spicula* biozone. As there is only one sample below the level 2433 m, poor in miospores, it would be unwise to draw a biozone boundary between these two levels. Consequently, sample 2445.75 m could be attributed either to the *Apiculiretusispora* subbiozone or to the *tripapillatus–spicula* biozone.

Apiculiretusispora synorea, only known in the *tripapillatus–spicula* biozone, is first observed in sample 2333.80 m, above the last occurrence of *Emphanisporites splendens*.

Apiculiretusispora perfecta first appears at the level 2264.60 m. Since *A. perfecta* and *Apiculiretusispora* sp. E are possible synonyms, therefore the base of *Apiculiretusispora* sp. E biozone could be provisionally drawn at this level. *Aneurospora* with prominent spines (e.g. *Aneurospora geikiei* from level 2136.35 m), also occur in the *Apiculiretusispora* sp. E biozone from the British Isles (Wellman and Richardson, 1996), which supports this correlation.

Chelinospora cassicula, from level 2041 m, has never been found below the Lochkovian MN biozone, but this is based on few data. In addition, the species *Breconisporites simplex*, *Cymbosporites paulus*, *Cymbosporites dittonensis*, *Iberoespora cantabrica*, *Synorisporites papillensis* and *Chelinospora retorrida*, previously unknown below the Lochkovian, are here observed in levels assigned to the lower and middle parts of the Pridoli by chitinozoans.

Richardson et al. (1981) drew the Silurian–Devonian boundary (on data in Al-Ameri's thesis, 1980), below the Tadrart Formation and in the upper part of the 'Alternances Argilo-gréseuses' Formation. This level is below the first occurrence of *Streelispora newportensis*, which is only known in the Lochkovian from Europe. The Libyan DN biozone of Al-Ameri is correlated with the MN biozone.

Streel et al. (1990) recorded *Chelinospora retorrida* in the upper part of the 'Alternances Argilo-gréseuses' Formation and his identification is confirmed by the present work. Streel et al. proposed a Lochkovian age for these strata as *C. retorrida* characterises the R interval biozone, above the N interval biozone defined by the occurrence of *Streelispora newportensis* (Steemans, 1989).

The present biostratigraphic data based on miospores are in contradiction with the results based on chitinozoans (Jaglin and Paris, 2002) and on acritarchs (Le Hérissé, 2002). This diachronism between the chitinozoan and acritarch biozones and the miospore biozones could reflect minor local miospore assemblage variations.

5. Phytogeographic implications

In contrast with the Devonian period, in Silurian times, Laurentia, Avalonia and Baltica were separated from the Gondwana by the Rheic Ocean. This palaeogeographic separation could be responsible for the endemism of some miospores species produced by land plants. However, marine palynomorphs are less affected by an oceanic barrier.

Some miospore species, previously considered as characteristic of the Lochkovian in Europe, occur earlier (Pridoli) on the Gondwana continent. The closure of the Rheic Ocean has allowed the vegetation to migrate from Gondwana to Avalonia during the earliest Lochkovian. Later in the Devonian, complete closure of the ocean allowed a more complete homogenisation of the miospore assemblages.

However, some other miospore data from Gondwana area might contradict the above hypothesis. The Pridoli layers from Brittany (Deunff and Chateauneuf, 1976) do not contain any of the above mentioned species, although these miospore assemblages are poor and badly preserved. These species are also absent in the Pridoli of Spain (Rodriguez, 1983). The Lochkovian Mitkov beds of Podolia have been correlated with the *Apiculiretusispora* sp. E biozone by Richardson et al. (1981). This correlation is based on a poor assemblage of miospores described by Arkhangelskaya (1980), but as yet there are no miospore data from the Pridoli of Podolia.

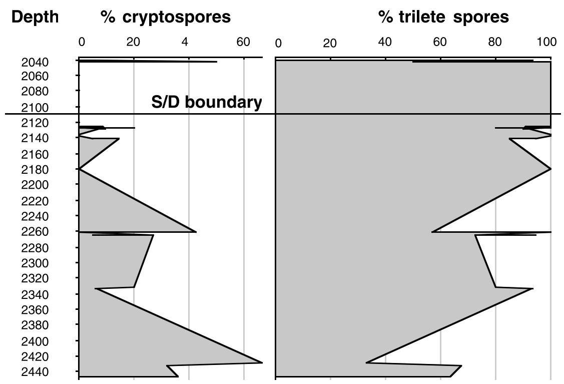

Fig. 6. Relative proportions of trilete spores versus cryptospores throughout the borehole A1-61.

6. Paleobotanical signification

Trilete spore taxa are much more abundant than cryptospores in all samples of the A1-61 borehole. With regard to the number of specimens, the difference is of even greater importance. Fig. 6 shows a clear progressive increase in the percentage of miospores relatively to the cryptospores from the oldest to the youngest levels. Even if a regressive trend is marked in the 'Alternances Argilo-gréseuses Formation', with terrestrial conditions at the top of the formation, constant marine conditions dominate the palynofacies throughout all the sections.

Wellman and Richardson (1996) observed a very different palynological assemblage from continental (lacustrine) sediments of similar age (*Apiculiretusispora* sp. E biozone). The numbers of cryptospore and miospore taxa are similar, however cryptospores are much more abundant than miospores. The cryptospore domination in continental assemblages from late Silurian and around the Silurian–Devonian boundary has also been observed by Fanning et al. (1991) and Richardson (1996).

Consequently, it appears that continental and coastal marine assemblages are characterised by inverse proportions of trilete spores and cryptospores. These differences between both palaeoenvironments could suggest that the plants producing trilete spores and those producing cryptospores are not thriving in the same biotope (Steemans, 1999a,b). The absence of many cryptospore species, or their extreme rarity in marine layers, suggests that the plants producing these cryptospores thrived in isolated biotopes of the fluvial system which transport the majority of these palynomorphs. This has been described as the 'Wellman effect' (Steemans, 1999a; Wellman et al., 2000).

7. Conclusions

Palynological assemblages of acritarchs, chitinozoans and miospores found together in the same samples, are of particularly importance as it allows correlation of the respective biozones and provides independent biostratigraphic control. A small number of miospore species important in the Lochkovian biostratigraphy of the Old Red Sandstone continent appear to occur earlier, in the Pridoli of the western margin of Gondwana. This age discrepancy of first miospore appearances between the two palaeocontinents could testify to the progressive closure of these tectonic plates. Four miospore biozones have been recognised within the continuous interval from the late Ludlow to the early Lochkovian. This zonation clarifies the evolution of different biostratigraphic concepts previously published on that matter.

The smaller proportion of cryptospores, compared to trilete spores in marine environments, by comparison to other work done on coeval continental sediments, confirms that the plants producing trilete spores and cryptospores inhabited, or at least dominated, different continental environments.

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Appendix

List of the miospore species

Ambitisporites avitus/dilutus morphon Steemans 1996
Ambitisporites tripapillatus Moreau-Benoit 1976
Amicosporites miserabilis Cramer 1966
Aneurospora cf. *A. bollandensis* Steemans 1989
Aneurospora geikiei Wellman and Richardson 1996
Aneurospora sp. 1
Aneurospora sp. 2
Aneurospora sp. 3
Aneurospora sp. 4
Aneurospora sp. 5
Apiculiretusispora perfecta Steemans 1989

Apiculiretusispora cf. *A. spicula* Richardson and Lister 1969
Apiculiretusispora synorea Richardson and Lister 1969
Apiculiretusispora sp. 1
Apiculiretusispora sp. 2
Archaeozonotriletes chulus (Cramer) Richardson and Lister 1969
Artemopyra robusta Wellman and Richardson 1996
Breconisporites simplex Wellman 1993
Chelinospora cassicula Richardson and Lister 1969
Chelinospora obscura Burgess and Richardson 1995
Chelinospora retorrida Turnau 1986
Chelinospora sp. A *in* Richardson and Ioannides, 1973
Chelinospora sp. 1
Chelinospora sp. 2
Chelinospora sp. 3
Clivosispora reticulata Rodriguez 1978
Clivosispora verrucata var. *convoluta* McGregor and Camfield 1986
Concentricosisporites agradabilis Rodriguez 1983
Concentricosisporites sagittarius (Rodriguez 1978) Rodriguez 1983
Confossuspora reniforma Strother 1995
Confossuspora sp.
Convolutispora sp.
Cymbosporites cf. *catillus in* Richardson and Lister (1969)
Cymbosporites dittonensis Richardson and Lister 1969
Cymbosporites multiconus Steemans 1989
Cymbosporites paulus McGregor and Camfield 1976
Cymbosporites paulus? in Wellman 1993
Cymbosporites sp. A *in* Richardson and Ioannides (1973)
Cymbosporites verrucosus Richardson and Lister 1969
Cymbosporites? sp. 1
Cymbosporites sp. 2
Dibolisporites sp.
Dictyotriletes gorgoneus Cramer 1967
Dictyotriletes sp.
Dyadospora murusdensa (Strother and Traverse) Burgess and Richardson 1991
Emphanisporites cf. *E. decoratus* Allen 1965
Emphanisporites neglectus Vigran 1964
Emphanisporites protophanus Richardson and Ioannides 1973
Emphanisporites rotatus (McGregor) McGregor 1973
Emphanisporites sp. C *in* Richardson and Ioannides (1973)
Emphanisporites splendens (Richardson and Ioannides) Richardson and Ioannides 1973
Emphanisporites sp.
Granulatisporites sp. 1
Granulatisporites sp. 2
Hispanaedicus lamontii Wellman 1993
Hispanaediscus verrucatus Cramer emend. Burgess and Richardson 1991
Hispanaediscus cf. *H. wenlockensis* Burgess and Richardson 1991
Iberoespora cantabrica Cramer and Diez 1975
Iberoespora noninspissatosa Steemans 1989
Iberoespora sp. 1
Iberoespora sp. 2
Laevolancis divellomedium (Chibrickova) Burgess and Richardson 1991
Lophozonotriletes? poecilomorphus Richardson and Ioannides 1973
Perotrilites laevigatus Steemans 1989
Quadrisporites variabilis (Cramer) Cramer and Diez 1972
Retusotriletes abundo Rodriguez 1978
Retusotriletes dubius (Eisenack) Richardson 1965
Retusotriletes maculatus McGregor and Camfield 1976
Retusotriletes sp. B *in* Richardson and Ioannides 1973
Retusotriletes triangulatus (Streel) Streel 1967
Retusotriletes sp. 1
Scylaspora downiei Burgess and Richardson 1995
Scylaspora chartulata (McGregor and Narbonne) Rubinstein and Steemans, comb. nov.
?Rugosphaera tuscarorensis Strother and Traverse 1979
Spore type A *in* Richardson and Ioannides 1973
Stellatispora inframurinata var. *cambrensis* Burgess and Richardson 1995

Stellatispora inframurinata var. *inframurinata* Burgess and Richardson 1995
cf. *?Stenozonotriletes furtivus* (Allen) McGregor and Camfield 1976
Synorisporites papillensis McGregor 1973
Synorisporites verrucatus Richardson and Lister 1969
Synorisporites? libycus Richardson and Ioannides 1973
?Synorisporites sp.
Tetrad sp.
Tetrahedraletes medinensis Strother and Traverse 1979

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