Comparison. Some extreme variants of *Lophozonotriletes media* Taugourdeau-Lantz, 1967, which show a similar exine and a much reduced ornamentation, could intergrade with *A. variabilis*. Consequently, the *A. variabilis* Morphon is defined here (Table 1).

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

Previous records. Archaeozonotriletes variabilis has been widely reported from Middle through Upper Devonian; e.g. upper Givetian – lower Frasnian of Argentina (Ottone 1996); middle Givetian – lower Frasnian (Grey 1991; Hashemi and Playford 2005); Frasnian of Belgium (Streel and Loboziak 1987); upper Givetian–Frasnian of Bolivia (Perez-Leyton 1990); lower Givetian – lowermost Famennian of Brazil (Loboziak *et al.* 1988; Loboziak *et al.* 1992*b*; Melo and Loboziak 2003; Breuer and Grahn 2011); Eifelian–lower Famennian of Canada (McGregor and Owens 1966; Owens 1971; McGregor and Uyeno 1972; McGregor and Camfield 1982); Givetian of China (Gao Lianda 1981), Poland (Turnau 1996; Turnau and Racki 1999) and Spitsbergen, Norway (Allen 1965); upper Givetian–upper Frasnian of France (Loboziak and Streel 1980, 1988; Loboziak *et al.* 1983); Eifelian–Givetian of Germany (Tiwari and Schaarschmidt 1975; Loboziak *et al.* 1990); middle Givetian of Greenland (Friend *et al.* 1983; Marshall and Hemsley 2003); middle Givetian – upper Famennian of Libya (Streel *et al.* 1988; Moreau-Benoit 1989); Givetian–Famennian of Morocco (Rahmani-Antari and Lachkar 2001); lower Frasnian of Russian Platform (Avkhimovitch *et al.* 1993); and uppermost Givetian – lower Frasnian of Scotland (Marshall *et al.* 1996).

Genus AURORASPORA Hoffmeister *et al.*, 1955

Type species. Auroraspora solisorta Hoffmeister *et al.*, 1955.

Auroraspora macromanifesta (Hacquebard) Richardson, 1960
Figure 10K

1925 Type A Lang, p. 255, pl. 1, figs 1–2.
1957 *Endosporites macromanifestus* Hacquebard, p. 317, pl. 3, figs 14–15.
1960 *Auroraspora macromanifestus* (Hacquebard) Richardson, p. 50, pl. 14, figs 1–2; text-fig. 6A.

Dimensions. 122–124 μm; two specimens measured.

Occurrence. MG-1; Awaynat Wanin II Formation; *lemurata-langii* to *triangulatus-catillus* zones.

Previous records. From middle Givetian–Frasnian of Algeria (Moreau-Benoit *et al.* 1993); Givetian–Mississippian of Canada (Hacquebard 1957; McGregor and Owens 1966; Owens 1971; McGregor and Uyeno 1972); upper Emsian – lower Givetian of Germany (Tiwari and Schaarschmidt 1975); upper Givetian – lower Frasnian of France (Brice *et al.* 1979; Loboziak and Streel 1980); upper Eifelian–Givetian of Poland (Turnau 1996; Turnau and Racki 1999); and middle Eifelian – lower Frasnian (Richardson 1965; Marshall 1988, 2000; Marshall *et al.* 1996; Marshall and Fletcher 2002).

Auroraspora minuta Richardson, 1965
Figure 10L–M

1965 *Auroraspora minuta* Richardson, p. 586, pl. 93, fig. 2.

Dimensions. 59(72)92 μm; 14 specimens measured.

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

Previous records. From middle Givetian of Algeria (Moreau-Benoit *et al.* 1993); upper Eifelian–middle Givetian (Breuer and Grahn 2011); Emsian–?lower Eifelian of Canada (McGregor and Owens 1966); lower Eifelian of Libya (Moreau-Benoit 1989); and Givetian of Scotland (Richardson 1965).

Genus BIORNATISPORA Lele and Streel, 1969

Type species. Biornatispora dentata Lele and Streel, 1969.

Comparison. Acinosporites Richardson, 1965 has convoluted pattern of muri that bear characteristically biform ornaments. *Dictyotriletes* Naumova, 1939 ex Ishchenko, 1952 is ornamented with a perfectly closed reticulum.

Biornatispora dubia (McGregor) Steemans, 1989
Figure 11A–D

1973 *Camptotriletes dubius* McGregor, p. 42, pl. 5, figs 9–11, 13–14.
non 1989 *Biornatispora dubia* (McGregor) Steemans, p. 104, pl. 22, figs 21–25.

Description. Amb is sub-circular to broadly triangular. Laesurae are simple or with low labra individually up to 1 μm wide, two-thirds to nine-tenths of the amb radius in length. Contact areas are laevigate. Distal and equatorial regions are ornamented with coni, truncate coni, bacula or biform tubercules generally 1–2 μm wide at base, 1–2.5 μm long, 1–4 μm apart, commonly interconnected by ridges 0.5–2.5 μm wide and high that form an incomplete reticulum. Muri thicken where the ornamentation is

rooted. Lumina of the reticulum 2–8 μm in greatest diameter. Exine is up to 2 μm thick at equator.

Dimensions. 29(37)51 μm; 30 specimens measured.

Remarks. Camptotriletes dubius McGregor, 1973 was transferred to the genus *Biornatispora* Lele and Streel, 1969 by Steemans (1989), who, however, as is evident from his description, erroneously applied the new combination *B. dubia* to another species of *Biornatispora*, namely *B. elegantula* sp. nov. The combination *B. dubia* (McGregor) Steemans, 1989 must not be applied to *B. elegantula* but must be retained for *C. dubius*.

Biornatispora dubia is a morphologically variable species. All gradations are observed between specimens characterized by small muri and ornament to ones showing thicker ornamentation. The appearance of the reticulum varies from an almost complete reticulum to an incomplete reticulum.

Comparison. Biornatispora elegantula sp. nov. is proximally granulate, finely sculptured and possesses a typical darker apical sub-triangular band. *B. dubia* is smaller than *B. dentata* (Streel) Lele and Streel, 1969 and has a more variable, less regularly disposed sculpture. It is distinguished from *Brochotriletes* sp. B *in* McGregor (1973) by its smaller size and low-ridged or incomplete foveo-reticulate sculpture.

Occurrence. BAQA-1, WELL-2, WELL-3, JNDL-3, JNDL-4, WELL-1, WELL-4, WELL-5, WELL-6 and WELL-7; Jauf Formation (Subbat to Murayr members); *ovalis-biornatus* to *annulatus-protea* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa Formation; *annulatus-protea* Zone.

Previous record. From Emsian of Eastern Canada (McGregor 1973).

Biornatispora elegantula sp. nov.
Figure 11E–I

1989 *Biornatispora dubia* (McGregor) Steemans, p. 104, pl. 22, figs 21–25.

Derivation of name. From *elegantulus* (Latin) meaning elegant, graceful; refers to the fine sculpture of the equatorial and distal regions.

Holotype. EFC P32/4 (Fig. 11G), slide 66812.

Paratype. EFC E41/2 (Fig. 11H), slide 03CW114; BAQA-1 core hole, sample 345.5 ft.

Type locality and horizon. BAQA-2 core hole, sample 50.2 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Biornatispora* sculptured with densely distributed, small coni or spines interconnected by thin ridges. Contact areas granulate and characterized by a darker apical sub-triangular band, with concave to straight margins, which extends between the ends of the laesurae.

Description. Amb is sub-circular. Laesurae are accompanied with low labra, individually 1.5–2.5 μm wide, one-half to three-quarters of the amb radius in length. As the labrate laesurae are commonly open, it gives a darker apical sub-triangular band, with concave to straight margins, which extends between the ends of the laesurae. Curvaturae perfectae are commonly confluent with the equator for part of their length and invaginate proximally to join the extremities of laesurae. Contact areas are granulate. Distal and equatorial regions are ornamented with coni or spines *c.* 0.5 μm wide at base, *c.* 0.5–1.5 μm long, 0.5–2 μm apart, commonly interconnected by ridges up to 1 μm wide and high that form an incomplete reticulum. Muri thicken where the discrete sculptural elements are rooted. Lumina of the reticulum 1–4 μm in greatest diameter. Exine is 0.5–1.5 μm thick.

Dimensions. 30(34)39 μm; 18 specimens measured.

Remarks. Biornatispora dubia (McGregor) Steemans, 1989 *sensu* Steemans (1989) is a later homonym of *B. dubia sensu* McGregor (1973; see above). *B. elegantula* sp. nov. is consequently nominated (nomen novum) to encompass the description of the specimens described in Steemans (1989) and here. Holotype and paratype are also designated.

Comparison. Biornatispora dubia (McGregor) Steemans, 1989 is more coarsely ornamented and does not have a darker apical sub-triangular band.

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

Previous record. From upper Lochkovian–Pragian of Belgium and upper Lochkovian–Emsian of Germany (Steemans 1989).

Biornatispora microclavata sp. nov.
Figure 11J–L

Derivation of name. From *microclavatus* (Latin), meaning sculptured with small club-shaped elements (clavae); refers to the sculpture of the equatorial and distal regions.

Holotype. EFC V36/4 (Fig. 11J), slide 03CW126.

Paratype. EFC E50/3 (Fig. 11L), slide 03CW126; BAQA-2 core hole, sample 50.2 ft.

Type locality and horizon. BAQA-2 core hole, sample 50.2 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Biornatispora* bearing small clavae or pila interconnected by low ridges.

Description. Amb is sub-circular. Laesurae are straight, simple or up to 2 μm wide, commonly three-fifths to four-fifths of the amb radius in length. Curvaturae are visible and sometimes bounded by a single continuous thin and translucent murus, up to 2.5 μm high. Contact areas are granular. Distal and equatorial regions are ornamented with clavae or pila (elements with a swollen tip), or more rarely bacula and parallel-sided spinae. Sculptural elements are 0.5–1 μm wide at base, 1–3 μm long, 1–3 μm apart, commonly interconnected by low ridges, generally *c.* 0.5 μm wide and high that form an incomplete reticulum. Irregular lumina of the reticulum are 3–8 μm in greatest diameter. Exine is 1–1.5 μm thick at equator.

Dimensions. 41(54)72 μm; 13 specimens measured.

Comparison. This species is easily recognizable because it is the only species of *Biornatispora* Lele and Streel, 1969 that is ornamented with pila.

Occurrence. BAQA-1 and BAQA-2; Jauf Formation (Sha'iba and Qasr members); *ovalis* Zone.

Genus BROCHOTRILETES Naumova, 1939 ex Ishchenko, 1952

Type species. *Brochotriletes magnus* Ishchenko, 1952.

Brochotriletes crameri sp. nov. Figure 11M–R

Derivation of name. In honour of the Dutch palynologist, Fritz H. Cramer, for his pioneering work on Gondwanan Lower Palaeozoic spores and acritarchs.

Holotype. EFC O54 (Fig. 11N), slide 68659.

Paratype. EFC Q38/3 (Fig. 11M), slide 68567; JNDL-3 core hole, sample 413.2 ft.

Type locality and horizon. JNDL-4 core hole, sample 277.6 ft; Jauf Formation at Domat Al-Jandal, Saudi Arabia.

Diagnosis. A *Brochotriletes* foveolate proximally and distally.

Description. Amb is sub-circular to sub-triangular. Laesurae are often open, straight, simple, extending to or almost to the equator. Exine is 1.5–3.5 μm thick. Proximal and distal regions are foveolate. Foveolae from both regions are round to oval in plan view, 3–6 μm in diameter, up to 2 μm deep and 2–4 μm apart. Number of foveolae on the equator are around 15. Exine between foveolae is laevigate.

Dimensions. 33(36)41 μm; nine specimens measured.

Comparison. *Coronospora reticulata* Richardson *et al.*, 2001 has kyrtome on the contact areas and is not reticulate proximally. *Brochotriletes* sp. B *in* Tekbali and Wood (1991) may correspond to specimens described above but there are only illustrations in the paper.

Occurrence. BAQA-1, JNDL-1, JNDL-3 and JNDL-4, Jauf (Subbat to Murayr members) and Jubah formations, *asymmetricus* to *svalbardiae-eximius* zones. A1-69; Ouan-Kasa and Awaynat Wanin I formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones.

Brochotriletes foveolatus Naumova, 1953 Figure 11S

1953 *Brochotriletes foveolatus* var. *major* Naumova, p. 58 (*cum syn.*), pl. 7, fig. 23–24.

Dimensions. 47(63)77 μm; 17 specimens measured.

Comparison. The absence of sculpture between foveolae distinguishes this species from *B. bellatulus* Steemans, 1989 and *B. robustus* (Scott and Rouse) McGregor, 1973. *Perforosporites*

FIG. 11. 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–D, *Biornatispora dubia* (McGregor) Steemans, 1989. A, WELL-7, 13614.1 ft, 62373, E34. B, JNDL-3, 499.5 ft, 03CW183, V37/3. C, WELL-3, 14159.5 ft, 60521, H34. D, JNDL-4, 331.9 ft, 03CW246, K38. E–I, *Biornatispora elegantula* sp. nov. E, BAQA-2, 50.8 ft, 66813, G29/4. F, BAQA-1, 345.5 ft, 03CW114, E41/2. G, Holotype, BAQA-2, 50.2 ft, 66812, P32/4. H, Paratype, BAQA-1, 395.2 ft, 66807, Y39/2. I, BAQA-1, 223.5 ft, 66783, P37. J–L, *Biornatispora microclavata* sp. nov. J, Holotype, BAQA-2, 50.2 ft, 03CW126, V36/4. K, BAQA-2, 52.0 ft, 03CW128, U44/1. L, Paratype, BAQA-2, 50.2 ft, 03CW126, H50/3. M–R, *Brochotriletes crameri* sp. nov. M, Paratype, JNDL-3, 413.2 ft, 68567, Q38/3. N, Holotype, JNDL-4, 277.6 ft, 68659, O54. O, JNDL-4, 471.6 ft, 68697, M42. P, JNDL-4, 316.4 ft, 68667, K44. Q, JNDL-1, 156.0 ft, 60840, F47/3. R, JNDL-4, 471.6 ft, 68697, N53. S, *Brochotriletes foveolatus* Naumova, 1953. BAQA-1, 345.5 ft, 03CW114, H54/4. T, *Brochotriletes hudsonii* McGregor and Camfield, 1976. JNDL-3, 462.0 ft, 68576, K54. U–V, *Brochotriletes robustus* (Scott and Rouse) McGregor, 1973. U, WELL-8, 16642.3 ft, 62407, S32. V, WELL-8, 16642.3 ft, 62406, Q45.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V

sp. *in* Allen (1965) is much larger and has a thicker exine. *B. hudsonii* McGregor and Camfield, 1976 is ornamented with more foveolae which are moreover smaller. *Chelinospora carnosa* sp. nov. is distinguished by the presence of constriction of the muri between the lumina.

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

Previous records. Brochotriletes foveolatus has been widely reported in Early through Middle Devonian palynofloras; e.g. Algeria (Boumendjel *et al.* 1988), Brazil (Melo and Loboziak 2003; Grahn *et al.* 2005; Mendlowicz Mauller *et al.* 2007; Steemans *et al.* 2008), Belgium (Steemans 1989), Canada (McGregor and Owens 1966; McGregor 1973; McGregor and Camfield 1976), France (Le Hérissé 1983; Steemans 1989), Germany (Steemans 1989), Libya (Moreau-Benoit 1989), Poland (Turnau *et al.* 2005) and Romania (Steemans 1989).

Brochotriletes hudsonii McGregor and Camfield, 1976
Figure 11T

1966 *Brochotriletes* sp. McGregor and Owens, pl. 1, figs 8–9.
? 1968 Spore no. 380 Magloire, pl. 1, fig. 9 pl. 2, fig. 2.
1970 *Brochotriletes* sp. McGregor *et al.*, pl. 1, figs 14–15.
1975 *Brochotriletes* sp. *in* McGregor; Sanford and Norris, pl. 1, figs 14–15.
1976 *Brochotriletes hudsonii* McGregor and Camfield, p. 12, pl. 3, figs 1–2.

Dimensions. 52(69)80 μm; 10 specimens measured.

Occurrence. BAQA-1, JNDL-3 and JNDL-4; Jauf Formation (Subbat and Hammamiyat members); *ovalis-biornatus* to *lindlarensis-sextantii* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone.

Previous records. From upper Lochkovian–Pragian of Canada (McGregor and Owens 1966; McGregor and Camfield 1976); upper Pragian of Germany (Steemans 1989); and Pragian–uppermost Emsian of Poland (Turnau 1986; Turnau *et al.* 2005).

Brochotriletes robustus (Scott and Rouse) McGregor, 1973
Figure 11U–V

1961 *Perforosporites robustus* Scott and Rouse, p. 978 (*pars*), pl. 113, figs 1–2.
1966 *Brochotriletes* spp. McGregor and Owens (*pars*), pl. 4, fig. 5.
1967 *Perforosporites robustus* Scott and Rouse; Beju, pl. 1, figs 23–24.
1973 *Brochotriletes robustus* (Scott and Rouse) McGregor, p. 40, pl. 5, figs 1, 6.
? 1983 *Brochotriletes* cf. *robustus* (Scott and Rouse) McGregor; Le Hérissé, p. 34, pl. 5, fig. 11.

Dimensions. 35(42)64 μm; eight specimens measured.

Comparison. This species is distinguished from *B. bellatulus* Steemans, 1989 by its smaller size and spinose sculpture. It is very close to it, and may represent an extreme member of the *B. bellatulus* population. Unfortunately, few specimens have been found.

Occurrence. JNDL-3, JNDL-4, WELL-3 and WELL-8; Jauf (Hammamiyat Member) and Jubah Formation; *lindlarensis-sextantii* Zone only as youngest specimens from the Jubah Formation are probably reworked.

Previous records. From upper Lochkovian–Emsian of Belgium (Steemans 1989); Emsian of Canada (McGregor and Owens, 1966; McGregor 1973; McGregor and Camfield 1976); and upper Lochkovian – lower Pragian of Germany (Steemans 1989).

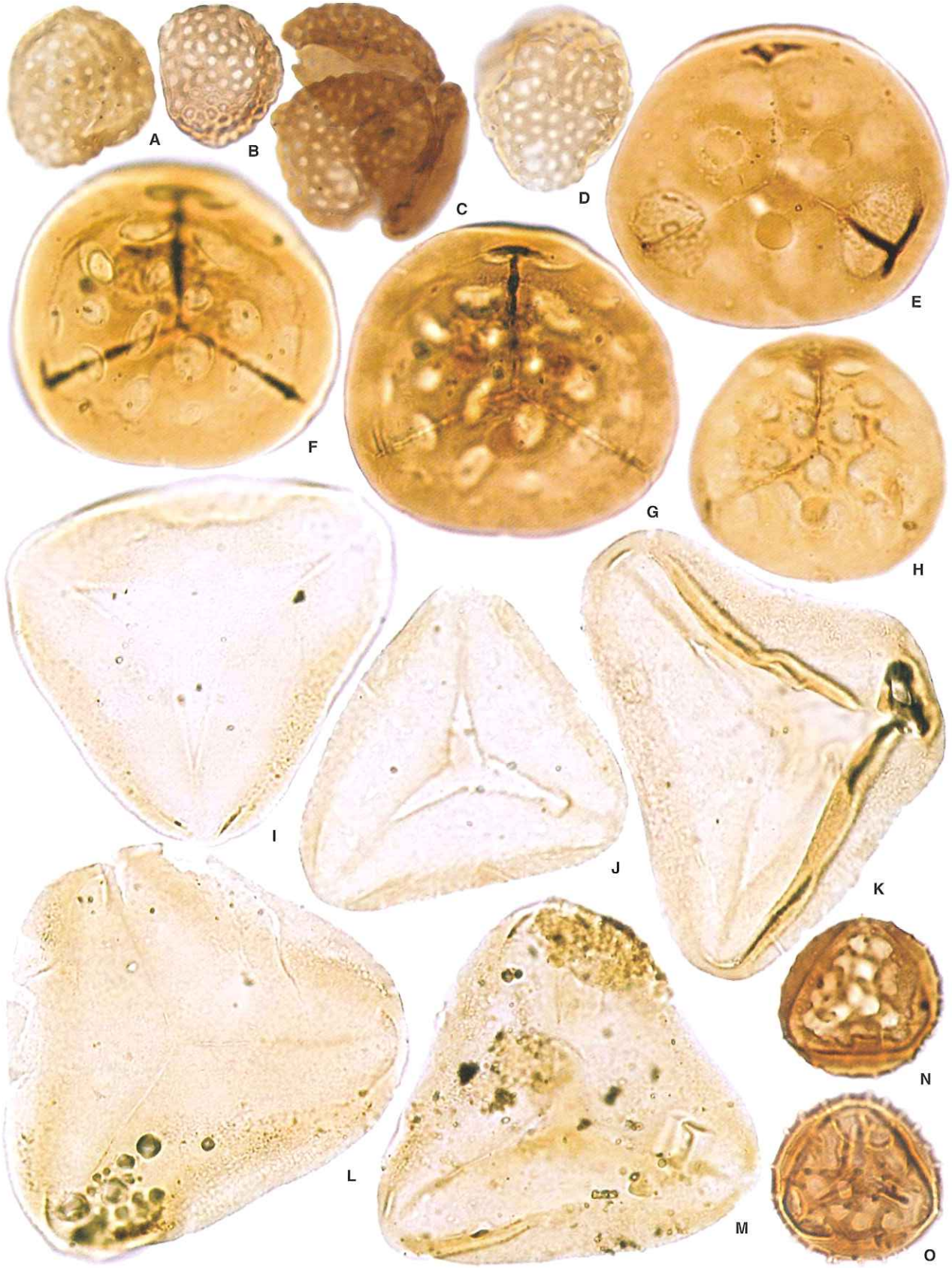
Brochotriletes tenellus sp. nov.
Figure 12A–D

Derivation of name. From *tenellus* (Latin), meaning delicate, wispy; refers to the size of the foveolae and the spore.

Holotype. EFC T32/2 (Fig. 12D), slide 68617.

Paratype. EFC T36/3 (Fig. 12B), slide 66782; BAQA-1 core hole, sample 222.5 ft.

FIG. 12. 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–D, *Brochotriletes tenellus* sp. nov. A, JNDL-4, 316.4 ft, 68667, L50. B, Paratype, BAQA-1, 222.5 ft, 66782, T36/3. C, JNDL-4, 484.1 ft, 68699, S24. D, Holotype, JNDL-4, 135.8 ft, 68617, T32/2. E–H, *Brochotriletes tripapillatus* sp. nov. E, Paratype, A1-69, 1109 ft, 27274, Q46/4. F–G, Holotype, A1-69, 1334 ft, 27127, O51. H, A1-69, 1109 ft, 27273, P53/3. I–M, *Camarozonotriletes asperulus* sp. nov. I, MG-1, 2247 m, 62941, O40/1. J, MG-1, 2278 m, 62936, G43. K, MG-1, 2295 m, 63007, M38/3. L, Paratype, MG-1, 2264 m, 62950, J47/2. M, Holotype, MG-1, 2160.6 m, 62747, X46/2. N–O, *Camarozonotriletes filatoffii* Breuer *et al.*, 2007*c*. N, BAQA-1, 227.1 ft, 03CW110, B25. O, BAQA-1, 346.8 ft, 66796, E37/3.


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

Type locality and horizon. JNDL-4 core hole, sample 135.8 ft; Jauf Formation at Domat Al-Jandal, Saudi Arabia.

Diagnosis. A small *Brochotriletes* sculptured with small regular circular to sub-circular, evenly distributed foveolae. Exine laevigate.

Description. Amb is rounded sub-triangular to sub-circular. Laesurae are not always perceptible, simple, straight and extending to equator. Exine is 0.5–1.5 μm thick equatorially and distally, thinner on contact areas of proximal face. Contact areas are laevigate. Distal and proximo-equatorial regions are foveolate. Foveolae are circular or sub-circular in plan view, U-shaped in profile, 0.5–2 μm in diameter, *c.* 0.5 μm deep, and 1.5–2 μm apart. Exine between foveolae is laevigate.

Dimensions. 25(30)40 μm; 20 specimens measured.

Comparison. Brochotriletes rarus Arkhangelskaya, 1978 is larger and shows small foveolae, usually less than 1 μm in diameter. *B. robustus* (Scott and Rouse) McGregor, 1973 is ornamented between the foveae with discrete elements, which are interconnected by barely perceptible fine muri.

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

Brochotriletes tripapillatus sp. nov.
Figure 12E–H

Derivation of name. From *tripapillatus* (Latin), meaning sculptured with three papillae; refers to the proximal papillae.

Holotype. EFC O51 (Fig. 12F–G), slide 27127.

Paratype. EFC Q46/4 (Fig. 12E), slide 27274; A1-69 borehole, sample 1109 ft.

Type locality and horizon. A1-69 borehole, sample 1109 ft; Awaynat Wanin II Formation in A1-69, Libya.

Diagnosis. A *Brochotriletes* bearing three proximal sub-circular papillae in the interradial areas.

Description. Amb is sub-circular. Laesurae, simple, straight, three-quarters to nine-tenths of the amb radius in length. Patinate exine is 2–6.5 μm thick equatorially and distally, thinner on contact areas. Contact areas are laevigate to infragranular. Sub-circular papillae, 4–9 μm in diameter, are developed on each interradial region, one-third to one-half of the distance from apical pole to equator. Distal surface is foveolate. Foveolae are circular to elongate or roughly polygonal in plan view, 4–9 μm in diameter and 1.5–5 μm apart. Exine between foveolae is laevigate.

Dimensions. 45(55)61 μm, three specimens measured.

Comparisons. Although the specimen figured as *Brochotriletes* sp. cf. *B. foveolatus* Naumova, 1953 *in* McGregor and Playford (1992, pl. 4, fig. 11) seems to have proximal sculpture, the species described above is the only representative of *Brochotriletes* Naumova, 1939 ex Ishchenko, 1952 known that shows proximal papillae.

Occurrence. A1-69; Awaynat Wanin II Formation; *undulatus* to *catillus* zones.

Genus CAMAROZONOTRILETES Naumova, 1939 ex Naumova, 1953

Type species. Camarozonotriletes devonicus Naumova, 1953.

Camarozonotriletes asperulus sp. nov.
Figure 12I–M

Derivation of name. From *asperulus* (Latin), meaning slightly rough; refers to the sculpture of the proximo-equatorial and distal regions.

Holotype. EFC X46/2 (Fig. 12M), slide 62747.

Paratype. EFC J47/2 (Fig. 12L), slide 62950; MG-1 borehole, sample 2264 m.

Type locality and horizon. MG-1 borehole, sample 2160.6 m; Awaynat Wanin III Formation at Mechiguig, Tunisia.

Diagnosis. A large triangular *Camarozonotriletes* sculptured with minute, closely spaced grana or coni.

Description. Amb is triangular. The corners are rounded, while the margins are slightly convex, straight or sometimes slightly concave. Exine is thin. Laesurae are sometimes open, distinct, simple, straight and extending to the inner margin of the cingulum. Curvaturae are not easily distinguishable. Cingulum is generally 1–3 μm wide equatorially opposite the laesurae and commonly 4–10 μm interradially. Contact faces are laevigate. Proximo-equatorial and distal regions are infragranular, sculptured with minute closely spaced grana or coni, less than 0.5 μm in diameter and sometimes barely visible. Cingulum is slightly darker than central area.

Dimensions. 42(69)85 μm; 17 specimens measured.

Comparison. Camarozonotriletes minutus Naumova ex Chibrikova, 1959 and *C. antiquus* Kedo, 1955 are smaller and are described as shagreenate. *C. parvus* Owens, 1971 is smaller and more rounded. *C. laevigatus* McGregor and Camfield, 1982 is unsculptured and also smaller. *C. rugulosus* Breuer *et al.*, 2007*c*

is commonly smaller and finely rugulate distally, but ornamentation is sometimes barely visible. *Camarozonotriletes*? *concavus* Loboziak and Streel, 1989 is smaller and the width of cingulum is barely reduced opposite the laesurae, which calls its allocation to the genus *Camarozonotriletes* Naumova, 1939 ex Naumova, 1953 into question. *Leiotriletes bonitus* Cramer, 1966*b* has the same thickening of the interradial margins but shows proximal thickenings along the laesurae. In addition, it is laevigate and smaller (*c.* 50 µm).

Occurrence. A1-69; Awaynat Wanin II Formation; *incognita* to *lemurata* zones. MG-1; Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations; *rugulata-libyensis* to *langii-concinna* zones.

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

Camarozonotriletes filatoffii Breuer *et al.*, 2007*c*
Figures 12N–O, 13A–B

2007*c* *Camarozonotriletes filatoffii* Breuer *et al.*, p. 49, pl. 4, figs 14–23; pl. 5, fig. 1.

Dimensions. 24(30)35 µm; 36 specimens measured.

Comparisons. Camarozonotriletes (*Rotaspora*) *retiformis* (Hashemi and Playford) comb. nov. is distally reticulate but not ornamented with spines. In contrast, *Rotaspora rara* (Raskatova) Hashemi and Playford, 2005 has the same type of spines but is not distally reticulate.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4 and WELL-7; Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones.

Previous record. From upper Pragian – lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller *et al.* 2007).

Camarozonotriletes parvus Owens, 1971
Figure 13C–F

1966 *Camarozonotriletes* sp. cf. *C. breviculus* Ishchenko; McGregor and Owens, pl. 9, fig. 5.
1971 *Camarozonotriletes parvus* Owens, p. 40, pl. 11, figs 1–4.
1972 *Camarozonotriletes* n. sp. McGregor and Uyeno, pl. 2, fig. 2.
non 1989 *Camarozonotriletes parvus* Owens; Steemans, p. 112, pl. 26, figs 4–8, 56.
non 2007 *Camarozonotriletes parvus* Owens; Mendlowicz Mauller *et al.*, pl. 5, fig. 7.

Dimensions. 28(36)43 µm; 15 specimens measured.

Comparison. The specimens described as *C. parvus* Owens, 1971 *in* Steemans (1989) are misidentified; they show higher pila and bacula. This misidentified species needs to be redefined because it is the key species of the Pa Interval Zone of Streel *et al.* (1987). This biozone remains valid but not its name. *C. minutus* Naumova ex Chibrikova, 1959 and *C. antiquus* Kedo, 1955 are described as shagreenate. In all other respects, they appear identical to *C. parvus*. *C. laevigatus* McGregor and Camfield, 1982 strongly resembles the latter but is unsculptured.

Occurrence. S-462 and WELL-8; Jubah Formation; *lemurata-langii* Zone but some specimens from S-462 may be caved in older strata. A1-69; Awaynat Wanin II Formation; *undulatus* Zone. MG-1; Awaynat Wanin III Formation; *langii-concinna* Zone.

Previous records. From middle Givetian of Algeria (Moreau-Benoit *et al.* 1993) and Parnaíba Basin, Brazil (Breuer and Grahn 2011); upper Eifelian–Frasnian of Canada (McGregor and Owens 1966; Owens 1971; McGregor and Uyeno 1972; McGregor and Camfield 1982); lower Eifelian – upper Frasnian of Libya (Moreau-Benoit 1989); and Givetian of Morocco (Rahmani-Antari and Lachkar 2001).

Camarozonotriletes (*Rotaspora*) *retiformis* (Hashemi and Playford) comb. nov.
Figure 13G

1972 ?*Reticulatisporites* sp. Kemp, p. 115, pl. 55, fig. 9.
1992 *Camarozonotriletes* spp. McGregor and Playford (*pars*), pl. 18, fig. 4 (*non* figs 1–3, 5).
2005 *Rotaspora retiformis* Hashemi and Playford, p. 362, pl. 7, figs 13–17.

Dimensions. 25–27 µm; two specimens measured.

Remarks. Although *Camarozonotriletes* Naumova, 1939 ex Naumova, 1953 is considered by Hashemi and Playford (2005) as a junior synonym of *Rotaspora* Schemel, 1950, the present species is transferred to the genus *Camarozonotriletes*. The criterion to differentiate the two genera is the differing body and equatorial crassitude colour densities, but it seems unconvincing as a taxonomic distinction according to Hashemi and Playford (2005).

Comparison. ?*Reticulatisporites* sp. *in* Kemp (1972), which is distally reticulate but not ornamented with spines, is synonymous with *Camarozonotriletes* (*Rotaspora*) *retiformis* (Hashemi and Playford) comb. nov.

Occurrence. JNDL-3 and JNDL-4; Jauf Formation (Hammamiyat Member); *lindlarensis-sextantii* Zone.

Previous records. From Pragian of Antarctica (Kemp 1972; Troth *et al.* 2011); and Emsian of Adavale Basin, Australia (Hashemi and Playford 2005).

Camarozonotriletes rugulosus Breuer *et al.*, 2007*c*
Figure 13H–I

2007*c* *Camarozonotriletes rugulosus* Breuer *et al.*, p. 49, pl. 5, figs 2–9.

Dimensions. 37(46)59 μm; 30 specimens measured.

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

Camarozonotriletes sextantii McGregor and Camfield, 1976
Figure 13J–K

1976 *Camarozonotriletes sextantii* McGregor and Camfield, p. 12 (*cum syn.*), pl. 4, figs 13–14, 16–18.
1982 *Craspedispora arctica* McGregor and Camfield, p. 28, pl. 5, figs 5–9; text-fig. 38.

Dimensions. 31(39)59 μm; 21 specimens measured.

Remarks. Two populations can be distinguished in our material. Size ranges of North African and Saudi Arabian specimens are 31–36 and 37–59 μm, respectively.

Comparison. Craspedispora arctica McGregor and Camfield, 1982 is herein considered as synonymous of *Camarozonotriletes sextantii*. *Craspedispora arctica* has notably straight to convex interradial margins of the contact area, while those of *Camarozonotriletes sextantii* are convex to more commonly concave. This feature does not constitute a discriminatory criterion to erect two different species as the shape of interradial margins may be similar in both species. *Craspedispora arctica* strongly resembles the specimens from the North African population.

Occurrence. JNDL-1, JNDL-3, JNDL-4, WELL-4, WELL-5, WELL-6 and WELL-7; Jauf (Hammamiyat and Murayr members) and Jubah formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones. A1-69; Ouan-Kasa and Awaynat Wanin I formations; *lindlarensis-sextantii* to *annulatus-protea* zones. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *annulatus-protea* to *svalbardiae-eximius* zones.

Previous records. Camarozonotriletes sextantii is eponymous for the Emsian *annulatus-sextantii* Assemblage Zone of the Old Red Sandstone Continent and adjacent regions (Richardson and McGregor 1986). *C. sextantii* has an almost worldwide distribution extending from Emsian into the lower Eifelian. It has been reported from many parts of the world; e.g. Algeria (Moreau-Benoit *et al.* 1993), Belgium (Steemans 1989), Brazil (Mendlowicz Mauller *et al.* 2007), Canada (McGregor and Camfield 1976), Germany (Steemans 1989), Libya (Moreau-Benoit, 1989), Morocco (Rahmani-Antari and Lachkar 2001), Poland (Turnau *et al.* 2005) and Saudi Arabia (Steemans 1995; Al-Ghazi 2007).

Camarozonotriletes? concavus Loboziak and Streel, 1989
Figure 13L–P

1989 *Camarozonotriletes? concavus* Loboziak and Streel, p. 175, pl. 1, figs 13–15.

Description. Amb is sub-triangular to triangular with rounded corners and generally concave to almost straight interradial margins. Laesurae are simple, straight and extend to the inner margin of cingulum. Cingulum, 2–5 μm wide, is slightly reduced at corners, slightly darker than central area of the spore. Exine is proximally laevigate, equatorially and distally infragranulate to granulate giving a spongy appearance. Sculptural elements are less than 1 μm wide and high, often barely perceptible and closely distributed.

Dimensions. 32(40)48 μm; 23 specimens measured.

Remarks. Sometimes, two slightly separated walls can be detected. Reduction in the cingulum width at corners is not often very conspicuous in this species, and attribution to *Camarozonotriletes* Naumova, 1939 ex Naumova, 1953 is therefore questionable (Loboziak and Streel 1989).

FIG. 13. 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, *Camarozonotriletes filatoffii* Breuer *et al.*, 2007*c*. A, BAQA-1, 308.3 ft, 03CW112, U26. B, BAQA-1, 223.5 ft, 03CW109, F30. C–F, *Camarozonotriletes parvus* Owens, 1971. C, MG-1, 2178 m, 62997, Y33/2. D, MG-1, 2160.6 m, 62747, J31. E, MG-1, 2180 m, 62971, M42/1. F, MG-1, 2178 m, 62997, P38/3. G, *Camarozonotriletes* (*Rotaspora*) *retiformis* (Hashemi and Playford) comb. nov. JNDL-4, 163.3 ft, 68625, U60. H–I, *Camarozonotriletes rugulosus* Breuer *et al.*, 2007*c*. H, JNDL-1, 172.7 ft, PPM007, R28/1. I, JNDL-1, 156.0 ft, 60840, V47/4. J–K, *Camarozonotriletes sextantii* McGregor, 1973. J, JNDL-4, 37.1 ft, 03CW184, R42. K, MG-1, 2639 m, 62779, M36/3. L–P, *Camarozonotriletes? concavus* Loboziak and Streel, 1989. L, A1-69, 1486 ft, 26977, R46. M, A1-69, 1483 ft, 26995, G38. N, A1-69, 1483 ft, 26995, B54. O, A1-69, 1486 ft, 26977, P40/3. P, WELL-1, 16354.0 ft, 61959, M36/1. Q–V, *Chelinospora carnosa* sp. nov. Q, BAQA-1, 395.2 ft, 03CW121, R38. R, Paratype, BAQA-2, 134.4 ft, 03CW137, P40/1. S, Holotype, BAQA-1, 395.2 ft, 62277, K48/2. T, BAQA-1, 395.2 ft, 62274, M49/4. U, BAQA-2, 133.0 ft, 03CW136, E30/1. V, BAQA-2, 133.0 ft, 03CW136, V42.


A
B
E
F
G
C
D
H
I
J
K
P
O
N
M
L
S
Q
R
T
U
V

Comparison. Among sculptured species, *C. antiquus* Kedo, 1955 has convex interradial margins. *C. parvus* Owens, 1971 has the cingulum clearly reduced in front of the laesurae and a more rounded general amb. *C. pusillus* Naumova ex Chibrikova, 1959 has ornamentation up to 1.5 μm high.

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

Previous records. From upper Eifelian–Frasnian of Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003; Breuer and Grahn 2011).

Genus CHELINOSPORA Allen, 1965

Type species. *Chelinospora concinna* Allen, 1965.

Chelinospora carnosa sp. nov.
Figure 13Q–V

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

Holotype. EFC K48/2 (Fig. 13S), slide 62277.

Paratype. EFC P40/1 (Fig. 13R), slide 03CW137; BAQA-2 core hole, sample 134.4 ft.

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

Diagnosis. A thick-walled *Chelinospora* sculptured with broad reticulum and large verrucae showing constrictions between each pair of junctions.

Description. Amb is sub-triangular to triangular. Laesurae are straight and simple, but often not observed because of the thinness of proximal exine, frequently torn. Exine is laevigate to infragranulate, 2–7 μm equatorially thick, thinner proximally. Patina is sculptured with broad reticulum. Muri are 2–7 μm wide and 1–4 μm high. At junctions, muri commonly widen into large rounded or flat-topped verrucae, 4–9 μm wide, up to 8 μm high, sometimes fused together. Lumina, polygonal or irregular in plan view, are 2–10 μm in greatest diameter. Muri show constrictions between each pair of junctions.

Dimensions. 37(55)69 μm; 16 specimens measured.

Comparison. The broad muri with distinct constrictions and more or less polygonal lumina distinguish this species from other species of *Chelinospora* Allen, 1965.

Occurrence. BAQA-1, BAQA-2 and WELL-7; Jauf Formation (Sha'iba to Subbat members); *papillensis-baqaensis* to *ovalis* zones.

Chelinospora concinna Allen, 1965
Figure 14A–C

? 1964 *Knoxisporites reticulatus* Vigran, p. 22, pl. 1, figs 10–12; pl. 2, figs 8–9.
1965 *Chelinospora concinna* Allen, p. 728, pl. 101, figs 12–20.

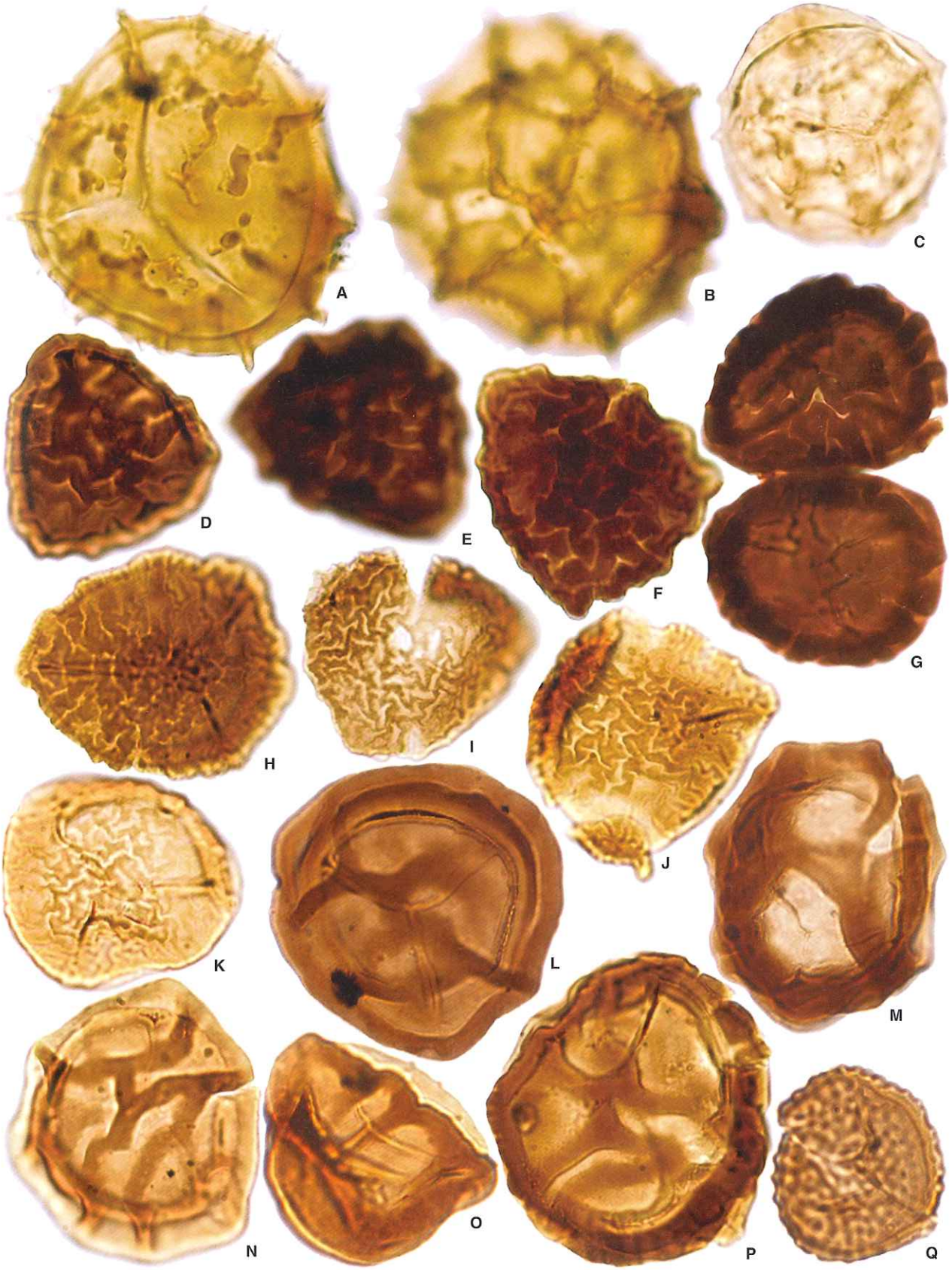
Dimensions. 36(51)65 μm; 22 specimens measured.

Remarks. There is considerable variation in width of the patina, thickness of muri and size of lumina.

Occurrence. S-462; Jubah Formation; *langii-concinna* Zone. A1-69; Awaynat Wanin II Formation; *langii-concinna* Zone. MG-1; Awaynat Wanin II and Awaynat Wanin III formations; *langii-concinna* Zone.

Previous records. *Chelinospora concinna* is eponymous for the upper Givetian – lower Frasnian TCo Oppel Zone of Western Europe (Streel *et al.* 1987). *C. concinna* has an almost worldwide distribution extending from Givetian into Frasnian and has been reported from many parts of the world; e.g. Bolivia (Perez-Leyton 1990), Brazil (Loboziak *et al.* 1988; Breuer and Grahn 2011), Canada (McGregor and Uyeno 1972), France (Brice *et al.* 1979; Loboziak and Streel 1980, 1988), Greenland (Friend *et al.* 1983; Marshall and Hemsley 2003), Spitsbergen, Norway (Vigran 1964; Allen 1965), Poland (Turnau 1996; Turnau and Racki 1999), Portugal (Lake *et al.* 1988), Russian Platform (Avkhimovitch *et al.* 1993; Arkhangelskaya and

FIG. 14. 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, *Chelinospora concinna* Allen, 1965. A–B, S-462, 1810–1815 ft, 63256, S50/1. C, MG-1, 2205 m, 62597, M43. D–G, *Chelinospora condensata* sp. nov. D, Holotype, BAQA-1, 371.1 ft, 03CW118, R48. E, BAQA-1, 371.1 ft, 03CW118, H42/1. F, Paratype, BAQA-1, 371.1 ft, 03CW118, H27/3. G, BAQA-1, 219.2 ft, 03CW107, G31/2. H–K, *Chelinospora densa* sp. nov. H, Paratype, BAQA-2, 50.8 ft, 03CW127, R23/4. I, BAQA-1, 408.3 ft, 03CW124, F29/2. J, BAQA-1, 416.6 ft, 03CW125, P30. K, Holotype, BAQA-2, 54.8 ft, 03CW129, P-Q36. L–P, *Chelinospora laxa* sp. nov. L, Holotype, JNDL-4, 499.1 ft, 68704, D27/1. M, BAQA-2, 50.8 ft, 66813, G54/4. N, Paratype, BAQA-2, 64.5 ft, 03CW132, X29. O, BAQA-2, 64.5 ft, 66818, V53/1. P, BAQA-2, 54.8 ft, 03CW129, U28/4. Q, *Chelinospora retorrida* Turnau, 1986. BAQA-2, 134.4 ft, 66826, H41/3.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q

Turnau 2003) and Scotland (Marshall and Allen 1982; Marshall *et al.* 1996).

Chelinospora condensata sp. nov.
Figure 14D–G

Derivation of name. From *condensatus* (Latin), meaning dense; refers to the colour of the body and the distal sculpture.

Holotype. EFC R48 (Fig. 14D), slide 03CW118.

Paratype. EFC H27/3 (Fig. 14F), slide 03CW118; BAQA-1 core hole, sample 371.1 ft.

Type locality and horizon. BAQA-1 core hole, sample 371.1 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A thick-walled *Chelinospora* sculptured with brain-like convoluted muri almost adjoining.

Description. Amb is sub-circular to triangular. Laesurae are straight, simple and extending to the inner edge of patina. Exine is laevigate to infragranulate, 3–5 μm thick equatorially, thinner proximally. Contact areas are laevigate. Patina is sculptured with brain-like convoluted muri almost adjoining, 1.5–4 μm wide and commonly less than 1 μm apart (rarely up to 2 μm). Muri become radially oriented over the equatorial and subequatorial regions.

Dimensions. 36(47)68 μm; 16 specimens measured.

Comparison. Chelinospora densa sp. nov. and *C. hemiesferica* (Cramer and Díez) Richardson *et al.*, 2001 have narrower distal muri. *C. vulgata* sp. nov. and *Chelinospora* cf. *hemiesferica* (Cramer and Díez) Richardson *et al.*, 2001 have the same muri, but these are loosely spaced. All these convolute forms of *Chelinospora* Allen, 1965 are not always distinguished easily. They may derived from a group of closely related plants and can be grouped into the *C. vulgata* Morphon defined here (Table 1).

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

Chelinospora densa sp. nov.
Figure 14H–K

Derivation of name. From *densus* (Latin) meaning dense; refers to the distal sculpture.

Holotype. EFC P-Q36 (Fig. 14K), slide 03CW129.

Paratype. EFC R23/4 (Fig. 14H), slide 03CW127; BAQA-2 core hole, sample 50.8 ft.

Type locality and horizon. BAQA-2 core hole, sample 54.8 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Chelinospora* sculptured with numerous, closely spaced, narrow brain-like convoluted muri.

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple or labrate (up to 2 μm wide) and extend to the inner edge of patina. Exine is laevigate or infragranulate, 3–7 μm equatorially thick, thinner proximally. Contact areas are laevigate, sometimes torn. Patina is sculptured with brain-like convoluted muri, 0.5–2 μm wide and up to 1.5 μm apart. Muri become radially oriented over the equatorial and subequatorial regions.

Dimensions. 37(47)62 μm; 10 specimens measured.

Comparison. The spores may be two-layered, and on some specimens some localized detachment of the outer layer is apparent (Fig. 14J) as in *C. hemiesferica* (Cramer and Díez) Richardson *et al.*, 2001. The latter, however, show a membranous curvatural zone bearing well-pronounced radial extensions of the distal muri. *C. vulgata* sp. nov. and *Chelinospora* cf. *hemiesferica* (Cramer and Díez) Richardson *et al.*, 2001 have wider muri.

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

Chelinospora laxa sp. nov.
Figure 14L–P

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

Holotype. EFC D27/1 (Fig. 14L), slide 68704.

Paratype. EFC X29 (Fig. 14N), slide 03CW132; BAQA-1 core hole, sample 64.5 ft.

Type locality and horizon. JNDL-4 core hole, sample 499.1 ft; Jauf Formation at Domat Al-Jandal, Saudi Arabia.

Diagnosis. A *Chelinospora* sculptured with loosely spaced broad muri, forming an irregular reticulum with broad lumina.

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple and extend to the inner edge of patina. Exine is laevigate to infragranulate, 3–6 μm equatorially thick, thinner proximally. Contact areas are laevigate. Patina is sculptured with convoluted muri widely distributed, 3–5 μm wide and from 1 to more than 10 μm apart. They form an irregular reticulate pattern.

Dimensions. 40(54)70 μm; 12 specimens measured.

Remarks. Depending on compression, specimens may give the appearance of having a zona (Fig. 14N).

Comparison. *Chelinospora cassicula* Richardson and Lister, 1969 and *C. lavidensis* Richardson *et al.*, 2001 show the same kind of irregular reticulate pattern but the former has narrower, high and fold-like muri and the latter is sculptured with narrower, low muri (1 μm or less wide). *C. vulgata* sp. nov. and *Chelinospora* cf. *hemiesferica* (Cramer and Díez) Richardson *et al.*, 2001 have narrower distal muri which are closely spaced and more numerous. *Chelinospora laxa* sp. nov. represents an end-member of the *C. vulgata* Morphon (Table 1).

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

Chelinospora retorrida Turnau, 1986
Figure 14Q

1969 ?*Chelinospora* sp. A Richardson and Lister, p. 243, pl. 41, fig. 15.
? 1983 *Synorisporites* cf. *dittonensis*; Rodriguez, pl. 1, fig. 13.
1986 *Chelinospora retorrida* Turnau, p. 339, pl. 1, figs 1–4.
1989 *Chelinospora retorrida* Turnau; Steemans, p. 118, pl. 29, figs 12–17.

Dimensions. 33–35 μm; two specimens measured.

Remarks. Steemans (1989) noted the presence of inspissations, rarely evident, on the interradial margins of the proximal face on 50 per cent of the specimens of *C. retorrida*. These could represent different varieties of *C. retorrida* (Steemans 1989), although this feature was not mentioned by Turnau (1986).

Comparison. ?*Chelinospora* sp. A *in* Richardson and Lister (1969) is similar to *C. retorrida* Turnau, 1986. ?*Archaeozonotriletes dubius* Richardson and Lister, 1969 has muri that represent an internal structure. *C. hemiesferica* (Cramer and Díez) Richardson *et al.*, 2001 is sculptured with closely spaced narrow muri, geniculate in plan, becoming radially oriented over the equatorial and subequatorial regions. *Chelinospora densa* sp. nov. is larger and has a thicker exine.

Occurrence. BAQA-2; Jauf Formation (Sha'iba Member); *papillensis-baqaensis* to *ovalis* zones.

Previous records. From lower Lochkovian – upper Pragian of Belgium (Steemans 1989); Lochkovian of Canada (Burden *et al.* 2002); upper Lochkovian of France, Germany and Romania (Steemans 1989); Lochkovian of Iran (Ghavidel-Syooki 2003), Saudi Arabia (Steemans 1995) and Wales (Richardson and Lister 1969); middle Přídolí of Libya (Rubinstein and Steemans 2002); and Lochkovian–Pragian of Poland (Turnau 1986; Turnau *et al.* 2005).

Chelinospora timanica (Naumova) Loboziak and Streel, 1989
Figure 15A–B

1953 *Archaeozonotriletes timanicus* Naumova, p. 81, pl. 12, fig. 14.
? 1962 *Convolutispora fromensis* Balme and Hassell, p. 8, pl. 1, figs 14–16.
? 1959 *Archaeozonotriletes polymorphus* Naumova var. *takatinicus* Chibrikova, p. 58, pl. 7, figs 2–3.
? 1962 *Archaeozonotriletes timanicus* Naumova var. *radiatus* Chibrikova, p. 412, pl. 7, fig. 1.
? 1965 *Convolutispora tegula* Allen, p. 705, pl. 97, figs 4–8.
1965 *Archaeozonotriletes ignoratus* Naumova; Hemer, pl. 2.
1965 *Archaeozonotriletes timanicus* Naumova var. no 1; Nazarenko, pl. 1, figs 49–50.
? 1965 *Tholisporites ancylus* Allen, p. 724 (*pars*), pl. 101, fig. 5 (*non* figs 1–4, 6–7).
? 1966 *Archaeozonotriletes laticolaris* Mikhailova, p. 209, pl. 3, fig. 4.
1982 *Archaeozonotriletes timanicus* Naumova; McGregor and Camfield, p. 20, pl. 3, figs 13–15.
1989 *Chelinospora timanica* (Naumova) Loboziak and Streel, p. 175, pl. 2., figs 8–9.
1992 *Archaeozonotriletes timanicus* Naumova; McGregor and Playford, pl. 4, figs 3–4.

Dimensions. 43(54)74 μm; 54 specimens measured.

Remarks. Numerous specimens are allocated to this species which may include several species defined in the literature and probably belonging to genera other than *Chelinospora* Allen, 1965. These forms are very variable and are not easily distinguishable. In such forms, it is difficult to determine whether the character of sculptural elements are positive or negative because variation between the two configurations seems to be continuous. Intergradations from *C. timanica* to other species of *Convolutispora* Hoffmeister *et al.*, 1955 genus most likely exist.

Comparison. The diagnosis of *Convolutispora fromensis* Balme and Hassell, 1962 is similar to that of *Chelinospora timanica*, but illustrations do not allow a direct comparison. *C. timanica* is difficult to distinguish from *Convolutispora tegula* Allen, 1965. The main difference is that the patina is dissected into elements (negative) in *Chelinospora timanica* while exine of *Convolutispora tegula* is sculptured with positive elements. The two characters are distinguishable with difficulty (see above). *C. tegula* may thus be included in the present taxon. *C. florida* Hoffmeister *et al.*, 1955 has a more extensively anastomosing muroid pattern, and wider lumina. *C. uistatas* Playford, 1962 has similar sculpture, but is much larger. *Convolutispora crassata*? (Naum-

ova) McGregor and Camfield, 1982 is not patinate. *C. subtilis* Owens, 1971 possesses narrower convolutae. *Archaeozonotriletes asymmetricus* Panshina, 1971 appears to be of similar basic construction but its large, flat, irregular tubercules are larger towards the equator where they are commonly fused with one another. Extreme forms of spores with convolute and verrucose sculpture, including notably species of *Convolutispora* Hoffmeister *et al.*, 1955, *Dibolisporites uncatus* (Naumova) McGregor and Camfield, 1982 and *Verrucosisporites scurrus* (Naumova) McGregor and Camfield, 1982, may intergrade with *Chelinospora timanica*. Indeed, all these species are morphologically very close and occur mostly in the same Givetian strata.

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

Previous records. From middle Givetian – lower Frasnian of Australia (Grey 1991; Hashemi and Playford 2005); upper Givetian –Frasnian of Bolivia (Perez-Leyton 1990); lower Givetian – lowermost Famennian of Brazil (Loboziak *et al.* 1988; Loboziak *et al.* 1992*b*; Melo and Loboziak 2003); Eifelian–lower Givetian of Canada (McGregor and Camfield 1982); upper Eifelian–Givetian of Germany (Loboziak *et al.* 1990); middle Givetian of Greenland (Friend *et al.* 1983; Marshall and Hemsley 2003); Givetian of Poland (Turnau 1996; Turnau and Racki 1999); Givetian–lower Frasnian of Russian Platform (Avkhimovitch *et al.* 1993); and uppermost Givetian–lower Frasnian of Scotland (Marshall *et al.* 1996).

Chelinospora vulgata sp. nov.
Figure 15C–G

Derivation of name. From *vulgatus* (Latin), meaning common; refers to its abundance in the lower Jauf Formation.

Holotype. EFC M-N41 (Fig. 15E), slide 03CW118.

Paratype. EFC W39/3 (Fig. 15D), slide 03CW118; BAQA-1 core hole, sample 371.1 ft.

Type locality and horizon. BAQA-1 core hole, sample 371.1 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A large *Chelinospora* sculptured with brain-like well-defined convoluted muri. Exine infragranulate.

Description. Amb is circular to sub-triangular. Laesurae are straight, simple or accompanied by labra, up to 3 μm in overall width, extending to the inner edge of patina. Exine is infragranulate, 2–8 μm thick equatorially, thinner proximally. Contact areas are laevigate, sometimes torn. Patina is sculptured with brain-like convoluted muri, 1–4 μm wide and 1–3 μm apart. Muri become radially oriented over the equatorial and subequatorial regions.

Dimensions. 43(55)71 μm; 17 specimens measured.

Comparison. Chelinospora laxa sp. nov. has fewer muri and *C. condensata* sp. nov. has the same type of muri, but these are more densely spaced. All these convolute forms of *Chelinospora* Allen, 1965 may be included in the *C. vulgata* Morphon (Table 1). They were probably derived from a group of closely related plants. *C. densa* sp. nov. and *C. hemiesferica* (Cramer and Díez) Richardson *et al.*, 2001 have narrower distal muri which are closely spaced. Nevertheless, the two species may intergrade within the same morphon.

Occurrence. BAQA-1, BAQA-2, JNDL-4 and WELL-3; Jauf Formation (Sha'iba to Subbat members); *papillensis-baqaensis* to *ovalis-biornatus* zones.

Chelinospora? sp. 1
Figure 15H–I

Description. Amb is circular to sub-circular. Laesurae are simple, straight, three-quarters to full central area radius in length. Contact areas are thinner and support a sparse ornament of broad rugulae and muri 2–4 μm wide. Patina, *c.* 3 μm thick equatorially and distally, is sculptured with irregularly distributed broad rounded muri, 2–5 μm wide and high, forming an imperfect to perfect reticulum. Lumina are irregular in plan view, commonly 3–10 μm in greatest diameter.

Dimensions. 49(52)56 μm; three specimens measured.

Remarks. A doubt remains about the assignment of this form to the genus *Chelinospora* Allen, 1965 as the contact areas show a sparse ornamentation of rugulae.

Comparison. Chelinospora concinna Allen, 1965 has narrower muri, larger lumina and commonly a thicker patina. *C. timanica* (Naumova) Loboziak and Streel, 1989 has also a thicker patina with a very irregular ornament pattern.

FIG. 15. 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, *Chelinospora timanica* (Naumova) Loboziak and Streel, 1989. A, MG-1, 2476 m, 63016, U36. B, MG-1, 2178 m, 62996, Q43. C–G, *Chelinospora vulgata* sp. nov. C, BAQA-2, 133.0 ft, 03CW136, J52. D, Paratype, BAQA-1, 371.1 ft, 03CW118, W39/3. E, Holotype, BAQA-1, 371.1 ft, 03CW118, M-N41. F, BAQA-1, 376.4 ft, 03CW119, J49. G, BAQA-1, 366.9 ft, 03CW117, J38/4. H–I, *Chelinospora*? sp. 1. H, A1-69, 971 ft, 62369, P44. I, A1-69, 971 ft, 62641, U52. J, *Cirratriradites*? *diaphanus* Steemans, 1989. BAQA-2, 50.2 ft, 03CW126, S26/2. K, *Clivosispora verrucata* McGregor, 1973 var. *convoluta* McGregor and Camfield, 1976. JNDL-4, 316.4 ft, 03CW244, K43/2. L–M, *Clivosispora verrucata* McGregor, 1973 var. *verrucata* McGregor and Camfield, 1976. L, BAQA-1, 395.2 ft, 66807, G39. M, JNDL-4, 87.2 ft, 03CW195, F34/1.


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

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

Genus CIRRATRIRADITES Wilson and Coe, 1940

Type species. *Cirratriradites maculatus* Wilson and Coe, 1940.

Cirratriradites? diaphanus Steemans, 1989
Figure 15J

1981 *Cirratriradites* sp. A Steemans, p. 53.
1981 *Cirratriradites* sp. A *in* Steemans; Streel *et al.*, pl. 3, figs 10–11.
1989 *Cirratriradites diaphanus* Steemans, p. 119, pl. 30, figs 4–9.
2006 Unidentified zonate spores Wellman, pl. 19, fig. d.

Dimensions. 46(58)71 μm; 10 specimens measured.

Remarks. There is some doubt about the allocation of this species to the genus *Cirratriradites* Wilson and Coe, 1940 because no distal foveolae are observed in the present population.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4, WELL-5, WELL-6 and WELL-7; Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Previous records. From upper Lochkovian – upper Pragian of Belgium (Steemans 1989); Lochkovian–lower Emsian of Brazil (Melo and Loboziak 2003; Grahn *et al.* 2005; Mendlowicz Mauller *et al.* 2007); upper Lochkovian – upper Pragian of Germany (Steemans 1989); middle Pragian – middle Emsian of Luxembourg (Steemans *et al.* 2000*a*); upper Lochkovian (Steemans 1989); and upper Pragian – ?lowermost Emsian of Scotland (Wellman 2006).

Genus CLIVOSISPORA Staplin and Jansonius, 1964

Type species. *Clivosispora variabilis* Staplin and Jansonius, 1964.

Clivosispora verrucata McGregor, 1973 var. *convoluta* McGregor and Camfield, 1976
Figure 15K

1976 *Clivosispora verrucata* McGregor var. *convoluta* McGregor and Camfield, p. 15, pl. 2, figs 13–21.

Dimensions. 36(44)63 μm; 11 specimens measured.

Comparison. Although ornamentation of *Chelinospora poecilomorpha* (Richardson and Ioannides) Richardson *et al.*, 2001 could be comparable, it exhibits muri produced by the terminal fusion of verrucae, circular, sub-circular, sub-polygonal to irregular in plan view. This species is also distinguished by its smaller size. *Clivosispora verrucata* var. *convoluta* seems to intergrade with *Clivosispora verrucata* McGregor, 1973 var. *verrucata* McGregor and Camfield, 1976.

Occurrence. BAQA-1, BAQA-2, JNDL-4, WELL-2, WELL-4 and WELL-7; Jauf Formation (Sha'iba to Subbat members); *papillensis-baqaensis* to *ovalis-biornatus* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone.

Previous records. From lower Přídolí – lower Emsian of Amazon and Paraná basins, Brazil (Mendlowicz Mauller *et al.* 2007; Steemans *et al.* 2008); Pragian–Emsian of Canada (McGregor and Camfield 1976) and Iran (Ghavidel-Syooki 2003); upper Pragian of Armorican Massif, France (Le Hérissé 1983); Ludlow or Přídolí of Libya (Rubinstein and Steemans 2002); upper Pragian – Emsian of Morocco (Rahmani-Antari and Lachkar 2001); and upper Pragian – ?lowermost Emsian of Scotland (Wellman 2006).

Clivosispora verrucata McGregor, 1973 var. *verrucata* McGregor and Camfield, 1976
Figure 15L–M

1954 Spore type C6 Radforth and McGregor, pl. 1, fig. 35.
1966 cf. *Clivosispora* McGregor and Owens, pl. 3, figs 16–17.
? 1968 Trilete verruquée sp. 1 Jardiné and Yapaudjian, pl. 1, fig. 23.
1970 *Clivosispora* sp. McGregor *et al.*, pl. 1, figs 28–29.
1973 *Clivosispora verrucata* McGregor, p. 54, pl. 7, figs 4–5, 10.
1976 *Clivosispora verrucata* McGregor var. *verrucata*; McGregor and Camfield, p. 15, pl. 3, figs 11–14.
non 1981 *Clivosispora verrucata* McGregor var. *verrucata*; Gao Lianda, pl. 2, fig. 3.

Dimensions. 36(43)55 μm; 16 specimens measured.

Comparison. This variety differs from *C. verrucata* McGregor, 1973 var. *convoluta* McGregor and Camfield, 1976 in that the distal sculpture consists of convolute muri. The two varieties are otherwise alike, and intergrade. *Chelinospora poecilomorpha* (Richardson and Ioannides) Richardson *et al.*, 2001 is distinguished by the terminal fusion of comparable verrucae that produce muri sometimes anastomosing in places. It is also smaller and the simple sutures are often barely perceptible because of its very thin proximal face. *Synorisporites verrucatus* Richardson and Lister, 1969 has a narrower cingulum and smaller verrucae.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-4, WELL-2, WELL-3, WELL-4, WELL-5, WELL-6 and WELL-7; Jauf Formation; *papillensis-baqaensis* to *annulatus-protea* zones.

Previous records. From lower Přídolí of Amazon Basin, Brazil (Steemans *et al.* 2008); Pragian–Emsian of Canada (McGregor and Owens 1966; McGregor 1973; McGregor and Camfield 1976) and Iran (Ghavidel-Syooki 2003); and uppermost Pragian – ?lowermost Emsian of Scotland (Wellman 2006).

Genus CONCENTRICOSISPORITES Rodriguez, 1983

Type species. *Concentricosisporites sagittarius* (Rodriguez) Rodriguez, 1983.

Concentricosisporites sagittarius (Rodriguez) Rodriguez, 1983
Figure 16A–C

1978*a* *Stenozonotriletes sagittarius* Rodriguez, p. 219, pl. 1, fig. 7.
1983 *Concentricosisporites sagittarius* (Rodriguez); Rodriguez, p. 36, pl. 3, fig. 15.

Dimensions. 28(38)47 μm; 10 specimens measured.

Occurrence. BAQA-1, BAQA-2, JNDL-4 and WELL-7; Jauf Formation (Sha'iba to Subbat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones. MG-1; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone.

Previous records. From upper Lochkovian of Solimões Basin, Brazil (Rubinstein *et al.* 2005); middle Přídolí of Libya (Rubinstein and Steemans 2002); upper Ludfordian – lower Lochkovian (Rodriguez 1978*a*, *b*; Richardson *et al.* 2001); and middle–upper Ludfordian of Pennsylvania, USA (Beck and Strother 2008).

Genus CONTAGISPORITES Owens, 1971

Type species. *Contagisporites optivus* (Chibrikova) Owens, 1971.

Contagisporites optivus (Chibrikova) Owens, 1971
Figures 16D, 47A–C

1959 *Archaeozonotriletes optivus* Chibrikova, p. 60, pl. 7, fig. 9.
1960 *Retusotriletes* sp. Taugourdeau-Lantz, p. 145, pl. 1, fig. 5.
1962 *Archaeozonotriletes optivus* var. *vorobjevensis* Chibrikova, p. 430, pl. 2, fig. 6.
1964 *Biharisporites spitsbergensis* Vigran, p. 12, pl. 2, figs 1–4.
1965 *Calyptosporites optivus* (Chibrikova) Allen, p. 736, pl. 104, figs 1–4.
1966 *Archaeozonotriletes* cf. *A. optivus* var. *vorobjevensis* Chibrikova; McGregor and Owens, pl. 16, figs 3–4.
1966 *Archaeozonotriletes optivus* Chibrikova; McGregor and Owens, pl. 17, fig. 6.
1967 *Rhabdosporites cuvillieri* Taugourdeau-Lantz, p. 54, pl. 3, figs 1–6.
1971 *Contagisporites optivus* (Chibrikova) var. *optivus* Owens, p. 52, pl. 16, figs 1–3.
1971 *Contagisporites optivus* var. *vorobjevensis* (Chibrikova) Owens, p. 53, pl. 16, figs 4–6.
1987 Megaspore (*Biharisporites*) of *Tanaitis furchihasta* Krassilov *et al.*, p. 173, pl. 4, figs 1–2; pl. 7, figs 1–2.

Dimensions. 200(223)250 μm; seven specimens measured.

Remarks. Although *C. optivus* var. *vorobjevensis* (Chibrikova) Owens, 1971 differs mainly from *C. optivus* (Chibrikova) var. *optivus* Owens, 1971 by its coarser, low verrucose or blunt pointed conate elements, both are grouped here together because they appear to intergrade and the difference is often impossible to discern under a transmitted light microscope. It is the first time that this megaspore is observed on the Gondwana (de Ville de Goyet *et al.* 2007; Steemans *et al.* 2011*b*).

Comparison. *Contagisporites optivus* (Chibrikova) Owens, 1971 differs from *Rhabdosporites langii* (Eisenack) Richardson, 1960 by its larger size, well-developed curvaturae and elevated labra.

Occurrence. S-462; Jubah Formation; *lemurata-langii* to *triangulatus-catillus* zones, although some specimens may be slightly caved. A1-69; Awaynat Wanin II Formation; *undulatus* to *triangulatus-catillus* zones.

Previous records. *Contagisporites optivus* 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). *C. optivus* has been mainly recorded from Givetian–Frasnian from Euramerica; e.g. Canada (McGregor and Owens 1966; Owens 1971; McGregor and Uyeno 1972), France (Brice *et al.* 1979; Loboziak and Streel 1980, 1988; Loboziak *et al.* 1983), Greenland (Friend *et al.* 1983; Marshall and Hemsley 2003), Spistsbergen, Norway (Vigran 1964; Allen 1965), Poland (Turnau 1996; Turnau and Racki 1999), Russian Platform (Avkhimovitch *et al.* 1993; Arkhangelskaya and Turnau 2003) and Scotland (Marshall *et al.* 1996; Marshall 2000). Outside Euramerica, it has only been reported from Givetian assemblages of Spain (Cramer 1969), Libya (de Ville de Goyet 2007; Steemans *et al.* 2011*b*) and China, which was originally claimed as Eifelian by Gao Lianda (1981).

Genus CONVOLUTISPORA Hoffmeister *et al.*, 1955

Type species. *Convolutispora florida* Hoffmeister *et al.*, 1955.

Convolutispora subtilis Owens, 1971
Figure 16E–G

1971 *Convolutispora subtilis* Owens, p. 35, pl. 9, figs 3–6.
1987 *Chelinospora* sp. Burjack *et al.*, pl. 2, fig. 1.
1988 *Chelinospora paravermiculata* Loboziak *et al.*, p. 355, pl. 3, figs 7–13.

Dimensions. 37(49)62 μm; seven specimens measured.

Comparison. *Chelinospora paravermiculata* Loboziak *et al.*, 1988 is herein considered as synonymous with *Convolutispora subtilis*.

Occurrence. MG-1; Awaynat Wanin II and Awaynat Wanin III formations; *undulatus* to *langii-concinna* zones.

Previous records. From Givetian–lower Frasnian of Paraná Basin, Brazil (Loboziak *et al.* 1988); upper Eifelian–Frasnian of Canada (Owens 1971; McGregor and Camfield 1982); Frasnian of Iran (Ghavidel-Syooki 2003); Givetian of Poland (Turnau 1996; Turnau and Racki 1999); lower Givetian of Russian Platform (Avkhimovitch *et al.* 1993); ?Eifelian–Givetian of Saudi Arabia (PB, pers. obs.); and uppermost Givetian – lower Frasnian of Scotland (Marshall *et al.* 1996).

Genus CORONASPORA Rodriguez emend. Richardson *et al.*, 2001

Type species. *Coronaspora mariae* Rodriguez, 1978*a*.

Coronaspora inornata sp. nov.
Figure 16H–M

Derivation of name. From *inornatus* (Latin), meaning without ornament; refers to the absence of distal sculptural elements.

Holotype. EFC V27 (Fig. 16I), slide 68704.

Paratype. EFC E34/4 (Fig. 16J), slide 68697; JNDL-4 core hole, sample 471.6 ft.

Type locality and horizon. JNDL-4 core hole, sample 499.1 ft; Jauf Formation at Domat Al-Jandal, Saudi Arabia.

Diagnosis. A *Coronaspora* with a broad kyrtome and a laevigate distal surface.

Description. Amb is circular to sub-triangular. Laesurae are straight, simple and extending to the inner edge of crassitude, which is invaginated at the radial apices. Equatorial crassitude is smooth to irregularly thickened, 3–6 μm wide. Proximal region is laevigate and bears a broad kyrtome on each interradial area. Kyrtome is distinct, formed by raised ridges (more or less semi-circular in profile) paralleling the laesurae and increasing in width (up to 8.5 μm wide) towards the spore apex in the interradial areas. Distal surface is laevigate.

Dimensions. 32(37)45 μm; 18 specimens measured.

Comparison. Differs from other members of the genus, with the exception of *C. primordiale* (Rodriguez) Rodriguez, 1983 in having a laevigate distal surface. *C. primodiale* has thick labra.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4 and WELL-7; Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones.

Genus CORYSTISPORITES Richardson, 1965

Type species. *Corystisporites multispinosus* Richardson, 1965.

Corystisporites collaris Tiwari and Schaarschmidt, 1975
Figures 16N, 47D–F

1975 *Corystisporites collaris* Tiwari and Schaarschmidt, p. 28, pl. 6, figs 2–5; text-fig. 18.

Dimensions. 72(74)77 μm; three specimens measured.

Comparison. *Corystisporites multispinosus* Richardson, 1965 has smaller regular spines, which do not posses any collars.

FIG. 16. 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, *Concentricosisporites sagittarius* (Rodriguez) Rodriguez, 1983. A, BAQA-1, 395.2 ft, 03CW121, H48. B, BAQA-2, 57.2 ft, 66817, X42/4. C, BAQA-1, 346.8 ft, 66795, V47/2. D, *Contagisporites optivus* (Chibrikova) Owens, 1971, magnification ×500. S-462, 2260–2265 ft, 63281, Q28/2. E–G, *Convolutispora subtilis* Owens, 1971. E, MG-1, 2264 m, 62950, J35. F, MG-1, 2160.6 m, 62747, X26. G, MG-1, 2181.2 m, 62525, V42. H–M, *Coronaspora inornata* sp. nov. H, JNDL-4, 495.2 ft, 68702, D26. I, Holotype, JNDL-4, 499.1 ft, 68704, V27. J, Paratype, JNDL-4, 471.6 ft, 68697, E34/4. K, JNDL-4, 306.3 ft, 68665, F26/4. L, BAQA-1, 406.0 ft, 66809, F39. M, WELL-7, 13738.5 ft, 62322, S37/2. N, *Corystisporites collaris* Tiwari and Schaarschmidt, 1975. A1-69, 1109 ft, 27274, O45/1. O, *Corystisporites undulatus* Turnau, 1996, magnification ×500. A1-69, 1277 ft, 62636, E35/3.


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

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

Previous records. From lower Eifelian – lower Givetian of Germany (Tiwari and Schaarschmidt 1975); and upper Eifelian–Givetian of Poland (Turnau 1996; Turnau and Racki 1999).

Corystisporites undulatus Turnau, 1996
Figures 16O, 17A, 47G–L

1989 *Hystricosporites mitratus* Allen; Loboziak and Streel, pl. 8, figs 3–4.
1996 *Corystisporites undulatus* Turnau, p. 117, pl. 1, fig. 1.

Dimensions. 75(110)156 μm; 15 specimens measured.

Remarks. The megaspore *Heliotriletes longispinosus* Fuglewicz and Prejbisz, 1981, which strongly resembles the microspore *C. undulatus*, is present in North Africa in same samples but was not studied here (de Ville de Goyet *et al.* 2007; Steemans *et al.* 2011*b*). These two species also co-occur in Poland.

Comparison. Loboziak and Streel (1989) misidentified specimens of *C. undulatus* from North Africa as *Hystricosporites mitratus* Allen, 1965. No typical grapnel-tipped *Hystricosporites* ornamentation was recognized on specimens in the restudied slides of Loboziak and Streel (1989). The figured specimen in Loboziak and Streel (1989, pl. 8, fig. 3) shows the characteristic morphology of *C. undulatus*.

Occurrence. WELL-8; Jubah Formation; *undulatus* Zone. A1-69; Awaynat Wanin II Formation; *undulatus* to *langii-concinna* zones. MG-1; Awaynat Wanin II and Awaynat Wanin III formations; *undulatus* to *langii-concinna* zones.

Previous record. From upper Eifelian of Poland (Turnau 1996).

Genus CRASPEDISPORA Allen, 1965

Type species. Craspedispora craspeda Allen, 1965.

Craspedispora ghadamesensis Loboziak and Streel, 1989
Figures 17B, 47M–O

1989 *Craspedispora ghadamesensis* Loboziak and Streel, p. 177, pl. 2, figs 1–4; pl. 9, fig. 4.

Dimensions. 71(80)95 μm; nine specimens measured.

Comparison. Craspedispora craspeda Allen, 1965 is smaller and has a laevigate or sparsely sculptured zona. *Samarisporites eximius* (Allen) Loboziak and Streel, 1989 has the same type of ornament but has a larger amb and the zona is as wide interradially as radially.

Occurrence. S-462; Jubah Formation; *triangulatus-catillus* Zone. 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 records. From Eifelian–Givetian of Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003; Breuer and Grahn 2011).

Craspedispora paranaensis Loboziak *et al.*, 1988
Figures 17C, 47P–R

1988 *Craspedispora paranaensis* Loboziak *et al.*, p. 355, pl. 2, figs 5–10.

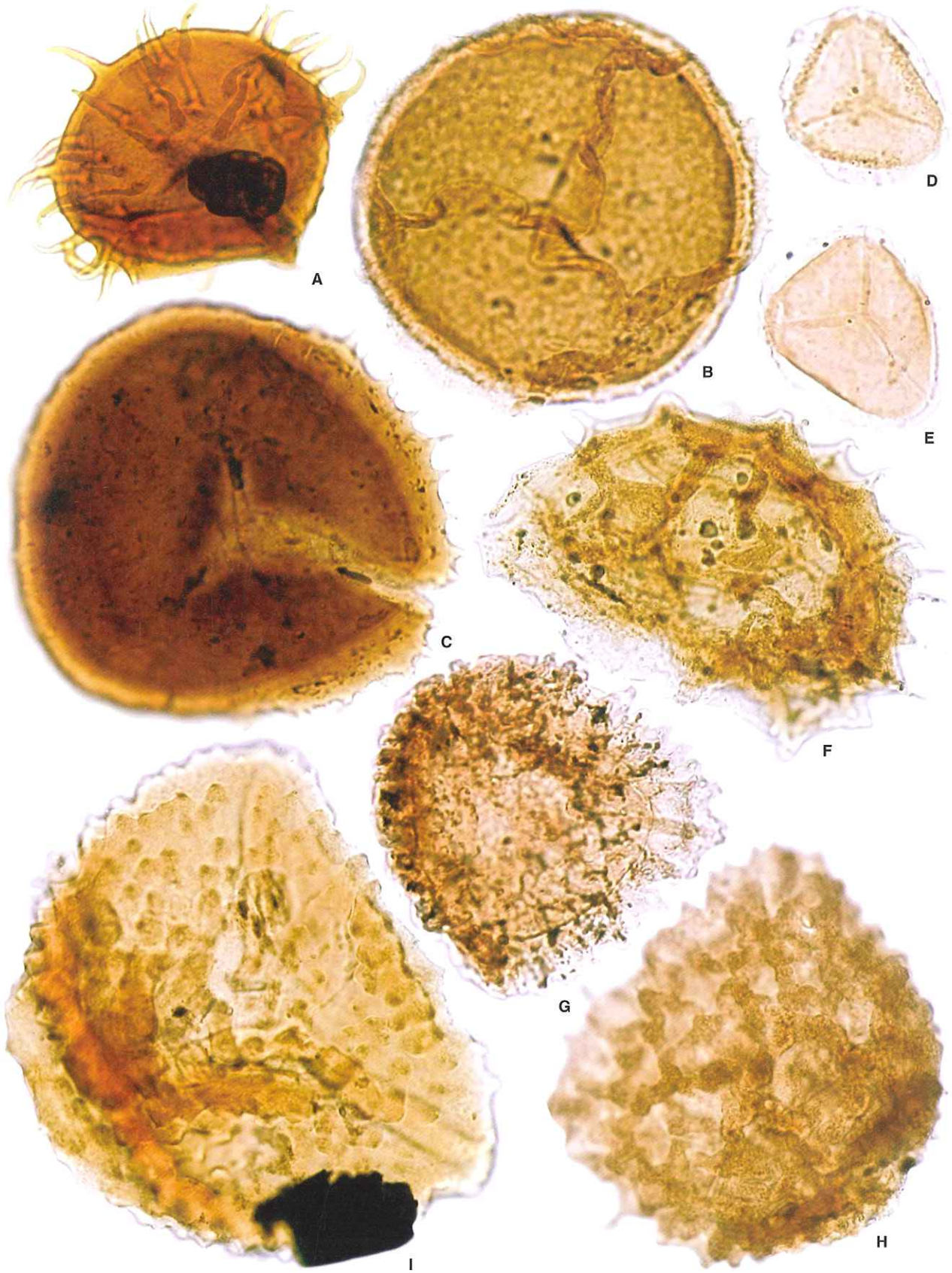
Dimensions. 70(88)120 μm; nine specimens measured.

Comparison. This species differs from *C. ghadamesensis* Loboziak and Streel, 1989 by possessing a larger and somewhat coalescent ornamentation on the zona.

Occurrence. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *triangulatus-catillus* zones.

Previous records. From upper Eifelian–Givetian of Brazil (Loboziak *et al.* 1988, 1992*b*; Melo and Loboziak 2003; Breuer and Grahn 2011) and Saudi Arabia (PB, pers. obs.); and Givetian–Frasnian of Tunisia (Loboziak *et al.* 1992*a*).

FIG. 17. 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, *Corystisporites undulatus* Turnau, 1996, magnification ×500. A1-69, 1277 ft, 62636, R29/2. B, *Craspedispora ghadamesensis* Loboziak and Streel, 1989. A1-69, 1596 ft, 26990, D44. C, *Craspedispora paranaensis* Loboziak *et al.*, 1988. A1-69, 1700 ft, 62632, R50. D–E, *Craspedispora* sp. *in* Paris *et al.* (1985). D, A1-69, 2108–2111 ft, 26913, L57-58. E, A1-69, 2039–2040 ft, 27279, M37/1. F–H, *Cristatisporites* (*Calyptosporites*) *reticulatus* (Tiwari and Schaarschmidt) comb. nov., magnification ×750. F, MG-1, 2264 m, 62951, L42/3. G, A1-69, 1109 ft, 27273, J35. H, MG-1, 2264 m, 62951, V31/3. I, *Cristatisporites streelii* sp. nov., magnification ×750. MG-1, 2241 m, 62964, T30/1.


A
B
C
D
E
F
G
H
I

Craspedispora sp. Paris *et al.*, 1985
Figure 17D–E

? 1966*a* *Perotrilites gordianus* Cramer, p. 266, pl. 3, fig. 64.
1985 *Craspedispora* sp. Paris *et al.*, pl. 18, fig. 9.

Description. Amb is sub-triangular to triangular with rounded corners. Laesurae are distinct, straight to slightly sinuous, up to 1.5 μm high, extending to the inner margin of the zona. Curvaturae not visible. Central body radius equals more or less nine-tenths of the amb radius. Exine of the central body is thin equatorially. The thin proximo-equatorial flange is commonly 2–4.5 μm wide interradially. The flange is generally narrower opposite the laesurae. Thin transverse attachment lines of the flange on the central body often can be distinguished on the proximal face. Proximal and distal surfaces are entirely laevigate.

Dimensions. 32(35)39 μm; three specimens measured.

Comparison. Perotrilites gordianus Cramer, 1966*a* may be the same species. *Craspedispora* sp. *in* Paris *et al.* (1985) is the same species and was found from equivalent Libyan material.

Occurrence. A1-69; Ouan-Kasa and Awaynat Wanin II formations; *lindlarensis-sextantii* to *annulatus-protea*, the single specimen from the Awaynat Wanin II Formation (*annulatus-protea* Zone) may be reworked.

Previous record. From lower or middle Emsian of Libya (Paris *et al.* 1985).

Genus CRISTATISPORITES Potonié and Kremp, 1954

Type species. Cristatisporites indignabundus (Loose) Potonié and Kremp, 1954.

Comparison. Samarisporites Richardson, 1965 is considered as a junior synonym of *Cristatisporites* by Playford (1971). *Samarisporites* includes forms with a wide variety of distal sculpture (e.g. coni, cristae and verrucae), which cannot be accommodated within *Cristatisporites*. The species described from this study in *Samarisporites* show a more flimsy and better individualized zona than the species described in *Cristatisporites*.

Cristatisporites (*Calyptosporites*) *reticulatus* (Tiwari and Schaarschmidt) comb. nov.
Figures 17F–H, 47S–U

1975 *Calyptosporites reticulatus* Tiwari and Schaarschmidt, p. 45., pl. 27, figs 2–4; pl. 28, fig. 1; text-fig. 35.
? 1989 *Acinosporites acanthomammillatus* Richardson; Loboziak and Streel, pl. 1, fig. 4.

Dimensions. 57(85)113 μm; 10 specimens measured.

Remarks. The genus *Calyptosporites* Richardson, 1962, which is considered as a junior synonym of *Grandispora* Hoffmeister *et al.* emend. Neves and Owens, 1966, is not the most appropriate genus for the species described here. *Calyptosporites reticulatus* Tiwari and Schaarschmidt, 1975 is transferred to the genus *Cristatisporites* Potonié and Kremp, 1954 as it is sculptured with ridges supporting spines.

Comparison. Acinosporites acanthomammillatus Richardson, 1965 illustrated in Loboziak and Streel (1989) was probably misidentified because it does not bear contorted anastomosing ridges as described by Richardson (1965) but rather ridges forming a subreticulate pattern. The specimen figured in Loboziak and Streel (1989) may be similar to *C. reticulatus*. *C. streelii* sp. nov., which is morphologically very similar, larger and does not possess a discernible inner body. These two taxa seem to intergrade in the *C. reticulatus* Morphon defined here (Table 1).

Occurrence. S-462, WELL-1 and WELL-8; Jubah Formation; *rugulata-libyensis* to *triangulatus-catillus* zones, although some specimens from S-462 may be caved. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *rugulata-libyensis* to *triangulatus-catillus* zones. MG-1; Ouan-Kasa and Awaynat Wanin II formations; *annulatus-protea* to *lemurata-langii* zones.

Previous record. From Eifelian of Germany (Tiwari and Schaarschmidt 1975).

Cristatisporites streelii sp. nov.
Figures 17I, 18A–B, 47V–X, 48A–C

? 1985 *Samarisporites* sp. B Paris *et al.*, pl. 20, fig. 6.
? 1988 *Acinosporites acanthomammillatus* Richardson; Loboziak *et al.*, pl. 1, fig. 12.

Derivation of name. In honour of the Belgian palynologist, Prof. Maurice Streel, for his pioneering Devonian palynology.

Holotype. EFC R42/3 (Figs 18A, 47W), slide 62849.

Type locality and horizon. MG-1 borehole, sample 2270 m; Awaynat Wanin II Formation at Mechiguig, Tunisia.

Paratype. EFC H44/3 (Figs 18B, 47V), slide 62964; MG-1 borehole, sample 2241 m.

Diagnosis. A *Cristatisporites* sculptured with cristae closely distributed in a subconcentric, sinuous or subreticulate pattern. Laesurae extending to equatorial margin commonly obscured by thick triradiate fold-like labra. Central body not well differentiated.

Description. Amb is sub-triangular. Laesurae are straight or sinuous, extending to equatorial margin and commonly obscured by triradiate fold-like labra *c.* 4–9 µm thick in total width. A central area can sometimes be delimited by thick folds, but an inner body is not clearly present. Sexine is laevigate, infragranular or shagreenate, sculptured distally and equatorially with fold-like ridges, up to 6 µm thick and high, bearing spines or biform elements (bulbous coni supporting an accuminate apical spine), commonly 1–5 µm wide at their base and 3–7 µm high. Cristae thus formed are sometimes closely distributed and constitute a subconcentric, sinuous or subreticulate pattern. On some specimens, the ridges may be barely visible.

Dimensions. 87(104)130 µm; 12 specimens measured.

Comparison. Acinosporites acanthomammillatus Richardson, 1965 illustrated in Loboziak *et al.* (1988) was probably misidentified because the specimen does not bear contorted anastomosing ridges as in the diagnosis of Richardson (1965) but rather ridges forming a subconcentric, sinuous or subreticulate pattern. The specimen figured in Loboziak and Streel, 1989 may be similar to *C. streelii*. *C. reticulatus* sp. nov. is somewhat smaller and shows very often a thin inner body, and cristae are instead distributed in a subreticulate pattern. Extreme variants could intergrade with *C. reticulatus* and form a morphon (Table 1).

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

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

Genus CYMBOSPORITES Allen, 1965

Type species. Cymbosporites cyathus Allen, 1965.

Cymbosporites asymmetricus Breuer *et al.*, 2007*c*
Figure 18C–D

2007*c* *Cymbosporites asymmetricus* Breuer *et al.*, p. 49, pl. 5, figs 15–19; pl. 6, figs 1–2.

Dimensions. 43(53)69 µm; 29 specimens measured.

Remarks. It is possible that the sexine, which is sometimes slightly locally detached, may be completely removed and the resulting spores would resemble specimens of *Retusotriletes* Naumova emend. Streel, 1964.

Comparison. Apiculiretusispora brandtii Streel, 1964 has a similar size and ornamentation, and sometimes also has asymmetrically placed laesurae, but differs in not being patinate. *Rhabdosporites minutus* Tiwari and Schaarschmidt, 1975 also possesses a similar ornamentation, but the sexine is totally detached from the nexine at the equator. These three species seem related and are included in the same morphon (Table 1).

Occurrence. BAQA-1, JNDL-1, JNDL-3, JNDL-4, WELL-1, WELL-3, WELL-5, WELL-6 and WELL-7; 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 *triangulatus-catillus* zones. MG-1; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *triangulatus-catillus* zones.

Previous record. From upper Pragian – lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller *et al.* 2007).

Cymbosporites catillus Allen, 1965
Figure 18E–F

1965 *Cymbosporites catillus* Allen, p. 727, pl. 100, figs 11–12.
non 1978*b* *Cymbosporites catillus* Allen; Rodriguez, p. 416, pl. 3, figs 17, 21.

Dimensions. 34(48)63 µm; 37 specimens measured.

Remarks. One monolete specimen of *C. catillus* was recorded.

Comparison. Cymbosporites cyathus Allen, 1965 has an ornamentation of larger coni. *C. cyathus* and *C. catillus*, which are generally found together in the same samples from the studied Saudi Arabian material, intergrade and consequently represent a morphon. The *C. catillus* Morphon is defined here (Table 1).

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

Previous records. From upper Givetian – lower Frasnian of Argentina (Ottone 1996); upper Eifelian – upper Givetian of Bolivia (Perez-Leyton 1990); lower Givetian – ?middle Famennian of Brazil (Loboziak *et al.* 1988; Loboziak *et al.* 1992*b*; Melo and Loboziak 2003); Givetian of Iran (Ghavidel-Syooki 2003) and Spisbergen, Norway (Allen 1965).

Cymbosporites cyathus Allen, 1965
Figure 18G–H

1965 *Cymbosporites cyathus* Allen, p. 725, pl. 101, figs 8–11.

Dimensions. 37(48)70 μm; 97 specimens measured.

Remarks. Some specimens show local detachments of sexine.

Comparison. Cymbosporites magnificus (McGregor) McGregor and Camfield, 1982 is larger, and may have fusion of ornament bases. *C. catillus* Allen, 1965 has a less developed ornamentation but some specimens intergrade with *C. cyathus* within the *C. catillus* Morphon (Table 1). *C. echinatus* Richardson and Lister, 1969 has a thinner patina and differs in the character of ornamentation.

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

Previous records. From middle Givetian of Algeria (Moreau-Benoit *et al.* 1993); lower Frasnian–Famennian of Bolivia (Perez-Leyton 1990); lower Givetian – ?middle Famennian of Amazon and Paraná basins, Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003); Eifelian (but likely Givetian) of China (Gao Lianda 1981); lower Eifelian – lower Givetian of Germany (Tiwari and Schaarschmidt 1975); middle Givetian – upper Frasnian of Libya (Moreau-Benoit 1989); and Givetian of Spitsbergen, Norway (Allen 1965).

Cymbosporites dammamensis Steemans, 1995
Figure 18I–J

? 1973 *Raistrickia* sp. McGregor, p. 35–36, pl. 4, figs 9–10.
1983 *Raistrickia* sp. A Le Hérissé, p. 24, pl. 4, figs 2, 8a–b.
1983 *Raistrickia* sp. B Le Hérissé, p. 25, pl. 4, fig. 3.
1983 *Raistrickia* sp. D Le Hérissé, p. 25, pl. 4, figs 6–7.
1995 *Cymbosporites dammamensis* Steemans, p. 101 (*pars*), pl. 2, figs 10–12 (only).

Dimensions. 27(34)43 μm; 20 specimens measured.

Comparison. The different specimens described by Le Hérissé (1983) are very similar to the species described by Steemans (1995). The ornamentation of *Raistrickia* sp. *in* McGregor (1973) is similar, but there is no dimensions for the thickness of the exine. *C. echinatus* Richardson and Lister, 1969 is larger and sculptured with biform spines. *Cymbohilates baqaensis* Breuer *et al.*, 2007*c* is similar but hilate. Some specimens, where the proximal face has been torn, are difficult to assign. Some specimens of *Cymbosporites dammamensis* not illustrated by Steemans (1995) were probably misidentified and should be reassigned to the hilate species because they have just slits as laesurae (PS, pers. obs.). *Raistrickia jaufensis* sp. nov. is more triangular and sculptured with widely distributed and generally larger bacula. *Verrucosisporites* sp. 1 is not patinate and bears verrucae that are generally wider at the base.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4 and WELL-7; Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Previous records. From upper Pragian – lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller *et al.* 2007); upper Pragian of Armorican Massif, France (Le Hérissé 1983); Lochkovian of Iran (Ghavidel-Syooki 2003); and Lochkovian–Pragian of Saudi Arabia (Steemans 1995).

Cymbosporites dittonensis Richardson and Lister, 1969
Figure 18K–N

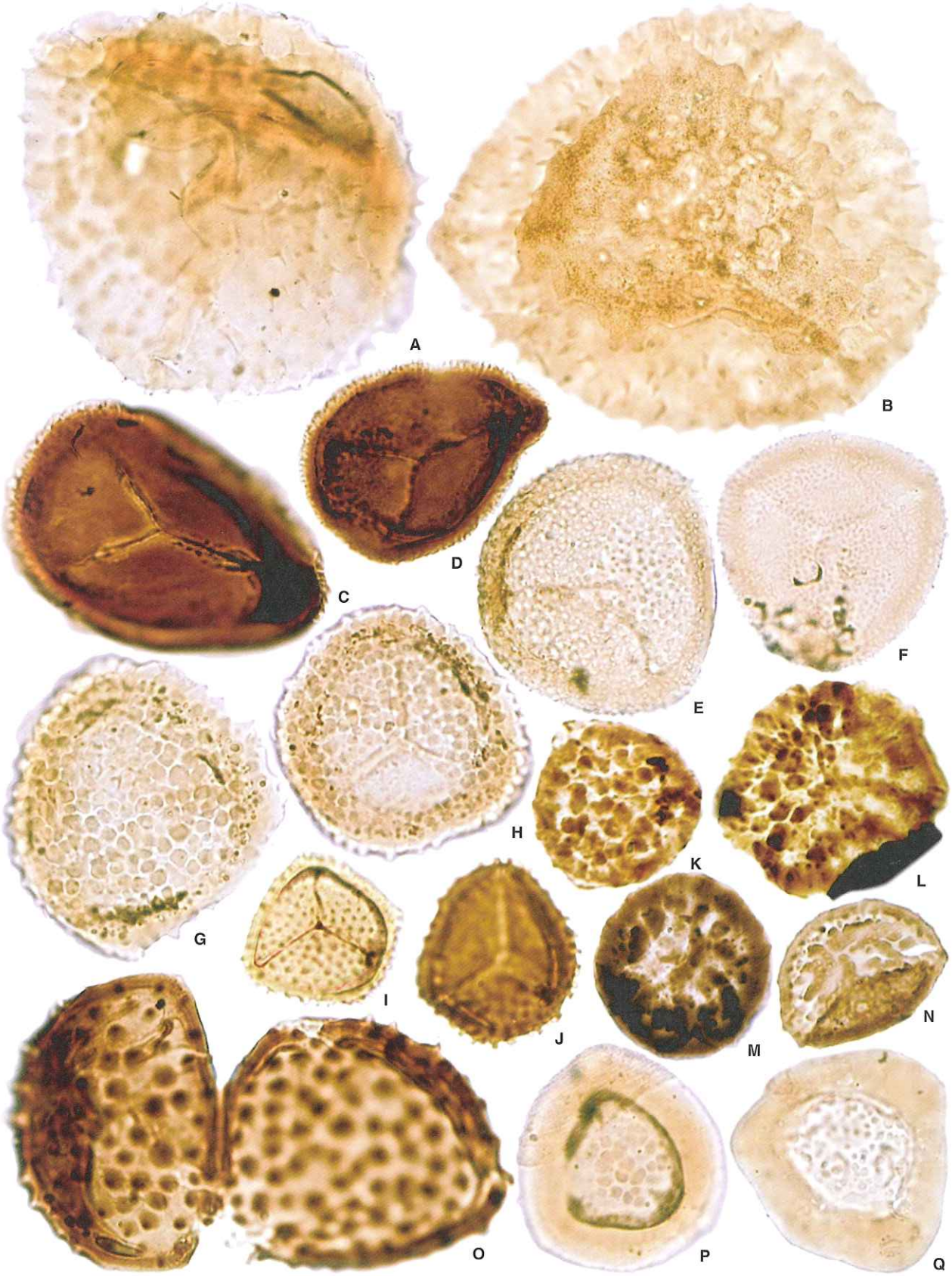
1969 *Cymbosporites dittonensis* Richardson and Lister, p. 241, pl. 41, figs 10–13.

Dimensions. 29(33)41 μm; 10 specimens measured.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4, WELL-2 and WELL-7; Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Previous records. From Lochkovian of Belgium (Steemans 1989), Armorican Massif, France (Steemans 1989), Poland (Turnau *et al.* 2005) and Wales (Richardson and Lister 1969); upper Lochkovian of Solimões Basin, Brazil (Rubinstein *et al.* 2005) and Germany (Steemans 1989); upper Pragian–Emsian of China (Lu Lichang and Ouyang Shu 1976; Gao Lianda

FIG. 18. 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, *Cristatisporites streelii* sp. nov., magnification ×750. A, Holotype, MG-1, 2270 m, 62849, R42/3. B, Paratype, MG-1, 2241 m, 62964, H44/3. C–D, *Cymbosporites asymmetricus* Breuer *et al.*, 2007*c*. C, JNDL-3, 294.0 ft, 03CW152, M29/1. D, JNDL-3, 341.0 ft, 03CW157, O32. E–F, *Cymbosporites catillus* Allen, 1965. E, MG-1, 2180 m, 62972, T37. F, S-462, 2010–2015 ft, 63399, N47. G–H, *Cymbosporites cyathus* Allen, 1965. G, S-462, 2010–2015 ft, 63399, E34/4. H, S-462, 2010–2015 ft, 63399, S53/1. I–J, *Cymbosporites dammamensis* Steemans, 1995. I, BAQA-1, 345.5 ft, 03CW114, W41/1. J, BAQA-1, 366.9 ft, 03CW117, H31/2. K–N, *Cymbosporites dittonensis* Richardson and Lister, 1969. K, WELL-7, 13614.1 ft, 62374, F46. L, WELL-7, 13614.1 ft, 62372, O28-29. M, WELL-2, 15893.9 ft, 63105, O49/4. N, MG-1, 2631.2 m, 62552, M47/2. O, *Cymbosporites echinatus* Richardson and Lister, 1969. BAQA-1, 366.9 ft, 03CW117, Q29. P–Q, *Cymbosporites ocularis* (Raskatova) comb. nov. P, MG-1, 2160.6 m, 62747, P43/4. Q, MG-1, 2181.2 m, 62524, V49.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q

1981); middle Přídolí of Libya (Rubinstein and Steemans 2002); and upper Pragian of Morocco (Rahmani-Antari and Lachkar 2001).

Cymbosporites echinatus Richardson and Lister, 1969
Figure 18O

1967 *Cymbosporites* Richardson, pl. 1, fig. f.
1969 *Cymbosporites echinatus* Richardson and Lister, p. 239, pl. 42, figs 1–5.
non 1983 *Cymbosporites echinatus* Richardson and Lister; Le Hérissé, p. 50, pl. 7, figs 10.

Dimensions. 52–54 μm; two specimens measured.

Remarks. Cymbosporites echinatus frequently occurs in tetrads according to Richardson and Lister (1969).

Comparison. Cymbosporites cyathus Allen, 1965 has a thicker patina and spinose-tipped ornamentation is more densely packed.

Occurrence. BAQA-1; Jauf Formation (Subbat Member); *ovalis* Zone.

Previous records. Lochkovian of Belgium (Steemans 1989) and Romania (Steemans 1989); and Přídolí of Wales (Richardson and Lister 1969).

Cymbosporites ocularis (Raskatova) comb. nov.
Figure 18P–Q

1993 *Archaeozonotriletes ocularis* Raskatova; Avkhimovitch *et al.*, pl. 8, fig. 9.

Dimensions. 40(41)42 μm; three specimens measured.

Remarks. Archaeozonotriletes ocularis Raskatova, 1969 is herein transferred into the genus *Cymbosporites* Allen, 1965. The latter consists of ornamented patinate spores while *Archaeozonotriletes* has a laevigate or punctate patina.

Occurrence. MG-1; Awaynat Wanin III Formation; *langii-concinna* Zone.

Previous record. From middle Givetian of the Russian Platform (Avkhimovitch *et al.* 1993).

Cymbosporites rarispinosus Steemans, 1989
Figure 19A–B

1981 *Cymbosporites* sp. G Steemans, p. 53, pl. 2, fig. 9.
1984 *Cymbosporites* sp. 1 Steemans and Gerrienne, pl. 2, fig. 11.
1989 *Cymbosporites rarispinosus* Steemans, p. 124, pl. 32, figs 26–28; pl. 33, figs 1–2.

Dimensions. 34(44)54 μm; 16 specimens measured.

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

Previous records. From upper Lochkovian–Emsian of Belgium (Steemans 1989); uppermost Pragian – lowermost Emsian of Parnaíba Basin (Grahn *et al.* 2005); and upper Lochkovian of Germany (Steemans 1989).

Cymbosporites senex McGregor and Camfield, 1976
Figure 19C–D

1970 New species McGregor *et al.*, pl. 1, fig. 7.
1976 *Cymbosporites? senex* McGregor and Camfield, p. 16, pl. 2, figs 1–4, text-fig. 14.

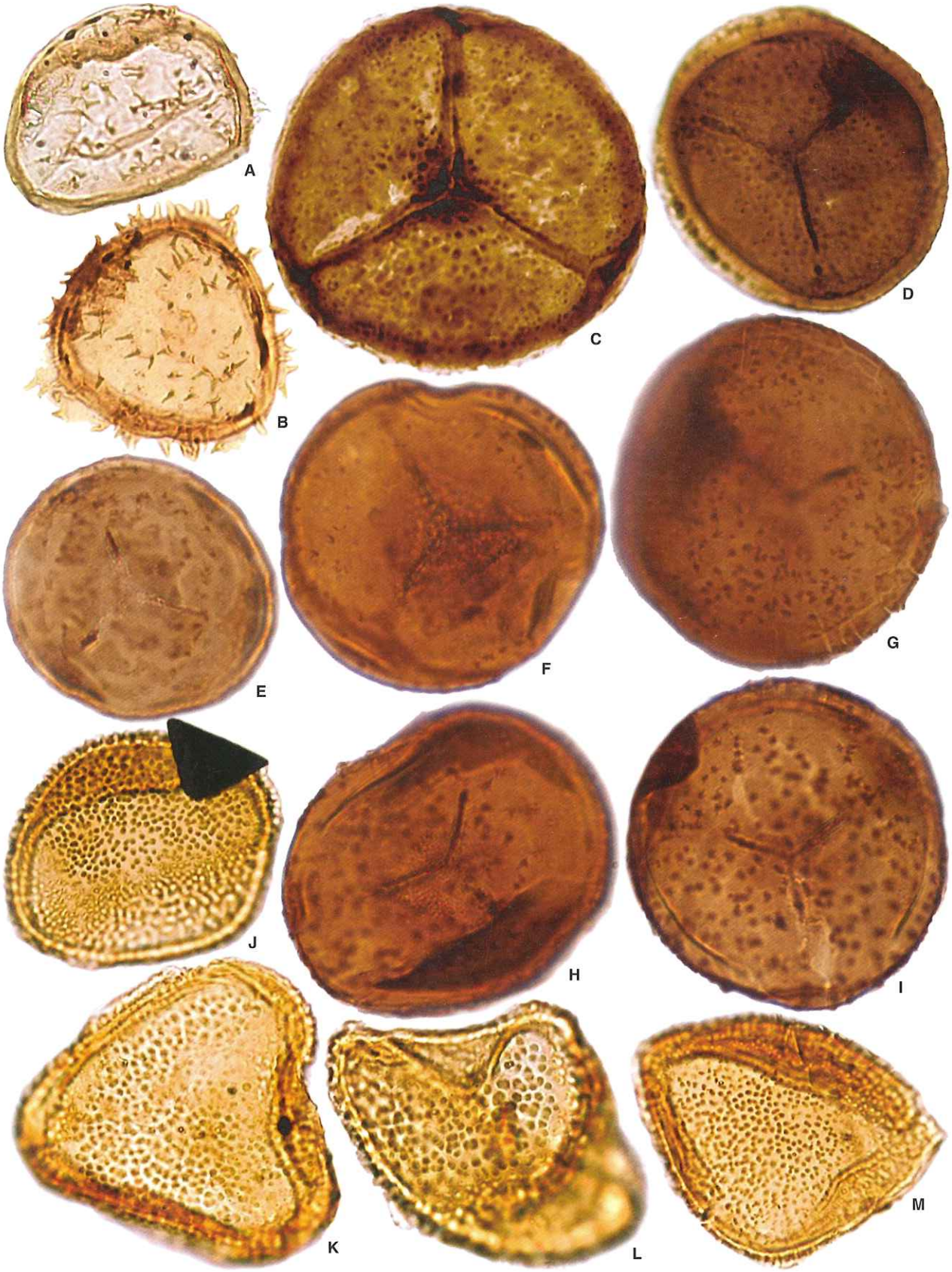
Dimensions. 47(60)72 μm; 28 specimens measured.

Remarks. Examination of the population presented here has proved that this form is clearly patinate and its attribution to the genus *Cymbosporites* is confirmed.

Comparison. Calyptosporites proteus McGregor and Camfield, 1976 is smaller, with sculpture consisting of grana and minute cones only. *Cymbohilates comptulus* Breuer *et al.*, 2007*c* is very similar and has the same size but is hilate.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-1, WELL-2, WELL-3, WELL-4, WELL-5, WELL-6 and

FIG. 19. 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, *Cymbosporites rarispinosus* Steemans, 1989. A, BAQA-2, 56.0 ft, 03CW130, U29/3. B, BAQA-2, 134.4 ft, 03CW137, P28/1. C–D, *Cymbosporites senex* McGregor and Camfield, 1976. C, WELL-7, 13670.8 ft, 62382, S-T32. D, BAQA-1, 285.5 ft, 03CW111, O25. E–I, *Cymbosporites stellospinosus* var. *minor* var. nov. E, BAQA-2, 133.0 ft, 66825, K37/1. F, BAQA-1, 161.0 ft, 66775, J53. G, Paratype, BAQA-1, 161.0 ft, 66775, G40/4. H, BAQA-1, 161.0 ft, 66775, S36. I, Holotype, BAQA-1, 161.0 ft, 66773, G42. J–M, *Cymbosporites variabilis* var. *densus* sp. et var. nov. J, BAQA-1, 366.9 ft, 62256, H32. K, BAQA-1, 219.2 ft, 62237, K35. L, BAQA-1, 345.5 ft, 62253, P30. M, Paratype, BAQA-1, 366.9 ft, 62255, H34/4.


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

WELL-7; Jauf and Jubah formations; *papillensis-baqaensis* to *svalbardiae-eximius* zones.

Previous records. From Pragian–Emsian of Canada (McGregor and Camfield 1976); and Emsian of Saudi Arabia (Al-Ghazi 2007; Breuer *et al.* 2007*c*).

Cymbosporites stellospinosus Steemans, 1989 var. *minor* var. nov.
Figure 19E–I

Derivation of name. From *minor* (Latin), meaning smaller; refers to the size of distal sculptural elements.

Holotype. EFC G42 (Fig. 19I), slide 66773.

Paratype. EFC G40/4 (Fig. 19G), slide 66775; BAQA-1 core hole, sample 161.0 ft.

Type locality and horizon. BAQA-1 core hole, sample 161.0 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A large *Cymbosporites stellospinosus* distally sculptured with irregularly distributed, minute spines in star-shaped clusters.

Description. Amb is sub-circular to circular. Laesurae are straight, simple, about two-thirds of the amb radius in length. Exine is proximally thin, equatorially and distally patinate, commonly 2–4 μm thick. Proximal surface is laevigate, sometimes differentially thickened. A sub-circular to sub-triangular apical zone (diameter about one-third of the amb diameter) surrounded by a curved, thicker band, 3–4 μm, characterized by a sharp inner outline and a commonly diffuse outer outline sometimes occurs. Patina is sculptured, irregularly distributed, short spines, 0.5–2 μm high and in star-shaped clusters (one to five), 0.5–5 μm apart.

Dimensions. 38(54)62 μm; 19 specimens measured.

Remarks. This form described herein is similar to *C. stellospinosus* Steemans, 1989 by having the same type of ornamentation but in smaller size. The two populations seem to constitute two different varieties of a same species: *C. stellospinosus* vars *stellospinosus* Steemans, 1989, in Western Europe, and *minor* var. nov., in Saudi Arabia.

Comparison. Cymbosporites stellospinosus var. *stellospinosus* Steemans, 1989 is smaller (31–36 μm) and the spines are longer (2–3 μm). *Cymbohilates cymosus* Richardson, 1996 has the same diagnostic clusters of short spines, but it occurs mainly in tetrads and sometimes as hilate monads. Its exine is also thinner (*c.* 1 μm thick).

Occurrence. BAQA-1, BAQA-2, JNDL-3 and JNDL-4; Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones.

Cymbosporites variabilis sp. nov.
Figures 19J–M, 20

Derivation of name. From *variabilis* (Latin), meaning changeable, variable; refers to the distribution of distal sculptural elements.

Holotype. EFC N29/2 (Fig. 20H), slide 03CW128.

Paratype. EFC H37 (Fig. 20I), slide 62250; BAQA-1 core hole, sample 345.5 ft.

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

Diagnosis. A *Cymbosporites* distally sculptured with grana, coni or small verrucae, variably distributed.

Remarks. Clivosispora variabilis and *Dictyotriletes biornatus* Breuer *et al.*, 2007*c* constitute the *D. biornatus* Morphon (Table 1). It includes *C. variabilis* vars *variabilis, densus* and *dispersus* sp. et var. nov., and *D. biornatus* vars *biornatus* and. *murinatus* var. nov. The ornament and its organization on the spore distal surface vary between the two end-members which correspond to two distinct genera: *Cymbosporites* Allen, 1965 and *Dictyotriletes* Naumova, 1939 ex Ishchenko, 1952. All intermediary forms between the two end-members co-occur in the assemblages. In the simplest form of the spore, sculptural elements are evenly distributed on the distal surface (*C. variabilis* var. *densus* sp. et var. nov.). In the intermediary forms (*C. variabilis* vars *dispersus* sp. et var. nov. and *C. variabilis* var. *variabilis* sp. et var. nov.), elements organize progressively and combine until they form a pseudoreticulum, the walls of which are constituted by lines

FIG. 20. 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, *Cymbosporites variabilis* var. *densus* sp. et var. nov. A, BAQA-1, 366.9 ft, 62257, F34. B, Holotype, BAQA-1, 366.9 ft, 62256, K42/2. C–G, *Cymbosporites variabilis* var. *dispersus* sp. et var. nov. C, BAQA-1, 366.9 ft, 62257, M51/2. D, BAQA-1, 345.5 ft, 62249, U45. E, BAQA-1, 366.9 ft, 62257, F-G42. F, Paratype, BAQA-1, 345.5 ft, 62248, R42/1. G, Holotype, BAQA-1, 395.2 ft, 03CW121, X43/1. H–L, *Cymbosporites variabilis* var. *variabilis* sp. et var. nov. H, Holotype, BAQA-2, 52.0 ft, 03CW128, N29/2. I, Paratype, BAQA-1, 345.5 ft, 62250, H37. J, BAQA-1, 345.5 ft, 62250, X38. K, BAQA-1, 308.3 ft, 03CW112, B36. L, BAQA-1, 345.5 ft, 62251, D45/2.


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

of discrete ornaments (*D. biornatus* Breuer *et al.*, 2007*c* var. *biornatus*). In the most complex spore form, ornaments merge to form elongated muri, which constitutes a perfectly closed reticulum (*D. biornatus* Breuer *et al.*, 2007*c* var. *murinatus* var. nov.). Thus, a progressive organization of the ornamentation appears from the simplest spores to the most complex ones.

Comparison. Cymbosporites catillus Allen, 1965 has a generally thicker patina and distinct laesurae straight accompanied by labra.

Cymbosporites variabilis var. *variabilis* sp. et var. nov.
Figure 20H–L

2007*a* *Cymbosporites*? sp. 3 Breuer *et al.*, text-fig. 13–C.
2007*b* Unnamed spore Breuer *et al.*, text-fig. 1–3.

Diagnosis. A *Cymbosporites variabilis* distally sculptured with grana, coni or small verrucae distributed into an irregular to almost imperfect reticulate pattern.

Description. Amb is sub-circular to roundly triangular. Laesurae are straight, simple, often indistinct, commonly three-fifths to four-fifths of the amb radius in length. Exine is proximally thin, equatorially and distally patinate, commonly 2–5 μm thick, homogeneous. Proximal surface is laevigate, often torn or collapsed. Patina is sculptured with grana, coni or small verrucae, 0.5–2 μm wide at base and high, 0.5–7 μm apart. Elements are distributed into an irregular to almost imperfect reticulate pattern. Elements are often merged at the base forming elongated elements or patches of several ornaments.

Dimensions. 47(57)68 μm; 34 specimens measured.

Comparison. C. variabilis var. *dispersus* sp. et var. nov. has more regularly distributed ornament. *Dictyotriletes biornatus* Breuer *et al.*, 2007*c* var. *biornatus* has all the ornament disposed in a perfect reticulate pattern. However, perfect lumina can occur locally in *C. variabilis* var. *variabilis*; others are incomplete or have isolated elements within the reticulum.

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

Cymbosporites variabilis var. *densus* sp. et var. nov.
Figures 19J–M, 20A–B

2007*a* *Cymbosporites* sp. 1 Breuer *et al.*, text-fig. 1: 3A.
2007*b* Unnamed spore Breuer *et al.*, text-fig. 1: 1.

Derivation of name. From *densus* (Latin), meaning dense; refers to the distribution of distal sculptural elements.

Holotype. EFC K42/2 (Fig. 20B), slide 62256.

Paratype. EFC H34/4 (Fig. 19M), slide 62255; BAQA-2 core hole, sample 366.9 ft.

Type locality and horizon. BAQA-1 core hole, sample 366.9 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Cymbosporites variabilis* distally sculptured with grana, coni or small verrucae evenly distributed and sometimes locally merged at their bases.

Description. Amb is sub-circular to roundly triangular. Laesurae are straight, simple, often indistinct, commonly two-thirds to four-fifths of the amb radius in length. Exine is proximally thin, equatorially and distally patinate, commonly 2–5 μm thick, homogeneous. Proximal surface is laevigate, often torn or collapsed. Patina is sculptured with densely distributed grana, coni or small verrucae, 0.5–2 μm wide at base and high, 0.5–2 μm apart. Elements are evenly distributed and sometimes locally merged at the base.

Dimensions. 47(58)73 μm; 54 specimens measured.

Remarks. C. variabilis var. *densus* constitutes an end-member of the *Dictyotriletes biornatus* Morphon (Table 1).

Comparison. C. variabilis var. *dispersus* sp. et var. nov. has more irregularly distributed ornaments. As the two species intergrade (see discussion above), it is sometimes difficult to discriminate between them.

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

Cymbosporites variabilis var. *dispersus* sp. et var. nov.
Figure 20C–G

2007*a* *Cymbosporites* sp. 2 Breuer *et al.*, text-fig. 1: 3B.
2007*b* Unnamed spore Breuer *et al.*, text-fig. 1: 2.

Derivation of name. From *disperses* (Latin), meaning dispersed; refers to the distribution of distal sculptural elements.

Holotype. EFC X43/1 (Fig. 20G), slide 03CW121.

Paratype. EFC R42/1 (Fig. 20F), slide 62248; BAQA-1 core hole, sample 345.5 ft.

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

Diagnosis. A *Cymbosporites variabilis* distally sculptured with grana, coni or small verrucae irregularly distributed and often merged at the base forming patches of several elements.

Description. Amb is sub-circular to roundly triangular. Laesurae are straight, simple, often indistinct, commonly three-fifths to four-fifths of the amb radius in length. Exine is proximally thin, equatorially and distally patinate, commonly 2–5 µm thick, homogeneous. Proximal surface is laevigate, often torn or collapsed. Patina is sculptured with grana, coni or small verrucae, 0.5–2 µm wide at base and high, 0.5–3 µm apart. Elements are irregularly packed and often merged at the base forming patches of several elements.

Dimensions. 45(56)70 µm; 46 specimens measured.

Comparison. C. variabilis var. *densus* sp. et var. nov. has more regularly distributed ornament. *C. variabilis* var. *variabilis* sp. et var. nov. shows clearly a more advanced organization of elements.

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

Cymbosporites variegatus sp. nov.
Figure 21A–F

1972 cf. *Cymbosporites cyathus* Allen; Mortimer and Chaloner, p. 11, pl. 1, fig. 4.
1989 *Verrucosisporites bulliferus* Richardson and McGregor; Loboziak and Streel, pl. 1, fig. 6.
? 1992 *Cymbosporites* sp. cf. *C. magnificus* (McGregor) McGregor and Camfield; McGregor and Playford, pl. 5, figs 5–6.
? 1992*a* *Geminospora piliformis* Loboziak *et al.*; Loboziak *et al.*, pl. 3, fig. 11.
2011 *Cymbosporites* sp. 1 Breuer and Grahn, pl. 2, fig. k.

Derivation of name. From *variegatus* (Latin), meaning variegated; refers to the size and type of distal sculptural elements.

Holotype. EFC F28/3 (Fig. 21E), slide 62940.

Paratype. EFC L51 (Fig. 21D), slide 62782; MG-1 borehole, sample 2315 m.

Type locality and horizon. MG-1 borehole, sample 2247 m; Awaynat Wanin II Formation at Mechiguig, Tunisia.

Diagnosis. A *Cymbosporites* sculptured with variable low verrucae or baculae, flat-topped or slightly rounded in profile, sub-circular, polygonal or irregular in plan view. Proximal surface infragranular to granular.

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple and extending to, or almost to, the inner margin of patina. Exine is proximally thin, equatorially and distally patinate, commonly 2–5 µm thick, homogeneous to infragranulate. Proximal surface is infragranular to granular. Patina is sculptured with variable low verrucae or baculae, flat-topped or slightly rounded in profile, sub-circular, polygonal or irregular in plan view, 0.5–4 µm wide, up to 1.5 µm high, 0.5–3 µm apart. Elements are sometimes irregularly packed with some small areas without any elements.

Dimensions. 38(48)60 µm; 26 specimens measured.

Remarks. Some specimens appear to have a partly separate inner body similar to that of the genus *Geminospora* Balme, 1962. This type of separation is typical of a thick patinate structure of *Cymbosporites* Allen, 1965.

Comparison. The sculptural elements of cf. *C. cyathus* Allen, 1965 *in* Mortimer and Chaloner (1972) are flat-topped as those of the species described herein. The specimens figured as *Cymbosporites* sp. cf. *C. magnificus* (McGregor) McGregor and Camfield, 1982 *in* McGregor and Playford (1992) could be similar, but no description of the observed specimens is given. The specimen figured as *Geminospora piliformis* Loboziak *et al.*, 1988 *in* Loboziak *et al.* (1992*a*) could be misinterpreted since it seems to bear low verrucae and to be single-layered. Consequently, it is similar to the species described herein. *G. piliformis* is two-layered and bears pila. *C. magnificus* (McGregor) McGregor and Camfield, 1982 is larger and sculptured with verrucae, mammae and rounded coni, discrete or joined laterally into short irregularly-trending ridges while *C. cyathus* Allen, 1965 bears mainly coni. *Verrucosisporites bulliferus* Richardson and McGregor, 1986 has generally larger verrucae (2.5–5 µm), is proximally laevigate and not patinate. *V. bulliferus* illustrated by Loboziak and Streel (1989) has been re-examined and is exactly the same as *C. variegatus*. As no *V. bulliferus* Richardson and McGregor, 1986 *sensu stricto* has been found in the studied material, the specimens described here cannot be confused with the index species of Richardson and McGregor (1986).

Occurrence. A1-69; Awaynat Wanin II Formation; *lemurata-langii* to *triangulatus-catillus* zones. MG-1; Awaynat Wanin II and Awaynat Wanin III formations; *lemurata-langii* to *langii-concinna* zones.

Previous records. From middle Givetian of Parnaíba Basin, Brazil (Breuer and Grahn 2011); Frasnian of Libya (Loboziak and Streel 1989); Givetian–Frasnian of Saudi Arabia (PB, pers. obs.); and Givetian of England (Mortimer and Chaloner 1972).

Cymbosporites wellmanii sp. nov.
Figure 21G–K

? 2000*b* *Aneurospora* sp. A Wellman *et al.*, p. 171, pl. 4, figs 8–9.

Derivation of name. In honour of the British palynologist, Dr. Charles H. Wellman, for his outstanding contribution to the understanding of the Silurian–Devonian spore assemblages, notably from Saudi Arabia.

Holotype. EFC K31 (Fig. 21J), slide 66825.

Paratype. Figure 21H, BAQA-2 core hole, sample 133.0 ft, slide 03CW136, EFC K31.

Type locality and horizon. BAQA-2 core hole, sample 133.0 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Cymbosporites* sculptured with densely distributed, slender pointed spines.

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple or labrate, usually 1–2 μm wide, three-fifths to four-fifths of the amb radius in length. Exine is proximally thin, distally and equatorially patinate, 2.5–6 μm thick equatorially. Proximal surface is laevigate to scabrate. Equatorial and distal are regions sculptured with slender pointed spines, densely distributed, 2.5–5 μm high, 0.75–2 μm wide at base and 1–2 μm apart.

Dimensions. 40(48)61 μm; nine specimens measured.

Comparison. Although *Aneurospora* sp. A *in* Wellman *et al.* (2000*b*) is smaller (33–41 μm), slightly thinner equatorially and distally, it could be similar to *C. wellmanii* (C. H. Wellman, pers. comm. 2009). *Dibolisporites eifeliensis* (Lanninger) McGregor, 1973 has a thinner exine and more widely distributed sculptural elements. Moreover, their basal part is bulbous or slightly to strongly tapering, and their apical part is not accuminate.

Occurrence. BAQA-2; Jauf Formation (Sha'iba Member); *papillensis-baqaensis* Zone.

Genus CYRTOSPORA Winslow, 1962

Type species. *Cyrtospora cristifera* (Luber) Van der Zwan, 1979.

Cyrtospora tumida sp. nov.
Figures 21L–N, 22A–C

Derivation of name. From *tumidus* (Latin), meaning swollen up; refers to the general aspect of the spore body.

Holotype. EFC T36/2 (Fig. 21N), slide 62736.

Paratype. EFC E32 (Fig. 21L), slide 62936; MG-1 borehole, sample 2278 m.

Type locality and horizon. MG-1 borehole, sample 2421 m; Awaynat Wanin I Formation at Mechiguig, Tunisia.

Diagnosis. A *Cyrtospora* with a patina of irregular shape in plan view and dissected into irregularly distributed, large, broad based, rounded verrucae, coni, tubercules or protuberances.

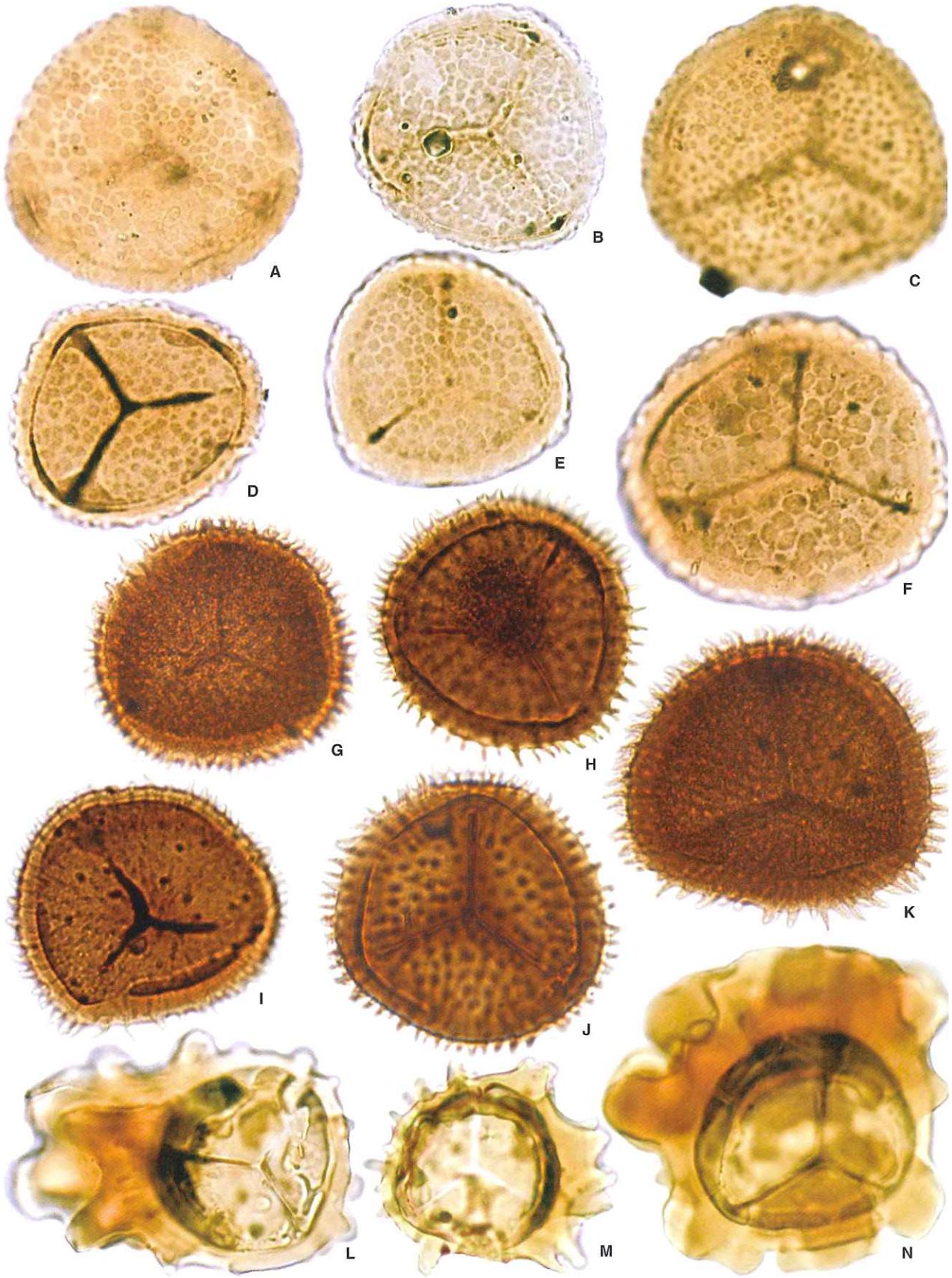
Description. Amb is sub-circular to sub-triangular. Laesurae are simple, straight, two-thirds to full central area radius in length. Patina, 2–21 μm thick, is homogeneous sometimes with scattered infrapuncta. Contact areas thinner than distal exine and laevigate. Patina is of irregular shape in plan view and dissected into irregularly distributed, large, broad based, rounded verrucae, coni, tubercules or protuberances, 1.5–28 μm wide at base, 1.5–14 μm high.

Dimensions. 39(59)72 μm; 11 specimens measured.

Remarks. Spores in this population do not belong to the genus *Archaeozonotriletes* Naumova emend. Allen, 1965 because their patina is far from being uniform.

Comparison. *Archaeozonotriletes variabilis* Naumova emend. Allen, 1965 also has a laevigate or finely punctate and irregular patina, which is not dissected into ornamentation or protuberances. Some specimens of *A. variabilis* (Fig. 10I–J) may locally show slightly convex and concave zones on the patina. *A. variabilis* is considered to intergrade with *C. tumida* in the same morphon (Table 1). *Lophozonotriletes media* Taugourdeau-Lantz, 1967 is densely punctate and bears equatorially blunt, pointed or rounded verrucae. The latter is rather cingulate, but extreme variants could intergrade with *C. tumida*. *C. cristifera* (Luber) Van der Zwan, 1979 has a distal ornamentation mainly consisting of bacula of variable shape, size, and, to a minor degree, coni and verrucae (1–8 μm high, 1–7 μm wide).

FIG. 21. 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–F, *Cymbosporites variegatus* sp. nov. A, MG-1, 2160.6 m, 62727, R40. B, MG-1, 2247 m, 62942, R40. C, MG-1, 2182.4 m, 62527, U-V40. D, Paratype, MG-1, 2315 m, 62782, L51. E, Holotype, MG-1, 2247 m, 62940, F28/3. F, MG-1, 2160.6 m, 62746, R28. G–K, *Cymbosporites wellmanii* sp. nov. G, BAQA-2, 134.4 ft, 66826, M29. H, Paratype, BAQA-2, 133.0 ft, 03CW136, O-P23. I, BAQA-2, 133.0 ft, 03CW136, G43/3. J, Holotype, BAQA-2, 133.0 ft, 66825, K31. K, BAQA-2, 133.0 ft, 66825, X33. L–N, *Cyrtospora tumida* sp. nov. L, Paratype, MG-1, 2278 m, 62936, E32. M, MG-1, 2456 m, 62737, H48. N, Holotype, MG-1, 2421 m, 62736, T36/2.


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

Occurrence. A1-69; Awaynat Wanin II Formation; *lemurata-langii* to *triangulatus-catillus* zones. MG-1; Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations; *rugulata-libyensis* to *langii-concinna* zones.

Previous record. Cyrtospora tumida has also been recorded from Givetian of Saudi Arabia (PB, pers. obs.).

Genus DENSOSPORITES (Berry) Butterworth *et al.* in Staplin and Jansonius (1964)

Type species. Densosporites covensis Berry, 1937.

Densosporites devonicus Richardson, 1960
Figures 22D, 48D–I

1960 *Densosporites devonicus* Richardson, p. 57, pl. 14, figs 10–11; text-fig. 7.
1965 *Densosporites orcadensis* Richardson, p. 580, pl. 92, figs 1–2.
1976 *Hymenozonotriletes propolyacanthus* Arkhangelskaya, p. 55, pl. 10, figs 3–4.
1976 *Densosporites orcadensis* Richardson; McGregor and Camfield, p. 17, pl. 6, fig. 3.

Dimensions. 77(96)126 μm; 23 specimens measured.

Remarks. In lateral compression, proximal face flattened-pyramidal, distal region strongly rounded (McGregor and Camfield 1982).

Comparison. Richardson (1965) gave the sculptural details and the relative widths of the light and dark zones of the cingulum as criteria for distinguishing *D. devonicus* from *D. orcadensis* Richardson, 1960. These criteria were used by Marshall and Allen (1982) in an attempt to substantiate the differences between the two species, but no systematic variation of these characters, as alleged by Richardson (1965). Thus, McGregor and Camfield (1982) and Marshall and Allen (1982) consider that *D. devonicus* and *D. orcadensis* intergrade and it is impractical to separate them. *D. weatherallensis* McGregor and Camfield, 1982 differs from *D. devonicus* in having broader spines that rarely expand at the tip, in the close spacing or basal fusion of its sculpture towards the distal pole and its less conspicuous dark zone. *D. inaequus* (McGregor) McGregor and Camfield, 1982 has more prominent spines, which do not bifurcate but have papillate tips. *D. concinnus* (Owens) McGregor and Camfield, 1982 is smaller in size and less elongate, with a predominantly pointed sculpture but intergrades with extreme variants of *D. devonicus* (McGregor and Camfield, 1982).

Occurrence. MG-1; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *langii-concinna* zones.

Previous records. Densosporites devonicus is eponymous for the late Eifelian – early Givetian *devonicus-naumovae* Assemblage Zone of the Old Red Sandstone Continent and adjacent regions (Richardson and McGregor 1986) and AD Oppel Zone of Western Europe (Streel *et al.* 1987). *D. devonicus* occurs from Eifelian into lower Frasnian and has been reported from Canada (McGregor and Uyeno 1972; McGregor and Camfield 1976; McGregor and Camfield 1982), Germany (Riegel 1973; Tiwari and Schaarschmidt 1975; Streel and Paproth 1982; Loboziak *et al.* 1990), Libya (Streel *et al.* 1988), Siptsbergen, Norway (Allen 1965), Poland (Turnau 1996; Turnau and Racki 1999), Russian Platform (Avkhimovitch *et al.* 1993), Saudi Arabia (PB, pers. obs.) and Scotland (Richardson 1965; Marshall and Allen 1982; Marshall *et al.* 1996; Marshall 2000; Marshall and Fletcher 2002).

Genus DIAPHANOSPORA Balme and Hassell, 1962

Type species. Diaphanospora riciniata Balme and Hassell, 1962.

Diaphanospora milleri sp. nov.
Figure 22E–K

2007*a* sp. 1 Breuer *et al.*, text-figs 1–4A–B.

Derivation of name. In honour of the American palynologist employed by Saudi Aramco, Merrell A. Miller, for his outstanding work on the acritarch and spore palynology from the Lower Palaeozoic.

Holotype. EFC N49/1 (Fig. 22J), slide 62317.

Paratype. EFC G27/2 (Fig. 22K), slide 03CW108; BAQA-1 core hole, sample 222.5 ft.

Type locality and horizon. WELL-7 well, sample 13689.7 ft; Jauf Formation at Uthmaniyah, Saudi Arabia.

FIG. 22. 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, *Cyrtospora tumida* sp. nov. A, MG-1, 2264 m, 62951, E46/4. B, MG-1, 2536 m, 62742, T32. C, MG-1, 2435 m, 63018, R40/3. D, *Densosporites devonicus* Richardson, 1960, magnification ×750. MG-1, 2247 m, 62942, H39/3. E–K, *Diaphanospora milleri* sp. nov. E, WELL-7, 13689.7 ft, 62317, Y42/1. F, WELL-7, 13689.7 ft, 62317, E33/4. G, WELL-7, 13689.7 ft, 62319, F-G29. H, BAQA-1, 346.8 ft, 66797, H41/3. I, WELL-2, 15919.7 ft, 63108, O28. J, Holotype, WELL-7, 13689.7 ft, 62317, N49/1. K, Paratype, BAQA-1, 222.5 ft, 03CW108, G27/2. L, *Diatomozonotriletes franklinii* McGregor and Camfield, 1982. A1-69, 1830 ft, 26961, U30/4. M–N, *Dibolisporites bullatus* (Allen) Riegel, 1973. M, BAQA-1, 223.5 ft, 03CW109, K29/4. N, WELL-7, 13738.5 ft, 62323, W32/1.


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

Diagnosis. A small *Diaphanospora* with a darker apical sub-triangular band on the spore body.

Description. Amb is sub-circular. Laesurae are straight, simple or rarely accompanied by narrow labra, *c.* 1 μm in overall width, three-fifths to three-quarters of the amb radius in length, connected by curvaturae perfectae not always well visible and often obscured by the folds of sexine. Nexine is laevigate, commonly 1–2 μm thick. A darker apical sub-triangular band, with straight, slightly concave or convex sides, extends to, or almost to, the end of the laesurae. This thickened area is up 3–6 μm wide interradially. An inner lighter sub-triangular area (with a thinner nexine), generally with slightly concave sides is present proximally and surrounded by the darkened band. Sexine extremely thin, transparent, closely appressed to the spore body and attached proximally close to the curvaturae. Surface of sexine randomly and finely folded.

Dimensions. 26(41)51 μm; 17 specimens measured.

Remarks. Specimens in which the outer layer is locally detached are not uncommon (Fig. 22E, G). Specimens in which the outer layer is missing are common in the less well-preserved palynological assemblages and consequently are similar to *Retusotriletes celatus* sp. nov. described below. The very delicate sexine may have been torn off by sedimentary or taphonomic processes. The two form-species *D. milleri* and *R. celatus* thus represent a unique biological species with the different states of preservation between both. They are grouped into the *D. milleri* Morphon (Table 1). They sometimes co-occur and have similar stratigraphical ranges.

Comparison. Diaphanospora riciniata and *D. perplexa* Balme and Hassell, 1962 are labrate and do not have a thickened apical area on the spore body.

Occurrence. BAQA-1, JNDL-3, JNDL-4, WELL-2, WELL-4 and WELL-7; Jauf Formation (Subbat and Hammamiyat members); *milleri* to *lindlarensis-sextantii* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone.

Genus DIATOMOZONOTRILETES Naumova emend. Playford, 1962

Type species. Diatomozonotriletes saetosus (Hacquebard and Barss) Hughes and Playford, 1961.

Diatomozonotriletes franklinii McGregor and Camfield, 1982
Figure 22L

1966 *Diatomozonotriletes devonicus* Naumova; Mikhailova, pl. 1, fig. 2.
1972 *Diatomozonotriletes devonicus* Naumova; McGregor and Uyeno, pl. 2, fig. 6.
1976 *Anapiculatisporites petilus* Richardson; Massa and Moreau-Benoit, pl. 3, fig. 4.
1979 *Anapiculatisporites petilus* Richardson; Moreau-Benoit, p. 32.
1985 *Anapiculatisporites petilus* Richardson; Massa and Moreau-Benoit, pl. 1, fig. 2.
1982 *Diatomozonotriletes franklinii* McGregor and Camfield, p. 36, pl. 7, figs 10–13.

Dimensions. 35(42)63 μm; 14 specimens measured.

Comparison. Diatomozonotriletes oligodontus Chibrikova, 1962 has predominantly wider, less closely spaced sculptural elements. *Diatomozonotriletes* sp. *in* Allen (1965) closely resembles *D. franklinii* McGregor and Camfield, 1982, except for a greater tendency towards concave-triangular amb. *Camarozonotriletes sextantii* McGregor and Camfield, 1976 has similar sculpture but has a prominent interradial cingulum.

Occurrence. BAQA-1, JNDL-3 and JNDL-4; Jauf Formation (Subbat and Hammamiyat members); *asymmetricus* to *lindlarensis-sextantii* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *triangulatus-catillus* 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 Emsian – lower Eifelian of Algeria (Moreau-Benoit *et al.* 1993); upper Emsian–Givetian of Amazon and Paraná basins, Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003); upper Eifelian – lower Givetian of Canada (McGregor and Uyeno 1972); Emsian–lower Givetian of Libya (Moreau-Benoit 1989); Emsian–Eifelian of Morocco (Rahmani-Antari and Lachkar 2001); and upper Eifelian of Russian Platform (Avkhimovitch *et al.* 1993).

Genus DIBOLISPORITES Richardson, 1965

Type species. Dibolisporites echinaceus (Eisenack) Richardson, 1965.

Comparison. Biharisporites Potonié, 1956 contains megaspores with similar sculpture. *Apiculiretusispora* Streel, 1964 shows a variable sculpture of small grani, coni or spinae, which measure less than 1 μm high.

Dibolisporites bullatus (Allen) Riegel, 1973
Figure 22M–N

1965 *Bullatisporites bullatus* Allen, p. 703, pl. 96, figs 5–7.
1973 *Dibolisporites bullatus* Allen; Riegel, p. 84, pl. 10, figs 10–12; pl. 11, figs 1–2.

Dimensions. 54(75)84 μm; 14 specimens measured.

Remarks. Although McGregor and Camfield (1982) consider *D. bullatus* as synonymous with *D. echinaceus* (Eisenack) Richardson, 1965, these two species are easily differentiated here and the synonymy is rejected.

Comparison. McGregor (1973) observed an intergradation from spores represented by the holotype of *D. echinaceus* to those of the holotype of *D. bullatus*, which is figured in Allen (1965). The two species are easily distinguishable, in this study, because the specimens of *D. echinaceus* are more densely ornamented with elongate, more or less parallel-sided spinae.

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

Previous records. From upper Givetian – lower Frasnian of France (Brice *et al.* 1979; Loboziak and Streel 1980); upper Emsian–Givetian of Germany (Riegel 1973; Loboziak *et al.* 1990); and Pragian–Eifelian of Spitsbergen, Norway (Allen 1965).

Dibolisporites echinaceus (Eisenack) Richardson, 1965
Figure 23A–B

1944 *Triletes echinaceus* Eisenack, p. 113, pl. 2, fig. 5.
? 1953 *Retusotriletes devonicus* Naumova, pl. 22, fig. 108.
? 1962 *Retusotriletes devonicus* Naumova var. *echinatus* Chibrikova, p. 393, pl. 1, fig. 9.
1965 *Dibolisporites echinaceus* Eisenack; Richardson, p. 568, P. 89, figs 5–6; text-figs 3B–D.
non 1973 *Dibolisporites bullatus* Allen; Riegel, p. 84, pl. 10, figs 10–12; pl. 11, figs 1–2.
1975 *Dibolisporites triangulatus* Tiwari and Schaarschmidt, p. 21, pl. 7, figs 3–4; pl. 8, figs 1–2; text-fig. 9.

Dimensions. 60(87)129 μm; 11 specimens measured.

Comparison. Dibolisporites triangulatus Tiwari and Schaarschmidt, 1975 is identical to *D. echinaceus* Richardson, 1965. *Retusotriletes devonicus* figured but not described by Naumova (1953) could be synonymous with *D. echinaceus*, but the details of the ornament cannot be seen. *R. devonicus* var. *echinatus* Chibrikova, 1962 could be also synonymous. *Dibolisporites* cf. *gibberosus* var. *major* (Kedo) Richardson, 1965 has shorter sculptural elements. *D. pseudoreticulatus* Tiwari and Schaarschmidt, 1975 has relatively high and wide curvatural ridges. Although *D. radiatus* Tiwari and Schaarschmidt, 1975 is considered as synonymous with *D. echinaceus* according to McGregor (1973), they are here distinguished because *D. radiatus* has larger sculptural elements disposed in a regular radial pattern. *D. varius* Tiwari and Schaarschmidt, 1975 has baculate ornamentation. Although *D. bullatus* (Allen) Riegel, 1973 is often placed in synonymy with *D. echinaceus*, it has more bulbous, wider spinae. All these species listed display only minor differences with *D. echinaceus*, so their assignation may be sometimes difficult.

Occurrence. BAQA-1, JNDL-1, JNDL-3 and JNDL-4; Jauf (Subbat to Murayr members) and Jubah formations; *ovalis* to *svalbardiae-eximius* zones. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *rugulata-libyensis* zones.

Previous records. Widely reported and often common in Early–Middle Devonian (particularly Middle Devonian) assemblages from many parts of the world; e.g. Algeria (Boumendjel *et al.* 1988; Moreau-Benoit *et al.* 1993), Belgium (Steemans 1989), Bolivia (Perez-Leyton 1990), Brazil (Mendlowicz Mauller *et al.* 2007), Canada (McGregor and Owens 1966; McGregor and Uyeno 1972; McGregor 1973; McGregor and Camfield 1976, 1982), China (Gao Lianda 1981), France (Brice *et al.* 1979; Loboziak and Streel 1980; Le Hérissé 1983), Germany (Lanninger 1968; Riegel 1968, 1973; Tiwari and Schaarschmidt 1975; Steemans 1989; Loboziak *et al.* 1990), Iran (Ghavidel-Syooki 2003), Libya (Paris *et al.* 1985; Streel *et al.* 1988; Moreau-Benoit 1989), Poland (Turnau 1986, 1996; Turnau and Racki 1999; Turnau *et al.* 2005), Saudi Arabia (Al-Ghazi 2007) and Scotland (Richardson 1965; Marshall 1988; Marshall and Fletcher 2002).

Dibolisporites eifeliensis (Lanninger) McGregor, 1973
Figure 23C–E

1966 cf. *Archaeotriletes setigerus* Kedo; McGregor and Owens, pl. 3, fig. 12.
1967 *Acanthotriletes inferus* Naumova; Beju, pl. 1, fig. 14.
1968 *Anapiculatisporites eifeliensis* Lanninger, p. 124, pl. 22, fig. 11.
1973 *Dibolisporites eifeliensis* (Lanninger) McGregor, p. 31, pl. 3, figs 17–22, 26.
non 1988 *Dibolisporites eifeliensis* (Lanninger) McGregor; Ravn and Benson, pl. 3, figs 16–23.

Dimensions. 29(42)60 μm; 20 specimens measured.

Comparison. Dibolisporites quebecensis McGregor, 1973 has smaller sculptural elements consisting of bacula and verrucae as well as tubercules. *Anapiculatisporites petilus* Richardson, 1965 has more widely spaced thinner pointed elements; about 15 around the periphery.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4, WELL-5, WELL-6 and WELL-7; Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqaensis* to *lindlarensis-sextantii* 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; *lindlarensis-sextantii* to *svalbardiae-eximius* zones.

Previous records. From upper Lochkovian–Emsian of Belgium (Steemans 1989); upper Lochkovian – lower Emsian of Paraná and Solimões basins, Brazil (Rubinstein *et al.* 2005; Mendlowicz Mauller *et al.* 2007); Emsian–Eifelian of Canada (McGregor and Owens 1966; McGregor 1973; McGregor and Camfield 1976); upper Pragian – lower Emsian of China (Gao Lianda 1981); upper Lochkovian – ?lowermost Pragian of Germany (Steemans 1989); Emsian of Iran (Ghavidel-Syooki 2003); Pragian–lowermost Eifelian of Libya (Paris *et al.* 1985; Moreau-Benoit 1989); upper Pragian–Eifelian of Morocco (Rahmani-Antari and Lachkar 2001); Pragian–?lowermost Eifelian of Poland (Turnau 1986; Turnau *et al.* 2005); and Emsian of Saudi Arabia (Al-Ghazi 2007).

Dibolisporites farraginis McGregor and Camfield, 1982
Figure 23F–G

1982 *Dibolisporites farraginis* McGregor and Camfield, p. 38, pl. 8, figs 3–4; text-fig. 54.

Dimensions. 42(60)77 μm; 18 specimens measured.

Remarks. Specimens assigned to this species belong to a more or less intergrading series from those with predominantly conate and small verrucose sculpture (*D. farraginis* and *D. uncatus* (Naumova) McGregor and Camfield, 1982) to those with large verrucate sculptural elements, and thus conform rather closely to the diagnosis of *Verrucosisporites scurrus* (Naumova) McGregor and Camfield, 1982 and *V. premnus* Richardson, 1965. All these forms belong to the *V. scurrus* Morphon defined by McGregor and Playford (1992). Therefore, the *D. farraginis* Morphon also defined by McGregor and Playford (1992) is included in the *V. scurrus* Morphon (Table 1).

Comparison. Dibolisporites farraginis is distinguished from *D. vegrandis* McGregor and Camfield, 1982 by larger, more elongate sculptural elements, and from *Dibolisporites* cf. *correctus* (Naumova) Richardson, 1965 by relatively narrower base, more varied sculptural elements. *D. uncatus* (Naumova) McGregor and Camfield, 1982 has larger sculptural elements but intergrades with *D. farraginis* as it was noted as a component of the *D. farraginis* Morphon in McGregor and Playford (1992, table 4). This morphon includes sub-circular forms sculptured with a mixture of mostly discrete grana, coni, spinae, biform elements and verrucae of various sizes and simple laesurae.

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

Previous records. From upper Eifelian – lower Givetian of Canada (McGregor and Camfield 1982); and lower Eifelian – lower Givetian of Libya (Moreau-Benoit 1989).

Dibolisporites (*Apiculiretusispora*) *gaspiensis* (McGregor) comb. nov.
Figure 23H–J

1966 cf. *Geminospora svalbardiae* (Vigran) Allen, McGregor and Owens, pl. 5, fig. 16.
1970 ?*Apiculiretusispora* sp. McGregor *et al.*, pl. 2, fig. 11.
1973 *Apiculiretusispora gaspiensis* McGregor, p. 28, pl. 3, figs 1–4.
1974 Large spores of *Chaleuria cirrosa* Andrews *et al.*, pp. 394, 398, pl. 56, figs 1, 2; pl. 57, fig. 4.
1976 *Apiculiretusispora gaspiensis* McGregor; McGregor and Camfield, p. 11, pl. 6, figs 11–12.

Dimensions. 53(65)80 μm; 16 specimens measured.

Remarks. McGregor (1973) described this form as two-layered. Nevertheless, specimens described here are single-layered, but the concentric equatorial folding sometimes gives the impression of a two-layered spore. This species is transferred to the genus *Dibolisporites* Richardson, 1965 because it is sculptured with short pila, bacula or biform elements up to 2 μm high and not spinae characteristic of the genus *Apiculiretusispora* (Streel) Streel, 1967.

Comparison. This species differs from *Apiculiretusispora arenorugosa* McGregor, 1973 and *A. plicata* (Allen) Streel, 1967 in possessing a thicker exine. *Geminospora svalbardiae* (Vigran) Allen, 1965 is distinctly two-layered.

Occurrence. JNDL-1, JNDL-3, JNDL-4 and WELL-3; Jauf (Subbat to Murayr members) and Jubah formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to

FIG. 23. 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, *Dibolisporites echinaceus* (Eisenack) Richardson, 1965, magnification ×750. A, A1-69, 1596 ft, 26989, R48/3. B, JNDL-1, 495.0 ft, PPM014, V35. C–E, *Dibolisporites eifeliensis* (Lanninger) McGregor, 1973. C, BAQA-1, 223.5 ft, 03CW109, F48/2. D, BAQA-1, 223.5 ft, 03CW109, J42. E, WELL-2, 15886.3 ft, 63102, G29/4. F–G, *Dibolisporites farraginis* McGregor and Camfield, 1982. F, A1-69, 1530 ft, 26984, O32/4. G, A1-69, 1416 ft, 26993, M44/2. H–J, *Dibolisporites* (*Apiculiretusispora*) *gaspiensis* (McGregor) comb. nov. H, JNDL-1, 172.7 ft, PPM007, N42. I, JNDL-1, 174.6 ft, 60848, L33/1. J, JNDL-1, 155.6 ft, 60838, T28/4. K, *Dibolisporites pilatus* Breuer *et al.*, 2007*c*. JNDL-1, 167.8 ft, 60843, L38/3.


A
B
C
D
E
F
G
H
I
J
K