Retusotriletes maculatus McGregor and Camfield, 1976
Figure 38B

1967 *Leiotriletes* sp. Mortimer, pl. 1b.
1968 Spore trilète à papilles proximales sp. 4 Jardiné and Yapaudjian, pl. 1, fig. 16.
1976 *Retusotriletes maculatus* McGregor and Camfield, p. 26, pl. 1, fig. 6.

Dimensions. 29(41)55 μm; 12 specimens measured.

Remarks. Mortimer (1967) and Jardiné and Yapaudjian (1968) figure similar spores. *Ambitisporites* sp. B *in* Richardson and Ioannides (1973) is smaller and has an equatorial crassitude. *R. ocellatus* McGregor (1973) has also proximal papillae but is much larger. *Ambitisporites eslae* (Cramer and Díez) Richardson *et al.*, 2001 is cingulate. *Scylaspora elegans* Richardson *et al.*, 2001 is proximally microrugulate.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4, and WELL-7; Jauf Formation; *papillensis-baqaensis* to *annulatus-protea* zones. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *lemurata-langii* zones, but the rare and isolated occurrence of some specimens are probably due to reworking. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *lindlarensis-sextantii* to *rugulata-libyensis* zones.

Previous records. From Lochkovian–upper Emsian of Bolivia (McGregor 1984; Perez-Leyton 1990); from lower Lochkovian–lower Emsian of Brazil (Rubinstein *et al.* 2005; Mendlowicz Mauller *et al.* 2007; Steemans *et al.* 2008); Lochkovian–Emsian of Canada (McGregor and Camfield 1976); Pragian–lower Emsian of Armorican Massif, France (Le Hérissé 1983); middle Přídolí–lowermost Eifelian of Libya (Moreau-Benoit 1989; Rubinstein and Steemans 2002); Lochkovian of Poland (Turnau *et al.* 2005); and Pragian from UK (Mortimer 1967).

Retusotriletes rotundus (Streel) Streel emend. Lele and Streel, 1969
Figure 38C

1964 *Phyllothecotriletes rotundus* Streel, pl. 1, figs 1–2.
1967 *Retusotriletes rotundus* (Streel) Streel, p. 25, pl. 1, fig. 11; pl. 2, figs 16–17.
1969 *Retusotriletes rotundus* (Streel) Streel emend. Lele and Streel, p. 94, pl. 1 figs 18–20.

Dimensions. 57(82)108 μm; 12 specimens measured.

Comparison. Retusotriletes tenerimedium Chibrikova, 1959 also has a differentiated proximal face but the thinner sub-triangular apical area extends to about one-third of the amb radius. Moreover, this species is smaller and equatorially thicker. The dark apical area of *R. goensis* Lele and Streel, 1969 may be larger and is not differentiated into two zones. *R. triangulatus* (Streel) Streel, 1967 has a sub-triangular thickened zone at the proximal pole but with concave sides.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4, S-462, WELL-3, WELL-4, WELL-7 and WELL-8; Jauf and Jubah formations; *papillensis-baqaensis* to *triangulatus-catillus* zones. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *lemurata-langii* zones. MG-1; Awaynat Wanin I Formation; *incognita* Zone.

Previous records. Widely dispersed and often common in Devonian (particularly Early–Middle Devonian) assemblages (Streel 1964, 1967; Riegel 1968; Cramer 1969; Lele and Streel 1969; McGregor 1973; McGregor and Camfield 1976, 1982; Marshall and Allen 1982; Le Hérissé 1983; Balme 1988; Boumendjel *et al.* 1988; Ravn and Benson 1988; Moreau-Benoit *et al.* 1993; Turnau 1996; Rahmani-Antari and Lachkar 2001; Marshall and Fletcher 2002; Hashemi and Playford 2005).

Retusotriletes tenerimedium Chibrikova, 1959
Figure 38D–G

1959 *Retusotriletes tenerimedium* Chibrikova, p. 52, pl. 5, figs 9–10.
1966 *Retusotriletes tenerimedium* Chibrikova; de Jersey, p. 7, pl. 2, fig. 4.
1967 *Retusotriletes triangulatus* (Streel) Streel; Richardson, pl. 2, fig.a.
1968 *Retusotriletes tenerimedium* Chibrikova; Schultz, p. 14, pl. 1, fig. 15.

FIG. 38. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A, *Retusotriletes goensis* Lele and Streel, 1969. JNDL-4, 285.5 ft, 68660, K27/1. B, *Retusotriletes maculatus* McGregor and Camfield, 1976. JNDL-4, 87.2 ft, 03CW195, P34/3. C, *Retusotriletes rotundus* (Streel) Streel emend. Lele and Streel, 1969. BAQA-1, 345.5 ft, 03CW114, O36. D–G, *Retusotriletes tenerimedium* Chibrikova, 1959. D, BAQA-1, 285.5 ft, 03CW111, C40/2. E, BAQA-1, 366.9 ft, 62257, M28. F, WELL-7, 13738.5 ft, 62322, U43. G, WELL-7, 13738.5 ft, 62325, G41. H–I, *Retusotriletes triangulatus* (Streel) Streel, 1967. H, BAQA-1, 371.1 ft, 03CW118, O23. I, BAQA-2, 50.8 ft, 03CW127, M33/2. J–L, *Retusotriletes* sp. 1. J, MG-1, 2205 m, 62597, S44/3. K, A1-69, 1293 ft, 63066, K32. L, S-462, 1910–1915 ft, 63260, E33/3.


A
B
C
D
E
F
G
H
I
J
K
L

Dimensions. 36(53)86 μm; 30 specimens measured.

Comparison. Ambitisporites (Archaicusporites) asturicus (Rodriguez) comb. nov. has a less pronounced sub-triangular darker apical zone and elevated curvaturae and is commonly smaller.

Occurrence. BAQA-1, BAQA-2, WELL-1, WELL-2, WELL-3, WELL-5, WELL-6 and WELL-7; Jauf Formation; *ovalis-biornatus* to *annulatus-protea* zones. A1-69; Awaynat Wanin II Formation; *undulatus* Zone. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone.

Previous records. From upper Emsian – lower Eifelian of the Russian Platform (Avkhimovitch *et al.* 1993); and Emsian of Germany (Schultz 1968).

Retusotriletes triangulatus (Streel) Streel, 1967
Figure 38H–I

1964 *Phyllothecotriletes triangulatus* Streel, p. 5, pl. 1, figs 3–5.
1967 *Retusotriletes triangulatus* (Streel) Streel, p. 24.
2006 *Retusotriletes* cf. *triangulatus* (Streel) Streel; Wellman, p. 175, pl. 10, figs i–k.

Dimensions. 40(66)87 μm; 22 specimens measured.

Comparison. Retusotriletes rotundus (Streel) Streel emend. Lele and Streel, 1969 has a sub-triangular apical area, with convex sides, which extends to one-fifth to one-third of the amb radius.

Occurrence. BAQA-1, BAQA-2, JNDL-4, S-462, WELL-1, WELL-2, WELL-3, WELL-4, WELL-5, WELL-6, WELL-7 and WELL-8; Jauf and Jubah formations; *papillensis-baqaensis* to *triangulatus-catillus* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *lindlarensis-sextantii* to *triangulatus-catillus* zones. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *lindlarensis-sextantii* to *rugulata-libyensis* zones.

Previous records. Widely dispersed and often common in Devonian (particularly Early–Middle Devonian) assemblages (Streel 1964, 1967; Riegel 1968; Lele and Streel 1969; Tiwari and Schaarschmidt 1975; Lu Lichang and Ouyang Shu 1976; Gao Lianda 1981; Streel *et al.* 1988; Turnau 1996; Turnau and Racki 1999; Turnau and Matyja 2001; Wellman 2006; Steemans *et al.* 2008).

Retusotriletes sp. 1
Figure 38J–L

Description. Amb is sub-circular. Laesurae are straight, simple, four-fifths to nine-tenths of the amb radius in length, connected near the equator by curvaturae perfectae. Exine is scabrate, 1–2 μm thick. An triangular apical area with more or less straight sides commonly occurs two-fifths to three-fifths of the amb radius along the laesurae. Outer margin of the apical area is delimited by a more or less diffuse darker zone, 1–4 μm wide. Interior to the triangular area at proximal pole has a wall thickness comparable to the remaining part of the spore body.

Dimensions. 51(62)81 μm; four specimens measured.

Comparison. Retusotriletes triangulatus (Streel) Streel, 1967 is characterized by a more pronounced dark sub-triangular apical area with concave sides. *R. rotundus* (Streel) Streel emend. Lele and Streel, 1969 has a proportionately less developed sub-triangular apical area with convex sides. *Calamospora atava* McGregor, 1973 figured in McGregor and Camfield, 1982 has a similar apical area, but does not have curvaturae and is commonly folded.

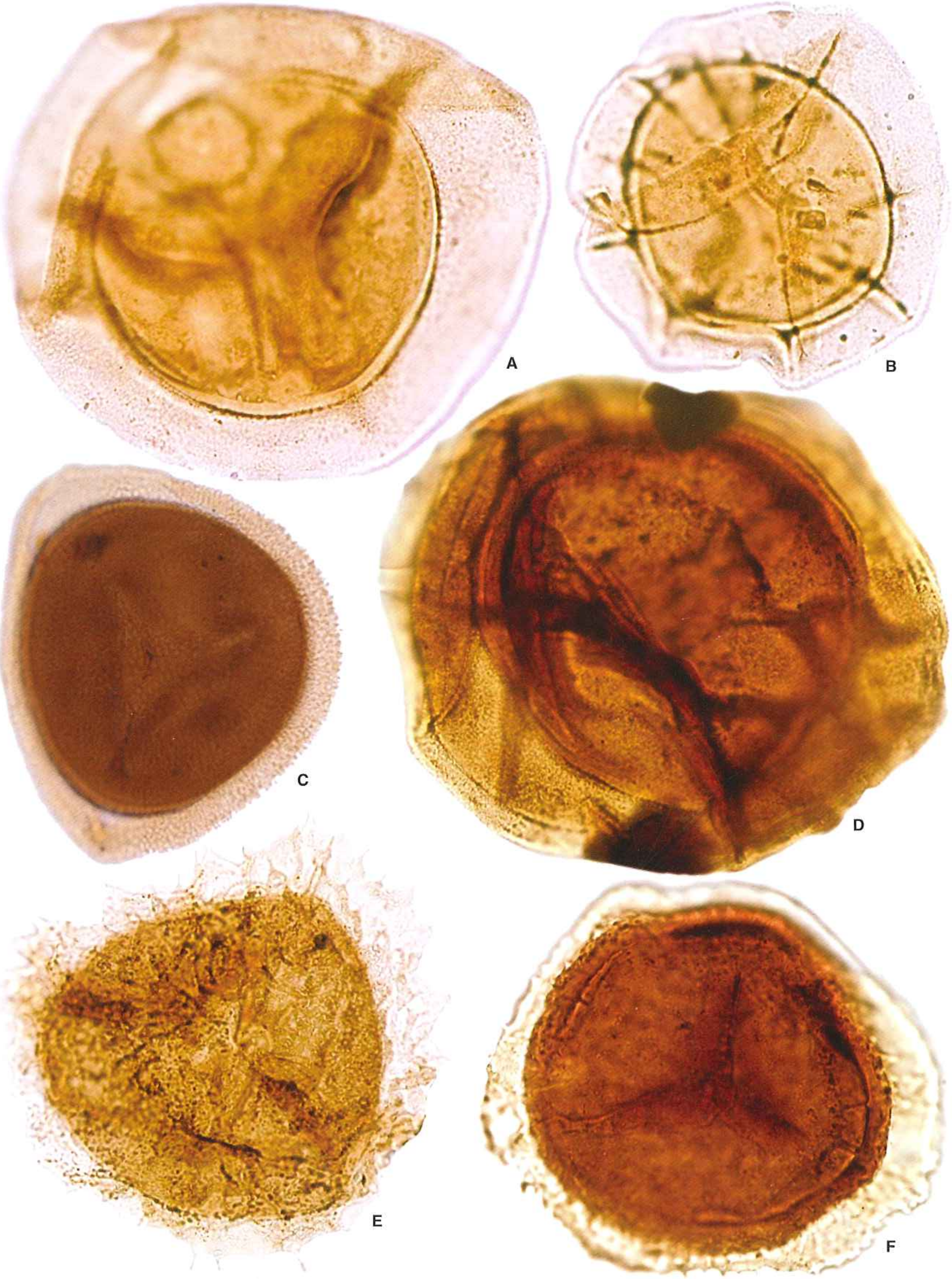
Occurrence. S-462; Jubah Formation; *triangulatus-catillus* to *langii-concinna* zones. A1-69; Awaynat Wanin II Formation; *triangulatus-catillus* Zone. MG-1; Awaynat Wanin II Formation; *langii-concinna* Zone.

Genus RHABDOSPORITES Richardson emend. Marshall and Allen, 1982

Type species. Rhabdosporites langii (Eisenack) Richardson, 1960.

Comparison. Camerate spores with coarser sculpture are included in other genera (e.g. *Grandispora* Hoffmeister *el al.* emend. Neves and Owens, 1966). In emending the generic concept of *Rhabdosporites*, Marshall and Allen (1982) were aware of the close similarity between small specimens of *Rhabdosporites* and *Geminospora* Balme (1962), which are mentioned by other authors (Lele and Streel 1969). *Geminospora* is typified by a thin-walled nexine either closely appressed to, or showing a variable degree of separation from, a sculptured sexine with a thickened distal surface. Further evidence for the similarity or inability to easily distinguish between *Rhabdosporites* and *Geminospora* comes from the study of *in situ* spores (Allen 1980), where spores assignable to both genera are recorded from closely related progymnosperms (Marshall and Allen 1982; Marshall 1996). Wellman (2009) concluded that there is

FIG. 39. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A–B, *Rhabdosporites langii* (Eisenack) Richardson, 1960. A, MG-1, 2258 m, 62947, Q46/2. B, MG-1, 2180 m, 62973, N44. C. *Rhabdosporites minutus* Tiwari and Schaarschmidt, 1975. JNDL-4, 346.3 ft, 68672, J34/1. D, *Rhabdosporites streelii* Marshall, 1996, magnification ×750. A1-69, 1322 ft, 27125, L36-37. E, *Samarisporites angulatus* (Tiwari and Schaarschmidt) Loboziak and Streel, 1989, magnification ×750. A1-69, 1596 ft, 26990, K40/2. F, *Samarisporites eximius* (Allen) Loboziak and Streel, 1989, magnification ×750. JNDL-1, 162.3 ft, 60841, W28/3.


A
B
C
D
E
F

a smooth evolutionary transition between *Apiculiretusispora* (Streel) Streel, 1967, *Rhabdosporites*, *Geminospora* and *Contagisporites* Owens, 1971.

Rhabdosporites langii (Eisenack) Richardson, 1960
Figure 39A–B

1925 Type B Lang, p. 256, pl. 1, figs 3–6.
1944 *Triletes langi* Eisenack, p. 112, pl. 2, fig. 4.
1959 Spores of *Milleria* (*Protopteridium*) *thomsonii* (Dawson) Lang; Obrhel, p. 387, pl. 2, fig. 6.
1960 *Rhabdosporites langi* (Eisenack) Richardson, p. 54, pl. 14, figs 8, 9, text-figs 4, 6B.
1963 *Rhabdosporites firmus* Guennel, p. 256, fig. 12.
1964 *Calyptosporites plicatus* Vigran, p. 19, pl. 6, fig. 4.
1965 *Rhabdosporites parvulus* Richardson, p. 588 (*pars*), pl. 93, figs 5–6.
1967 Spores of *Tetraxylopteris schmidtii* Beck; Bonamo and Banks, p. 765, figs 34–36, 38, 40.
1969 ?*Rhabdosporites parvulus* Richardson; Lele and Streel, p. 103, pl. 3, fig. 66–68.
1971 *Rhabdosporites micropaxillus* Owens, p. 49, pl. 15, figs 3–7.
1971 Spores of *Milleria* (*Protopteridium*) *thomsonii* (Dawson) Lang; Leclercq and Bonamo, p. 98, pl. 36, figs 24–33.
1972 *Rhabdosporites* n. sp. McGregor and Uyeno, pl. 3, fig. 5.
1974 *Rhabdosporites* sp. Hamid, p. 202, pl. 10, fig. 1.
1975 *Rhabdosporites* sp. Tiwari and Schaarschmidt, p. 40, pl. 21, fig. 7.
1977 Spores of *Rellimia thomsonii* (Dawson) Leclercq and Bonamo; Bonamo, p. 1277, figs 6–7.

Dimensions. 62(93)128 μm; 69 specimens measured.

Remarks. Rhabdosporites parvulus Richardson, 1965 differs in being smaller and has in addition a nexine-to-sexine size ratio different from typical *R. langii.* Populations of *R. langii* in this study include continuous size variation including specimens as small as *R. parvulus.* As in Marshall and Allen (1982) and Marshall (1996), *R. parvulus* is regarded as a junior synonym of *R. langii.* However, the situation is more complex. According to Marshall (1996), the specimens attributed by Richardson (1965) to *R. parvulus* include both *Geminospora lemurata* Balme emend. Playford, 1983 and small specimens of *R. langii.*

Studies of *in situ* spores indicated that dispersed *R. langii* was produced by at least two different, but closely related, aneurophytalean progymnosperms. The spores of these two plant species cannot be distinguished on purely morphological grounds, although there are possibly some minor differences at the ultrastructural level (Wellman 2009).

Comparison. Rhabdosporites minutus Tiwari and Schaarschmidt, 1975 is commonly smaller and less folded. In addition, this species often has an asymmetrical appearance with an elongate subtriangular or oval amb. Normally, the separation of *G. lemurata* and *R. langii* presents no difficulty as the latter is significantly larger and has a nexine that is significantly smaller than the sexine and thus well-developed cameration. In addition, its sexine is thinner and folded with the folds continuous across a significant proportion of the sexine diameter. Typically specimens of *G. lemurata* show only a small separation between nexine and sexine with the sexine being relatively rigid because of its greater thickness such that the nexine is usually centrally placed. *G. svalbardiae* (Vigran) Allen, 1965 is often folded as in *R. langii* but has a slightly thicker sexine and its ornamentation is coarser.

Occurrence. S-462, WELL-1 and WELL-8; Jubah Formation; *lemurata-langii* to *langii-concinna* zones. A1-69; Awaynat Wanin II Formation; *lemurata-langii* to *langii-concinna* zones. MG-1; Awaynat Wanin II and Awaynat Wanin III formations; *lemurata-langii* to *langii-concinna* zones.

Previous records. Rhabdosporites langii is eponymous for the early Eifelian *velata-langii* Assemblage Zone of the Old Red Sandstone Continent and adjacent regions (Richardson and McGregor 1986). *R. langii* has an almost worldwide distribution extending into the Frasnian.

Rhabdosporites minutus Tiwari and Schaarschmidt, 1975
Figure 39C

1975 *Rhabdosporites minutus* Tiwari and Schaarschmidt, p. 39, pl. 21, figs 4–6.

Dimensions. 42(60)84 μm; 39 specimens measured.

Comparison. Rhabdosporites langii (Eisenack) Richardson, 1960 is larger, commonly having smaller body in relation to the saccus, the latter being much folded. *R. scamnus* Allen, 1965 is larger and is typically folded distally. *Apiculiretusispora brandtii* Streel, 1964 has the same type of sculpture and the sexine is irregularly detached from nexine on some specimens, whereas *R. minutus* has a sexine completely detached equatorially from the spore body. The two species could belong to a same spore lineage as suggested by Wellman (2009). Therefore, the two species are included in the *A. brandtii* Morphon (Table 1).

Occurrence. BAQA-1, JNDL-1, JNDL-3, JNDL-4 and WELL-4; Jauf (Subbat to Murayr members) and Jubah formations; *asymmetricus* to *svalbardiae-eximius* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *lindlarensis-sextantii* to *lemurata-langii* zones. MG-1; Ouan-Kasa, Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations; *annulatus-protea* to *langii-concinna* zones.

Previous records. From lower Eifelian – lower Givetian of Germany (Tiwari and Schaarschmidt 1975); middle–upper

Emsian of Luxembourg (Steemans *et al.* 2000*a*); and Emsian of Saudi Arabia (Al-Ghazi 2007).

Rhabdosporites streelii Marshall, 1996
Figure 39D

1969 ?*Rhabdosporites Langi* (Eisenack) Richardson; Lele and Streel, p. 102, pl. 3, fig. 65.
1996 *Rhabdosporites streelii* Marshall, p. 177 (*cum syn.*), pl. 3, figs 1–5.

Dimensions. 111(133)184 μm; four specimens measured.

Remarks. As *R. streelii* occurs within sporangia (Bonamo and Banks 1967) containing also *R. langii* (Eisenack) Richardson, 1960, it could be regarded as a variant of *R. langii. R. streelii* is created by splitting of the nexine into ectonexine and endonexine. It represents a distinct evolutionary development within the sporangia of *Rhabdosporites* (Richardson) Marshall and Allen, 1982. As its stratigraphical range is short, it constitutes a potential stratigraphical index species (Marshall 1996).

Comparison. Rhabdosporites streelii is clearly separable from all other species of *Rhabdosporites* by the possession of three detached layers.

Occurrence. A1-69; Awaynat Wanin II Formation; *undulatus* Zone.

Previous records. From the Pepinster Formation of Belgium (Lele and Streel 1969), which is considered as upper Eifelian by Laloux *et al.* (1996); lower Givetian of Parnaíba Basin, Brazil (Breuer and Grahn 2011); middle Eifelian – middle Givetian of Libya (Moreau-Benoit 1989); and Givetian of Scotland (Richardson 1965; Marshall and Allen 1982).

Genus SAMARISPORITES Richardson, 1965

Type species. Samarisporites orcadensis (Richardson) Richardson, 1965.

Remarks. The nature of zonae-cingula is difficult to apprehend in compressed specimens under a transmitted light microscope. Indeed, different layers in multilayered spores may have differing optical properties, and this can be misleading when attempting to interpret wall thickness and spore structure. This problem is enhanced when coupled with optical effects resulting from compressional artefacts (Wellman 2001).

Comparison. The definition of *Cristatisporites* Potonié and Kremp, 1954 restricts the distal sculpture to being dominantly mammoid, i.e. coni or spinae which are fused together at their bases into ridges carrying the spinose projections.

Samarisporites angulatus (Tiwari and Schaarschmidt) Loboziak and Streel, 1989
Figures 39E, 52M–O

1975 *Calyptosporites angulatus* Tiwari and Schaarschmidt, p. 44, pl. 26, figs 4–5, pl. 27, fig. 1.
1989 *Samarisporites angulatus* (Tiwari and Schaarschmidt) Loboziak and Streel, p. 191, pl. 5, figs 8–9.

Dimensions. 84(102)131 μm; 18 specimens measured.

Comparison. Samarisporites eximius (Allen) Loboziak and Streel, 1989 often has smaller spines and its equatorial flange is more or less uniform around the central body but some specimens intergrade with *S. angulatus.* Therefore, the two species are included in the *S. eximius* Morphon defined here (Table 1).

Occurrence. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *rugulata-libyensis* zones. MG-1; Awaynat Wanin I Formation; *rugulata* Zone.

Previous records. From Eifelian of Paraná Basin, Brazil (Loboziak *et al.* 1988); upper Emsian–lower Givetian (Tiwari and Schaarschmidt 1975; Loboziak *et al.* 1990); and ?upper Eifelian–Givetian of Saudi Arabia (PB, pers. obs.).

Samarisporites eximius (Allen) Loboziak and Streel, 1989
Figures 39F, 40A and 52P–R

1965 *Perotrilites eximius* Allen, p. 731, pl. 102, figs 11–13.
1980*b* *Grandispora velata* (Eisenack) McGregor; Moreau-Benoit, p. 40, pl. 12, fig. 3.
1982 *Grandispora eximia* (Allen) McGregor and Camfield, p. 44, pl. 10, figs 2, 6–7; text- fig. 64.
1989 *Samarisporites eximius* (Allen) Loboziak and Streel, p. 192, pl. 4, figs 1–4.
non 1995 *Samarisporites eximius* (Allen) Loboziak and Streel; Rodriguez *et al.*, pl. 1, fig. 2.

Dimensions. 95(116)145 μm; 25 specimens measured.

Comparison. Samarisporites praetervisus (Naumova) Allen, 1965 possesses a pseudoreticulate pattern formed by rugulae comprised of spines similar to *S. eximius.* Extreme forms of *S. eximius* intergrade with *S. praetervisus* and *S. angulatus* (Tiwari and Schaarschmidt) Loboziak and Streel, 1989, which show larger spines and a more triangular flange. Therefore, the *S. eximius* Morphon is defined here (Table 1).

Occurrence. JNDL-1, S-462 and WELL-1; Jubah Formation; *svalbardiae-eximius* to *langii-concinna* zones. A1-69; Awaynat Wanin

I and Awaynat Wanin II formations; *svalbardiae-eximius* to *triangulatus-catillus* zones. MG-1; Ouan-Kasa, Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations; *svalbardiae-eximius* to *langii-concinna* zones.

Previous records. From upper Eifelian–Famennian of Bolivia (Perez-Leyton 1990); Eifelian–Frasnian of Paraná Basin, Brazil (Loboziak *et al.* 1988); upper Eifelian – lower Givetian of Canada (McGregor and Camfield 1982); upper Emsian–Givetian of Germany (Riegel 1973; Loboziak *et al.* 1990); upper Emsian to lowermost Eifelian – lower Givetian of Libya (Moreau-Benoit 1989); and Emsian–Eifelian of Spistbergen, Norway (Allen 1965).

Samarisporites praetervisus (Naumova) Allen, 1965
Figures 40B–C, 52S–U

1953 *Hymenozonotriletes praetervisus* Naumova, p. 40, pl. 4, fig. 8.
1965 *Samarisporites praetervisus* (Naumova) Allen, p. 714, pl. 98, figs 9–10.
1980*b* *Grandispora praetervisa* (Naumova) Moreau-Benoit, p. 37, pl. 11, fig. 5.
1985 ?*Calyptosporites* sp. A Paris *et al.*, pl. 20, fig. 8.
non 1995 *Samarisporites praetervisus* (Naumova) Allen; Rodriguez *et al.*, pl. 1, fig. 1.

Dimensions. 79(98)114 μm; 10 specimens measured.

Comparison. Samarisporites eximius (Allen) Loboziak and Streel, 1989 differs only by the possession of discrete elements on the distal surface of the central body however they can be locally fused in rugulae. Extreme forms of *S. praetervisus* (Naumova) Allen, 1965 probably intergrade with *S. eximius* in the *S. eximius* Morphon (Table 1). *S. orcadensis* Richardson, 1960 is considerably larger.

Occurrence. S-462; Jubah Formation; *lemurata-langii* to *triangulatus-catillus* zones. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *lemurata-langii* zones. MG-1; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *triangulatus-catillus* zones.

Previous records. From lower Givetian of Algeria (Boumendjel *et al.* 1988); uppermost Eifelian–lower Givetian of Amazon Basin, Brazil (Melo and Loboziak 2003); Eifelian–middle Givetian of Libya (Paris *et al.* 1985; Streel *et al.* 1988; Moreau-Benoit 1989); and Givetian of Spistbergen, Norway (Allen 1965).

Samarisporites triangulatus Allen, 1965
Figures 40D–E, 52V–X

1964 *Cirratriradites* sp. Vigran, p. 24, pl. 3, fig. 6.
1965 *Samarisporites triangulatus* Allen, p. 716, pl. 99, figs 1–6.

Dimensions. 40(60)94 μm; 40 specimens measured.

Remarks. In the studied material, *S. triangulatus* is preserved in proximo-distal or in lateral compression when specimens have very high laesurae.

Comparison. The distinctive equatorial flange separates this species from other species assigned to *Samarisporites* Richardson, 1965.

Occurrence. S-462, WELL-1 and WELL-8; Jubah Formation; *triangulatus-catillus* to *langii-concinna* zones, specimens from S-462 may be caved in older strata. A1-69; Awaynat Wanin II Formation; *triangulatus-catillus* to *langii-concinna* zones. MG-1; Awaynat Wanin II and Awaynat Wanin III formations; *triangulatus-catillus* to *langii-concinna* zones.

Previous records. Samarisporites triangulatus is eponymous for the upper Givetian – lower Frasnian *optivus-triangulatus* Assemblage Zone of the Old Red Sandstone Continent and adjacent regions (Richardson and McGregor 1986), the middle Givetian – lower Frasnian TA and TCo Oppel zones of Western Europe (Streel *et al.* 1987). *S. triangulatus* has a worldwide distribution extending through the Givetian and Frasnian, locally reaching the Famennian. From middle Givetian of Algeria (Moreau-Benoit *et al.* 1993); upper Givetian – lower Frasnian of Argentina (Ottone 1996), Portugal (Lake *et al.* 1988) and Russian Platform (Avkhimovitch *et al.* 1993); middle Givetian – lower Frasnian of Australia (Balme 1988; Grey 1991; Hashemi and Playford 2005); middle Givetian–Famennian of Belgium (Becker *et al.* 1974; Streel and Loboziak 1987; Gerrienne *et al.* 2004); upper Givetian –Famennian of Bolivia (Perez-Leyton 1990); Givetian–upper Tournaisian of Brazil (Loboziak *et al.* 1988, 1992*b*; Melo and Loboziak 2003); upper Givetian – upper Frasnian of France (Brice *et al.* 1979; Loboziak and Streel 1980, 1988; Loboziak *et al.* 1983); Givetian of Germany (Loboziak *et al.* 1990) and Poland (Turnau 1986, 1996; Turnau and Racki 1999); middle Givetian of Greenland (Friend *et al.* 1983; Marshall and Hemsley 2003); Frasnian–?lower Famennian of Libya (Paris *et al.* 1985; Streel *et al.* 1988); Givetian–Frasnian of Spistbergen, Norway (Vigran 1964; Allen 1965); and uppermost Givetian–lower Frasnian of Scotland (Marshall *et al.* 1996).

FIG. 40. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A, *Samarisporites eximius* (Allen) Loboziak and Streel, 1989, magnification ×750. JNDL-1, 167.8 ft, PPM006, O34/2. B–C, *Samarisporites praetervisus* (Naumova) Allen, 1965, magnification ×750. B, A1-69, 1334 ft, 27127, K48. C, MG-1, 2258 m, 62947, M39/2. D–E, *Samarisporites triangulatus* Allen, 1965. D, A1-69, 1277 ft, 62636, X31/1. E, A1-69, 1277 ft, 62637, Q37/3. F–G, *Samarisporites tunisiensis* sp. nov. F, MG-1, 2741.4 m, 62611, L28/1. G, Paratype, MG-1, 2741.4 m, 62612, W28.


A
B
D
C
E
F
G

Samarisporites tunisiensis sp. nov.
Figures 40F–G, 41A and 52Y–AA

1992*a* *Samarisporites* sp. Loboziak *et al.*, pl. 1, fig. 1.

Derivation of name. From *tunisiensis* (Latin), meaning from Tunisia; refers to its geographical occurrence.

Holotype. EFC P39/2 (Figs 41A, 52Z), slide 62611.

Paratype. EFC W28 (Fig. 40G), slide 62612; MG-1 borehole, sample 2741.4 m.

Type locality and horizon. MG-1 borehole, sample 2741.4 m; Ouan-Kasa Formation at Mechiguig, Tunisia.

Diagnosis. A sub-triangular *Samarisporites* sometimes with a bizonate appearance. Distal surface sculptured with small coni or spines, more densely distributed on the distal hemisphere of the central body than on the zona.

Description. Amb is sub-triangular. Laesurae are straight or slightly sinuous, elevated, up to 7 μm high, often extending on to the equatorial flange, and frequently to the equatorial margin. The central body is sub-circular to sub-triangular, and its diameter equals three-fifths to two-thirds of the total amb diameter. The equatorial flange is wider opposite the laesurae (12–24 μm wide) than interradially (6–14 μm wide). Exine may sometimes be folded radially. Camerate structure can give a bizonate appearance. Camera width equals one-fifth to two-fifths of the zona width. Proximal surface laevigate, distal surface supporting coni or spines, 0.5–1.5 μm wide, 1–2.5 μm high and 1–3 μm apart. Ornament on the distal hemisphere of the central body is more densely distributed than those on the zona. Groups of sculptural elements on the central body can be fused at their bases making short ridges.

Dimensions. 73(82)88 μm; six specimens measured.

Comparison. Samarisporites eximius (Allen) Loboziak and Streel, 1989 possesses a thicker central body and its ornamentation is commonly larger. *S. angulatus* (Tiwari and Schaarschmidt) Loboziak and Streel, 1989 has considerably larger sculptural elements. *Perotrilites caperatus* (McGregor) Steemans, 1989 has smaller ornamentation, often barely visible.

Occurrence. MG-1; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone.

Samarisporites sp. 1
Figure 41B

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple, extending half or almost to the inner margin of the zona. Curvaturae are not visible. The central body diameter equals three-fifths to four-fifths of the total amb diameter. Maximum width of the equatorial flange is 12–22 μm. Zona is folded radially. Exine of the central body is punctate and 2.5–5 μm thick equatorially. Distal hemisphere of central body is sculptured with polygonal verrucae, commonly 2–5 μm wide (rarely up to 8 μm) and closely packed.

Dimensions. 90(98)107 μm; three specimens measured.

Occurrence. A1-69; Awaynat Wanin I Formation; *svalbardiae-eximius* Zone. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone.

Samarisporites sp. 2
Figures 41C, 52AB–AD

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple and elevated up to 8 μm high at the pole, decreasing in height to or almost to the outer margin of the zona. Curvaturae are not visible. The central body diameter equals more or less three-quarters of the total amb diameter. The equatorial flange is laevigate to infragranulate and can be slightly wider opposite the laesurae than interradially; its maximum width is up to 25 μm. Distal surface of zona is ornamented with spines, 1–2.5 μm wide at base, 2–5.5 μm high and 1.5–5 μm apart. Exine of the central body is 4–7 μm thick equatorially. Exine of body is entirely laevigate except the equatorial part, which is ornamented with the same spines as the zona.

Dimensions. 116(120)123 μm; three specimens measured.

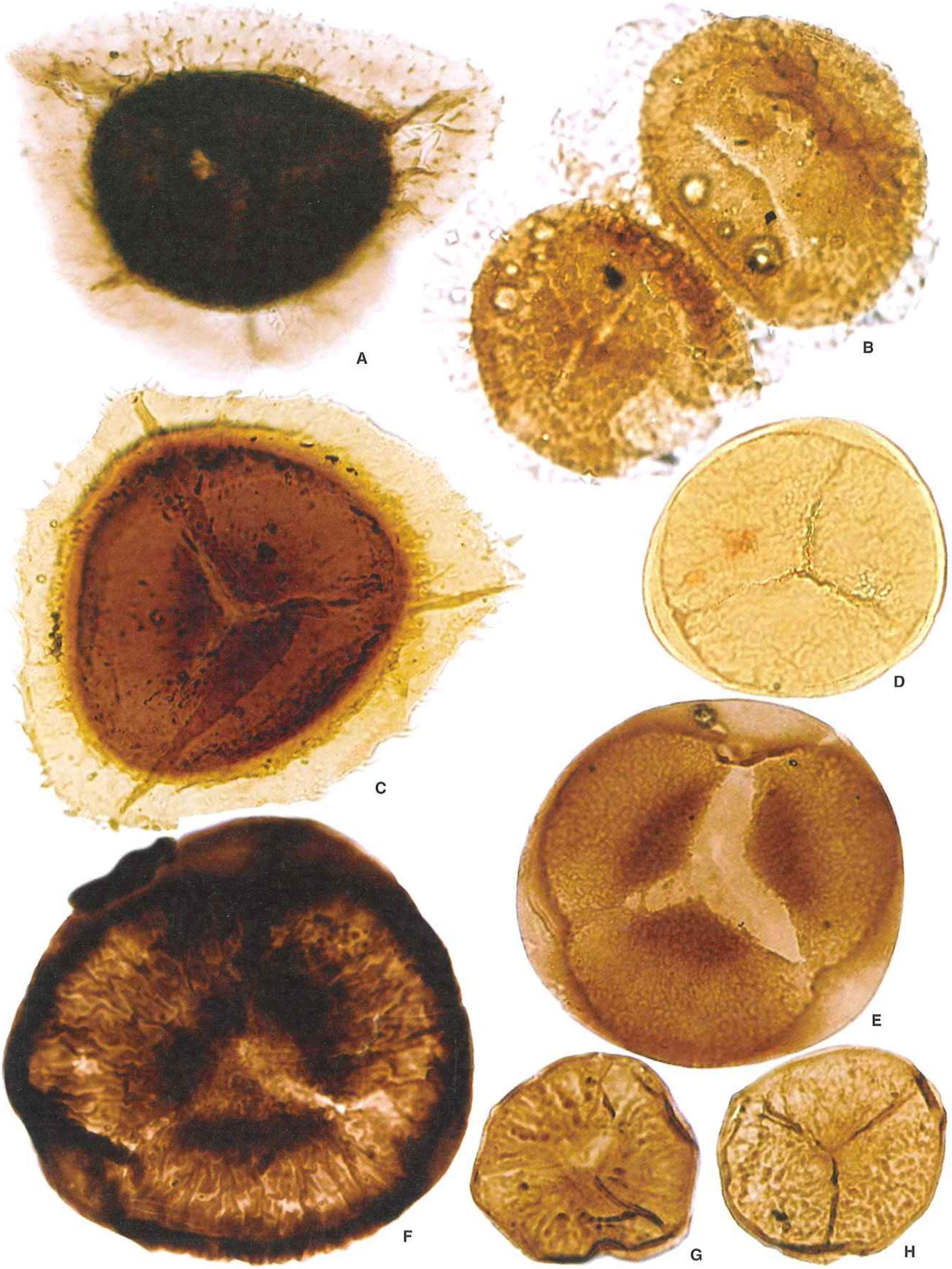
Comparison. Samarisporites eximius (Allen) Loboziak and Streel, 1989 possesses a distally ornamented central body as *S. praetervisus* (Naumova) Allen, 1965, which has a smaller ornamentation in addition.

Occurrence. A1-69; Awaynat Wanin I Formation; *svalbardiae-eximius* to *rugulata-libyensis* zones.

Genus SCYLASPORA Burgess and Richardson, 1995

Type species. Scylaspora scripta Burgess and Richardson, 1995.

FIG. 41. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A, *Samarisporites tunisiensis* sp. nov. Holotype, MG-1, 2741.4 m, 62611, P39/2. B, *Samarisporites* sp. 1, magnification ×750. A1-69, 1962 ft, 27277, K37/4. C, *Samarisporites* sp. 2, magnification ×750. A1-69, 1596 ft, 26989, G38/1. D, *Scylaspora costulosa* Breuer *et al.*, 2007*c*. JNDL-4, 419.3 ft, 03CW261, U37/3. E–F, *Scylaspora rugulata* (Riegel) Breuer *et al.*, 2007*c*. E, WELL-8, 16649.3 ft, 62416, Q47/2. F, A1-69, 1530 ft, 26985, E32/4. G–H, *Scylaspora* sp. 1. G, MG-1, 2631.2 m, 62551, O30. H, MG-1, 2631.2 m, 62553, J48.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H

Comparison. *Emphanisporites* McGregor, 1961 has proximal sculpture of radially aligned muri.

Scylaspora costulosa Breuer *et al.*, 2007c
Figure 41D

2005 *Retusotriletes rugulatus* Riegel; Hashemi and Playford, p. 337, pl. 2, fig. 1.
2007c *Scylaspora costulosa* Breuer *et al.*, p. 50, pl. 10, figs 1–5.

Dimensions. 45(65)91 μm; 24 specimens measured.

Comparison. The specimen of *Retusotriletes rugulatus* Riegel, 1973 illustrated in Hashemi and Playford (2005) has radially oriented sinuous muri and does not has a darker sub-triangular area at the proximal pole as described in Riegel (1973). *R. rugulatus in* Hashemi and Playford (2005) corresponds to the description of *S. costulosa* and it is considered as synonymous.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4, WELL-6 and WELL-7; Jauf Formation; *papillensis-baqaensis* to *annulatus-protea* zones.

Previous records. From Emsian of Adavale Basin, Australia (Hashemi and Playford 2005); and upper Pragian – lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller *et al.*, 2007).

Scylaspora rugulata (Riegel) Breuer *et al.*, 2007c
Figure 41E–F

1965 *Retusotriletes dubius* (Eisenack); Richardson p. 564 (*pars*), pl. 88, fig. 6.
1966 *Retusotriletes* sp. McGregor and Owens (*pars*), pl. 9, fig. 2.
1967 *Retusotriletes* sp. 1 Hemer and Nygreen, pl. 2, fig. 6.
1971 *Retusotriletes dubius* (Eisenack) Richardson; Owens, p. 12 (*pars*), pl. 1, fig. 10.
1973 *Retusotriletes rugulatus* Riegel, p. 82, pl. 10, figs 2–5.
1974 *Stenozonotriletes extensus* Naumova; Hamid, pl. 10, fig. 3.
non 2005 *Retusotriletes rugulatus* Riegel; Hashemi and Playford, p. 337, pl. 2, fig. 1.
2007c *Scylaspora rugulata* (Riegel) Breuer *et al.*, p. 50.

Dimensions. 53(67)85 μm; 12 specimens measured.

Comparison. *Emphanisporites* sp. *in* Tiwari and Schaarschmidt (1975) appears similar to *S. rugulata* except for its prominent elevated labra. *Retusotriletes biarealis* McGregor, 1964 is thinner and bears a faintly defined radial pattern in the contact areas. *S. costulosa* has less prominent and less angular rugulae.

Occurrence. S-462, WELL-1 and WELL-8; Jubah Formation; *rugulata-libyensis* to *triangulatus-catillus* zones. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *rugulata-libyensis* to *triangulatus-catillus* zones. MG-1; Awaynat Wanin I and Awaynat Wanin II formations; *rugulata-libyensis* to *triangulatus-catillus* zones.

Previous records. From middle Givetian of Belgium (Gerrienne *et al.* 2004); Eifelian–lower Givetian of Canada (McGregor and Owens 1966; Owens 1971; McGregor and Camfield 1982); upper Givetian – lower Frasnian of France (Brice *et al.* 1979; Loboziak and Streel 1980, 1988); Eifelian–Givetian of Germany (Riegel 1973; Loboziak *et al.* 1990); lower Eifelian – lower Givetian of Libya (Streel *et al.* 1988); lower Eifelian – upper Givetian of Poland (Turnau 1986, 1996; Turnau and Racki 1999; Turnau and Matyja 2001); and Eifelian – lower Frasnian of Scotland (Richardson 1965; Marshall 1988, 2000; Marshall *et al.* 1996; Marshall and Fletcher 2002).

Scylaspora sp. 1
Figure 41G–H

cf. 1995 *Scylaspora scripta* Burgess and Richardson, p. 17, pl. 7, figs 5–9.

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple, up to 2 μm wide, extending almost to the equator. Exine is 1–2 μm thick equatorially. Contact areas are sculptured with low, rounded, sinuous to convolute and anastomosing muri, 0.5–1.5 μm wide and commonly less than 1 μm apart. Muri are radially aligned near equator, but randomly orientated towards the proximal pole. Distal surface is laevigate.

Dimensions. 40–42 μm; two specimens measured.

Comparison. *Scylaspora scripta* Burgess and Richardson, 1995 is equatorially and distally sculptured with scattered to regularly distributed grana and tiny verrucae. *S. downiei* Burgess and Richardson, 1991 is smaller with predominantly verrucate proximal sculpture. *S. costulosa* Breuer *et al.*, 2007c is larger.

Occurrence. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Genus SQUAMISPORA Breuer *et al.*, 2007c

Type species. *Squamispora arabica* Breuer *et al.*, 2007c.

Comparison. *Diducites* Van Veen, 1981 is two-layered with a very thin outer layer folding and wrinkling frequently resulting as a rugulate appearance. *Squamispora* cannot be compared to genera such *Verrucosisporites* Ibrahim, 1933 because the flakes do not constitute real positive sculptural elements.

Squamispora arabica Breuer *et al.*, 2007*c*
Figure 42A–B

2007*c* *Squamispora arabica* Breuer *et al.*, p. 51, pl. 10, figs 6–10.

Dimensions. 39(51)63 μm; 43 specimens measured.

Remarks. Squamispora arabica may occur in clusters of several specimens. Some local detachment of the scaly layer can occur. Consequently, total detachment of this outer layer possibly could resemble specimens of *Leiotriletes* Naumova emend. Potonié and Kremp, 1954 in poorly preserved assemblages, but *S. arabica* specimens are also recorded in such assemblages from eastern Saudi Arabia (PB, pers. obs.).

Occurrence. JNDL-1; Jubah Formation; *svalbardiae-eximius* Zone.

Genus STELLATISPORA Burgess and Richardson, 1995

Type species. Stellatispora inframurinata (Richardson and Lister) Burgess and Richardson, 1995.

Stellatispora multicostata Breuer *et al.*, 2007*c*
Figure 42C–D

2007*c* *Stellatispora multicostata* Breuer *et al.*, p. 51, pl. 11, figs 1–4.

Dimensions. 54(74)93 μm; 17 specimens measured.

Occurrence. BAQA-1, JNDL-3, JNDL-4, WELL-4 and WELL-7; Jauf Formation (Subbat and Hammamiyat members); *asymmetricus* to *lindlarensis-sextantii* zones.

Genus SYNORISPORITES Richardson and Lister, 1969

Type species. Synorisporites downtonensis Richardson and Lister, 1969.

Synorisporites cf. *S. lobatus* Rodriguez, 1978*a*
Figure 42E–F

cf. 1978*a* *Synorisporites lobatus* Rodriguez, p. 216, pl. 1, figs 13–14.

Description. Trilete spores with sub-circular to sub-triangular amb. Laesurae straight, accompanied by labra, up to 2.5 μm wide individually, extending to the inner margin of the cingulum. Cingulum 3–5 μm wide. Proximal surface laevigate and distal surface sculptured with a convoluted sub-circular thickening, about three-fifths of the amb diameter. Additional verrucae, 1.5–5 μm wide may be present on the distal surface.

Dimensions. 39(48.5)58 μm; three specimens measured.

Remarks. According to its diagnosis, *S. lobatus* Rodriguez, 1978*a* is smaller and its sub-circular thickening is developed on the proximal face. The location of the thickening may be misinterpreted as it was observed on compressed specimens.

Occurrence. MG-1; Ouan-Kasa Formation; *lindlarensis-sextantii* to *svalbardiae-eximius* zones.

Previous record. Similar specimens have been found from upper Emsian–lower Eifelian of Paraná Basin, Brazil (PB, pers. obs.).

Synorisporites papillensis McGregor, 1973
Figure 42G–H

1966 Unidentified McGregor and Owens, pl. 2, fig. 32.
? 1968 Spore trilète à papilles proximales sp. 5 Jardiné and Yapaudjian, pl. 1, fig. 7.
1969 *Synorisporites* sp. A Richardson and Lister, p. 234, pl. 41, figs 1–2.
1973 *Synorisporites papillensis* McGregor, p. 51, pl. 6, figs 26–29.
1976 *Synorisporites ?papillensis* McGregor; McGregor and Camfield, p. 28, pl. 1, figs 24, 27.

Dimensions. 24(32)43 μm; 55 specimens measured.

Comparison. Synorisporites tripapillatus Richardson and Lister, 1969 is smaller and has a distal sculpture consisting of convolute and anastomosing muri. Jardiné and Yapaudjian (1968) figure an undescribed species resembling *S. papillensis. ?Knoxisporites riondae* Cramer and Díez, 1975 is characterized by a distal annulus which may be very faint. The taxonomic attribution of intermediary specimens is difficult because these two species intergrade and are placed in the *S. papillensis* Morphon defined here (Table 1).

Occurrence. WELL-1, BAQA-1, BAQA-2, WELL-2, WELL-3, JNDL-1, JNDL-3, JNDL-4, WELL-4 and WELL-7; Jauf and Jubah Formation; *papillensis-baqaensis* to *svalbardiae-eximius* zones. A1-69; Ouan-Kasa and Awaynat Wanin I formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *annulatus-protea* to *rugulata-libyensis* zones but the highest occurrences are probably reworked.

Previous records. From lower Lochkovian – upper Pragian of Belgium (Steemans 1989); upper Lochkovian – lower Emsian of Paraná and Solimões basins, Brazil (Rubinstein *et al.* 2005; Mendlowicz Mauller *et al.* 2007); Lochkovian–Emsian of Canada (McGregor and Owens 1966; McGregor 1973; McGregor and Camfield 1976); Pragian of Armorican Massif, France (Le Hérissé 1983); middle Přídolí of Libya (Rubinstein and Steemans 2002); Emsian of Saudi Arabia (Al-Ghazi 2007); and Lochkovian of Wales (Richardson and Lister 1969).

Synorisporites verrucatus Richardson and Lister, 1969
Figure 42I–J

1969 *Synorisporites verrucatus* Richardson and Lister, p. 233, pl. 40, figs 10–12.
1981 *Synorisporites* cf. *verrucatus* Richardson and Lister; Steemans, pl. 1, figs 12–13.

Dimensions. 28(33)40 μm; seven specimens measured.

Comparison. Synorisporites tripapillatus Richardson and Lister, 1969 is smaller and has a distal sculpture of convolute and anastomosing muri, and three proximal interradial papillae. *S. papillensis* McGregor, 1973 has also proximal papillae. *Synorisporites? libycus* Richardson and Ioannides, 1973 have larger verrucae.

Occurrence. A1-69; Ouan-Kasa and Awaynat Wanin I formations; *annulatus-protea* to *svalbardiae-eximius* zones. Ouan-Kasa and Awaynat Wanin I formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones.

Previous records. From Silurian–Pragian of Algeria (Boumendjel *et al.* 1988); lower Lochkovian of Belgium (Steemans 1989); Lochkovian of Bolivia (McGregor 1984); upper Lochkovian – lower Emsian of Paraná and Solimões basins, Brazil (Rubinstein *et al.* 2005; Mendlowicz Mauller *et al.* 2007); Emsian of Canada (McGregor 1973), Lochkovian–Pragian of Armorican Massif, France (Le Hérissé 1983; Steemans 1989); ?Ludlow–middle Přídolí of Libya (Rubinstein and Steemans 2002); Lower Silurian–Pragian of Saudi Arabia (Steemans 1995); Wenlock–lower Pragian of Spain (Rodriguez 1978*b*); and Přídolí of Wales (Richardson and Lister 1969).

Genus VERRUCIRETUSISPORA Owens, 1971

Type species. Verruciretusispora dubia (Eisenack) Richardson and Rasul, 1978.

Verruciretusispora dubia (Eisenack) Richardson and Rasul, 1978
Figure 42K

1978 *Verruciretusispora dubia* (Eisenack) Richardson and Rasul, p. 443 (cum syn.), pl. 1, fig. 6.

Dimensions. 52(56)58 μm; four specimens measured.

Occurrence. JNDL-1, JNDL-4 and WELL-7; Jauf (Subbat and Hammamiyat members) and Jubah formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones.

Previous records. From Emsian–lower Givetian of Australia (Hashemi and Playford 2005); Emsian–lower Givetian of Canada (McGregor and Owens, 1966; Owens 1971; McGregor and Uyeno 1972; McGregor 1973; McGregor and Camfield 1982); Emsian of Germany (Lanninger 1968); middle–upper Emsian of Luxembourg (Steemans *et al.* 2000*a*); Emsian–Givetian of Poland (Turnau 1986, 1996; Turnau and Racki 1999; Turnau *et al.* 2005); and upper Eifelian – lower Frasnian of Scotland (Marshall 1988, 2000; Marshall *et al.* 1996; Marshall and Fletcher 2002).

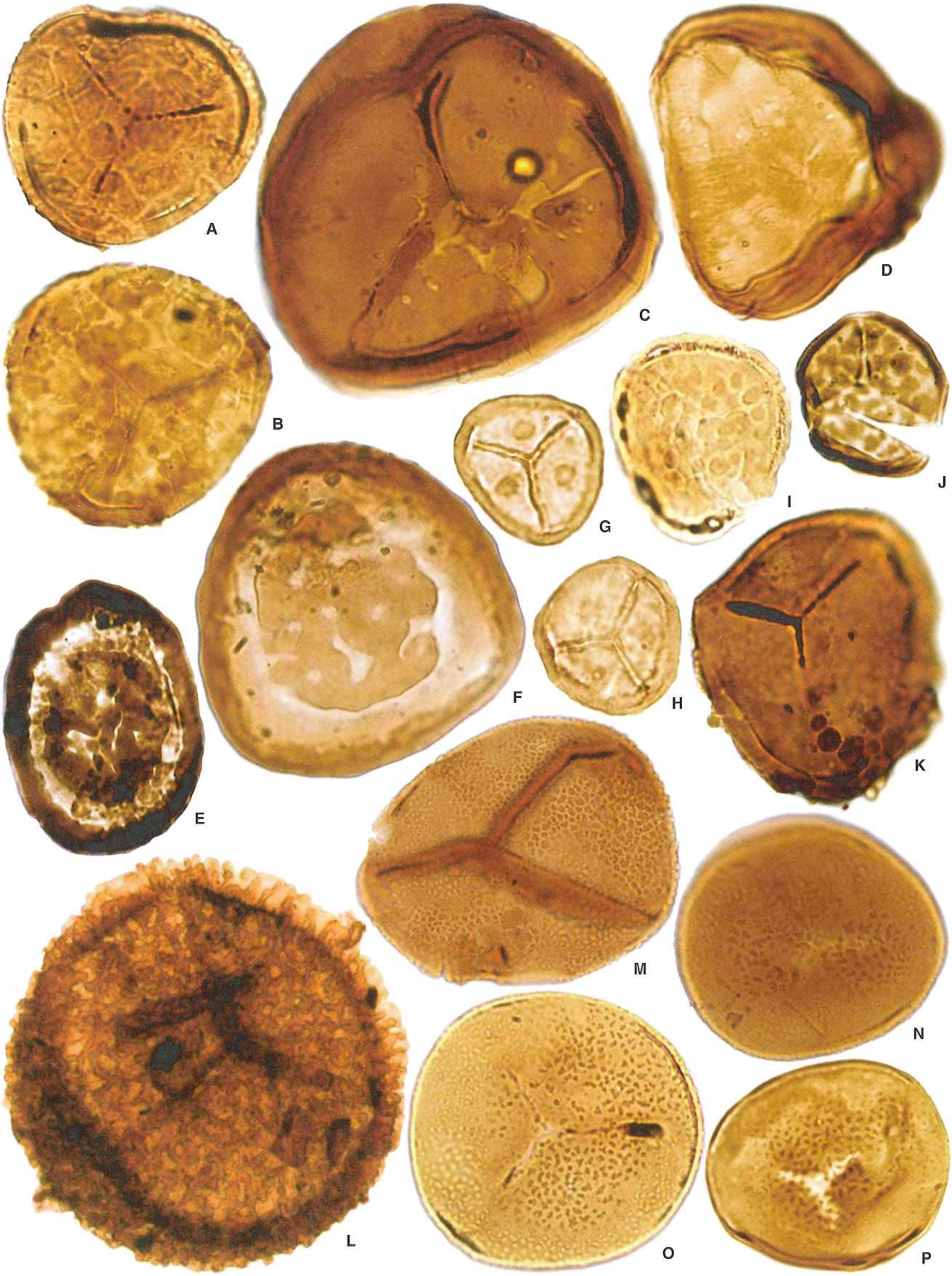
Genus VERRUCISPORITES Chi and Hills, 1976

Type species. Verrucisporites medius Chi and Hills, 1976.

Verrucisporites ellesmerensis (Chaloner) Chi and Hills, 1976
Figures 42L, 52AE–AG

1959 *Biharisporites ellesmerensis* Chaloner, p. 322, pl. 55, fig. 2, text-fig. 1.
1976 *Verrucisporites ellesmerensis* (Chaloner) Chi and Hills, p. 701, pl. 2, figs 9–16; pl. 3, figs 1– 6.

FIG. 42. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A–B, *Squamispora arabica* Breuer *et al.*, 2007*c*. A, JNDL-1, 174.6 ft, 60848, B43/3. B, JNDL-1, 172.7 ft, PPM007, F33/3. C–D, *Stellatispora multicostata* Breuer *et al.*, 2007*c*. C, JNDL-4, 448.6 ft, 68693, R38. D, JNDL-4, 52.3 ft, 03CW188, J38/2. E–F, *Synorisporites* cf. *S. lobatus* Rodriguez, 1978*a*. E, MG-1, 2631.2 m, 62551, F37/4. F, MG-1, 2728 m, 62855, R49. G–H, *Synorisporites papillensis* McGregor, 1973. G, BAQA-1, 222.5 ft, 03CW108, W51/3. H, BAQA-1, 222.5 ft, 03CW108, M30/2. I–J, *Synorisporites verrucatus* Richardson and Lister, 1969. I, A1-69, 2039–2041 ft, 27279, J53/4. J, MG-1, 2631.2 m, 62552, K34-35. K, *Verruciretusispora dubia* (Eisenack) Richardson and Rasul, 1978. JNDL-1, 177.0 ft, PPM009, J39. L, *Verrucisporites ellesmerensis* (Chaloner) Chi and Hills, 1976, magnification ×250. S-462, 1710–1715 ft, 63222, H31. M–P, *Verrucosisporites nafudensis* sp. nov. M, JNDL-4, 331.9 ft, 68669, Q26/3. N, Paratype, JNDL-4, 495.2 ft, 68702, Y40/2. O, Holotype, BAQA-2, 50.8 ft, 03CW127, H30/4. P, BAQA-1, 227.1 ft, 03CW110, N35.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2007 *Verrucisporites yabrinensis* Marshall *et al.*, p. 77, pl. 1, figs 1–11, pl. 2, figs 1–2, 9–10, text- fig. 2A.

Dimensions. 265(299)350 μm; 26 specimens measured.

Remarks. Chi and Hills (1976) define three varieties of *V. ellesmerensis* which are slightly different in detail, but the dimensions of ornamentation intergrade. As the specimens described here are very variable, they may belong to the different defined varieties. Consequently, they were not separated into varieties because the morphological changes seem to be continuous.

Comparison. Verrucisporites yabrinensis Marshall *et al.*, 2007 was erected because its ornament does not correspond exactly to one of the three varieties of *V. ellesmerensis* defined by Chi and Hills, 1976. Indeed, Marshall *et al.* (2007) compare their population only with *V. ellesmerensis* (Chaloner) var. *conatus* Chi and Hills, 1976 which have longer sculptural elements. According to J. E. A. Marshall (pers. comm. 2007), the dimensions of the ornament of *V. yabrinensis* correspond rather to those of *V. ellesmerensis* var. *parvus* but the sculpture is fused like that of *V. ellesmerensis* var. *ellesmerensis*. Thus, the characteristics of ornament of *V. yabrinensis* are included at least in the original definition of *V. ellesmerensis*, i.e. at the specific level. In addition, Marshall *et al.* (2007) also erected a Saudi species different from Arctic Canada because they thought that heterosporous plants are geographically limited by the large size of the megaspore (J. E. A. Marshall, pers. comm. 2007). Although heterosporous plants have little potential to migrate, presence of some identical megaspore species on Gondwana and Euramerica suggests that there was no palaeogeographical barriers to prevent their migration during the Middle Devonian (Steemans *et al.* 2011*b*). Consequently, *V. yabrinensis*, which shows a certain morphological variability, needs to be objectively considered here as a junior synonym of *V. ellesmerensis*.

Occurrence. S-462 and WELL-8; Jubah Formation; *triangulatus-catillus* to *langii-concinna* zones (Marshall *et al.* 2007).

Previous records. From Givetian–Frasnian of Canada (Chi and Hills 1976); and middle Givetian of Libya (Moreau-Benoit 1989).

Genus VERRUCOSISPORITES Ibrahim emend. Smith, 1971

Type species. Verrucosisporites verrucosus (Ibrahim) Ibrahim, 1933.

Verrucosisporites nafudensis sp. nov.
Figure 42M–P

Derivation of name. From *nafudensis* (Latin) meaning from the Nafud Basin; refers to its geographical occurrence.

Holotype. EFC H30/4 (Fig. 42O), slide 03CW127.

Paratype. EFC Y40/2 (Fig. 42N), slide 68702; JNDL-4 core hole, sample 495.2 ft.

Type locality and horizon. BAQA-2 core hole, sample 50.8 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Verrucosisporites* sculptured with small flat-topped verrucae and coni, sub-circular to angular and irregular in plan view.

Description. Amb is sub-circular. Laesurae are straight, simple, one-half to four-fifths of the amb radius in length. Curvaturae are barely visible. Exine is 0.5–2 μm thick. Proximal surface is laevigate. Equatorial and distal regions are sculptured with flat-topped verrucae and coni, irregular in plan view, 0.5–3 μm wide at base, 0.5–1 μm high and 0.5–2.5 μm apart. Sculptural elements are discrete or locally fused at base.

Dimensions. 43(54)68 μm; 15 specimens measured.

Comparison. Verrucosisporites polygonalis Lanninger, 1968 has an ornamentation polygonal to more rounded in plan view and closely spaced resulting in a polygonal pattern. *Cyclogranisporites retisimilis* Riegel, 1968 has a darker apical area, sub-triangular with concave sides.

Occurrence. BAQA-1, BAQA-2 and JNDL-4; Jauf Formation (Sha'iba to Subbat members); *papillensis-baqaensis* to *ovalis-biornatus* zones.

Verrucosisporites onustus sp. nov.
Figure 43A–E

Derivation of name. From *onustus* (Latin), meaning swollen; refers to the apices of the proximo-equatorial sculptural elements.

Holotype. EFC J34/2 (Fig. 43E), slide 03CW128.

FIG. 43. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A–E, *Verrucosisporites onustus* sp. nov. A, Paratype, BAQA-2, 54.8 ft, 03CW129, H50. B, BAQA-1, 345.5 ft, 03CW114, R41/2. C, BAQA-2, 57.2 ft, 66817, D50/4. D, BAQA-2, 56.0 ft, 03CW130, G27-28. E, Holotype, BAQA-2, 52.0 ft, 03CW128, J34/2. F–I, *Verrucosisporites polygonalis* Lanninger, 1968. F, MG-1, 2713 m, 62811, Q40. G, BAQA-1, 371.1 ft, 03CW117, R25/4. H, JNDL-1, 495.0 ft, PPM014, H30/4. I, BAQA-1, 169.1 ft, 03CW103, Q29. J–K, *Verrucosisporites premnus* Richardson, 1965. J, MG1, 2405 m, 62821, V51/1. K, MG-1, 2456 m, 62737, Y40. L–N, *Verrucosisporites scurrus* (Naumova) McGregor and Camfield, 1982. L, MG-1, 2161.8 m, 62528, M45/4. M, A1-69, 1483 ft, 26994, H31/2. N, A1-69, 1334 ft, 27127, K40.


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Paratype. EFC H50 (Fig. 43A), slide 03CW129; BAQA-2 core hole, sample 54.8 ft.

Type locality and horizon. BAQA-2 core hole, sample 52.0 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Verrucosisporites* sculptured with unevenly distributed verrucae and pila, sub-polygonal to sub-circular to in plan view and with explaned apices.

Description. Amb is sub-circular. Laesurae are straight and simple, seven-tenths to three-fourths of the amb radius in length. Exine is 1–2.5 μm thick equatorially. Proximo-equatorial and distal regions are sculptured with verrucae and pilae commonly 0.5–2.5 μm at base, 1–4.5 μm wide at apice, 1–3.5 μm high. Basal width of ornament is smaller than height. Sculptural elements usually have expanded apices, 1–4.5 μm wide, slightly rounded or flat-topped in profile, sub-polygonal to more rounded in plan view and unevenly distributed. Proximal region granulate.

Dimensions. 44(61)75 μm; 12 specimens measured.

Comparison. Verrucosisporites polygonalis Lanninger, 1968 is slightly different by having regularly less high, parallel-sided verrucae, which are evenly distributed and closely spaced, resulting in a polygonal pattern.

Occurrence. BAQA-1 and BAQA-2; Jauf Formation (Sha'iba to Subbat members); *papillensis-baqaensis* to *ovalis* zones.

Verrucosisporites polygonalis Lanninger, 1968
Figure 43F–I

1968 *Verrucosisporites polygonalis* Lanninger, p. 128, pl. 22, fig. 19.
1973 *Verrucosisporites ?polygonalis* Lanninger; McGregor, p. 37 (*cum syn.*), pl. 4, figs 15, 21– 22.

Dimensions. 31(50)90 μm; 21 specimens measured.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4, WELL-6 and WELL-7; Jauf Formation; *papillensis-baqaensis* to *annulatus-protea* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa Formation; *annulatus-protea* to *svalbardiae-eximius* zones.

Previous records. From Emsian of Algeria (Moreau-Benoit *et al.* 1993) and Australia (Hashemi and Playford 2005); lower Pragian–Emsian of Belgium (Steemans 1989); upper Pragian – lower Emsian of the Paraná and Parnaíba basins, Brazil (Grahn *et al.* 2005; Mendlowicz Mauller *et al.* 2007); Pragian–Emsian of Canada (McGregor and Owens 1966; McGregor 1973; McGregor and Camfield 1976), Iran (Ghavidel-Syooki 2003), Poland (Turnau 1986; Turnau *et al.* 2005) and Saudi Arabia (Steemans 1995; Al-Ghazi 2007); lower Pragian–Emsian of Germany (Steemans 1989); upper Pragian of Armorican Massif, France (Le Hérissé 1983); Emsian–lowermost Eifelian of Libya (Moreau-Benoit 1989); and upper Pragian – upper Emsian of Luxembourg (Steemans *et al.* 2000*a*).

Verrucosisporites premnus Richardson, 1965
Figure 43J–K

1965 *Raistrikia* sp. A Richardson, p. 574, pl. 90, fig. 3.
1965 *Raistrikia* cf. *clavata* Hacquebard; Richardson, p. 575, pl. 90, fig. 5.
1965 *Verrucosisporites premnus* Richardson, p. 572, pl. 90, figs 1–2.
non 1968 *Verrucosisporites premnus* Richardson; Lanninger, p. 128, pl. 22, fig. 20.

Dimensions. 30(53)85 μm; 20 specimens measured.

Remarks. Verrucosisporites premnus is included in the *V. scurrus* Morphon (Table 1) defined by McGregor and Playford (1992). The latter comprises species characterized by varied, closely spaced or fused, evenly or asymmetrically distributed coni, bacula or verrucae. These taxa have simple laesurae and a sub-circular amb. Consequently, some transitional specimens are difficult to assign to species.

Comparison. Raistrikia sp. A and *Raistrickia* cf. *clavata* Hacquebard, 1957 *in* Richardson (1965) have most features in common with *V. premnus.* The major point of difference between these forms and *V. premnus* is that they may bear spatulate or club-shaped sculptural elements in addition to bacula. The variation of ornamentation allowed by the diagnosis of *V. premnus* makes separation of *Raistrikia* sp. A and *Raistrickia* cf. *clavata* Hacquebard, 1957 *in* Richardson (1965) difficult, unrealistic and thus they are considered as synonymous (McGregor and Camfield 1982). *V. scurrus* (Naumova) McGregor and Camfield, 1982 has smaller sculptural elements that are commonly tapered in profile.

Occurrence. WELL-1 and S-462; Jubah Formation; *rugulata-libyensis* to *langii-concinna* zones, some specimens from S-462 may be caved in older strata. A1-69; Awaynat Wanin II Formation; *lemurata-langii* to *triangulatus-catillus* zones. MG-1; Awaynat Wanin I and Awaynat Wanin II formations; *rugulata-libyensis* to *langii-concinna* zones.

Previous records. From middle Givetian of Algeria (Moreau-Benoit *et al.* 1993), Australia (Grey 1991) and Belgium (Gerrienne *et al.* 2004); upper Givetian–Famennian of Bolivia (Perez-Leyton 1990); upper Eifelian – lowermost Famennian of the Amazon and Parnaíba basins, Brazil (Loboziak *et al.* 1992*b*, Melo and Loboziak 2003); middle Eifelian – lower Givetian of Canada (McGregor and Camfield 1982); upper Givetian – lower Frasnian of France (Brice *et al.* 1979; Loboziak and Streel 1988); Eifelian–

Givetian of Germany (Loboziak *et al.* 1990); Eifelian–lower Givetian of Iran (Ghavidel-Syooki 2003); lower Eifelian – middle Givetian of Libya (Moreau-Benoit 1989); upper Eifelian–Givetian of Poland (Turnau 1996; Turnau and Racki 1999); upper Givetian – lower Frasnian of Portugal (Lake *et al.*, 1988); and Givetian–lower Frasnian of Scotland (Richardson 1965; Marshall *et al.* 1996; Marshall 2000).

Verrucosisporites scurrus (Naumova) McGregor and Camfield, 1982
Figure 43L–N

1965 *Raistrickia aratra* Allen, p. 701, pl. 96, figs 3–4.
1982 *Verrucosisporites scurrus* (Naumova) McGregor and Camfield, p. 61 (*cum syn.*), pl. 18, figs 10–17, 22; text-fig. 96.

Dimensions. 35(51)90 μm; 19 specimens measured.

Remarks. Specimens herein assigned to this species belong to a more or less intergrading series from those with predominantly conate and small verrucose sculpture (see *Dibolisporites farraginis* McGregor and Camfield, 1982 and *D. uncatus* (Naumova) McGregor and Camfield, 1982) to those with large verrucate sculptural elements, and thus conform rather closely to the diagnosis of *V. scurrus* and *V. premnus* Richardson, 1965. All these forms are included in the *V. scurrus* Morphon (Table 1).

Comparison. Extreme forms of *V. scurrus* (Naumova) McGregor and Camfield, 1982 intergrade with *D. uncatus* (Naumova) McGregor and Camfield, 1982, *V. premnus*, *V. tumulentis* Clayton and Graham, 1974 and possibly *Chelinospora timanica* (Naumova) Loboziak and Streel, 1989. Typically *D. uncatus* has predominantly somewhat smaller and less crowded conate spinose sculpture. *V. premnus* has larger, predominantly flat-topped, baculate-spatulate sculpture. *C. timanica* has predominantly convolute sculpture and a thicker wall. *Raistrickia nigra* Love, 1960 bears more regularly spaced ornamentation of about the same size on each specimen. *R. commutata* sp. nov. has more widely spaced, and more elongate baculate sculptural elements.

Occurrence. S-462, WELL-1 and WELL-8; Jubah Formation; *rugulata-libyensis* to *langii-concinna* zones. A1-69; Awaynat Wanin II Formation; *rugulata-libyensis* to *langii-concinna* zones. MG-1; Ouan-Kasa, Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations; *annulatus-protea* to *langii-concinna* zones.

Previous records. From upper Givetian – lower Frasnian of Argentina (Ottone 1996); lower Givetian–lower Frasnian of Australia (Grey 1991; Hashemi and Playford 2005); upper Eifelian–Givetian of Russian Platform (Avkhimovitch *et al.* 1993; Arkhangelskaya and Turnau 2003); middle Givetian of Belgium (Gerrienne *et al.* 2004); upper Eifelian – lower Frasnian of Bolivia (Perez-Leyton 1990); Givetian–lowermost Famennian of Brazil (Loboziak *et al.* 1988, 1992*b*; Melo and Loboziak 2003); Eifelian–lower Givetian of Canada (McGregor and Camfield 1982); Eifelian–Givetian of Germany (Loboziak *et al.* 1990); lower Eifelian – upper Frasnian of Libya (Paris *et al.* 1985; Streel *et al.* 1988; Moreau-Benoit 1989); Givetian–Frasnian of Spitsbergen, Norway (Vigran 1964; Allen 1965); Givetian of Poland (Turnau 1996; Turnau and Racki 1999); and upper Eifelian – lower Frasnian of Scotland (Richardson 1965; Marshall 1988, 2000; Marshall *et al.* 1996).

Verrucosisporites stictus sp. nov.
Figure 44A–G

Derivation of name. From *stictus* (Latin), meaning spotted; refers to the character of the verrucate ornamentation.

Holotype. EFC V41 (Fig. 44B), slide 62272.

Paratype. EFC O28/1 (Fig. 44E), slide 03CW121; BAQA-1 core hole, sample 395.2 ft.

Type locality and horizon. BAQA-1 core hole, sample 395.2 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Verrucosisporites* densely sculptured by verrucae, closely appressed or fused at base, surmounted by 1 or more minute coni. Proximal region bearing a kyrtome on each interradial area.

Description. Trilete spores with sub-circular to sub-triangular amb. Laesurae straight, simple and extending almost to the equator. Proximal region laevigate and bearing a kyrtome on each interradial area. Equatorial and distal regions sculptured with densely distributed verrucae, 1.5–4 μm wide at base, 1–2.5 μm high, generally less than 0.5 μm apart. Sculptural elements discrete, sub-circular or polygonal in plan view, rounded or slightly tapered with rounded or more or less flat apices in profile view, surmounted by 1 or more minute coni, *c.* 0.5 μm wide and high, at each apex.

Dimensions. 29(44)53 μm; 18 specimens measured.

Remarks. On well-preserved specimens, the apex of verrucae, where the coni are present, appears as a paler spot in polar view. This phenomenon is interpreted to be the result of light reflection. On more badly preserved specimens, this phenomenon is not observed.

Comparison. Verrucosisporites sp. 1 does not possess kyrtomes on its proximal face and is less densely sculptured.

Occurrence. BAQA-1, BAQA-2, JNDL-3 and WELL-4; Jauf Formation (Sha'iba to Subbat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone.

Verrucosisporites sp. 1
Figure 44H–J

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple and extend to the equator. Exine 1–2 μm thick. Proximal region is laevigate. Equatorial and distal regions are sculptured with evenly distributed verrucae or truncated coni, 1.5–5 μm wide at base, 2–5 μm high and 0.5–3 μm apart. Sculptural elements are circular or sub-circular in plan view, parallel-sided or slightly tapered with flat or rounded apices in profile view, sometimes surmounted by 1 or 2 minute coni at each apex.

Dimensions. 34(39)45 μm; four specimens measured.

Comparison. Cymbosporites dammamensis Steemans, 1995 is patinate and bears small bacula generally with bifurcate-shaped apices. *V. stictus* sp. nov. possesses a kyrtome in each interradial area.

Occurrence. BAQA-1, JNDL-4 and WELL-4; Jauf Formation (Subbat and Hammamiyat members); *ovalis-biornatus* to *lindlarensis-sextantii* zones.

Genus ZONOTRILETES Luber and Waltz, 1938

Type species. None designated.

Zonotriletes armillatus Breuer *et al.*, 2007c
Figure 44K–M

2007c *Zonotriletes armillatus* Breuer *et al.*, p. 51, pl. 11, figs 9–12, pl. 12, figs 1–2.

Dimensions. 43(64)109 μm; 35 specimens measured.

Occurrence. JNDL-1, Jubah Formation, *svalbardiae-eximius* Zone. MG-1, Awaynat Wanin I Formation, *rugulata-libyensis* Zone.

Previous record. From upper Eifelian – lower Givetian of Parnaíba Basin, Brazil (Breuer and Grahn 2011).

Zonotriletes brevivelatus sp. nov.
Figure 44N–Q, 45A–B

1968 *Zonotriletes* sp. 1 Jardiné and Yapaudjian, pl. 2, fig. 6.
1976 *Perotriletes* sp. Massa and Moreau-Benoit, pl. 1, fig. 5.

Derivation of name. From *brevi-* and *velatus* (Latin), meaning bearing a narrow flange; refers to the flange.

Holotype. EFC Q46/3 (Fig. 44O), slide 62779.

Paratype. EFC D55/1 (Fig. 44P), slide 26912; A1-69 borehole, sample 2108–2111 ft.

Type locality and horizon. MG-1 borehole, sample 2639 m; Ouan-Kasa Formation at Mechiguig, Tunisia.

Diagnosis. A simple *Zonotriletes* with a narrow proximo-equatorial flange.

Description. Amb is sub-circular to sub-triangular. Laesurae are distinct, straight, simple or sometimes bordered with labra *c.* 0.5 μm wide individually, extending almost to the inner margin of the zona. Curvaturae are often visible. The central body diameter equals is commonly three-quarters to nine-tenths of the total amb diameter. Exine of the central body is 2–5 μm thick equatorially. The proximo-equatorial flange is commonly 2–8 μm wide and is uniformly wide but is often folded back locally. Thin transverse attachment lines of the flange on the central body can sometimes be distinguished on the proximal face. Proximal and distal surfaces are entirely laevigate.

Dimensions. 49(59)71 μm; 22 specimens measured.

Comparison. This species differs from other species of *Zonotriletes* Luber and Waltz, 1938 by its regular narrow zona. *Z. simplicissimus* Breuer *et al.*, 2007c is more robust and possesses wide labra bordering laesurae. Its flange is generally narrower opposite the laesurae.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-4 and WELL-7, Jauf (Sha'iba to Hammamiyat members) and Jubah formations; *ovalis-biornatus* to *svalbardiae-eximius* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone. MG-1, Ouan-Kasa and Awaynat Wanin I formations; *svalbardiae-eximius* to *rugulata-libyensis* zones.

FIG. 44. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A–G, *Verrucosisporites stictus* sp. nov. A, BAQA-2, 50.8 ft, 66813, E41. B, Holotype, BAQA-1, 395.2 ft, 62272, V41. C, BAQA-1, 227.1 ft, 03CW110, K39/1. D, BAQA-1, 395.2 ft, 03CW121, X45. E, Paratype, BAQA-1, 395.2 ft, 03CW121, O28/1. F, BAQA-1, 395.2 ft, 62275, Q29-30. G, BAQA-2, 134.4 ft, 03CW137, N27/4. H–J, *Verrucosisporites* sp. 1. H, JNDL-4, 419.3 ft, 03CW261, M35/3. I, JNDL-4, 163.7 ft, 03CW212, V33/4. J, JNDL-4, 411.5 ft, 03CW259, T45/2. K–M, *Zonotriletes armillatus* Breuer *et al.*, 2007c. K, JNDL-1, 155.6 ft, 60837, O34. L, JNDL-1, 172.7 ft, 60846, T32. M, JNDL-1, 155.6 ft, PPM003, T42/4. N–Q, *Zonotriletes brevivelatus* sp. nov. N, MG-1, 2639 m, 62780, R37/1. O, Holotype, MG-1, 2639 m, 62779, Q46/3. P, Paratype, A1-69, 2108–2111 ft, 26912, D55/1. Q, A1-69, 2108–2111 ft, 26913, J44/4.


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Previous records. From Lochkovian–Pragian of Algeria (Jardiné and Yapaudjian 1968); and Pragian–Emsian of Libya (Massa and Moreau-Benoit 1976).

Zonotriletes rotundus sp. nov.
Figure 45C–G

Derivation of name. From *rotundus* (Latin), meaning rounded; refers to the distal sculpture.

Holotype. EFC O41/2 (Fig. 45C), slide 62781.

Paratype. EFC H51/3 (Fig. 45F), slide 26976; A1-69 borehole, sample 1486 ft.

Type locality and horizon. MG-1 borehole, sample 2315 m; Awaynat Wanin II Formation at Mechiguig, Tunisia.

Diagnosis. A sub-circular *Zonotriletes* with a flange of the same width along the amb. Distal surface contains a distinct annular thickening.

Description. Amb is sub-circular to sub-triangular. Laesurae are distinct, straight to slightly sinuous, simple and rarely elevated up to 2 μm, extending or almost to the inner margin of the zona. Curvaturae are not visible. The central body diameter equals commonly seven-tenths to three-quarters of the total amb diameter. Exine of the central body is commonly 1–3 μm thick equatorially. The thin proximo-equatorial flange is generally 5–20 μm wide but up to 24 μm for the larger specimens. The flange can be folded back opposite the laesurae and radially folded. Thin transverse attachment lines of the flange on the central body may be distinguished on the proximal face. An annulus is present on the distal face and is 6–10 μm wide. The annulus diameter equals two-fifths to three-fifths of the central body diameter. In some specimens, the annulus is barely perceptible and may be represented by a rounded darker area. Proximal and distal surfaces are laevigate.

Dimensions. 55(83)110 μm; 20 specimens measured.

Comparison. Zonotriletes armillatus Breuer *et al.*, 2007*c* has a more triangular appearance and a generally less wide flange which is always narrower opposite the laesurae.

Occurrence. JNDL-1, JNDL-3 and JNDL-4; Jauf (Hammamiyat and Murayr members) and Jubah formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *triangulatus-catillus* zones. MG-1; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *triangulatus-catillus* zones.

Previous record. From upper Eifelian – lower Givetian of Parnaíba Basin, Brazil (Breuer and Grahn 2011).

Zonotriletes simplicissimus Breuer *et al.*, 2007*c*
Figure 45H–I

? 1968 *Zonotriletes* sp. 3 Jardiné and Yapaudjian, pl. 2, fig. 2.
2007*c Zonotriletes simplicissimus* Breuer *et al.*, p. 52, pl. 12, figs 3–7.

Dimensions. 38(59)82 μm; 26 specimens measured.

Occurrence. JNDL-1 and S-462, Jubah Formation, *svalbardiae-eximius* to *rugulata-libyensis* zones. A1-69; Awaynat Wanin II Formation; *rugulata-libyensis* Zone.

Previous record. From upper Eifelian – lower Givetian of Parnaíba Basin, Brazil (Breuer and Grahn 2011).

Zonotriletes venatus sp. nov.
Figure 46A–C

1968 *Zonotriletes* sp. 2 Jardiné and Yapaudjian, pl. 2, fig. 1.
1988 *Perotrilites* sp. cf. *Zonotriletes* sp. 2 *in* Jardiné and Yapaudjian; Boumendjel *et al.*, pl. 1, fig. 1.

Derivation of name. From *venatus* (latin), meaning veined; refers to the flange.

Holotype. EFC T33 (Fig. 46B), slide 62552.

Paratype. EFC Q36/3 (Fig. 46A), slide 62552; MG-1 borehole, sample 2631.2 m.

Type locality and horizon. MG-1 borehole, sample 2631.2 m; Ouan-Kasa Formation at Mechiguig, Tunisia.

Diagnosis. A large *Zonotriletes* with a very wide veined, striated, equatorial flange.

FIG. 45. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A–B, *Zonotriletes brevivelatus* sp. nov. A, MG-1, 2639 m, 62780, L39. B, JNDL-4, 328.3 ft, 03CW245, P35/4. C–G, *Zonotriletes rotundus* sp. nov. C, Holotype, MG-1, 2315 m, 62781, O41/2. D, JNDL-1, 155.6 ft, 60837, C50/1. E, A1-69, 1950 ft, 27276, R41. F, Paratype, A1-69, 1486 ft, 26976, H51/3. G, JNDL-1, 155.6 ft, 60837, Q34/4. H–I, *Zonotriletes simplicissimus* Breuer *et al.*, 2007*c*. H, JNDL-1, 172.7 ft, PPM007, D31; the transverse attachment lines of the flange on the central body are distinguishable. I, JNDL-1, 177.0 ft, 60849, G35/4.


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Description. Zonate trilete spores with sub-circular to sub-triangular amb. Laesurae distinct, straight to slightly sinuous, sometimes elevated, extending to the outer margin of the zona. Curvaturae not visible. The central body diameter equals two-fifths to three-fifths of the total amb diameter. Exine of the central body relatively thin equatorially. The equatorial flange is finely veined and striated. Proximal and distal surfaces entirely laevigate.

Dimensions. 77(130)176 μm; 10 specimens measured.

Comparison. Zonotriletes sp. 1 is usually smaller and has a narrower zona.

Remarks. The equatorial flange is thin and very large; as a result, it is often broken and/or folded.

Occurrence. BAQA-1 and JNDL-4; Jauf Formation (Qasr to Subbat members); *ovalis-biornatus* to *lindlarensis-sextantii* zones. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone.

Previous records. From Lochkovian–Pragian of Algeria (Jardiné and Yapaudjian 1968; Boumendjel *et al.* 1988); lower Lochkovian – lower Emsian of Brazil (Grahn *et al.* 2005; Mendlowicz Mauller *et al.* 2007; Steemans *et al.* 2008).

Zonotriletes sp. 1
Figure 46D–E

Description. Amb is sub-circular to sub-triangular. Laesurae are distinct, straight to slightly sinuous, simple or bordered with labra up to 3 μm wide individually and extending to the outer margin of the zona. Curvaturae are not visible. The central body diameter equals three-fifths to four-fifths of the total amb diameter. Exine of the central body is 2–5 μm thick equatorially. Zona is divided entirely or partially into three individual proximo-equatorial flanges, the maximum width (commonly 14–25 μm) of which is opposite the laesurae. Zona laevigate to infragranular, generally folded back opposite the laesurae, resulting in a tri-lobed appearance. Thin transverse attachment lines of the flange on the central body can be distinguished on the proximal face. Proximal and distal surfaces of the central body are laevigate.

Dimensions. 65(82)102 μm; five specimens measured.

Comparison. Alatisporites? trisacculus sp. nov. is more rounded and possess three individual sacci. Furthermore, the maximum width of the zona is opposite the laesurae.

Occurrence. JNDL-1; Jubah Formation; *svalbardiae-eximius* Zone. A1-69; Awaynat Wanin I Formation; *svalbardiae-eximius* Zone.

BIOSTRATIGRAPHY

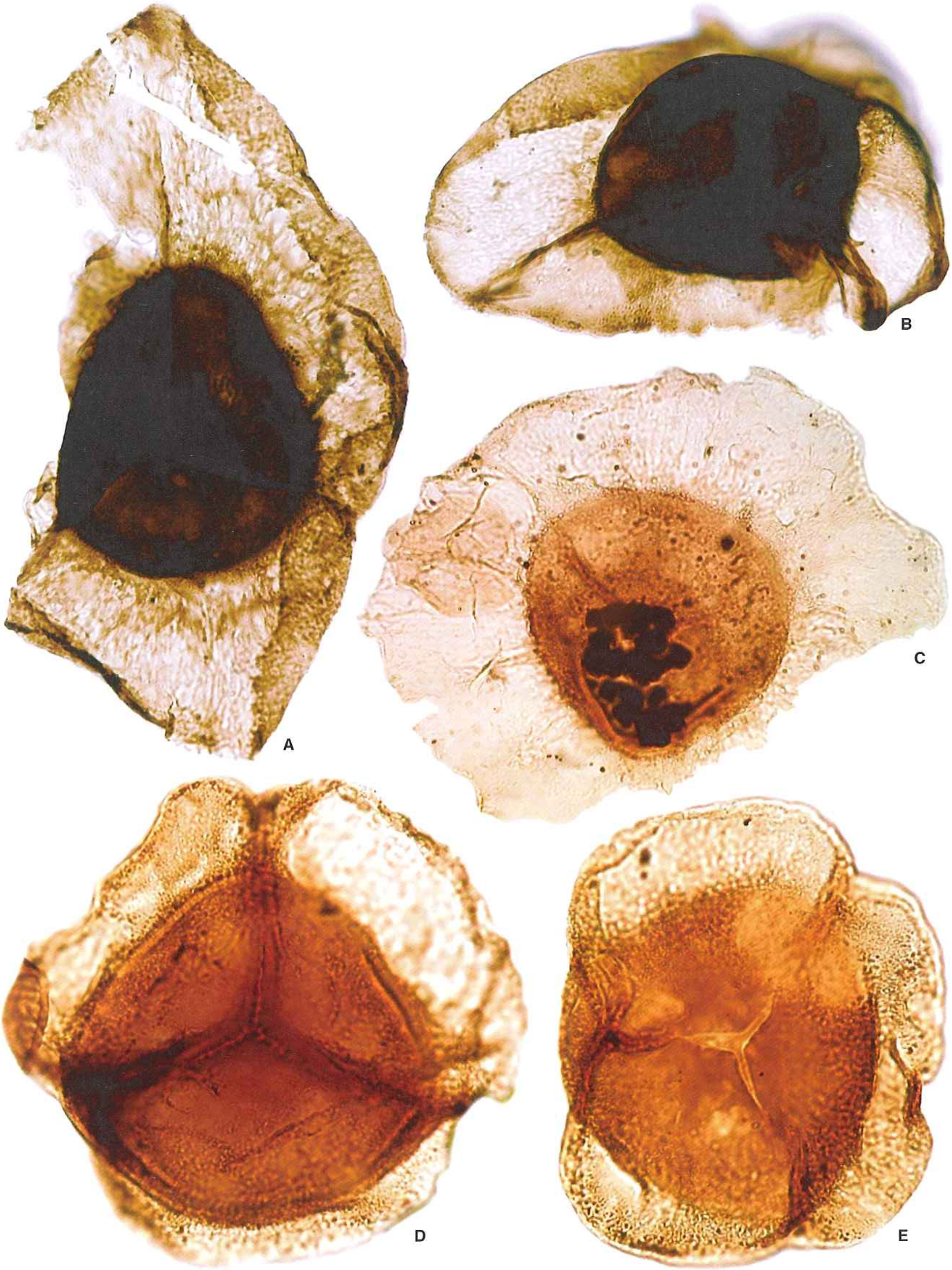
The two main Devonian spore zonations defined by Richardson and McGregor (1986) and Streel *et al.* (1987) from Euramerican material are commonly used in most of the palynological studies (see above). Loboziak and Melo (2002) simplified the Western European biozonation of Streel *et al.* (1987) to apply it to western Gondwanan localities. In addition, they associated the ranges of some endemic spores which could represent useful zonal markers for the regional biozonation (Loboziak and Streel 1995*a*). In north-western Gondwana, Massa and Moreau-Benoit (1976) and Moreau-Benoit (1989) established also a unique detailed biozonation (see above). The palynological analyses show here that the reference spore zones usually used in Euramerica are not all recognized in the Gondwanan coeval sections. It is due to the absence or the rarity of several index species.

In this work, about 88 per cent of species from the North African assemblages are also found in Saudi Arabia. Among the 205 different taxa described herein, about 48 per cent are found elsewhere outside Gondwana (cosmopolitan species) and the remaining 52 per cent are restricted to Saudi Arabia, North Africa or more generally to Gondwana (endemic species). In terms of number of specimens, these endemic taxa may represent a percentage greater again of the whole spore assemblages. Almost since their origin, land plant taxa have not been cosmopolitan, and therefore the lateral extension of correlation by spores is risky (Traverse 2007). Precise transcontinental correlation is sometimes difficult, intercontinental correlation is again more difficult and sometimes impossible (except in very broad terms). As one of the main problems for spore-based palynostratigraphy and biostratigraphy in general is provincialism, a new biozonation based on the own characteristics of the spore assemblages described here could allow more accurate local/regional correlations and also tentative intercontinental correlations.

New biozonation for north-western Gondwana

The known ranges of the nominal species and main characteristic species occurring in North Africa and Saudi Arabia are plotted in a composite stratigraphical chart in Figures 53 and 54. The plotted stratigraphical ranges of these characteristic taxa do not represent a mean based on their local range in each section but is their total

FIG. 46. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A–C, *Zonotriletes venatus* sp. nov., magnification ×750. A, Paratype, MG-1, 2631.2 m, 62552, Q36/3. B, Holotype, MG-1, 2631.2 m, 62552, T33. C, BAQA-1, 406.0 ft, 03CW123, L23/3. D–E, *Zonotriletes* sp. 1. D, JNDL-1, 156.0 ft, PPM004, K38/1. E, JNDL-1, 162.3 ft, 60844, L34.


A
B
C
D
E

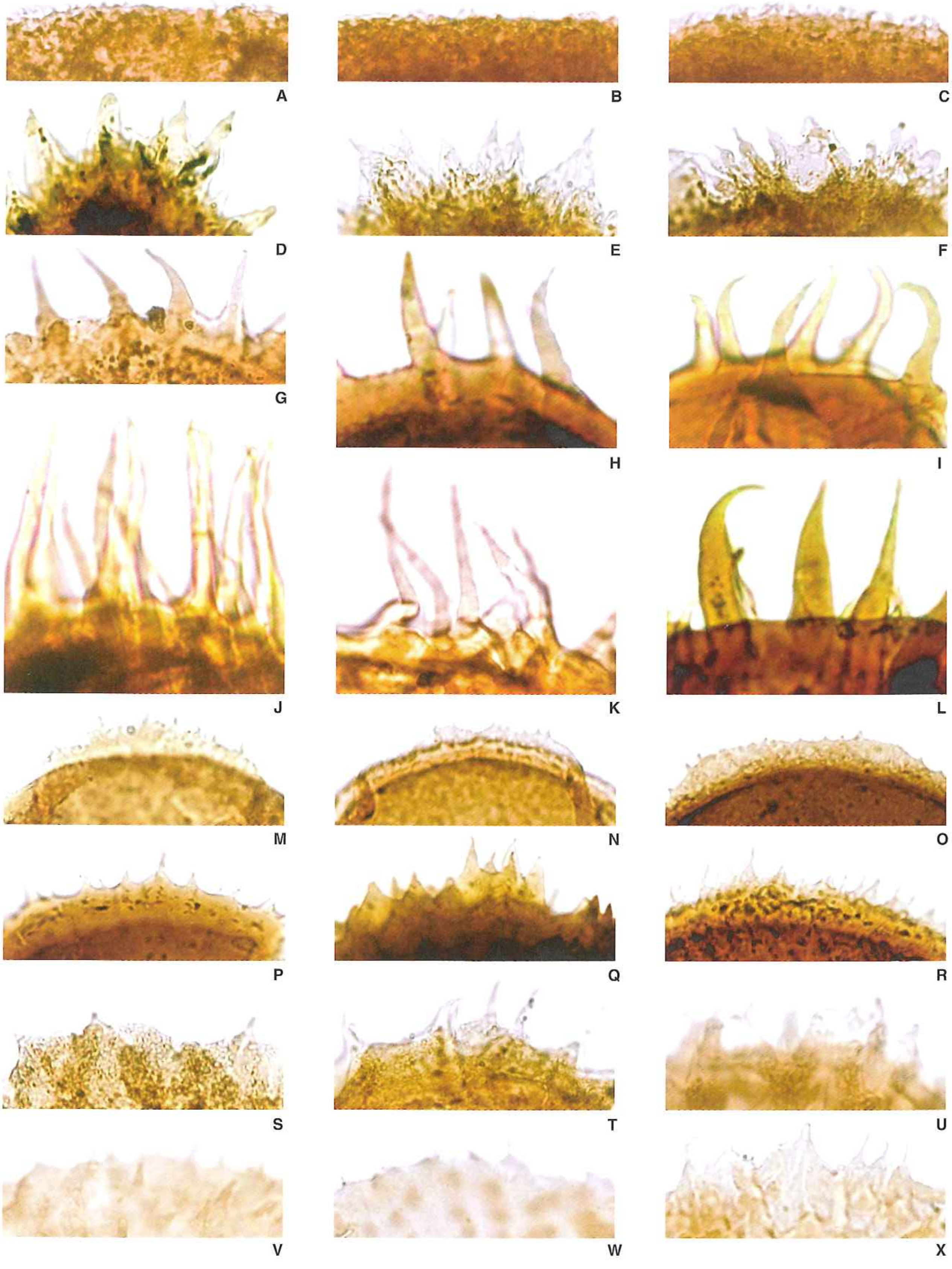
stratigraphical range. The first and last occurrences of each taxon are taken into account in all cored sections. By studying, analyzing and comparing stratigraphical range of spores species and composition of different assemblages of the studied sections, a new biozonation can be defined for north-western Gondwana. As each type of biozones has different advantages and disadvantages, different types of biozones are combined to establish the most useful biozonation. The assemblage zones are used to subdivide the stratigraphical column on a large scale. Firstly, their advantage is that they are probably the most easily applicable for long-distance (intercontinental) correlation to other studies. Secondly, some general characteristics or trends of the assemblages may be included in order to be useful also in a local/regional use. Finally, several index species may be designated for the recognition of the zone. Although the assemblage zones boundaries defined here are based on one single index species and consequently correspond in theory to an interval zone, each biozone is described as an assemblage zone because stratigraphically useful species and general characteristics of the assemblages are included in the characterization of these biozones. Therefore, in spite of the eventual absence of the index species in a studied section, the assemblage zone might be recognizable. The assemblage zones are themselves divided into subzones when it is possible for a more accurate stratigraphy. These subzones are either interval or acme zones. The interval zones are not useful if their index taxon is absent for any reason, but they can be very useful for local/regional correlations. However, a note of caution is expressed regarding the use of interval zones because it is quite possible that the age of first occurrences may vary spatially due to immigration/migration or subtle biogeographical, ecological or facies effects (Wellman 2006). Nevertheless, the use of interval zones is still the only way to correlate spores with other palaeontological groups such as conodonts and foraminifera. As regards the acme or abundance zones, their use is tenuous and probably more of ecological significance than anything else but they are above all useful for local correlation. The new proposed scheme based on a combination of diverse types of biozones consists of nine assemblage zones, nine interval zones and one acme zone spanning from upper Pragian to lower Frasnian. Thanks to this new biozonation, the studied sections from the three distinct regions are correlated (Fig. 55).

From base to top, the assemblages are defined and compared to biozones defined in the literature (Fig. 56), especially the two main Devonian spore zonations defined on Euramerica by Richardson and McGregor (1986) and Streel *et al.* (1987) and the operational palynological zonation used by Saudi Aramco (Al-Hajri *et al.* 1999). The age of each assemblage is discussed, but the biostratigraphical correlations remain approximative (Fig. 56), as there are any outcrops or sections that allow to correlate the different biozones. Indeed few precise independent palaeontological dating is available for the studied areas; therefore, we have to keep in mind that the suggested ages are only based on the comparisons with reference spore biozones, which themselves are dated independently. The use of the high-resolution conodont-based international Devonian stratigraphy allows to date the spore zonation from Western Europe of Streel *et al.* (1987; Streel and Loboziak 1996; Streel *et al.* 2000).

Description of the palynological zones and subzones

The name given to each spore zones comprises (1) the names of one or two characteristic taxa referred to as 'nominal species', and (2) a statement of the kind of zone. The nominal species are chosen for various reasons: lateral widespread and abundant occurrence (acme zone), restriction to a definite stratigraphical interval, characteristic first appearance or extinction. Stratigraphical range of nominal species is given in Figure 53. On its first citation, the name of the zone is given in full, for example the *Acinosporites lindlarensis–Camarozonotriletes sextantii* Assemblage Zone. In subsequent citations the name of the zone is abbreviated: the *lindlarensis-sextantii* Zone.

FIG. 47. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A–C, *Contagisporites optivus* (Chibrikova) Owens, 1971. A, S-462, 2110–2115 ft, 63273, N40/1. B, S-462, 2260–2265 ft, 63281, Q28/2. C, S-462, 2110–2115 ft, 63272, O31. D–F, *Corystisporites collaris* Tiwari and Schaarschmidt, 1975. D, A1-69, 1109 ft, 27274, O45/1. E, S-462, 1760–1765 ft, 63255, P36/1. F, A1-69, 971 ft, 62639, T32. G–L, *Corystisporites undulatus* Turnau, 1996. G, A1-69, 1109 ft, 27273, E50/4. H, A1-69, 971 ft, 62641, K46/2. I, A1-69, 1277 ft, 62636, R29/2. J, MG-1, 2205 m, 62595, G30/2. K, MG-1, 2295 m, 63005, X51/3. L, A1-69, 1277 ft, 62636, E35/3. M–O, *Craspedispora ghadamesensis* Loboziak and Streel, 1989. M, A1-69, 1322 ft, 27125, K54/2. N, A1-69, 1596 ft, 26990, D44. O, A1-69, 1700 ft, 62634, M37/2. P–R, *Craspedispora paranaensis* Loboziak *et al.*, 1988. P, A1-69, 1700 ft, 62632, R50. Q, A1-69, 1700 ft, 62633, T43/2. R, A1-69, 1596 ft, 26989, T39. S–U, *Cristatisporites (Calyptosporites) reticulatus* (Tiwari and Schaarschmidt) comb. nov. S, MG-1, 2713 m, 62811, H36. T, MG-1, 2264 m, 62951, L42/3. U, MG-1, 2285 m, 62846, L46. V–X, *Cristatisporites streelii* sp. nov. V, Paratype, MG-1, 2241 m, 62964, H44/3. W, Holotype, MG-1, 2270 m, 62849, R42/3. X, MG-1, 2375 m, 62773, L33.



Synorisporites papillensis–Cymbohilates baqaensis *Assemblage Zone*

Reference section. Borehole BAQA-2: samples 133.0 and 134.4 ft.

Distribution. Lower part of the Sha'iba Member, Jauf Formation, Saudi Arabia. This biozone is only recognized in two samples. Its lower stratigraphical limit of this assemblage is presently unknown, as it occurs at the lowest depth sampled.

Description. The most characteristic trilete spores are: *Am-*

ites papillensis, *Verrucosisporites onustus* and *V. polygonalis*. Cryptospores are rather well diversified and common including above all *Cymbohilates baqaensis*, *C. comptulus* and *Gneudnaspora divellomedia* var. *minor*). Although all these species persist upwards in the succeeding *Latosporites ovalis–Dictyotriletes biornatus* Assemblage Zone, the *papillensis-baqaensis* is primarily distinguished by the absence of laevigate monolete spores. This assemblage can also be recognized by the occurrence of *Cymbosporites wellmanii* and *Dictyotriletes granulatus*, which are exclusive to it. The spores of this section are mainly simple laevigate spores, simple spores sculptured with discrete elements and proximal interradial papillae are common.

Comparison with reference biozones. The co-occurrence of *Verrucosisporites polygonalis* and *Dictyotriletes emsiensis* is the criterion to correlate this assemblage to the *polygonalis-emsiensis* Assemblage Zone of Richardson and McGregor (1986). The presence of *Dictyotriletes subgranifer* indicates more precisely the Su Interval Zone of Streel *et al.* (1987).

Stage. Upper Pragian.

Latosporites ovalis–Dictyotriletes biornatus *Assemblage Zone*

Reference section. No section recorded entirely the *ovalis-biornatus* Zone but the combination of core holes BAQA-2 (from 64.5 ft) and BAQA-1 (to 161 ft) can serve as a reference section since these sections are easily correlated by lithostratigraphic and sedimentologic data.

Distribution. Upper Sha'iba, Qasr, lower and middle Subbat members, Jauf Formation, Saudi Arabia.

Zone base definition. Its lower boundary is based on the

through the assemblage are: *Artemopyra recticosta*, *Biornatispora dubia*, *Brochotriletes crameri*, *B. hudsonii*, *B. tenellus*, *Coronaspora inornata*, *Cymbosporites asymmetricus*, *Diaphanospora milleri* Morphon, *Dibolisporites bullatus*, *Dictyotriletes biornatus* Morphon, *D. favosus*, *Emphanisporites schultzii*, *Latosporites ovalis*, *Leiozosterospora* cf. *L. andersonii*, *Reticuloidosporites antarcticus Retusotriletes tenerimedium*, *Rhabdosporites minutus* and *Stellatispora multicostata*. *Apiculiretusispora brandtii* becomes more common. The trilete spores are still dominated by simple forms but are more and more diversified. Spores become larger (up to more than 130 μm). Cavate spores are present from the base of the assemblage with *Leiozosterospora* cf. *L. andersonii*. Although a unique specimen of sculptured monolete spore (*Devonomonoletes* sp. 1), which is a poorly-known species, is recorded in the underlying the *papillensis-baqaensis* Zone, the *ovalis-biornatus* Zone is characterized by the first significant inception of monolete spores (*Latosporites ovalis*) and followed later by the short-ranged reticulate form *Reticuloidosporites antarcticus* only known in Gondwana. The cryptospores still constitute a significant component.

FIG. 48. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification ×1000 except where mentioned otherwise. A–C, *Cristatisporites streelii* sp. nov. A, MG-1, 2241 m, 62964, T30/1. B, MG-1, 2285 m, 62845, J27. C, A1-69, 1322 ft, 27126, O37/1. D–I, *Densosporites devonicus* Richardson, 1960. D, MG-1, 2292 m, 63023, T29. E, MG-1, 2483 m, 62802, C37/4. F, MG-1, 2315 m, 62783, Q42. G, MG-1, 2456 m, 62739, G44. H, MG-1, 2295 m, 63007, E47/1. I, MG-1, 2527 m, 63003, G34/2. J–O, *Grandispora cassidea* (Owens) Massa and Moreau-Benoit, 1976. J, MG-1, 2465 m, 62852, R43/2. K, MG-1, 2518 m, 62805, N27/4. L, MG-1, 2161.8 m, 62529, J49/1. M, MG-1, 2536 m, 62740, L40. N, MG-1, 2161.8 m, 62528, X52/2. O, MG-1, 2639 m, 62778, T42. P–X, *Grandispora douglastownensis* McGregor, 1973. P, A1-69, 1962 ft, 27278, O39. Q, A1-69, 1962 ft, 27278, P44/3. R, A1-69, 1962 ft, 27277, U54/3. S, JNDL-1, 174.6 ft, PPM008, T32. T, JNDL-1, 177.0 ft, 60850, P45/4. U, JNDL-1, 162.3 ft, 60841, K44. V, JNDL-1, 156.0 ft, PPM004, P36/3. W, JNDL-1, 167.8 ft, PPM006, N37. X, WELL-1, 16327.6 ft, 61944, E49. Y–AA. *Grandispora fibrilabrata* Balme, 1988. Y, S-462, 1810–1815 ft, 63257, R48. Z, S-462, 1860–1865 ft, 63258, P27/1. AA, S-462, 2010–2015 ft, 63266, S34.