rugulata-libyensis zones. MG-1; Awaynat Wanin I Formation; *incognita* Zone.

Previous records. From Emsian–Givetian of Canada (McGregor and Owens 1966; McGregor 1973; McGregor and Camfield 1976).

Dibolisporites pilatus Breuer *et al.*, 2007c
Figure 23K

2007c *Dibolisporites pilatus* Breuer *et al.*, p. 50, pl. 6, figs 10–13.

Dimensions. 54(68)79 μm; 29 specimens measured.

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

Dibolisporites tuberculatus sp. nov.
Figure 24A–F

1988 *Dibolisporites eifeliensis* (Lanninger) McGregor; Ravn and Benson, pl. 3, figs 16–23.

Derivation of name. From *tuberculatus* (Latin), meaning made up of tubercules; refers to the baculate distal surface.

Holotype. EFC O43/2 (Fig. 24B), slide 60849.

Paratype. EFC Q39 (Fig. 24F), slide 60845; JNDL-1 core hole, sample 172.7 ft.

Type locality and horizon. JNDL-1 core hole, sample 177.0 ft; Jubah Formation at Domat Al-Jandal, Saudi Arabia.

Diagnosis. A robust *Dibolisporites* sculptured with bacula, tubercules and biform elements. Sculptural elements consisting of a tapering conical stem, surmounted by an expanded tip.

Description. Amb is circular to sub-circular. Laesurae straight, simple or accompanied by labra, up to 3 μm in overall width, three-fifths to nine-tenths of the amb radius in length. Curvaturae are often visible or perceptible. Exine is 1.5–3 μm thick equatorially. Proximo-equatorial regions are sculptured with biform elements, tubercules, bacula 1.5–4.5 μm high, 1–3.5 μm wide at base, 1–5 μm apart. Biform elements, sub-circular in plan view, consist of a tapering conical stem, surmounted by an expanded tip less than 2 μm in diameter. Contact areas are laevigate, scabrate or granulate.

Dimensions. 43(56)69 μm; 24 specimens measured.

Comparison. Ravn and Benson (1988) figured specimens as *D. eifeliensis* (Lanninger) McGregor, 1973. Although no description of the latter is present, they have sculptural elements that are too coarse for *D. eifeliensis* (Lanninger) McGregor, 1973 *sensu stricto*. On the contrary, they have the same sculpture as *D. tuberculatus* sp. nov. described here. *D. quebecensis* McGregor, 1973 has smaller tubercules and bacula. Sculptural elements of *D. eifeliensis* have either a smaller or no expansion at the tip.

Occurrence. JNDL-1, JNDL-3, JNDL-4 and S-462; Jauf (Hammamiyat and Murayr members) and Jubah formations; *lindlarensis-sextantii* to *rugulata-libyensis* Zone. A1-69; Awaynat Wanin II Formation; *incognita* to *triangulatus-catillus* zones. MG-1; Awaynat Wanin I Formation; *rugulata* Zone.

Previous records. From upper Eifelian of Parnaíba Basin, Brazil (Breuer and Grahn 2011); and ?Emsian–Eifelian of Georgia, USA (Ravn and Benson, 1988).

Dibolisporites turriculatus Balme, 1988
Figure 24G

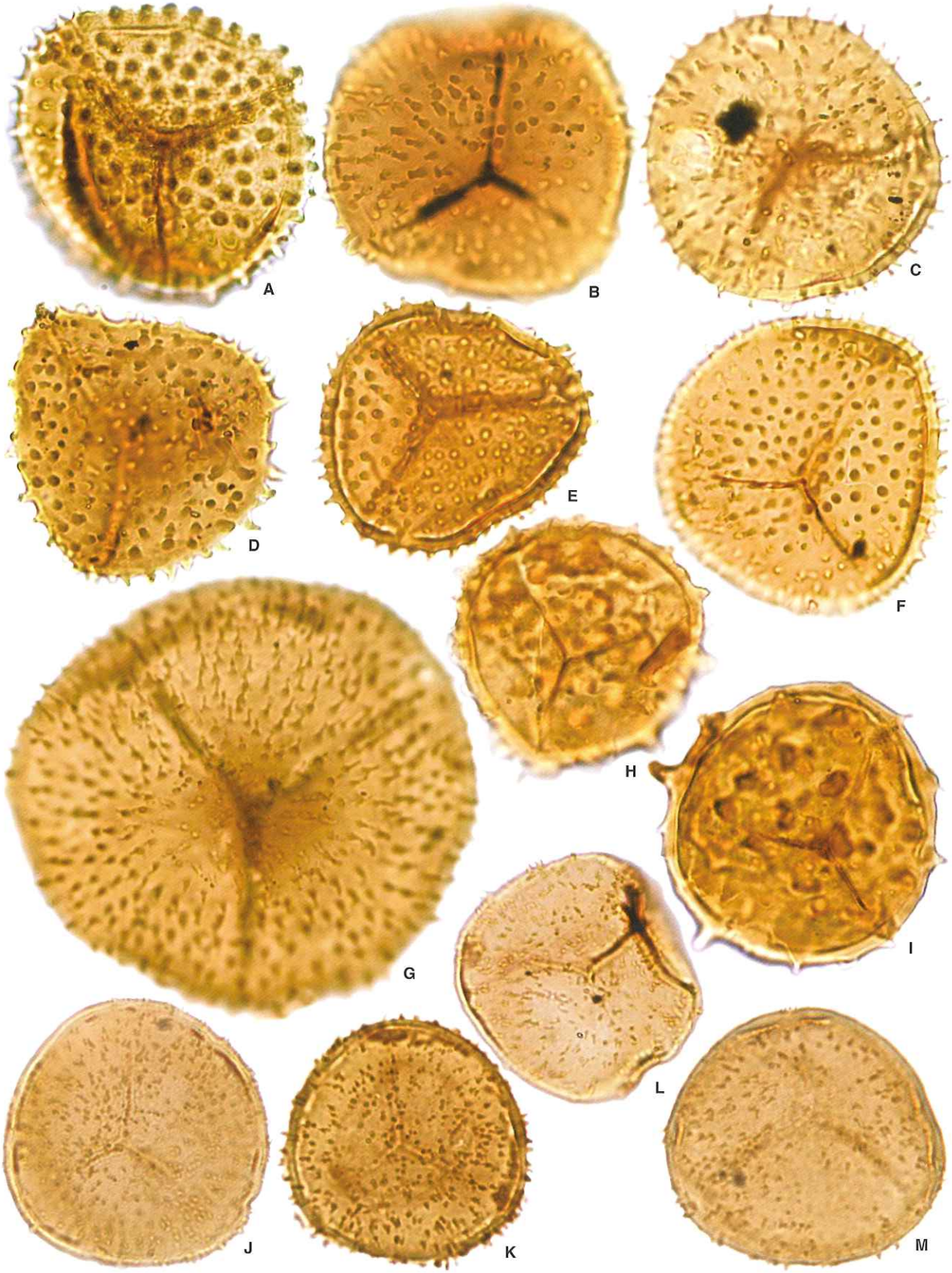
1962 *Apiculatisporis* sp. Balme, p. 4, pl. 1, fig. 14.
1975 *Dibolisporites* sp. Grey, fig. 61 h.
1988 *Dibolisporites turriculatus* Balme, p. 128, pl. 5, figs 10–14.
1992 *Dibolisporites* sp. cf. *D. turriculatus* Balme; Grey, pl. 14, figs 5–6.

Dimensions. 63(82)114 μm; 20 specimens measured.

Remarks. Balme (1988) described some specimens showing laesurae set in a slightly thinner proximal concavo-triangular area, but this character is not recognized in the population studied here.

Comparison. Dibolisporites eifeliensis (Lanninger) McGregor, 1973 is smaller. Although *D. tuberculatus* sp. nov. is smaller and has more massive sculptural elements, extreme forms characterized

FIG. 24. 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, *Dibolisporites tuberculatus* sp. nov. A, JNDL-1, 172.7 ft, 60845, D50/3. B, Holotype, JNDL-1, 177.0 ft, 60849, O43/2. C, JNDL-1, 177.0 ft, 60850, P32. D, JNDL-1, 177.0 ft, 60850, J31/1. E, JNDL-1, 174.6 ft, 60847, C41/3. F, Paratype, JNDL-1, 172.7 ft, 60845, Q39. G, *Dibolisporites turriculatus* Balme, 1988. A1-69, 1277 ft, 62636, O53/3. H–I, *Dibolisporites uncatus* (Naumova) McGregor and Camfield, 1982. H, A1-69, 1322 ft, 27126, M40. I, A1-69, 1277 ft, 62637, V-W42. J–M, *Dibolisporites verecundus* sp. nov. J, BAQA-2, 50.8 ft, 66813, G35. K, BAQA-2, 133.0 ft, 03CW136, N30. L, Holotype, BAQA-2, 52.0 ft, 03CW128, L44/3. M, Paratype, BAQA-2, 64.5 ft, 66818, K33/3.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by thinner sculpture have the same ornamentation as *D. turriculatus*.

Occurrence. WELL-1; Jubah Formation; *lemurata-langii* to *triangulatus-catillus* zones. 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 lower Eifelian – lower Frasnian of Australia (Balme 1962, 1988; Hashemi and Playford 2005).

Dibolisporites uncatus (Naumova) McGregor and Camfield, 1982
Figure 24H–I

1953 *Acanthotriletes uncatus* Naumova, pp. 26, 28, pl. 1, figs 23–24; pl. 5, fig. 36.
1960 *Verrucosisporites variabilis* McGregor, p. 30, pl. 11, fig. 15.
1964 *Lophotriletes uncatus* (Naumova) Vigran, p. 13, pl. 1, figs 3–4.
1964 Unnamed; Regali, text-fig. 2–6.
1965 *Verrucosisporites* cf. *uncatus* (Naumova) Richardson, p. 572, pl. 89, fig. 13.
1967 *Raistrickia* sp. Scott and Doher, fig. 3m.
1971 *Dibolisporites variabilis* (McGregor) Smith, p. 83.
1982 *Dibolisporites uncatus* (Naumova) McGregor and Camfield, p. 38, pl. 8, figs 5–6, 11; text-fig. 55.

Dimensions. 30(52)68 μm; 13 specimens measured.

Remarks. This taxon belongs to the *V. scurrus* Morphon (Table 1) defined by McGregor and Playford (1992). Specimens assigned to this species belong to a more or less intergrading series from those with predominantly conate and small verrucose sculpture (*D. farraginis* McGregor and Camfield, 1982) to those with large verrucate sculptural elements, and thus conform rather closely to the definition of *V. scurrus*.

Comparison. Extreme forms of *Verrucosisporites scurrus* (Naumova) McGregor and Camfield, 1982 intergrade with *D. uncatus*. *V. scurrus* has slightly larger, more closely spaced sculptural elements, a greater proportion of them flat-topped. *V. premnus* Richardson, 1965 has much larger, mostly flat-topped, non-biform verrucae and bacula. *D. farraginis* McGregor and Camfield, 1982 has smaller sculptural elements but intergrades with *D. uncatus* within the *D. farraginis* Morphon. *Convolutispora crassata*? (Naumova) McGregor and Camfield, 1982 has larger, commonly more closely crowded sculptural elements fused into ridges.

Occurrence. S-462 and WELL-8; Jubah Formation; *lemurata-langii* to *langii-concinna* zones. A1-69; Awaynat Wanin II Formation; *rugulata-libyensis* 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 Givetian–lower Frasnian of Paraná Basin, Brazil (Loboziak *et al.* 1988); upper Givetian – lower Frasnian of France (Brice *et al.* 1979; Loboziak and Streel, 1980, 1988); upper Eifelian – lower Givetian of Canada (McGregor and Camfield, 1982); uppermost Eifelian of Germany (Loboziak *et al.* 1990); Frasnian of Spitsbergen, Norway (Vigran 1964); and Givetian of Scotland (Richardson 1965).

Dibolisporites verecundus sp. nov.
Figure 24J–M

Derivation of name. From *verecundus* (Latin) meaning inconspicuous, moderate; refers to the small scattered distal ornamentation.

Holotype. EFC L44/3 (Fig. 24L), slide 03CW128.

Paratype. EFC K33 (Fig. 24M), slide 66818; BAQA-2 core hole, sample 64.5 ft.

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

Diagnosis. A *Dibolisporites* sculptured with irregularly scattered small spinae and coni.

Description. Amb is circular to sub-circular. Laesurae are straight, simple, around four-fifths of the amb radius in length. Exine 1–2 μm thick equatorially. Proximo-equatorial and distal regions are sculptured with irregularly scattered spinae and coni, up to 2 μm high, 0.5–1 μm wide at base. Sculptural elements are sub-circular in plan view and 0.5–6 μm apart. Contact areas are laevigate to infragranulate.

Dimensions. 37(43)50 μm; 16 specimens measured.

Comparison. Cymbosporites rarispinosus Steemans, 1989 is patinate and sculptured with larger spinae.

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

Dibolisporites sp. 1
Figure 25A–C

2007*c* *Dibolisporites echinaceus* (Eisenack) Richardson; Breuer *et al.*, pl. 6, fig. 8.

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple and two-thirds to three-quarters of the amb

radius in length. Exine is 1–2 µm thick equatorially. Proximo-equatorial and distal regions are sculptured with a mixture of densely distributed parallel-sided elements, tubercules, bacula, spinae, 0.5–3 µm high, 0.5–1 µm wide at base. Sculptural elements are sub-circular to polygonal in plan view and generally *c.* 0.5 µm apart. Different types of ornament may occur on a single specimen. Contact areas are granulate.

Dimensions. 28(42)50 µm; nine specimens measured.

Remarks. On some specimens (Fig. 25A), ornamentation appears longer in interradial areas.

Comparison. Dibolisporites echinaceus (Eisenack) Richardson, 1965 has a larger amb (61–129 µm) and laevigate or infragranular contact areas.

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

Dibolisporites sp. 2
Figure 25D–E

Description. Amb is sub-circular to sub-circular. Laesurae are straight, simple, about three-quarters of the amb radius in length. Curvaturae often are visible or perceptible. Exine is 1–2 µm thick equatorially. Proximo-equatorial and distal regions are sculptured with scattered spinae 1.5–3.5 µm high, 1–2 µm wide at base. Sculptural elements are sub-circular in plan view and 1–3 µm apart. Contact areas are granulate.

Dimensions. 23(30)37 µm; four specimens measured.

Comparison. Dibolisporites eifeliensis (Lanninger) McGregor, 1973 is larger with no accuminate-tipped elements.

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

Dibolisporites sp. 3
Figure 25F–G

Description. Amb is circular to sub-circular. Laesurae are straight, simple, extending to, or almost to, the equator. Exine 1–2 µm thick equatorially. Proximo-equatorial and distal regions are sculptured with irregularly scattered spinae and coni, 1.5–3.5 µm high, 1–3 µm wide at base. Sculptural elements are sub-circular in plan view and 0.5–10 µm apart. Contact areas are laevigate.

Dimensions. 32–44 µm; two specimens measured.

Comparison. Cymbosporites rarispinosus Steemans, 1989 is patinate and sculptured with spinae that flare more at the base and show a more flexuous appearance.

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

Genus DICTYOTRILETES Naumova, 1939 ex Ishchenko, 1952

Type species. Dictyotriletes bireticulatus (Ibrahim) Potonié and Kremp, 1955.

Dictyotriletes biornatus Breuer *et al.*, 2007*c* var. *biornatus*
Figure 25H–J

2007*c* *Dictyotriletes biornatus* Breuer, p. 50, pl. 7, figs 1–9.

Description. Amb is sub-circular to triangular. Laesurae are rarely visible. Exine is 1–3 µm thick and thinner proximally, laevigate. Proximo-equatorial and distal are regions are reticulate. Muri of reticulum formed by orientated discrete rows of grana (1–2 µm wide and high) that are commonly slightly merged at the base. Polygonal lumina of reticulum are 4–9 µm in greatest diameter, about 30 to 40 in total number.

Dimensions. 47(58)72 µm; 55 specimens measured.

Comparison. Dictyotriletes biornatus Breuer *et al.*, 2007*c* var. *murinatus* var. nov. show a further merger of grana so as to form solid muri. Specimens of *Cymbosporites variabilis* var. *variabilis* sp. et var. nov. have no real lumina but rather pseudolumina with some grana occurring inside. All these forms are related and belong to the *D. biornatus* Morphon (Table 1; see discussion in *C. variabilis* sp. nov.).

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

Dictyotriletes biornatus Breuer *et al.*, 2007*c* var. *murinatus* nov. var.
Figure 25K–N

2007*a* *Dictyotriletes* sp. 1 Breuer *et al.*, text-figs 1–3E.
2007*b* Unnamed spore Breuer *et al.*, text-figs 1–5.

Derivation of name. From *murinatus* (Latin), meaning made up of muri; refers to the reticulate distal surface.

Holotype. EFC G37/3 (Fig. 25N), slide 03CW124.

Paratype. EFC J27/1 (Fig. 25M), slide 62275; BAQA-1 core hole, sample 395.2 ft.

Type locality and horizon. BAQA-1 core hole, sample 408.3 ft; Jauf Formation at Baq'a, Saudi Arabia.

Diagnosis. A *Dictyotriletes biornatus* with muri of reticulum constituted by discontinuous or irregular, low elongated elements, generally resulting of the merger of several discrete grana.

Description. Amb is sub-circular to sub-triangular. Exine is 1–3 μm thick equatorially. Exine is thinner proximally, laevigate. Proximo-equatorial and distal regions are reticulate. Muri of reticulum are comprised of discontinuous or irregular elongated elements, 0.5–2 μm high and wide. The elongated elements appear generally to be the result of the merger of several discrete elements. In addition, some discrete elements (grana) may be present in low numbers lined up on the reticulum. Sculptural elements vary in thickness and shape. Polygonal lumina of reticulum are 4–9 μm in greatest diameter, about 30 to 40 in number.

Dimensions. 40(53)67 μm; 27 specimens measured.

Remarks. Dictyotriletes biornatus var. *murinatus* represents the end-member of a lineage comprising several form-species (see discussion in *Cymbosporites variabilis* sp. nov.).

Comparison. Dictyotriletes biornatus Breuer *et al.*, 2007 var. *biornatus* is considered as sculptured with muri only formed by grana, which are slightly merged at base. *D. emsiensis* (Allen) McGregor, 1973 has more robust, continuous and regular muri.

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

Dictyotriletes emsiensis (Allen) McGregor, 1973
Figure 25O

1965 *Reticulatisporites emsiensis* Allen, p. 705, pl. 97, figs 9–11.
? 1967 ?*Dictyotriletes* Richardson, pl. 4, fig. c.
non 1968 *Reticulatisporites emsiensis* Allen; Lanninger, p. 131, pl. 23, fig. 4.
1973 *Dictyotriletes emsiensis* (Allen) McGregor, p. 42, pl. 5, fig. 15.
1976 *Dictyotriletes* cf. *D. emsiensis* (Allen) McGregor; McGregor and Camfield, p. 21, pl. 3, figs 5–6.

Dimensions. 44(64)80 μm; 21 specimens measured.

Remarks. The *D. emsiensis* Morphon defined by Rubinstein *et al.* (2005) includes the species *D. emsiensis*, *D. granulatus* Steemans, 1989, some specimens incorrectly attributed to *D. subgranifer* McGregor, 1973, and other specimens in open nomenclature. These species share very similar morphological features. They are characterized by a proximo-equatorial reticulum, with robust muri that are commonly widened and bear papillae or spinae at the junctions.

Comparison. Dictyotriletes subgranifer McGregor, 1973 has narrower, lower muri that are serrated along the upper edge, and not widened or papillate at the junctions. In addition, the lumina tend to be smaller in diameter in *D. subgranifer*. Although *D. granulatus* Steemans, 1989 is closely comparable with *D. emsiensis*, it is smaller and has a granulate proximal face. *D. biornatus* Breuer *et al.*, 2007*c* var. *murinatus* var. nov. has lower muri.

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. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *annulatus-protea* to *svalbardiae-eximius* zones.

Previous records. Dictyotriletes emsiensis is eponymous for the Pragian polygonalis-emsiensis Assemblage Zone of the Old Red Sandstone Continent and adjacent regions (Richardson and McGregor 1986) and the early Pragian E Interval Zone of Western Europe (Streel *et al.* 1987). *D. emsiensis* has an almost worldwide distribution and has been reported from Pragian of Algeria (Boumendjel *et al.* 1988); upper Pragian – lower Eifelian of Argentina (Le Hérissé *et al.* 1997; Rubinstein and Steemans

FIG. 25. 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, *Dibolisporites* sp. 1. A, BAQA-1, 406.0 ft, 03CW123, D23. B, BAQA-2, 50.8 ft, 03CW127, P25/3. C, BAQA-1, 406.0 ft, 03CW123, E50. D–E, *Dibolisporites* sp. 2. D, BAQA-2, 50.2 ft, 03CW126, G44/4. E, BAQA-2, 52.0 ft, 03CW128, F32/3. F–G, *Dibolisporites* sp. 3. F, A1-69, 1830 ft, 26962, L43. G, A1-69, 1596 ft, 26990, H48/4. H–J, *Dictyotriletes biornatus* Breuer *et al.*, 2007*c* var. *biornatus*. H, JNDL-4, 495.2 ft, 03CW275, L41/4. I, BAQA-1, 366.9 ft, 62259, D44/3. J, BAQA-1, 308.3 ft, 62244, D46. K–N, *Dictyotriletes biornatus* Breuer *et al.*, 2007*c* var. *murinatus* var. nov. K, BAQA-1, 345.5 ft, 62251, U32/1. L, BAQA-1, 345.5 ft, 62252, H46. M, Paratype, BAQA-1, 395.2 ft, 62275, J27/1. N, Holotype, BAQA-1, 408.3 ft, 03CW124, G37/3. O, *Dictyotriletes emsiensis* (Allen) McGregor, 1973. MG-1, 2180 m, 62973, H34/2. P–Q, *Dictyotriletes favosus* McGregor and Camfield, 1976. P, WELL-7, 13614.1 ft, 62372, S45. Q, JNDL-4, 364.6 ft, 03CW252, T37. R, *Dictyotriletes ?gorgoneus* Cramer, 1966*a in* McGregor (1973). BAQA-2, 64.5 ft, 66818, J42. S, *Dictyotriletes granulatus* Steemans, 1989. BAQA-2, 133.0 ft, 66825, L28. T–U, *Dictyotriletes hemeri* sp. nov. T, Paratype, S-462, 2460–2465 ft, 63293, W41. U, WELL-8, 16642.3 ft, 62407, E37.


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2007; Amenábar 2009); ?upper Lochkovian – upper Pragian of Belgium (Steemans 1989); Lochkovian–Eifelian of Bolivia (McGregor 1984); lower Lochkovian – lower Eifelian of Amazon, Parnaíba and Solimões basins, Brazil (Melo and Loboziak 2003; Grahn *et al.* 2005; Rubinstein *et al.* 2005; Steemans *et al.* 2008); Pragian–Emsian of Canada (McGregor 1973; McGregor and Camfield 1976); upper Pragian – lower Emsian of China (Gao Lianda 1981); Pragian–lower Emsian of Armorican Massif, France (Le Hérissé 1983); upper Lochkovian–Emsian of Germany (Steemans 1989); upper Pragian–Emsian of Morocco (Rahmani-Antari and Lachkar 2001); Emsian of Spitsbergen, Norway (Allen 1965); and Pragian of Saudi Arabia (Steemans, 1995).

Dictyotriletes favosus McGregor and Camfield, 1976
Figure 25P–Q

? 1973 *Dictyotriletes* sp. McGregor, p. 44, pl. 6, figs 1–2.
1976 *Dictyotriletes favosus* McGregor and Camfield, p. 21, pl. 2, figs 5–6.
1989 *Chelinospora favosa* (McGregor and Camfield) Steemans, p. 117, pl. 29, figs 1–3.
non 2005 *Chelinospora favosa* (McGregor and Camfield) Steemans; Rubinstein *et al.*, pl. 2, fig. 4.

Dimensions. 36(43)52 μm; 22 specimens measured.

Remarks. The Saudi Arabian population of *D. favosus* is smaller in overall size than that from Canada described by McGregor and Camfield (1976).

Comparison. Synonymy with *Dictyotriletes* sp. *in* McGregor (1973) is uncertain because it has slightly more robust muri with more pronounced elongations at their junctions.

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

Previous records. From uppermost Pragian – lowermost Emsian of Parnaíba Basin, Brazil (Grahn *et al.* 2005); upper Lochkovian – ?lowermost Pragian of Belgium (Steemans 1989); Pragian–Emsian of Canada (McGregor and Camfield 1976); Lochkovian of France (Steemans 1989); upper Lochkovian–Emsian of Germany (Steemans 1989); and Pragian of Saudi Arabia (Steemans 1995).

Dictyotriletes ?gorgoneus Cramer, 1966*a* in McGregor (1973)
Figures 25R, 26A

1954 Unnamed; Radforth and McGregor, pl. 2, fig. 61.
1965 *Reticulatisporites* sp. cf. *Dictyotriletes minor* Naumova; Allen, p. 706, pl. 97, figs 12–13.
1966 *Reticulatisporites* sp. cf. *Dictyotriletes minor* Naumova *in* Allen; McGregor and Owens, pl. 3, fig. 18.
? 1966*a* *Dictyotriletes gorgoneus* Cramer; p. 265, pl. 3, figs 69, 72.
? 1966 *Dictyotriletes minor* Naumova var. *nigritellus* Nadler, pl. 1, fig. 8.
1967 *Dictyotriletes* sp. McGregor, pl. 1, fig. 4.
1973 *Dictyotriletes ?gorgoneus* Cramer; McGregor, p. 43, pl. 5, figs 12, 17.
1979 *Dictyotriletes ?gorgoneus* Cramer; Lessuise *et al.*, p. 337, pl. 5, figs 16–17.

Dimensions. 26(33)37 μm; 16 specimens measured.

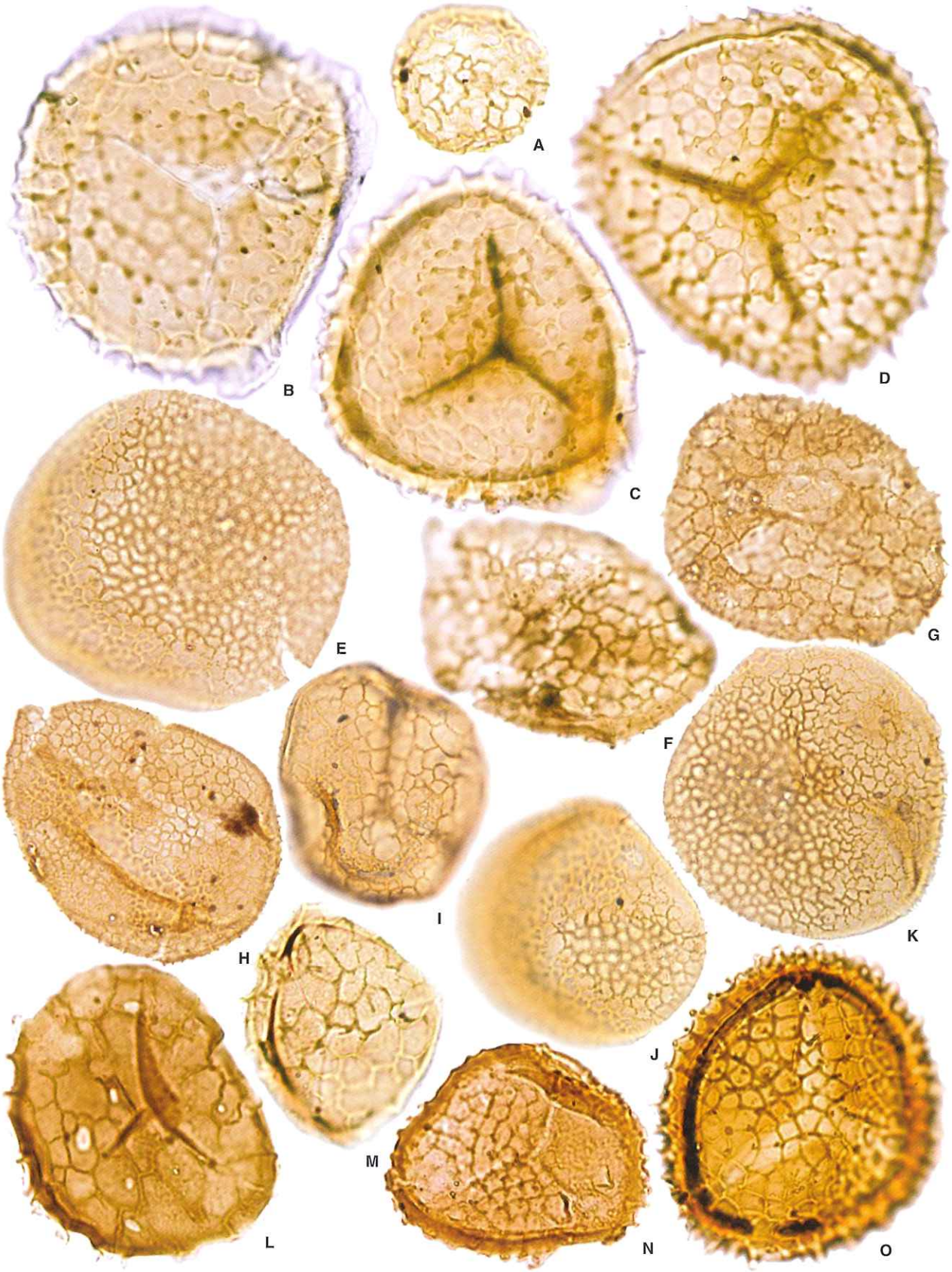
Remarks. In McGregor (1973), assignment to *D. gorgoneus* Cramer, 1966*a* is questioned because Cramer did not report a trilete mark on this species as in the Canadian specimens.

Comparison. Reticulatisporites sp. cf. *Dictyotriletes minor* Naumova, 1953 *in* Allen (1965) is considered here as similar to *D. ?gorgoneus* Cramer, 1966*a in* McGregor (1973). Allen (1965) mentioned the higher muri of *D. minor* Naumova, 1953 but expressed some doubt that this feature is of sufficient importance to distinguish his specimens from those assigned by Naumova to *D. minor*. The latter also has wider muri than *D. ?gorgoneus* Cramer, 1966*a in* McGregor (1973).

Occurrence. BAQA-1, BAQA-2 and WELL-4; Jauf Formation (Sha'iba to Subbat members); *ovalis* Zone.

Previous records. From upper Lochkovian – upper Emsian of Belgium (Lessuise *et al.* 1979; Steemans 1989); Emsian of Canada (McGregor and Owens 1966; McGregor 1973); lower Pragian–Emsian of Germany (Steemans, 1989); and Emsian–Givetian of Sipstbergen, Norway (Allen 1965).

FIG. 26. 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, *Dictyotriletes ?gorgoneus* Cramer, 1966*a in* McGregor (1973). BAQA-2, 50.8 ft, 03CW127, W40/3. B–D, *Dictyotriletes hemeri* sp. nov. B, S-462, 2510–2515 ft, 63297, T41/4. C, S-462, 2460–2465 ft, 63293, J32. D, Holotype, S-462, 2460–2465 ft, 63293, L45/3. E–K, *Dictyotriletes marshallii* sp. nov. E, Paratype, JNDL-4, 355.4 ft, 68673, D26/3. F, MG-1, 2639 m, 62780, B48/4. G, JNDL-3, 413.2 ft, 68567, E36/4. H, JNDL-4, 341.2 ft, 68671, Q53. I, JNDL-4, 179.9 ft, 68634, F45. J, JNDL-4, 163.7 ft, 68626, S54. K, Holotype, JNDL-4, 402.4 ft, 68682, M36. L–M, *Dictyotriletes subgranifer* McGregor, 1973. L, BAQA-1, 366.9 ft, 03CW117, G28. M, BAQA-1, 376.4 ft, 03CW119, O26/3. N–O, *Dictyotriletes* sp. 1. N, BAQA-1, 366.9 ft, 62259, F39/4. O, BAQA-1, 366.9 ft, 62259, T41-42.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Dictyotriletes granulatus Steemans, 1989
Figure 25S

? 1968 Spore no 2565 Magloire, pl. 5, fig. 11.
? 1975 *Dictyotriletes* sp. L Rauscher and Robardet, pl. 11, figs 13–14.
1979 *Dictyotriletes* sp. A D'Erceville, p. 94, pl. 3, fig. 6.
1989 *Dictyotriletes granulatus* Steemans, p. 133, pl. 36, figs 6–10.
2005 *Dictyotriletes emsiensis* Morphon (*pars*); Rubinstein *et al.*

Dimensions. 26–32 μm; two specimens measured.

Remarks. True specimens of *D. granulatus* Steemans, 1989 are included in the *D. emsiensis* Morphon defined by Rubinstein *et al.* (2005).

Comparison. Dictyotriletes sp. A *in* Richardson and Lister (1969) seems very similar but exhibits less elevated muri. *D. subgranifer* McGregor, 1973 has also granulate contact areas, but the grana are usually smaller. In addition, *D. subgranifer* has serrated muri along the upper edge. *D. emsiensis* (Allen) McGregor, 1973 is larger and does not show a granulate proximal face.

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

Previous records. From upper Lochkovian of Solimões Basin, Brazil (Rubinstein *et al.* 2005); and lower Lochkovian of Armorican Massif, France (Steemans 1989).

Dictyotriletes hemeri sp. nov.
Figures 25T–U, 26B–D

? 1966 *Dictyotriletes* sp. McGregor and Owens, pl. 4, figs 1–2.
1969 Indeterminate spore Cramer, pl. 2, fig. 28.
? 1973 *Dictyotriletes* sp. McGregor, p. 44, pl. 6 figs 1–2.
? 1992 *Dictyotriletes australis*? de Jersey; McGregor and Playford, pl. 7, figs 15–16.

Derivation of name. In honour of the American palynologist employed by Saudi Aramco, Darwin O. Hemer, who first studied the S-462 borehole.

Holotype. EFC L45/3 (Fig. 26D), slide 63293.

Paratype. EFC W41 (Fig. 25T), slide 63293; S-462 borehole, sample 2460–2465 ft.

Type locality and horizon. S-462 borehole, sample 2460–2465 ft; Jubah Formation in S-462, Saudi Arabia.

Diagnosis. A *Dictyotriletes* with lumina sub-circular to polygonal in plan view. Muri low and wider at junctions. Bacula with flared bases at the muri junctions. The tops of bacula flat or slightly concave, with bifurcate shape.

Description. Amb is sub-circular. Laesurae are straight and simple, three-fifths to four-fifths of the amb radius in length. Exine is 1–4 μm thick equatorially, sexine locally detached on some specimens. Contact areas are laevigate or infragranular. Proximo-equatorial and distal regions are reticulate. Lumina of reticulum are sub-circular to polygonal in plan view, 2–8 μm (rarely up to 12 μm) in greatest diameter. Muri are low, less than 1.5 μm wide at base, wider at junctions. Bacula occur with flared bases at the muri junctions, 0.5–3.5 μm high, 0.5–2.0 wide at base. The tops of bacula are flat or slightly concave, with bifurcate shape.

Dimensions. 46(59)80 μm; 24 specimens measured.

Comparison. Cramer (1969) illustrated, though not described, an indeterminate spore similar to *D. hemeri*. *Dictyotriletes* sp. figured in McGregor and Owens (1966) and McGregor (1973) resemble the specimens described here, but they have rounded and smaller protrusions at the muri junctions. McGregor and Playford (1992) figure a specimen resembling *D. hemeri* (except for the proximal dark triangular area) without giving a description. *D. australis* de Jersey, 1966 is smaller and devoid of discrete ornamentation at muri junctions. Some extreme specimens of *D. hemeri* may have a foveolate appearance and somewhat resemble *Brochotriletes bellatulus* Steemans, 1989, but they are distinguished from it by the tops of sculptural elements commonly being bifurcate.

Occurrence. WELL-1, S-462 and WELL-8; Jubah Formation; *rugulata-libyensis* to *triangulatus-catillus* zones, some specimens from S-462 may be caved into older strata.

Previous record. From Eifelian–Givetian of Spain (Cramer 1969).

Dictyotriletes marshallii sp. nov.
Figure 26E–K

Derivation of name. In honour of the British palynologist, Dr. John E. A. Marshall, for his outstanding contribution to the understanding of the Devonian spore assemblages and vegetational history.

Holotype. EFC M36 (Fig. 26K), slide 68682.

Paratype. D26/3 (Fig. 26E), slide 68673; JNDL-4 core hole, sample 355.4 ft.

Type locality and horizon. JNDL-4 core hole, sample 402.4 ft; Jauf Formation at Domat Al-Jandal, Saudi Arabia.

Diagnosis. A *Dictyotriletes* with small irregular lumina in plan view. Muri narrow, low and serrated. Proximal surface infragranular.

Description. Amb is sub-circular. Laesurae are straight, simple and seven-tenths to nine-tenths of the amb radius in length. Exine is 1–2 µm thick equatorially. Contact areas is infragranulate. Grana are less than 0.5 µm wide. Distal surface is reticulate. Muri are 0.5–1 µm high and wide at base, serrated along the upper edge. Sculptural elements (spines or coni), which constitute the serration, are less than 0.5 µm wide, often *c.* 0.5 µm high (rarely as high as 1.5 µm). Lumina are irregular in plan view, 1.5–6 µm in diameter, various in size and shape on a same specimen, *c.* 30–70 situated at equator.

Dimensions. 39(51)64 µm; 13 specimens measured.

Comparison. Dictyotriletes subgranifer McGregor, 1973 has larger lumina and their number is also fewer.

Occurrence. JNDL-3 and JNDL-4; Jauf Formation (Subbat and Hammamiyat members); *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Dictyotriletes subgranifer McGregor, 1973
Figure 26L–M

1973 *Dictyotriletes subgranifer* McGregor, p. 43 (*cum syn.*), pl. 5, figs 16, 18–20.

Dimensions. 34(54)80 µm; 17 specimens measured.

Comparison. Dictyotriletes emsiensis (Allen) McGregor, 1973 has more robust muri that are commonly widened at the junctions, and not serrated along the upper edge.

Occurrence. BAQA-1, BAQA-2, JNDL-3 and JNDL-4; Jauf Formation; *papillensis-baqaensis* to *lindlarensis-sextantii* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *lindlarensis-sextantii* Zone, some isolated occurrence of specimens in the youngest part of the section are due to reworking. MG-1; Ouan-Kasa, Awaynat Wanin, and Awaynat Wanin II formations; *annulatus-protea* Zone, the isolated occurrence of specimens in the youngest part of the section are probably due to reworking.

Previous records. Dictyotriletes subgranifer is eponymous for the upper Pragian – lower Emsian Su Interval Zone of Western Europe (Streel *et al.* 1987). *D. subgranifer* has an almost worldwide distribution extending from Pragian to upper Emsian. It has been reported from many parts of the world; e.g. Belgium (Steemans 1989), Brazil (Grahn *et al.* 2005; Mendlowicz Mauller *et al.* 2007), Canada (McGregor and Owens 1966; McGregor 1973; McGregor and Camfield 1976), China (Gao Lianda 1981), Armorican Massif, France (Le Hérissé 1983), Germany (Steemans 1989), Luxembourg (Steemans *et al.* 2000*a*), Morocco (Rahmani-Antari and Lachkar 2001), Poland (Turnau 1986; Turnau *et al.* 2005), Saudi Arabia (Al-Ghazi 2007), Scotland (Wellman 2006) and USA (Ravn and Benson 1988).

Dictyotriletes sp. 1
Figure 26N–O

Description. Trilete patinate spores with sub-circular to sub-triangular amb. Laesurae straight and simple, extending to the inner edge of the patina. Exine 1–4 µm equatorially thick. Contact areas laevigate. Patina reticulate. Lumina of reticulum, polygonal in plan view, 2–6 µm in greatest diameter. Muri low, less than 1 µm wide at base, Bacula with bifurcate tips at the muri junctions, 1–3 µm high, 0.5–2 µm wide at base.

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

Comparison. The reticulum of described specimens looks like very much that of *D. hemeri* sp. nov., but ornamentation at muri junctions of the latter is less clearly bifurcate. In addition, it is not patinate. We have thus separated these specimens from those of *D. hemeri.*

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

Genus ELENISPORIS Arkhangelskaya, 1985

Type species. Elenisporis biformis (Arkhangelskaya) Jansonius and Hills, 1987.

Comparison. This genus differs from *Emphanisporites* McGregor, 1961 in having an equatorial cingulum, the less clearly delimited muri on the proximal face, which are not radially oriented on the proximal surface, but rather abut against the laesurae.

Elenisporis gondwanensis sp. nov.
Figure 27A–C

Derivation of name. From *gondwanensis* (Latin), meaning from Gondwana; refers to its palaeogeographical occurrence.

Holotype. EFC K36/2 (Fig. 27C), slide 62845.

Paratype. EFC R39 (Fig. 27B), slide 62821, MG-1 borehole, sample 2405 m.

Type locality and horizon. MG-1 borehole, sample 2285 m; Awaynat Wanin II Formation at Mechiguig, Tunisia.

Diagnosis. An *Elenisporis* with laesurae characterized by triradiate sinuous fold-like labra. Proximal surface supporting radial sculpture of somewhat tortuous muri and distal surface sculptured with various and variable elements such as coni, spines, bacula or rounded verrucae.

Description. Amb is sub-circular. Laesurae are simple and straight but characterized by triradiate sinuous fold-like labra from the outer layer, *c.* 2–7 μm high in total width, about three-quarters of the amb radius in length. Curvaturae join the laesurae and are suggested by a narrow crassitude, 2–4 μm thick along the curvaturae, the outer edge of which can be denticulate. Proximal surface supports sculpture of somewhat tortuous muri, of uneven width but approximately uniform to their very end, 1–2.5 μm (rarely up to 4 μm) wide and more or less parallel to each other from the crassitude to laesurae. As they are closely spaced, they are often barely distinguishable. Distal surface is sculptured with various elements such as coni, spines, bacula or rounded verrucae, 1–6 μm high and up to 1–2 μm wide at their base, commonly 1–3 μm apart. Exine is 2–7 μm thick. Some specimens show two clearly differentiated wall layers; layers are tightly appressed distally, but local detachments sometimes occur equatorially.

Dimensions. 65(81)92 μm; 17 specimens measured.

Comparison. Elenisporis biformis (Arkhangelskaya) Jansonius and Hills, 1987 shows wider muri. It is finely granulate and is sometimes sculptured distally with small, short elements. *Elenisporis* sp. 1 has also wider rolls and is more poorly sculptured distally.

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

Elenisporis sp. 1
Figure 27D–E

Description. Amb is sub-circular to sub-triangular. Laesurae are straight to sinuous, characterized by triradiate fold-like labra *c.* 4–9 μm high in total width, extending to the crassitude. Curvaturae join the laesurae and are suggested by a narrow crassitude, 2–4 μm thick along the curvaturae. Proximal surface supports sculpture of somewhat tortuous muri, of uneven width but approximately uniform to their very end, 2–6 μm wide and more or less paralleled from the crassitude to laesurae. Distal surface is sculptured with small, sometimes barely noticeable, widely spaced spines, 0.5–3 μm high and up to 1 μm wide at their base. Exine is 4–8 μm thick.

Dimensions. 71(92)110 μm; six specimens measured.

Comparison. Elenisporis biformis (Arkhangelskaya) Jansonius and Hills, 1987 is very similar to *Elenisporis* sp. 1 but has narrow, straight laesurae, and its cingulum is thicker. *E. gondwanensis* sp. nov. has thinner muri and is sculptured distally with larger elements.

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

Genus EMPHANISPORITES McGregor, 1961

Type species. Emphanisporites rotatus McGregor emend. McGregor, 1973.

Remarks. Wall ultrastructure of some *Emphanisporites* species are discussed in details in Taylor *et al.* (2011). This study likely suggests that this genus comprises spores produced by various plant groups, which adopted the emphanoid condition (possessing proximal radially disposed muri) by convergence.

Emphanisporites annulatus McGregor, 1961
Figure 27F

1956 Unnamed Radforth and McGregor, pl. 1, fig. 6.
1961 *Emphanisporites annulatus* McGregor, p. 3, pl. 1, figs 5–6.
1962 *Radiaspora* sp. Balme, p. 6, pl. 1, fig. 13.
1963 *Emphanisporites erraticus* (Eisenack) McGregor; Chaloner, p. 103, fig. 1.
1967 *Emphanisporites* cf. *erraticus* McGregor; Daemon *et al.*, p. 106, pl. 1, fig. 10.

Dimensions. 41(48)60 μm; 15 specimens measured.

Occurrence. JNDL-1, JNDL-3, S-462, WELL-1 and WELL-8; Jauf (Murayr Member) and Jubah formations; *annulatus-protea* to *lemurata-langii* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *lemurata-langii* zones. MG-1; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *lemurata-langii* zones.

Previous records. Emphanisporites annulatus is eponymous for the Emsian *annulatus-sextantii* Assemblage Zone of the Old Red

FIG. 27. 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, *Elenisporis gondwanensis* sp. nov. A, MG-1, 2270 m, 62849, L47. B, Paratype, MG-1, 2405 m, 62821, R39. C, Holotype, MG-1, 2285 m, 62845, K36/2. D–E, *Elenisporis* sp. 1. D, MG-1, 2456 m, 62739, O48. E, MG-1, 2270 m, 62848, X34. F, *Emphanisporites annulatus* McGregor, 1961. JNDL-1, 174.6 ft, 60847, G31. G–H, *Emphanisporites* cf. *E. biradiatus* Steemans, 1989. G, JNDL-4, 448.6 ft, 03CW267, G37/1. H, JNDL-1, 155.6 ft, 60838, M51.


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Sandstone Continent and adjacent regions (Richardson and McGregor 1986) and the early Emsian AB Oppel Zone of Western Europe (Streel *et al.* 1987). *E. annulatus* has a worldwide distribution extending from Emsian to the lower Frasnian.

Emphanisporites cf. *E. biradiatus* Steemans, 1989
Figure 27G–H

cf. 1989 *Emphanisporites biradiatus* Steemans, p. 136, pl. 37, figs 11–13.

Dimensions. 37–47 μm; two specimens measured.

Comparison. Emphanisporites biradiatus Steemans, 1989 is granulate distally and possesses six to eight pairs of muri per each interradial area, whereas the present specimens are entirely laevigate and show about four pairs of muri per interradial area. *E. rotatus* McGregor emend. McGregor, 1973 occasionally presents some pairs of muri.

Occurrence. JNDL-1 and JNDL-4. Jauf (Subbat Member) and Jubah formations; *asymmetricus* and *svalbardiae-eximius* zones.

Emphanisporites decoratus Allen, 1965
Figure 28A

1965 *Emphanisporites decoratus* Allen, p. 708, pl. 97, figs 15–18.
1981 *Emphanisporites* sp. K Steemans, p. 53, pl. 2, fig. 3.
2006 *Emphanisporites* cf. *decoratus* Allen; Wellman, p. 186, pl. 15, figs g–i.

Dimensions. 31(44)59 μm; nine specimens measured.

Comparison. The characteristics of *Emphanisporites* cf. *decoratus* Allen, 1965 *in* Wellman (2006) can be accommodated in the variability shown by the population studied here. *E. neglectus* Vigran, 1964 is occasionally sculptured, but then, only with very fine granules. *E. novellus* McGregor and Camfield, 1976 and *E. micrornatus* Richardson and Lister, 1969 var. *micrornatus* Steemans and Gerrienne, 1984 differ in finer granulate ornamentation. *E. micrornatus* var. *sinuosus* Steemans and Gerrienne, 1984 exhibits sinuous radial muri.

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

Previous records. From upper Emsian – lower Eifelian of Argentina (Amenábar 2009); upper Lochkovian – upper Pragian of Belgium (Steemans 1989); Pragian–Emsian of Canada (McGregor and Camfield 1976); upper Pragian of Armorican Massif, France (Le Hérissé 1983); Emsian of Germany (Schultz 1968); Pragian of Spitsbergen, Norway (Allen 1965); and Pragian–?lowermost Emsian of Scotland (Wellman 2006).

Emphanisporites cf. *E. edwardsiae* Wellman, 2006
Figure 28B–C

cf. 2006 *Emphanisporites edwardsiae* Wellman, p. 188, pl. 16, figs a–f.

Dimensions. 57(65)71 μm; four specimens measured.

Comparison. Emphanisporites edwardsiae Wellman, 2006 does not have a thin triangular area inside the apical darker area as showed by the present specimens. *Retusotriletes phillipsii* Clendening *et al.*, 1980 possesses scattered grana on the proximal face and muri are straight to sinuous. *Scylaspora rugulata* (Riegel) Breuer *et al.*, 2007*c* is sculptured with fine, more or less radially oriented rugulate or subreticulate muri.

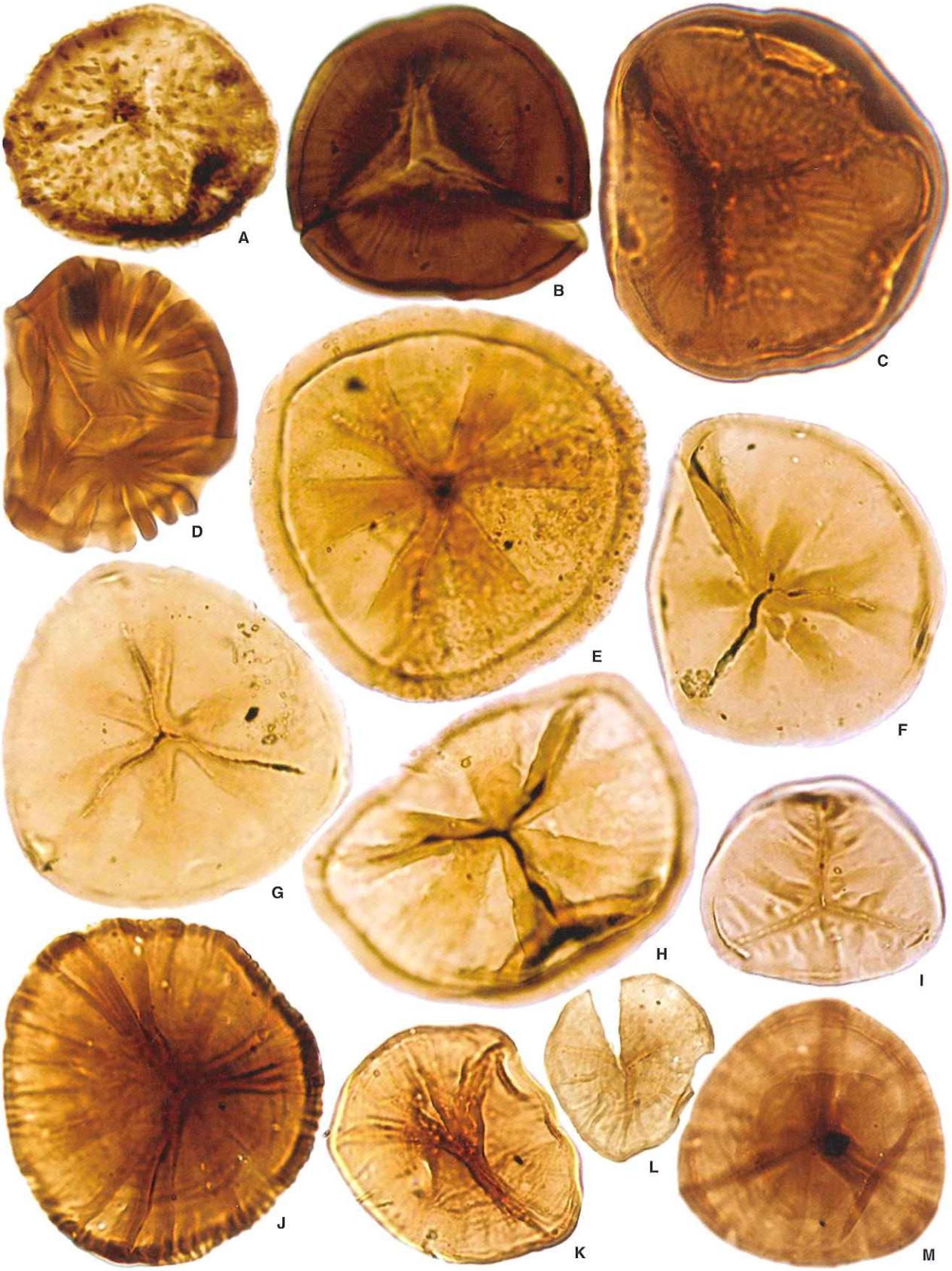
Occurrence. BAQA-1; Jauf Formation (Subbat Member); *milleri* to *lindlarensis-sextantii* zones.

Emphanisporites erraticus (Eisenack) McGregor, 1961
Figure 28D

1944 *Triletes erraticus* Eisenack, p. 114, pl. 2, fig. 9.
1954 Unnamed Radforth and McGregor, pl. 2, fig. 59.
1956 Unnamed Radforth and McGregor, pl. 3, fig. 1.
1961 *Emphanisporites erraticus* (Eisenack) McGregor, p. 4, pl. 1, figs 7–11.
1967 *Emphanisporites* cf. *erraticus* (Eisenack) McGregor; Richardson, pl. 4, fig. a.

Dimensions. 41(48)55 μm; nine specimens measured.

FIG. 28. 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, *Emphanisporites decoratus* Allen, 1965. WELL-7, 13689.7 ft, 62316, Q50/1. B–C, *Emphanisporites* cf. *E. edwardsiae* Wellman, 2006. B, BAQA-1, 285.5 ft, 03CW111, D-E23. C, BAQA-1, 161.0 ft, 66773, W47. D, *Emphanisporites erraticus* McGregor, 1961. JNDL-3, 327.0 ft, 68555, S40. E–H, *Emphanisporites laticostatus* sp. nov. E, MG-1, 2161.8 m, 62528, M33. F, Holotype, MG-1, 2161.8 m, 62528, S38. G, MG-1, 2181.2 m, 62524, S49. H, Paratype, MG-1, 2161.8 m, 62528, V36/4. I, *Emphanisporites mcgregorii* Cramer, 1966*a*. MG-1, 2181.2 ft, 62525, V42/3. J–M, *Emphanisporites plicatus* sp. nov. J, Paratype, JNDL-1, 155.6 ft, 60838, M52. K, JNDL-1, 495.0 ft, 60854, F43/3. L, JNDL-3, 249.0 ft, 68543, Q24/2. M, JNDL-4, 163.3 ft, 68625, L37/4.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Comparison. *Emphanisporites schultzii* McGregor, 1973 possesses also a proximal rosette pattern but does not have a distal annulus.

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

Previous records. From Emsian of Canada (McGregor and Owens 1966; McGregor 1973), Germany (Lanninger 1968; Schultz 1968) and Poland (Turnau 1986; Turnau *et al.* 2005); lower or middle Emsian of Libya (Paris *et al.* 1985); and Eifelian–Givetian of Spain (Cramer 1966*a*).

Emphanisporites laticostatus sp. nov.
Figure 28E–H

2011 *Emphanisporites* sp. 2 Breuer and Grahn, pl. 2, fig. q.

Derivation of name. From *lati-* and *costatus* (Latin), meaning sculptured with wide costae or muri; refers to the proximal muri.

Holotype. EFC S38 (Fig. 28F), slide 62528.

Paratype. EFC V36/4 (Fig. 28H), slide 62528; MG-1 borehole, sample 2161.8 m.

Type locality and horizon. MG-1 borehole, sample 2161.8 m; Awaynat Wanin III Formation at Mechiguig, Tunisia.

Diagnosis. A large, robust *Emphanisporites* with few and wide muri.

Description. Amb is circular to sub-triangular. Laesurae are straight or slightly undulating, simple, three-fifths to four-fifths of the amb radius in length. Laesurae are commonly bordered by muri. Exine is 2–5 μm thick equatorially. Proximal radially arranged muri are 3–12 μm in greatest width, low, tapering towards proximal pole. Muri extend from the proximal pole and fade inside the contact area before reaching the equator. Each contact area presents usually three muri. Distal surface is laevigate.

Dimensions. 61(67)75 μm; 13 specimens measured.

Comparison. *Emphanisporites laticostatus* is clearly distinguishable from all other species of *Emphanisporites* by the possession of few robust muri.

Occurrence. S-462; Jubah Formation; *langii-concinna* Zone. MG-1; Awaynat Wanin III Formation; *langii-concinna* Zone.

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

Emphanisporites mcgregorii Cramer, 1966*a*
Figure 28I

1961 *Emphanisporites* sp. McGregor, pl. 1, fig. 12.
1966*a* *Emphanisporites mcgregorii* Cramer, p. 263, pl. 3, fig. 59.
1968 *Emphanisporites spinaeformis* Schultz, p. 27, pl. 3, figs 10–10a.
1968 *Emphanisporites* sp. 1 Jardiné and Yapaudjian, pl. 1, fig. 3.
non 1968 *Emphanisporites macgregori* Schultz, p. 28, pl. 3, figs 12–12a.
non 1968 *Emphanisporites macgregori* Schultz; Lanninger, p. 136, pl. 23, fig. 15.

Dimensions. 36(46)55 μm; 12 specimens measured.

Comparison. Proximal muri of *E. mcgregorii* are aligned approximately parallel to one another, extending from the equator to the margin of laesurae forming a herringbone pattern, whereas muri of *E. rotatus* McGregor emend. McGregor, 1973 are radially distributed.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, S-462, WELL-1, WELL-4 and WELL-8; Jauf and Jubah formations; *papillensis-baqaensis* to *triangulatus-catillus* zones. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *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 – middle Givetian of Algeria (Moreau-Benoit *et al.* 1993); upper Lochkovian–Emsian of Belgium (Steemans 1989); upper Pragian – lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller *et al.* 2007); upper Pragian–Eifelian of Germany (Lanninger 1968; Riegel 1968; Steemans 1989); Pragian–lower Eifelian of Libya (Moreau-Benoit 1989); Emsian of Poland (Turnau 1986); and Pragian–Givetian of Spain (Cramer 1966*a*, 1969).

Emphanisporites plicatus sp. nov.
Figures 28J–M, 29A

Derivation of name. From *plicatus* (Latin), meaning folded; refers to the distal surface.

Holotype. EFC D43 (Fig. 29A), slide 60847.

Paratype. EFC M52 (Fig. 28J), slide 60838; JNDL-1 core hole, sample 155.6 ft.

Type locality and horizon. JNDL-1 core hole, sample 174.6 ft; Jubah Formation at Domat Al-Jandal, Saudi Arabia.

Diagnosis. An *Emphanisporites* with a distal surface concentrically folded.

Description. Amb is circular to sub-triangular. Laesurae are straight, simple or accompanied with low, narrow labra, up to 1.5 µm wide individually, extending to or almost to the equator. Exine is 1–3.5 µm equatorially thick. Proximal radially arranged muri, 0.5–2.5 µm wide at equator, are low and taper towards proximal pole. Each contact area contains between 8–16 muri. Distal surface laevigate and bears fine, concentric folds.

Dimensions. 35(47)63 µm; 19 specimens measured.

Remarks. Emphanisporites rotatus McGregor emend. McGregor, 1973 is similar. The presence of the distal concentric folds on *E. plicatus* occurs only on these specimens and is regarded as the principal characteristic feature of this new species.

Occurrence. JNDL-1, JNDL-3 and JNDL-4; Jauf (Hammamiyat and Murayr members) and Jubah formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones.

Emphanisporites rotatus McGregor emend. McGregor, 1973
Figures 6I–J, 29B

1973 *Emphanisporites rotatus* McGregor emend. McGregor, p. 46 (*cum syn.*), pl. 6, figs 9–13.

Dimensions. 34(44)55 µm; 32 specimens measured.

Remarks. Rare monolete specimens have been found (pl. 2, figs 9–10).

Occurrence. Emphanisporites rotatus is found in all sections from *papillensis-baqaensis* to *langii-concinna* zones.

Previous record. Emphanisporites rotatus has been widely reported from upper Silurian through the entire Devonian from many parts of the world.

Emphanisporites schultzii McGregor, 1973
Figure 29C

1966 *Emphanisporites* sp. McGregor and Owens, pl. 4, fig. 10.
non 1966*a* *Emphanisporites mcgregorii* Cramer, p. 263, pl. 3, fig. 59.
1967 *Emphanisporites* sp. McGregor, pl. 1, fig. 2.
1968 *Emphanisporites macgregori* Schultz, p. 28, pl. 3, figs 12–12a.
1968 *Emphanisporites pseudoerraticus* Schultz, p. 29, pl. 3, figs 15–15a.
1970 *Emphanisporites* sp. McGregor, pl. 31, fig. 2.
1973 *Emphanisporites schultzii* McGregor, p. 48, pl. 6, fig. 14.

Dimensions. 36(52)75 µm; 13 specimens measured.

Comparison. According to Schultz (1968), *E. schultzii* differs from *E. pseudoerraticus* Schultz, 1968 notably in that the centre of the rosette pattern of each contact area is not strongly displaced towards the proximal pole. *E. pseudoerraticus* is, however, considered here as a junior synonym of *E. schultzii* because the centre of the rosette pattern seems relatively variable in its position from the current material. *E. erraticus* (Eisenack) McGregor, 1961 has a distal annulus.

Occurrence. BAQA-1, JNDL-3, JNDL-4, WELL-3, WELL-4, WELL-7 and WELL-8; Jauf (Subbat to Hammamiyat members) and Jubah formations; *ovalis-biornatus* to *lindlarensis-sextantii* zones. MG-1; Awaynat Wanin I Formation; *rugulata* Zone but the specimen is probably reworked.

Previous records. From middle Pragian–Emsian of Belgium (Steemans 1989); Emsian of Canada (McGregor and Owens 1966; McGregor 1973; McGregor and Camfield 1976); upper Pragian–Emsian of Germany (Lanninger 1968; Schultz 1968; Steemans 1989); upper Pragian – lower Emsian of Luxembourg (Steemans *et al.* 2000*a*); and Emsian of Poland (Turnau 1986).

Emphanisporites sp. 1
Figure 29D–E

? 1981 *Emphanisporites rotatus* McGregor var. B; Streel *et al.*, pl. 1, figs 15–16.

Description. Amb is sub-circular. Laesurae are straight, simple and extend almost to the equator. Exine is laevigate or infragranular, 2–4 µm thick equatorially. Proximal radially arranged muri are 4–13 µm wide at equator, up to 5 µm high, tapering towards proximal pole. Muri extend from the proximal pole and over the equator, resulting in strongly undulating equator in plan view. Each contact area contains between 3–5 muri. Distal face laevigate.

Dimensions. 48(62)78 µm; four specimens measured.

Comparison. Emphanisporites rotatus McGregor, 1961 var. B *in* Streel *et al.* (1981), which shows muri extending over the equator, may be similar. *E. robustus* McGregor, 1961 has muri that extend from the proximal pole to, but not beyond, the equator.

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

Genus GEMINOSPORA Balme, 1962

Type species. *Geminospora lemurata* Balme emend. Playford, 1983.

Geminospora convoluta sp. nov.
Figure 29F–J

Derivation of name. From *convolutus* (Latin), meaning convoluted; refers to the sculptured distal surface.

Holotype. EFC V29/2 (Fig. 29J), slide 60849.

Paratype. EFC M37/2 (Fig. 29F), slide PPM006; JNDL-1 core hole, sample 167.8 ft.

Type locality and horizon. JNDL-1 core hole, sample 177.0 ft; Jubah Formation at Domat Al-Jandal, Saudi Arabia.

Diagnosis. A *Geminospora* densely sculptured with cones, spines and biform processes round to polygonal in plan view, closely spaced and joined to form convoluted ridges of varied length.

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, simple or bordered by labra up to 3 μm in total thickness, extending to the outer margin of the inner body. The inner body diameter equals three-quarters to nine-tenths of the total amb diameter. Nexine is 1–3 μm thick, laevigate. Sexine is 1.5–3 μm thick, densely sculptured proximo-equatorially and distally with cones, spines and biform processes (flask-shaped or mammate). Sculptural elements on the distal hemisphere are round to polygonal in plan view, 1–3 μm wide at their base, 1–2 μm high, closely spaced and joined to form ridges of varied length. Proximal surface is laevigate or with scattered grana. Specimens are very often folded.

Dimensions. 52(69)84 μm; nine specimens measured.

Comparison. *Acinosporites lindlarensis* Riegel, 1968 is morphologically similar, but its ornamentation is larger and the sexine is often partially separated from the nexine. *G. libyensis* Moreau-Benoit, 1980*b* is sculptured with shorter elements and has a nexine closely appressed to sexine.

Occurrence. JNDL-1; Jubah Formation; *annulatus-protea* to *svalbardiae-eximius* zones. A1-69; Awaynat Wanin II Formation; *svalbardiae-eximius* Zone.

Geminospora lemurata Balme emend. Playford, 1983
Figures 6K–L, 29K–L

1962 *Geminospora lemurata* Balme, p. 5, pl. 1, figs 5–10.
non 1965 *Geminospora svalbardiae* (Vigran) Allen, p. 696, pl. 94, figs 12–16.
1965 *Geminospora tuberculata* (Kedo) Allen, p. 696, pl. 94, figs 10–11.
1965 *Rhabdosporites parvulus* Richardson, p. 588 (*pars*), pl. 93, figs 5–6.
1982 *Geminospora micromanifesta* var. *minor* (Naumova) McGregor and Camfield, p. 40, pl. 8, figs 14–15, 19–22.
1983 *Geminospora lemurata* Balme emend. Playford, p. 316, text-figs 1–9.
non 2007*c* *Geminospora lemurata* Balme emend. Playford; Breuer *et al.*, pl. 8, figs 7–9.

Dimensions. 40(53)72 μm; 47 specimens measured.

Remarks. Fairly uncommon monolete specimens (Figs 6K–L) and rare tetralete specimens have been found. Rare occurrence of asymmetrically trilete, dilete and monolete specimens was also reported by Playford (1983, text-fig. 4A–C). These forms accounted for less than 0.05 per cent of the *G. lemurata* population studied by Playford.

Comparison. Specimens of *G. micromanifesta* var. *minor* (Naumova) McGregor and Camfield, 1982 possess a spectrum of morphological variations comparable to specimens of *Geminospora lemurata* Balme, 1962 emended by Playford (1983). *G. lemurata* 'early form' *in* Marshall (1996) differ from typical *G. lemurata* in being both smaller (mean 55 μm), only very rarely showing any appreciable separation between the nexine and sexine, the two layers being appressed although still distinguishable and possessing a thicker sexine (2–7 μm) where measured at the equatorial margin. *Rhabdosporites langii* (Eisenack) Richardson, 1960 has a generally thinner sexine and a less rigid appearance. In addition, it is larger. *G. svalbardiae* (Vigran) Allen, 1965 is not considered here as synonymous with *G. lemurata* because it can be distinguished from the typical *lemurata* form. *G. svalbardiae* has a generally thinner sexine resulting in more numerous folds.

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

FIG. 29. 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, *Emphanisporites plicatus* sp. nov. Holotype, JNDL-1, 174.6 ft, 60847, D43. B, *Emphanisporites rotatus* McGregor emend. McGregor, 1973. BAQA-1, 222.5 ft, 03CW108, L32/2. C, *Emphanisporites schultzii* McGregor, 1973. JNDL-1, 156.0 ft, 60839, H47/1. D–E, *Emphanisporites* sp. 1. D, MG-1, 2181.2 m, 62524, E45. E, MG-1, 2314 m, 62799, W39/2. F–J, *Geminospora convoluta* sp. nov. F, Paratype, JNDL-1, 167.8 ft, PPM006, M37/3. G, JNDL-1, 495.0 ft, PPM014, K37/1. H, JNDL-1, 495.0 ft, 60855, K48. I, JNDL-1, 177.0 ft, 60849, D42/2. J, Holotype, JNDL-1, 177.0 ft, 60849, V29/2. K–L, *Geminospora lemurata* Balme emend. Playford, 1983. K, S-462, 2060–2065 ft, 63270, N28/4. L, S-462, 1470–1475 ft, 63212, R32/3.


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Wanin II and Awaynat Wanin III formations; *lemurata-langii* to *langii-concinna* zones.

Previous records. *Geminospora lemurata* is eponymous for the Givetian *lemurata-magnificus* Assemblage Zone of the Old Red Sandstone Continent and adjacent regions (Richardson and McGregor 1986) and the early Givetian Lem Interval Zone of Western Europe (Streel *et al.* 1987). *G. lemurata* has a worldwide distribution extending through the Givetian and Frasnian, possibly reaching the basal Famennian.

Geminospora libyensis Moreau-Benoit, 1980*b*
Figure 30A

1976 *Geminospora libyensis* n. sp. Massa and Moreau-Benoit, pl. 6, fig. 4.
1980*b* *Geminospora libyensis* Moreau-Benoit, p. 44, pl. 13, fig. 6.

Dimensions. 66(94)115 μm; four specimens measured.

Comparison. *Acinosporites lindlarensis* Riegel, 1968 has the same sculpture, but the sexine is never separated as well as in specimens of *Geminospora libyensis*.

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

Previous records. From middle Givetian of Algeria (Moreau-Benoit *et al.* 1993); and upper Emsian – lower Givetian of Libya (Moreau-Benoit, 1989).

Geminospora punctata Owens, 1971
Figure 30B–C

1965 Unidentified spore types Kerr *et al.*, pl. 4, figs 15–16.
1966 *Geminospora* sp. McGregor and Owens, pl. 15, figs 7–10.
1971 *Geminospora punctata* Owens, p. 61, pl. 19, figs 1–9.

Dimensions. 43(57)80 μm; 16 specimens measured.

Comparison. *Geminospora lemurata* Balme emend. Playford, 1983 is closely comparable in general construction but has a discrete, positive ornamentation.

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

Previous records. From Eifelian–upper Tournaisian of Brazil (Loboziak *et al.* 1988, 1992*b*; Melo and Loboziak 2003); Frasnian of Canada (McGregor and Owens 1966; Owens 1971) and Iran (Ghavidel-Syooki 2003); uppermost Eifelian–Givetian of Germany (Loboziak *et al.* 1990); and Givetian of Poland (Turnau and Racki 1999).

Geminospora svalbardiae (Vigran) Allen, 1965
Figure 30D–F

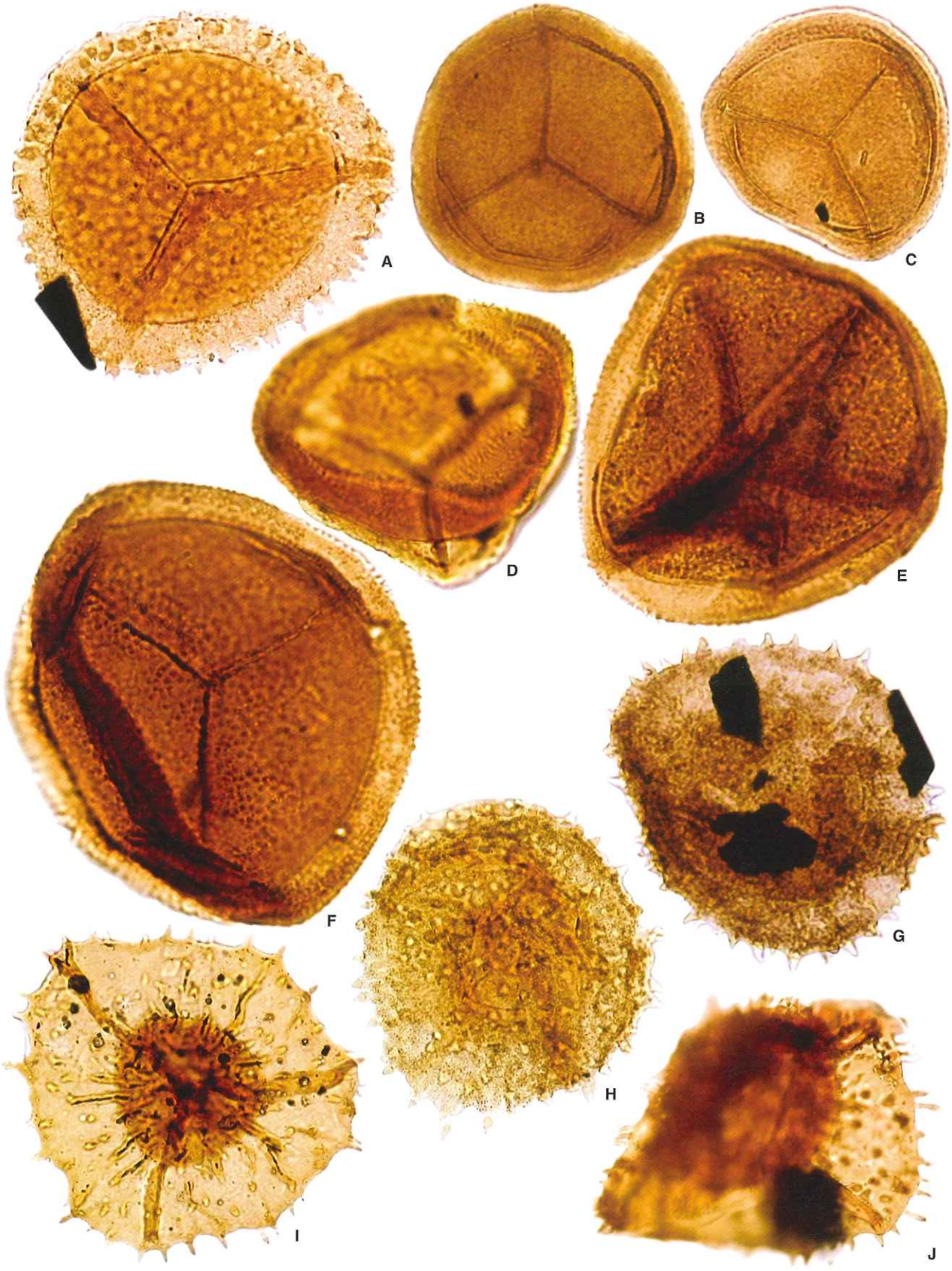
1964 *Lycospora svalbardiae* Vigran, p. 23, pl. 3, figs 4–5, pl. 4, figs 1–2.
1965 *Geminospora svalbardiae* (Vigran) Allen, p. 696, pl. 94, figs 12–16.
non 1974 *Geminospora svalbardiae* (Vigran) Allen; Becker *et al.*, pl. 16, figs 16–19.
1988 *Geminospora lemurata* Balme emend. Playford; Boumendjel *et al.*, pl. 1, figs 18–19.
? 1996 *Geminospora lemurata* Balme emend. Playford 'early form'; Marshall, p. 171, pl. 2, figs 2–5.
2007*c* *Geminospora lemurata* Balme emend. Playford; Breuer *et al.*, pl. 8, figs 7–9.

Dimensions. 49(68)87 μm; 44 specimens measured.

Comparison. *Geminospora lemurata* Balme emend. Playford, 1983 is often smaller and has generally a thicker sexine resulting in a more rigid spore. Specimens of *G. lemurata* 'early form' *in* Marshall (1996) seems to be similar to those of *G. svalbardiae*, but they have an equatorially thicker sexine (2–7 μm).

Occurrence. Saudi Arabia: JNDL-1; Jubah Formation; *svalbardiae-eximius* Zone. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *lemurata* zones. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *svalbardiae-eximius* to *rugulata-libyensis* zones.

FIG. 30. 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, *Geminospora libyensis* Moreau-Benoit, 1980*b*, magnification ×750. MG-1, 2483 m, 62802, S46/4. B–C, *Geminospora punctata* Owens, 1971. B, A1-69, 1322 ft, 27126, P51. C, A1-69, 1322 ft, 27125, O34/1. D–F, *Geminospora svalbardiae* (Vigran) Allen, 1965. D, JNDL-1, 172.7 ft, PPM007, W31/4. E, JNDL-1, 172.7 ft, PPM007, L37/1. F, JNDL-1, 167.8 ft, PPM006, H33. G–H, *Grandispora cassidea* (Owens) Massa and Moreau-Benoit, 1976, magnification ×500. G, MG-1, 2161.8 m, 62529, J49/1. H, MG-1, 2465 m, 62852, R43/2. I–J, *Grandispora douglastownensis* McGregor, 1973, magnification ×500. I, A1-69, 1962 ft, 27277, U54/3. J, JNDL-1, 174.6 ft, PPM008, T32.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Previous records. From Emsian–lower Eifelian of Algeria (Moreau-Benoit *et al.* 1993); upper Eifelian – middle Givetian of Parnaíba Basin, Brazil (Breuer and Grahn 2011); Emsian–upper Frasnian of Libya (Moreau-Benoit 1989); Emsian–Frasnian of Spitsbergen, Norway (Vigran 1964; Allen 1965); and upper Givetian of Scotland (Marshall and Allen 1982).

Genus GRANDISPORA Hoffmeister *et al.* emend. Neves and Owens, 1966

Type species. Grandispora spinosa Hoffmeister *et al.*, 1955.

Remarks. Large, camerate spores with apparently similar exinal sculpture are common in Emsian to Givetian rocks, and considerable weight is ascribed to sculpture as a criterion for circumscribing species. However, most authors do not record the range of variation in shape and size of the sculptural elements. Consequently, it is difficult to make meaningful comparisons between many of the described species of this complex on the basis of ornamentation. In addition, relatively minor differences in sculpture form and distribution are apt to become untenable because of intergradation of many specimens from several populations of spores (McGregor 1973).

Grandispora cassidea (Owens) Massa and Moreau-Benoit, 1976
Figures 30G–H, 48J–O

1966 *Spinozonotriletes* sp. McGregor and Owens, pl. 18, fig. 8.
1971 *Spinozonotriletes cassideus* Owens, pl. 17, figs 3–5; text-fig. 11.
1976 *Grandispora cassidea* (Owens) Massa and Moreau-Benoit, table-fig. 5.
1980*b* *Grandispora cassidea* (Owens) Moreau-Benoit, p. 31, pl. 10, fig. 6; pl. 15, fig. 5.
1989 *Spinozonotriletes* cf. *cassideus* Owens; Moreau-Benoit, p. 13.

Dimensions. 95(123)163 μm; seven specimens measured.

Comparison. Grandispora incognita (Kedo) McGregor and Camfield, 1976 is comparable in general architecture, but the sculptural elements are more slender.

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

Previous records. From Givetian–Frasnian of Paraná and Parnaíba basins, Brazil (Loboziak *et al.* 1988; Breuer and Grahn 2011); Frasnian of Canada (McGregor and Owens 1966; Owens 1971); middle Givetian–lower Frasnian of Libya (Moreau-Benoit 1989); and Givetian of Saudi Arabia (PB, pers. obs.).

Grandispora douglastownensis McGregor, 1973
Figures 30I–J, 48P–X

? 1968 *Calyptosporites pilaspinosus* Lanninger, p. 153, pl. 26, fig. 1.
1973 *Grandispora douglastownense* McGregor, p. 62, pl. 8, figs 8–9, 12–14.
? 1988 *Grandispora* sp. B; Ravn and Benson, p. 191, pl. 6, figs 1–2.

Dimensions. 88(126)156 μm; 21 specimens measured.

Comparison. Grandispora diamphida Allen, 1965 is smaller, and the inner body is larger relative to the total diameter of the spore in the specimens illustrated. *G. naumovae* (Kedo) McGregor, 1973 has longer spines. *G. libyensis* Moreau-Benoit, 1980*b* is slightly larger with a strongly thickened sexine. Its general amb shape tends to be more triangular. *G. protea* (Naumova) Moreau-Benoit, 1980*b* has smaller, generally bulbous and widely distributed sculptural elements, but some specimens show intergradation with the population of *G. douglastownensis* described here. The two species are included in the *G. protea* Morphon defined here (Table 1). The possibility that *G. douglastownensis* and *G. ?macrotuberculata* (Arkangelskaya) McGregor, 1973, the synonymy of which is questioned herein with *G. protea* (Naumova) Moreau-Benoit, 1980*b*, represent end-members of the same complex is also supported by analysis of their gross structure and ultrastructure (Wellman and Gensel 2004).

Occurrence. JNDL-1 and WELL-1; Jubah Formation; *svalbardiae-eximius* to *triangulatus-catillus* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *svalbardiae-eximius* zones. MG-1; Awaynat Wanin I Formation; *rugulata-libyensis* Zone.

Previous records. From upper Emsian – lower Eifelian of Algeria (Moreau-Benoit *et al.* 1993); Frasnian of Bolivia (Perez-Leyton 1990); upper Emsian – lower Givetian of Amazon and Parnaíba basins, Brazil (Loboziak *et al.* 1992*b*; Melo and Loboziak 2003); Emsian–Givetian of Canada: (McGregor 1973; McGregor and Camfield 1976, 1982); Givetian of France (Loboziak and Streel 1980); Eifelian of Germany (Loboziak *et al.* 1990); upper Emsian – lower Givetian (Ghavidel-Syooki 2003); and Emsian–middle Givetian of Libya (Moreau-Benoit 1989).

Grandispora fibrilabrata Balme, 1988
Figures 31A–C, 48Y–AA

1988 *Grandispora? fibrilabrata* Balme, p. 140, pl. 9, figs 6–8.

Dimensions. 87(95)105 µm; 12 specimens measured.

Remarks. The population of this species described by Balme (1988) is larger (144–255 µm). Although Balme (1988) was not certain of the allocation of this species to *Grandispora* Hoffmeister *et al.* emend. Neves and Owens, 1966, the specimens described here present all typical characters for this genus.

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

Previous record. From lower Frasnian of Carnarvon Basin, Australia (Balme 1988).

Grandispora gabesensis Loboziak and Streel, 1989
Figures 30D, 49A–C

1989 *Grandispora gabesensis* Loboziak and Streel, p. 181, pl. 6, figs 2–4; pl. 9, figs 17–20.

Dimensions. 65(96)133 µm; 13 specimens measured.

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

Previous records. From upper Emsian–Frasnian of Algeria (Moreau-Benoit *et al.* 1993); Givetian of Paraná Basin, Brazil (Loboziak *et al.* 1988); and Emsian of Morocco (Rahmani-Antari and Lachkar 2001).

Grandispora incognita (Kedo) McGregor and Camfield, 1976
Figures 31E–G, 49D–L

1955 *Archaeozonotriletes incognitus* Kedo, p. 33, pl. 4, fig. 9.
1976 *Grandispora incognita* (Kedo) McGregor and Camfield, p. 23, pl. 6, figs 9, 10.
1976 *Grandispora tomentosa* Taugourdeau-Lantz; McGregor and Camfield, p. 24, pl. 6, figs 4, 5, 8.
1976 *Grandispora* cf. *G. tomentosa* Taugourdeau-Lantz; McGregor and Camfield, p. 24, pl. 7, figs 2, 3.
1992 *Grandispora tomentosa* Taugourdeau-Lantz; McGregor and Playford, pl. 15, fig. 10.

Dimensions. 84(127)227 µm; 15 specimens measured.

Comparison. McGregor and Camfield (1976) illustrated both *Grandispora tomentosa* Taugourdeau-Lantz, 1967 and *Grandispora* cf. *G. tomentosa* Taugourdeau-Lantz, 1967, which are similar to specimens figured as *G. incognita*. *G. cassidea* (Owens) Massa and Moreau-Benoit, 1976 has broad-based conate or spines with a bulbous appearance. *G. naumovae* (Kedo) McGregor, 1973 has longer spinae comparatively to the amb, but some specimens intergrade with *G. incognita*. The *G. incognita* Morphon is thus defined and include specimens characterized by slender spinae (Table 1).

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

Previous records. From Givetian–Frasnian of Paraná Basin, Brazil (Loboziak *et al.* 1988); Eifelian–Givetian of Canada (McGregor and Camfield 1976); and Givetian of Iran (Ghavidel-Syooki 2003).

Grandispora inculta Allen, 1965
Figures 31H, 49M

1965 *Grandispora inculta* Allen, p. 734, pl. 103, figs 7–9.

Dimensions. 57–64 µm; two specimens measured.

Occurrence. S-462, WELL-1 and WELL-8; Jubah Formation; *triangulatus-catillus* Zone. A1-69; Awaynat Wanin II Formation; *lemurata-langii* Zone.

Previous records. From Emsian–Frasnian of Algeria (Boumendjel *et al.* 1988; Moreau-Benoit *et al.* 1993); Frasnian of Bolivia (Perez-Leyton 1990); Givetian–lower Frasnian of Paraná Basin, Brazil (Loboziak *et al.* 1988); upper Eifelian – lower Givetian of Canada (McGregor and Camfield 1982); upper Givetian – upper Frasnian of France (Brice *et al.* 1979; Loboziak and Streel 1980, 1988; Loboziak *et al.* 1983); Emsian–middle Givetian of Libya (Paris *et al.* 1985; Streel *et al.* 1988; Moreau-Benoit 1989); Eifelian–Givetian of Morocco (Rahmani-Antari and Lachkar 2001); Givetian of Spitsbergen, Norway (Allen 1965); upper Eifelian–Givetian of Poland (Turnau 1996; Turnau and Racki 1999); upper Eifelian of Russian Platform (Avkhimovitch *et al.* 1993) and Scotland (Marshall 1988).

Grandispora libyensis Moreau-Benoit, 1980*b*
Figures 32A–B, 49N–Y, 50A–I

1967 *Spinozonotriletes echinatus* Moreau-Benoit, p. 230, pl. 3, fig. 51; pl. 4, figs 52–53.
1967 *Spinozonotriletes mamillatus* Moreau-Benoit, p. 231, pl. 4, figs 54–55.
1967 *Grandispora* sp. Daemon *et al.*, p. 115, pl. 3, figs 37–39.

1969 *Hymenozonotriletes* sp. no 2388 Lanzoni and Magloire, pl. 7, fig. 19, pl. 8, fig. 1.
1974 *Spinozonotriletes echinatus* Moreau-Benoit; Moreau-Benoit, p. 203, pl. 15, fig. 6.
1974 *Spinozonotriletes mamillatus* Moreau-Benoit; Moreau-Benoit, p. 203, pl. 15, fig. 7.
? 1974 *Spinozonotriletes* cf. *echinatus* Moreau-Benoit; Bär and Riegel, p. 44, pl. 1, fig. 14.
1976 *Grandispora echinata* (Moreau-Benoit) Massa and Moreau-Benoit, pl. 4, fig. 1; table-fig. 5.
1980*b* *Grandispora libyensis* Moreau-Benoit, p. 33, pl. 11, figs 2–3.
1989 *Spinozonotriletes libyensis* (Moreau-Benoit) Coquel and Moreau-Benoit, p. 96, pl. 3, fig. 5; pl. 4, fig. 3.

Dimensions. 133(166)194 μm; 22 specimens measured.

Remarks. It appears that specimens of *G. libyensis* show a continuous morphological variation in ornamentation, intergrading from morphotypes with rather slender spines to ones characterized by bulbous biform elements. Although the two end-members exist, all intermediate forms are present. The morphotype characterized by the most massive sculptural elements seems to appear later than the morphotype with more slender ornaments, but in the youngest samples, the two end-members co-occur (Breuer *et al.* 2007*a*).

Comparison. Grandispora douglastownensis McGregor, 1973 is slightly smaller and not as distinctly thickened equatorially. Moreover, the ornamentation is less bulbous at the base. *G. velata* (Richardson) McGregor, 1973 is more widely sculptured with commonly smaller pointed spinae and coni. In addition, the sexine is not equatorially thickened as in *G. libyensis*.

Occurrence. S-462; Jubah Formation; *triangulatus-catillus* to *langii-concinna* zones. 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 records. From Emsian – lower Visean of Algeria (Boumendjel *et al.* 1988; Coquel and Moreau-Benoit 1989; Moreau-Benoit *et al.* 1993); upper Givetian – lower Frasnian of Argentina (Ottone 1996); upper Eifelian–Frasnian of Amazon and Paraná basins, Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003); late Emsian–?Tournaisian of Libya (Paris *et al.* 1985; Coquel and Moreau-Benoit 1986, 1989; Streel *et al.* 1988; Moreau-Benoit 1989); and upper Famennian–Tournaisian of Morocco (Rahmani-Antari and Lachkar 2001).

Grandispora maura sp. nov.
Figures 32C–E, 50J–L

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

Holotype. EFC K37/3 (Figs 32C, 50K), slide 62942.

Paratype. EFC Q51/4 (Fig. 32E), slide 63025; MG-1 borehole, sample 172.7 ft.

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

Diagnosis. A three-layered *Grandispora* sculptured with closely spaced small spines, parallel-sided or tapered upwards, rounded- or acute-tipped, or biform elements with a more bulbous base supporting a delicate minute tip.

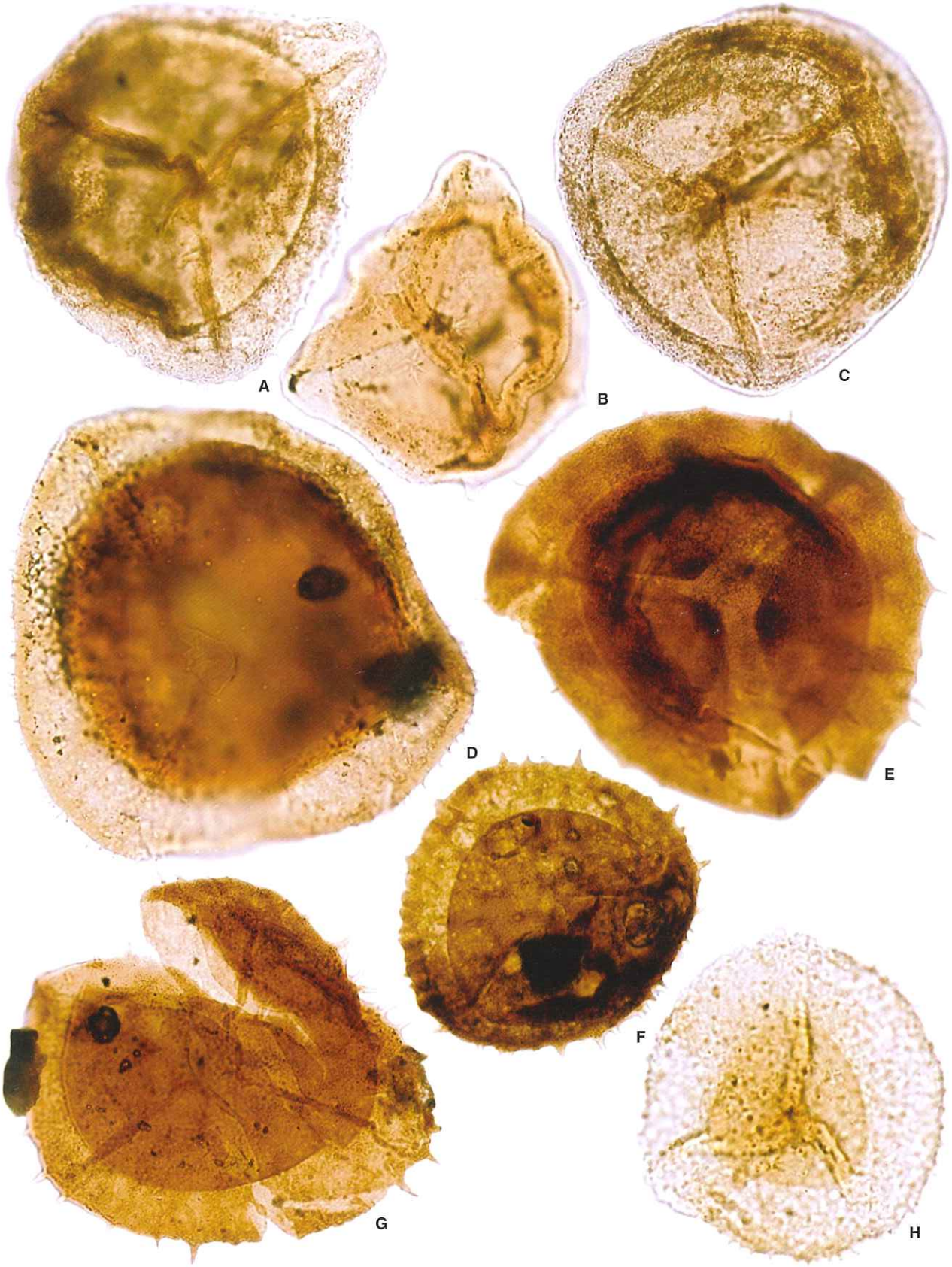
Description. Amb is sub-circular. Laesurae are straight, accompanied by labra, 1.5–4 μm in total width and extending to equator of inner body. The inner body diameter three-quarters to nine-tenths of the total amb diameter. Diameter of the middle layer about nine-tenths of the total amb diameter. The middle layer is rarely appressed to the inner body. Inner body is laevigate and middle layer commonly infragranular to granular. Outer layer is laevigate, but sculptured distally and equatorially with closely spaced small spines, parallel-sided or tapered upwards, rounded- or acute-tipped, or biform elements with a more bulbous base supporting a delicate minute tip. Elements are up to 3 μm high, up to 1.5 μm wide at base and 1–2 μm apart. Ornamentation can be coalescent equatorially. Specimens are often folded distally.

Dimensions. 65(76)90 μm; eight specimens measured.

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

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

FIG. 31. 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, *Grandispora fibrilabrata* Balme, 1988, magnification ×750. A, S-462, 2010–2015 ft, 63266, S34. B, S-462, 1570–1575 ft, 63215, N45. C, S-462, 1860–1865 ft, 63259, P32/4. D, *Grandispora gabesensis* Loboziak and Streel, 1989, magnification ×750. A1-69, 1962 ft, 27278, H51. E–G, *Grandispora incognita* (Kedo) McGregor and Camfield, 1976, magnification ×500. E, A1-69, 1530 ft, 26984, S39. F, A1-69, 1540 ft, 26987, H37/1. G, A1-69, 1540 ft, 26988, N40/3. H, *Grandispora inculta* Allen, 1965. S-462, 2060–2065 ft, 63270. N30/3.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Previous record. From Frasnian of Saudi Arabia (PB, pers. obs.).

Grandispora naumovae (Kedo) McGregor, 1973
Figures 32F, 33A and 50M–U

1925 Spore type H Lang, p. 257, pl. 1, figs 18–19.
1955 *Archaeozonotriletes naumovii* Kedo, p. 33, pl. 4, fig. 8.
1965 ?*Spinozonotriletes* cf. *naumovii* (Kedo) Richardson, p. 583, pl. 92, figs 3–5; text-fig. 7.
1966 ?*Spinozonotriletes* cf. *naumovii* (Kedo) Richardson; McGregor and Owens, pl. 7, fig. 5.
1966 *Spinozonotriletes* sp. cf. *S. naumovii* (Kedo) Richardson; de Jersey, p. 18, pl. 9, figs 1–4, 6.
1966 *Spinozonotriletes tuberculatus* Neves and Owens, p. 356, pl. 3, figs 4–5.
? 1967 *Spinozonotriletes naumovii* (Kedo); Hemer and Nygreen, pl. 2, fig. 9.
1968 *Spinozonotriletes* cf. *naumovii* (Kedo) Richardson; Lanninger, p. 150, pl. 25, fig. 10.
? 1969 *Spinozonotriletes* cf. *tuberculatus* Neves and Owens; Peppers and Damberger, p. 16, pl. 5, fig. 1.
? 1969 *Spinozonotriletes* cf. *naumovii* (Kedo) Richardson; Peppers and Damberger, p. 16, pl. 5, fig. 2.
1970 *Spinozonotriletes naumovii* (Kedo) Richardson; McGregor *et al.*, pl. 2, fig. 13.
1973 *Grandispora* ?*naumovii* (Kedo) McGregor, p. 61, pl. 9, figs 1–3.
1986 *Grandispora naumovii* (Kedo) McGregor; Richardson and McGregor, pl. 13, fig. 1.

Dimensions. 87(110)135 μm; 10 specimens measured.

Remarks. The range of variation in this species includes those with mostly rather small, delicate spines and those with large, rigid spines. Mostly commonly, but not invariably, the larger spores bear the most robust spines.

Comparison. Grandispora incognita (Kedo) McGregor and Camfield, 1976 has generally smaller spinae, which are also shorter comparatively to amb, but the two species intergrade in the *G. incognita* Morphon (Table 1).

Occurrence. S-462; Jubah Formation; *langii-concinna* Zone. A1-69; Awaynat Wanin I and Awaynat Wanin II formations; *svalbardiae-eximius* to *langii-concinna* zones.

Previous records. From lower Frasnian of Australia (Balme 1988); Emsian–Eifelian of Canada (McGregor and Owens 1966; McGregor 1973); Emsian of Germany (Lanninger 1968); Givetian of Poland (Turnau and Racki 1999) and Scotland (Richardson 1965; Marshall and Allen 1982).

Grandispora permulta (Daemon) Loboziak *et al.*, 1999
Figures 33B–C, 50V–X and 51A–F

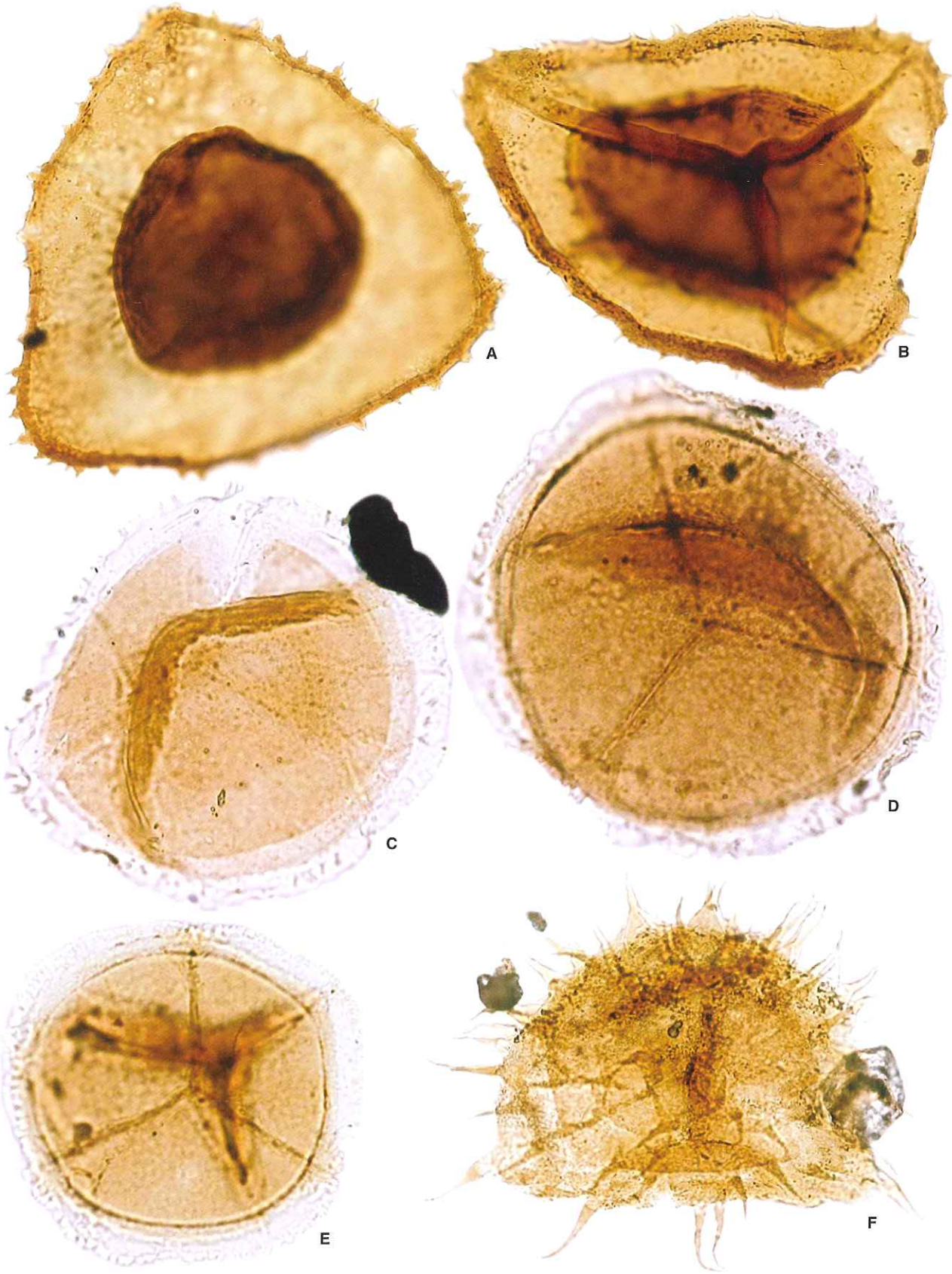
1967 *Calyptosporites* sp. A Daemon *et al.*, p. 114, pl. 3, figs 31–34.
1967 *Calyptosporites* sp. B Daemon *et al.*, p. 114, pl. 3, figs 35–36.
1974 *Calyptosporites* sp. B Bär and Riegel, pl. 1, fig. 13.
1974 *Contagisporites permultus* Daemon, p. 574, pl. 3, figs 4–5.
1980*b* *Grandispora velata* (Eisenack) McGregor (*pars*); Moreau-Benoit, pl. 12, fig. 3.
1985 *Grandispora macrotuberculata* (Arkhangelskaya) McGregor; Massa and Moreau-Benoit, pl. 1, fig. 6.
1985 *Grandispora* sp. A Paris *et al.*, pl. 24, figs 8–9.
1985 *Grandispora* sp. B Paris *et al.*, pl. 24, fig. 10.
1987 *Grandispora* sp. A Schrank, pl. 1, fig. 11.
1989 *Grandispora riegelii* Loboziak and Streel, p. 190, pl. 5, figs 1–5, pl. 9, figs 10–13.
1992 *Grandispora riegelii* Loboziak and Streel; Loboziak *et al.*, pl. 1, fig. 16.
1995*a* *Grandispora riegelii* Loboziak and Streel; Loboziak and Streel, pl. 1, fig. 1.
1995*b* *Grandispora riegelii* Loboziak and Streel; Loboziak and Streel, pl. 1, fig. 1.
1999 *Grandispora permulta* (Daemon) Loboziak *et al.*, p. 99, pl. 1, figs 1–6.

Dimensions. 68(99)125 μm; 30 specimens measured.

Comparison. Grandispora inculta Allen, 1965 is smaller and bears mainly coni. *G. gabesensis* Loboziak and Streel, 1989 has spinae and capilli in addition to coni and biform elements. Its ornamentation is also larger than in specimens of *G. permulta* (Daemon) Loboziak *et al.*, 1999.

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

FIG. 32. 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, *Grandispora libyensis* Moreau-Benoit, 1980*b*, magnification ×500. A, A1-69, 1416 ft, 26993, K31/3. B, A1-69, 1416 ft, 26993, G31/3. C–E, *Grandispora maura* sp. nov. C, Holotype, MG-1, 2247 m, 62942, K37/3. D, MG-1, 2181.2 m, 62525, N34/4. E, Paratype, MG-1, 2292 m, 63025, Q51/4. F, *Grandispora naumovae* (Kedo) McGregor, 1973, magnification ×500. A1-69, 1530 ft, 26984, J34/2.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Previous records. From middle Givetian of Algeria (Moreau-Benoit *et al.* 1993); upper Givetian – lower Frasnian of Argentina (Ottone 1996); upper Eifelian – lower Frasnian of Bolivia (Perez-Leyton 1990); Eifelian–Frasnian of Amazon and Paraná basins, Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003); and lower Eifelian – lower Givetian of Libya (Paris *et al.* 1985; Streel *et al.* 1988).

Grandispora protea (Naumova) Moreau-Benoit, 1980*b*
Figures 33D–E, 51G–R

1953 *Hymenozonotriletes proteus* Naumova, p. 40, pl. 4. fig. 5.
1955 *Hymenozonotriletes proteus* var. *eximius* Kedo, p. 31, pl. 4, fig. 3.
1965 *Calyptosporites proteus* (Naumova) Allen, p. 735, pl. 103, figs 10–11.
1968 *Calyptosporites proteus* (Naumova) Allen, Lanninger, p. 153, pl. 25, fig. 14.
1968 *Calyptosporites proteus* (Naumova) Allen; Riegel, p. 91, pl. 20, figs 2–4.
? 1968 ?*Hymenozonotriletes* sp.; Jardiné and Yapaudjian, pl. 2, fig. 9.
? 1973 *Grandispora* ?*macrotuberculata* (Arkhangelskaya) McGregor, p. 59, pl. 8, figs 1–5.
1975 *Calyptosporites proteus* (Naumova) Allen; Tiwari and Schaarschmidt, p. 41, pl. 23, fig. 1; text-fig. 30.
1976 *Grandispora protea* (Naumova) Massa and Moreau-Benoit, pl. 4, fig. 1; table-fig. 5.
1980*b* *Grandispora protea* (Naumova), Moreau-Benoit p. 37, pl. 11, fig. 6.

Dimensions. 73(122)152 μm; 22 specimens measured.

Comparison. Forms that may be similar are ?*Hymenozonotriletes* sp. *in* Jardiné and Yapaudjian (1968) and *G.* ?*macrotuberculata* (Arkhangelskaya) McGregor, 1973. *G. megaformis* (Richardson) McGregor, 1973 is larger and has wider ornaments. *G. velata* (Richardson) McGregor, 1973 is very similar in size, but has an ornamentation of much smaller spinae and coni, which have acute rather than rounded apices. *G. megaformis* has the same ornamentation but is larger in diameter. *Calyptosporites microspinosus* (Richardson) Richardson, 1962 is considerably larger and has small bifurcate spinae. *G. douglastownensis* McGregor, 1973 has longer spinae and is more densely sculptured, but some specimens intergrade with *G. protea*; the two species are thus included here in the *G. protea* Morphon (Table 1).

Occurrence. JNDL-1; Jauf (Murayr Member) and Jubah formations; *annulatus-protea* to *rugulata-libyensis* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *rugulata-libyensis* zones. MG-1; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *rugulata-libyensis* zones.

Previous records. Grandispora protea is eponymous for the upper Emsian – lower Eifelian AP Oppel Zone of Western Europe (Streel *et al.* 1987). *G. protea* has an almost worldwide distribution extending from upper Emsian into the Frasnian. It is notably reported in Algeria (Moreau-Benoit *et al.* 1993), Argentina (Ottone 1996), Belgium (Gerrienne *et al.* 2004), Bolivia (Perez-Leyton 1990), Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003), Canada (McGregor and Uyeno 1972; McGregor and Camfield 1976, 1982), Germany (Riegel 1968, 1973; Tiwari and Schaarschmidt 1975; Loboziak *et al.* 1990), Libya (Moreau-Benoit 1989), Spitsbergen, Norway (Allen 1965), Poland (Turnau 1986, 1996), Russian Platform (Avkhimovitch *et al.* 1993) and Scotland (Marshall and Allen 1982; Marshall 1988; Marshall and Fletcher 2002).

Grandispora rarispinosa Moreau-Benoit, 1980*b*
Figures 33F–H, 51S–X

1976 *Grandispora rarispinosa* Massa and Moreau-Benoit, pl. 5, fig. 7.
1980*b* *Grandispora rarispinosa* Moreau-Benoit, p. 38, pl. 12, fig. 1.

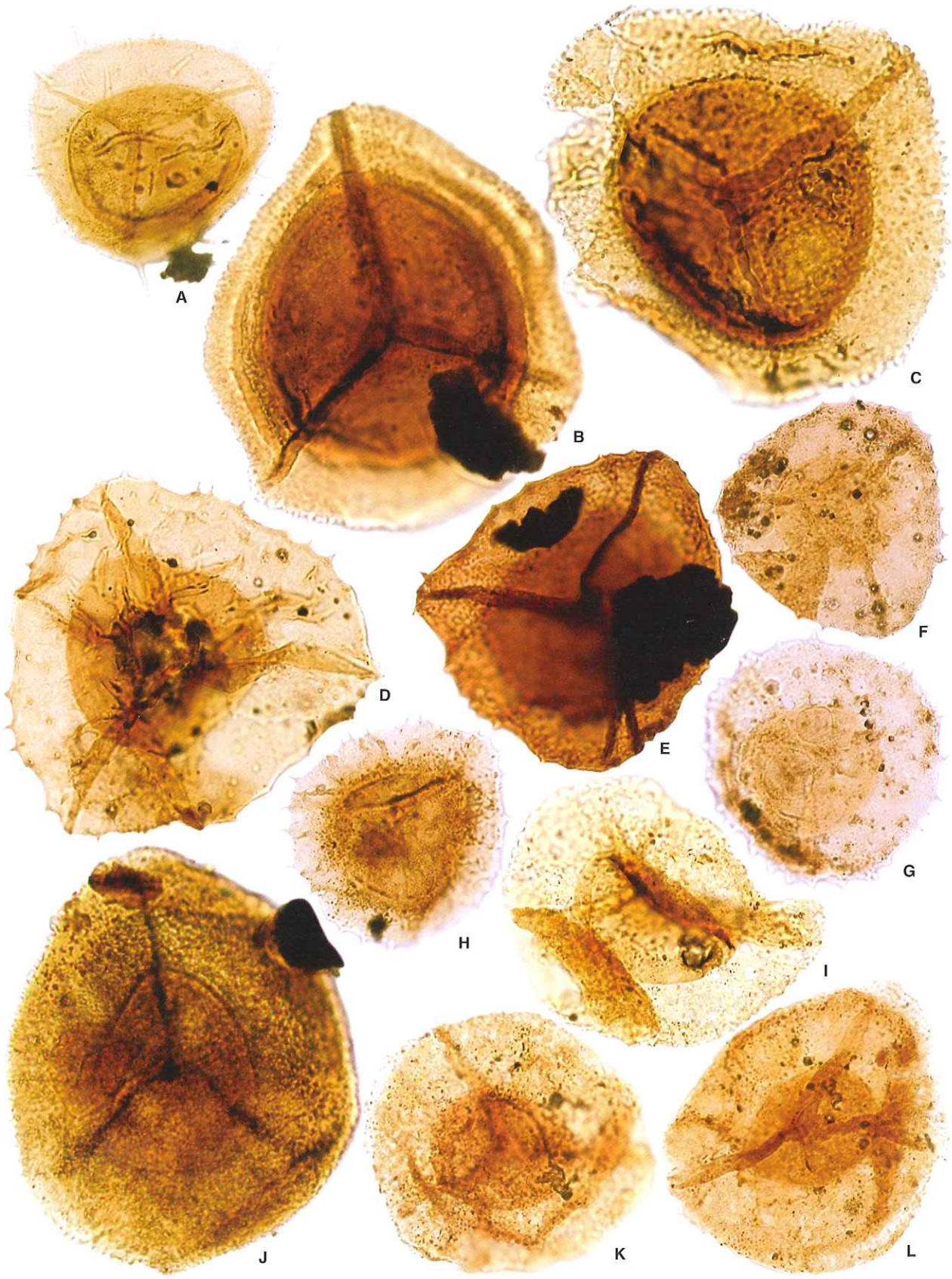
Dimensions. 66(86)108 μm; seven specimens measured.

Comparison. Grandispora protea (Naumova) Moreau-Benoit, 1980*b* is larger and does not have the spongy appearing sexine.

Occurrence. S-462; Jubah Formation; *langii-concinna* Zone. MG-1; Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations; *incognita* to *langii-concinna* zones.

Previous records. From lower–middle Givetian of Algeria (Boumendjel *et al.* 1988; Moreau-Benoit *et al.* 1993); and lower Eifelian – upper Frasnian of Libya (Moreau-Benoit 1989).

FIG. 33. 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, *Grandispora naumovae* (Kedo) McGregor, 1973, magnification ×500. S-462, 1660–1665 ft, 63219, L38/4. B–C, *Grandispora permulta* (Daemon) Loboziak *et al.*, 1999, magnification ×750. B, A1-69, 1277 ft, 62637, V49/1. C, A1-69, 1296 ft, 62643, G34/1. D–E, *Grandispora protea* (Naumova) Moreau-Benoit, 1980*b*, magnification ×500. D, A1-69, 1962 ft, 27278, T36/3. E, JNDL-1, 155.6 ft, PPM003, D32. F–H, *Grandispora rarispinosa* Moreau-Benoit, 1980*b*, magnification ×500. F, MG-1, 2182.4 m, 62527, Q32. G, MG-1, 2285 m, 62845, L26/3. H, MG-1, 2413 m, 62776, R35/2. I–L, *Grandispora* (*Calyptosporites*) *stolidota* (Balme) comb. nov., magnification ×500. I, MG-1, 2375 m, 62772, O25. J, A1-69, 1322 ft, 27126, Q39/3. K, MG-1, 2476 m, 63015, F44. L, MG-1, 2476 m, 63015, P38.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Grandispora (Calyptosporites) stolidota (Balme) comb. nov.
Figures 33I–L, 51Y–AA

1988 *Calyptosporites stolidotus* Balme, p. 141, pl. 10, figs 8–10.

Dimensions. 103(125)161 μm; 14 specimens measured.

Remarks. Since *Calyptosporites* Richardson, 1962 is considered as a junior synonym of *Grandispora* Hoffmeister *et al.* emend. Neves and Owens, 1966, *C. stolidotus* Balme, 1988 is here transferred.

Comparison. According to Balme (1988), *G. uyenoi* McGregor and Camfield, 1982 and *Rhabdosporites* sp. *in* McGregor and Camfield, 1982 were the same morphology as *G. stolidota*. *G. uyenoi* differs in possessing curvaturate contact faces, and *Rhabdosporites* sp. *in* McGregor and Camfield, 1982 has a more uniform sculpture without biform elements.

Occurrence. S-462 and WELL-1; Jubah Formation; *rugulata-libyensis* to *triangulatus-catillus* zones but some specimens from S-462 may be caved in older strata. A1-69; Awaynat Wanin II Formation; *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 middle Givetian – lower Frasnian of Australia (Balme 1988; Grey 1991).

Grandispora velata (Richardson) McGregor, 1973
Figures 34A–B, 51AB–AD and 52A–C

1944 *Triletes velatus* Eisenack p. 108 (*pars*), pl. 1, figs 1–3.
1960 *Cosmosporites velatus* (Eisenack); Richardson, p. 52, pl. 14, fig. 4.
1962 *Calyptosporites velatus* (Eisenack); Richardson, p. 192.
1965 *Calyptosporites velatus* (Eisenack); Richardson, p. 587, pl. 93, fig. 4.
1973 *Grandispora velata* (Richardson) McGregor, p. 61, pl. 8, figs 10–11.

Dimensions. 106(131)170 μm; 18 specimens measured.

Comparison. *Grandispora libyensis* Moreau-Benoit, 1980*b* is densely sculptured with commonly larger spinae which can be bulbous. In addition, the sexine is thickened equatorially.

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

Previous records. *Grandispora velata* is eponymous for the lower Eifelian *velata-langii* Assemblage Zone of the Old Red Sandstone Continent and adjacent regions (Richardson and McGregor 1986). *R. langii* has a worldwide distribution extending into the Frasnian. *G. velata* is widely reported from upper Emsian through Frasnian from many parts of the world; e.g. Argentina (Amenábar 2009), Australia (Hashemi and Playford 2005), Russian Platform (Avkhimovitch *et al.* 1993), Belgium (Lessuise *et al.* 1979), Bolivia (Perez-Leyton 1990), Brazil (Loboziak *et al.* 1988), 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, 1988), Germany (Riegel 1968, 1973; Tiwari and Schaarschmidt 1975), Greenland (Friend *et al.* 1983; Marshall and Hemsley 2003), Iran (Ghavidel-Syooki 2003), Libya (Streel *et al.* 1988), Poland (Turnau 1996), Portugal (Lake *et al.* 1988), Spain (Cramer 1969), Scotland (Richardson 1965; Marshall and Allen 1982; Marshall 1988; Marshall and Fletcher 2002) and Georgia, USA (Ravn and Benson 1988).

Genus GRANULATISPORITES Ibrahim emend. Potonié and Kremp, 1954

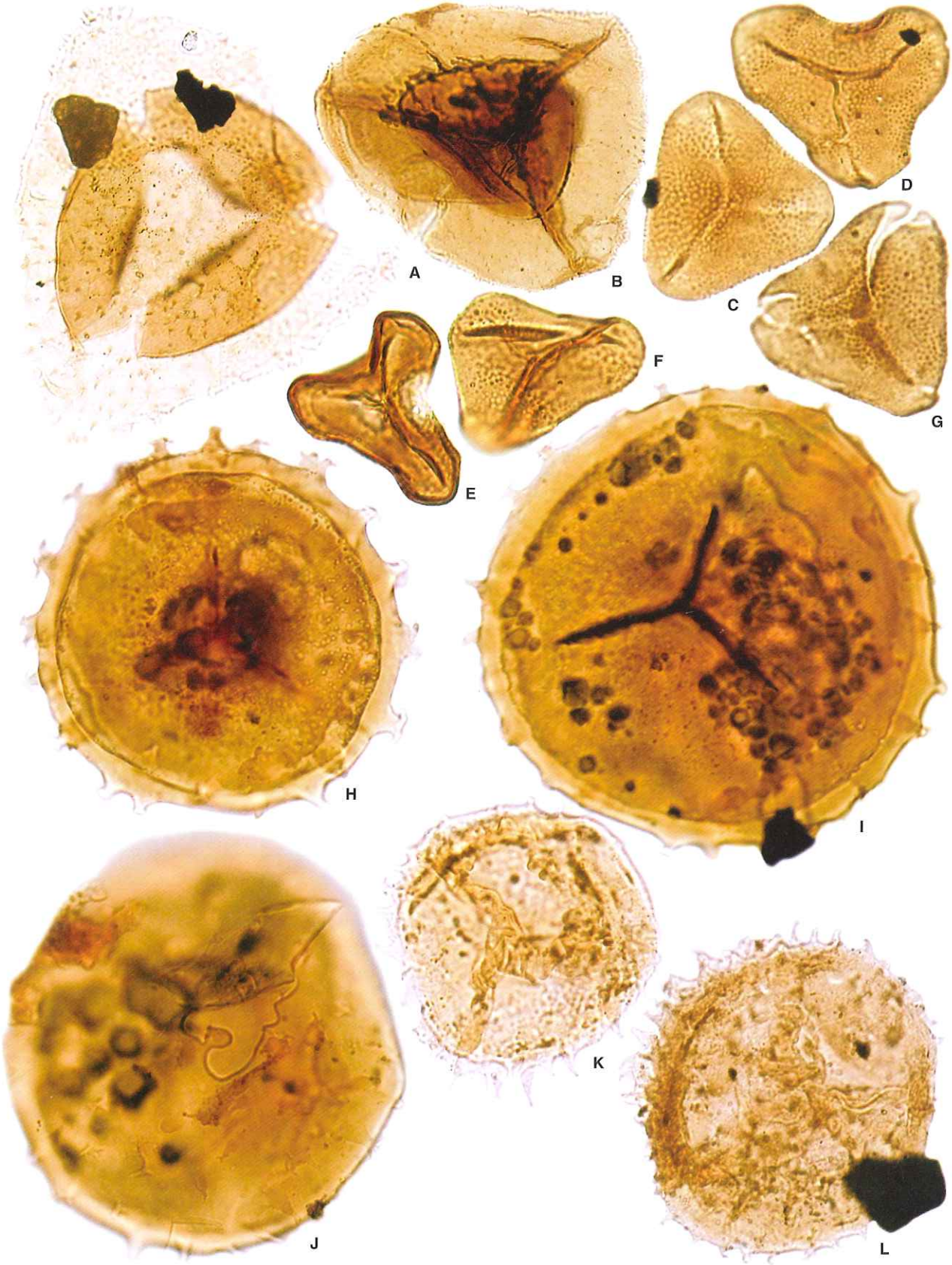
Type species. *Granulatisporites granulatus* Ibrahim, 1933.

Granulatisporites concavus sp. nov.
Figure 34C–G

? 1976 *Granulatisporites muninensis* Allen; Massa and Moreau-Benoit, pl. 3, fig. 5.
? 1991 *Granulatisporites muninensis* Allen; Grigani *et al.*, pl. 10, figs 3–4.
? 2003 *Granulatisporites granulatus* Ibrahim; Melo and Loboziak, pl. 5, fig. 13.

Derivation of name. From *concavus* (Latin); refers to the concave shape of the spore body.

FIG. 34. 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, *Grandispora velata* (Richardson) McGregor, 1973, magnification ×500. A, A1-69, 1530 ft, 26984, H40/1. B, A1-69, 1416 ft, 26992, U47/2. C–G, *Granulatisporites concavus* sp. nov. C, A1-69, 2039–2041 ft, 27279, M-N43. D, Paratype, JNDL-1, 162.3 ft, PPM005, C29/4. E, JNDL-1, 156.0 ft, 60840, N27-28. F, JNDL-1, 495.0 ft, 60855, L36/3. G, Holotype, A1-69, 1483 ft, 26995, R33/3. H–J, *Hystricosporites brevispinus* sp. nov., magnification ×750. H, Holotype, MG-1, 2295 m, 63007, P37. I, Paratype, MG-1, 2375 m, 62772, H34/1. J, MG-1, 2222.7 m, 62680, P37; focus on the distal face. K–L, *Hystricosporites* sp. 1, magnification ×750. K, MG-1, 2160.6 m, 62746, N49. L, MG-1, 2160.6 m, 62727, E49.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Holotype. EFC R33/3 (Fig. 34G), slide 26995.

Paratype. EFC F41 (Fig. 34D), slide 26987; A1-69 borehole, sample 1540 ft.

Type locality and horizon. A1-69 borehole, sample 1483 ft; Awaynat Wanin II Formation in A1-69, Libya.

Diagnosis. A triangular *Granulatisporites* with the margins concave or straight. Distal and equatorial regions sculptured with densely distributed grana.

Description. Amb is triangular. The corners are rounded, while the margins are concave or straight. Exine 0.5–1 μm thick. Laesurae are simple, straight, three-quarters to nine-tenths of the amb radius in length. Curvaturae are visible. Distal and equatorial sculpture are composed of densely distributed grana less than 0.5 μm high, less than 1 μm wide at their base, and 0.5–1 μm apart.

Dimensions. 31(36)40 μm; six specimens measured.

Comparison. Granulatisporites muninensis Allen, 1965 has a triangular amb with straight to slightly convex margins. *G. muninensis* illustrated in Massa and Moreau-Benoit (1976) and Grignani *et al.* (1991) may correspond to species described herein; however, no description was given. As the original paper where *G. granulatus* Ibrahim, 1933 was defined is not available, it cannot be compared. The specimen of *G. granulatus* illustrated in Melo and Loboziak (2003) may be similar to *G. concavus*, but no description was given.

Occurrence. Saudi Arabia. JNDL-1; Jauf (Murayr Member) and Jubah formations; *annulatus-protea* to *svalbardiae-eximius* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *lindlarensis-sextantii* to *lemurata* Zone.

Genus HYSTRICOSPORITES McGregor, 1960

Type species. Hystricosporites delectabilis McGregor, 1960.

Hystricosporites brevispinus sp. nov.
Figures 34H–J, 52D–F

Derivation of name. From *brevi-* and *spinus* (Latin); refers to the sculptural elements of short spines.

Holotype. EFC P37 (Figs 34H, 52D), slide 63007.

Paratype. EFC H34/1 (Figs 34I, 52E), slide 62772; MG-1 borehole, sample 2375 m.

Type locality and horizon. MG-1 borehole, sample 2295 m; Awaynat Wanin II Formation at Mechiguig, Tunisia.

Diagnosis. A thick-walled *Hystricosporites* sculptured with short multifurcate grapnel-tipped process terminations.

Description. Amb is circular to sub-circular. Laesurae are straight, approximately one-half to two-thirds of the amb radius in length, accompanied by smooth, labra, 2–4.5 μm in total width. Curvaturae are indistinct. Exine is 3–6 μm thick equatorially and laevigate. Proximo-equatorial and distal surfaces are sculptured with multifurcate grapnel-tipped ornament, 2–9 μm long, 2–10 μm wide at their base. Sculptural elements are 15–25 around the equatorial margin; their bases are robust, grapnel-tipped or often divided upwards into two or three parts, which are themselves grapnel-tipped. The first divided branches are 1–3 μm long and their grapnel-shaped tips are smaller. On the less well-preserved specimens, the grapnel-shaped tips are commonly broken.

Dimensions. 77(91)108 μm; four specimens measured.

Comparison. This thick-walled species does not resemble any species of *Hystricosporites* McGregor, 1960. The unique feature, which defines this genus, is the very short divided sculptural elements.

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

Hystricosporites sp. 1
Figures 34K–L, 52G–I

Description. Amb is circular to sub-circular. Laesurae are straight to sinuous, generally accompanied by elevated labra, 7–25 μm high. Exine is 2.5–5 μm thick equatorially and laevigate. Proximo-equatorial and distal surfaces are ornamented with grapnel-tipped spines, commonly 4–8 μm (rarely as much as 10 μm) long, 1.5–4 μm wide at their base, 3–6 μm apart.

Dimensions. 63(79)95 μm; four specimens measured.

Remarks. This form may correspond rather to the definition of the genus *Nikitinsporites* Chaloner, 1959, it is placed in the genus *Hystricosporites* McGregor, 1960 because the elevated labra do not form here an apical prominence as required for *Nikitinsporites*.

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

Genus IBEROESPORA Cramer and Díez, 1975

Type species. Iberoespora cantabrica Cramer and Díez, 1975.

Iberoespora cantabrica Cramer and Díez, 1975
Figure 35A

1968 Spore trilète à papilles proximales sp. 2 Jardiné and Yapaudjian, pl. 1, figs 8–9.
1975 *Iberoespora cantabrica* Cramer and Díez, p. 339, pl. 2, figs 24, 26–28, 30–31.
1980*a* ?*Geminospora* sp. A Moreau-Benoit, p. 73, pl. 10, fig. 8.
1980*a* ?*Geminospora* sp. B Moreau-Benoit, p. 73, pl. 10, fig. 9.
1981 *Iberoespora glabella* Cramer and Díez; Steemans, pl. 1, figs 8–9.

Dimensions. 26(33)41 µm; seven specimens measured.

Comparison. Specimens identified here as *Iberoespora* cf. *I. guzmani* Cramer and Díez, 1975 have a cingulum well-divided by short radially oriented muri and do not seem to have proximal inspissations.

Occurrence. BAQA-2; Jauf Formation (Sha'iba Member); *papillensis-baqaensis* to *ovalis* zones. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Previous records. From lower Lochkovian – upper Pragian of Belgium (Steemans 1989); upper Lochkovian of Solimões Basin, Brazil (Rubinstein *et al.* 2005); lower Lochkovian – lower Emsian of Armorican Massif, France (Le Hérissé 1983; Steemans 1989); lower Lochkovian of Germany (Steemans 1989); middle Přídolí of Libya (Rubinstein and Steemans 2002); and Lochkovian–lower Pragian of Spain (Cramer and Díez 1975; Rodriguez 1978*b*).

Iberoespora cf. *I. guzmani* Cramer and Díez, 1975
Figure 35B–E

cf. 1975 *Iberoespora guzmani* Cramer and Díez, p. 340, pl. 2, figs 23, 25, 32.

Description. Amb is circular to sub-triangular. Laesurae are rarely visible, straight, accompanied by narrow labra, up to 1 µm wide in overall width, extending to the inner margin of cingulum. Cingulum is 2–4 µm wide, divided in short radially oriented muri, 0.5–2 µm wide giving a crenulate appearance to the cingulum. A narrow, straight-edged and flat-bottomed, slightly sinuous furrow, generally 1–2 µm wide, separates the cingulum from the distal face of the spore body. Distal face is sculptured with convolute rugulae, generally 1–2.5 µm wide and less than 1 µm apart, resulting in a pseudoreticulum.

Dimensions. 32(39)45 µm; eight specimens measured.

Remarks. Iberoespora guzmani Cramer and Díez, 1975 clearly exhibits inspissations on the interradial areas, whereas the Saudi Arabian specimens seem to possess none. The proximal face, however, may have been torn because the laesurae are rarely observed.

Comparison. Iberoespora noninspissatosa Steemans, 1989 does not have inspissations and seems very similar to specimens described here, but it does not possess short radially oriented muri on the cingulum. The studied specimens belonging to *I. cantabrica* Cramer and Díez, 1975 are proximally sculptured with inspissations and do not have a crenulate cingulum.

Occurrence. JNDL-4, WELL-4 and WELL-7; Jauf Formation (Hammamiyat Member); *lindlarensis-sextantii* Zone.

Genus JHARIATRILETES Bharadwaj and Tiwari, 1970

Type species. Jhariatriletes baculosus Bharadwaj and Tiwari, 1970.

Comparison. Bacutriletes Potonié, 1956 lacks a well-defined contact areas; its inner structure is not known. *Biharisporites* Potonié, 1956 is spinose (spinae, coni rather than bacula). *Raistrickia* Schopf *et al.* emend. Potonié and Kremp, 1954 is single-layered and is usually used for baculate microspores.

Jhariatriletes (*Verruciretusispora*) *emsiensis* (Moreau-Benoit) comb. nov.
Figures 35F–H, 52J–L

1976 Mégaspore 1 Massa and Moreau-Benoit, table-fig. 5.
1979 *Verruciretusispora emsiensis* Moreau-Benoit, p. 43, pl. 6, figs 1–2.

Dimensions. 92(177)223 µm; eight specimens measured.

Comparison. Mégaspore 1 *in* Massa and Moreau-Benoit (1976) and *Verruciretusispora emsiensis* Moreau-Benoit, 1979, which are described from the same area, are similar to the specimens described here. The genus *Jhariatriletes* Bharadwaj and Tiwari, 1970 is more appropriate because its species are two-layered unlike *Verruciretusispora* Owens, 1971. In addition, this last genus is used for microspores. Although *Dibolisporites pilatus* Breuer *et al.*, 2007*c* is a microspore, it is also relatively thick walled and has the same kind of distal sculpture. It differs from *J. emsiensis* by its smaller size and single-layered homogenous exine.

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

Genus KNOXISPORITES Potonié and Kremp emend. Neves, 1961

Type species. *Knoxisporites hagenii* Potonié and Kremp, 1954.

?*Knoxisporites riondae* Cramer and Díez, 1975
Figure 35I–J

1968 Spore trilète à papilles soudées sp. 3 Jardiné and Yapaudjian, pl. 1, fig. 10.
1968 Spore trilète à papilles distinctes sp. 3 Jardiné and Yapaudjian, pl. 1, fig. 11.
1972 ?*Aneurospora* sp. Kemp, p. 115 (*pars*), pl. 55, fig. 10.
1975 ?*Knoxisporites riondae* Cramer and Díez, p. 341, pl. 1, figs 14, 16–17.
1983 *Knoxisporites*? *riondae* Cramer and Díez; Le Hérissé, p. 45, pl. 8, figs 10–12.
1983 *Knoxisporites*? cf. *riondae* Cramer and Díez; Le Hérissé, p. 45, pl. 8, figs 16–19.
? 1985 *Aneurospora* sp. B Paris *et al.*, pl. 18, fig. 7.

Dimensions. 28(31)35 μm; 15 specimens measured.

Comparison. *Knoxisporites*? *riondae* Cramer and Díez, 1975 and *Knoxisporites*? cf. *riondae* Cramer and Díez, 1975 described by Le Hérissé (1983) seem to represent extreme forms of the same species because they differ from each other only by the presence of additional distal verrucae. Paris *et al.* (1985) figured a specimen that resembles those of the population described here by having a distal annulus, but no description was given. *Synorisporites papillensis* McGregor, 1973 does not exhibit a distal annulus but sometimes sub-circular verrucae. As these two species intergrade, they are included in the *S. papillensis* Morphon defined here (Table 1).

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

Previous records. From the Horlick Formation of Antarctica (Kemp 1972), the age of which is considered as Pragian by Troth *et al.* (2011) based on correlation of chitinozoans and spore assemblages from South America; upper Pragian of Belgium (Steemans 1989); upper Pragian – lower Emsian of Paraná and Parnaíba basins, Brazil (Grahn *et al.* 2005; Mendlowicz Mauller *et al.* 2007); upper Pragian – lower Emsian of Armorican Massif, France (Le Hérissé 1983); and Ludlow–lowermost Lochkovian of Spain (Cramer and Díez 1975; Rodriguez 1978*b*).

Genus LEIOZOSTEROSPORA Wellman, 2006

Type species. *Leiozosterospora andersonii* Wellman, 2006.

Leiozosterospora cf. *L. andersonii* Wellman, 2006
Figure 35K–N

cf. 2006 *Leiozosterospora andersonii* Wellman, p. 194, pl. 18, figs g–i.

Description. Amb is sub-circular. Laesurae are straight, accompanied by labra, up to 1 μm wide, and associated with a narrow strip, 0.5–1 μm wide, of thinner exine on either side, extending to, or almost to, the edge of the zona. Curvaturae are sometimes visible. The inner body is sub-circular, and its diameter usually equals about one-half to three-quarters of the total amb diameter.

Dimensions. 43(67)77 μm; 16 specimens measured.

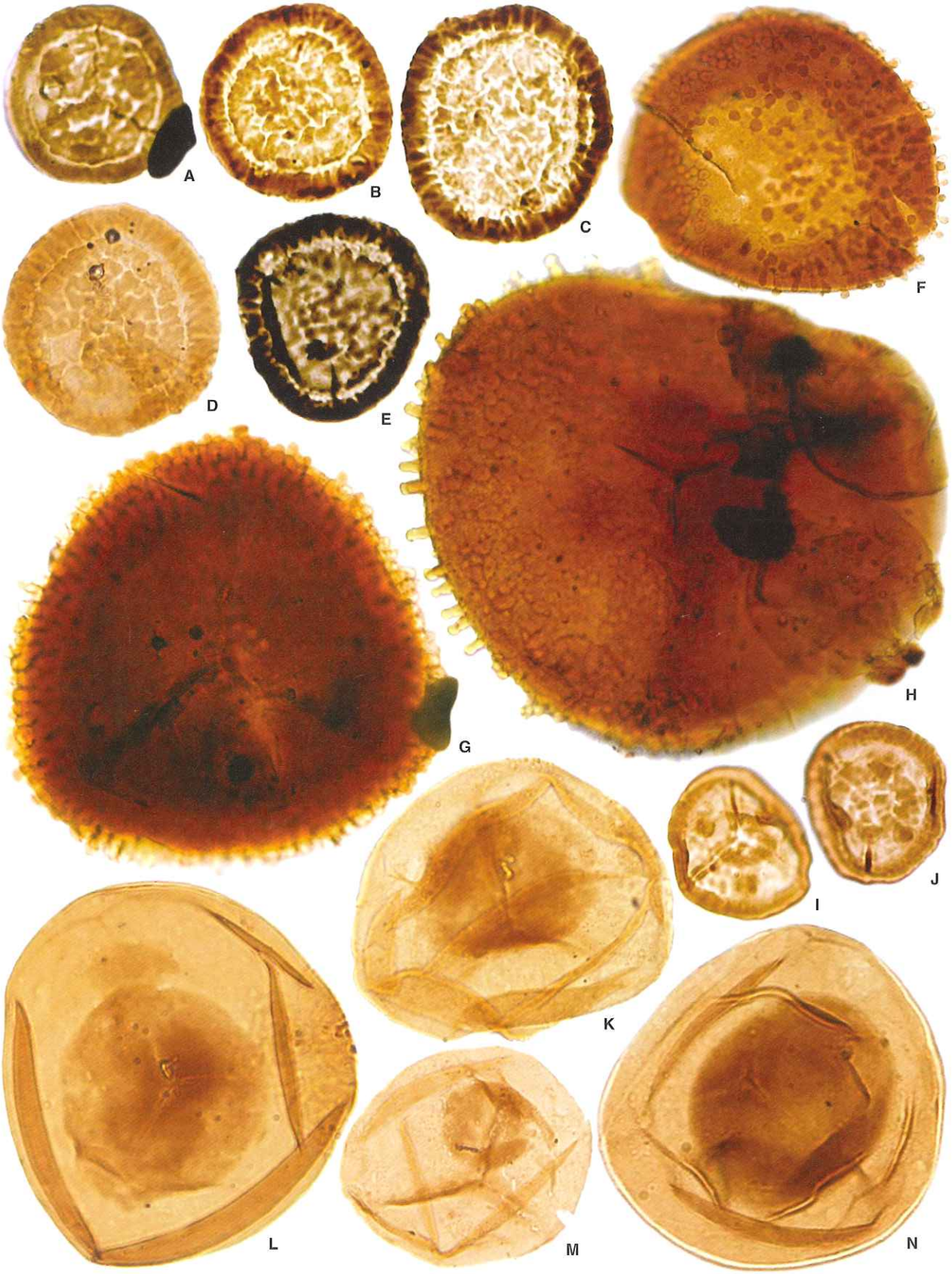
Comparison. According to C. H. Wellman (pers. comm. 2007) *L. andersonii* Wellman, 2006 is subtly different from the specimens described here. Indeed, the latter does not possess curvaturae and laesurae extend to the equator of the zona where they join a narrow limbus. *Auroraspora minuta* Richardson, 1965 is pseudosaccate with an inner body, only slightly smaller than the sexine. Its sexine is laevigate, infrapunctate or occasionally infragranular.

Occurrence. BAQA-2, JNDL-4 and WELL-5; Jauf Formation (Sha'iba to Hammamiyat members); *ovalis-biornatus* to *lindlarensis-sextantii* zones.

Genus LOPHOTRILETES (Naumova) Potonié and Kremp, 1954

Type species. *Lophotriletes gibbosus* (Ibrahim) Potonié and Kremp, 1954.

FIG. 35. 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, *Iberoespora cantabrica* Cramer and Díez, 1975. MG-1, 2631.2 m, 62252, V50.5. B–E, *Iberoespora* cf. *I. guzmani* Cramer and Díez, 1975. B, WELL-7, 13614.1 ft, 62372, K25. C, WELL-7, 13689.7 ft, 62319, O47/3. D, JNDL-4, 120.0 ft, 68612, K47. E, WELL-4, 16224.7 ft, 62090, O39. F–H, *Jhariatriletes* (*Verruciretusispora*) *emsiensis* (Moreau-Benoit) comb. nov., magnification ×500. F, A1-69, 1962 ft, 27278, J42. G, A1-69, 1962 ft, 27277, T45/4. H, A1-69, 1962 ft, 27277, Q40. I–J, ?*Knoxisporites riondae* Cramer and Díez, 1975. I, BAQA-1, 366.9 ft, 03CW117, S42-43. J, BAQA-1, 366.9 ft, 03CW117, K27/1. K–N, *Leiozosterospora* cf. *L. andersonii* Wellman, 2006. K, JNDL-4, 120.0 ft, 68612, Q59. L, BAQA-2, 64.5 ft, 66818, T48. M, JNDL-4, 221.8 ft, 68646, G33; the inner body diameter is abnormally small compared to the total amb diameter. N, BAQA-2, 64.5 ft, 03CW132, N49.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Lophotriletes devonicus (Naumova ex Chibrikova) McGregor and Camfield, 1982
Figure 36A–B

1982 *Lophotriletes devonicus* (Naumova ex Chibrikova) McGregor and Camfield, p. 54 (*cum syn.*), pl. 15, figs 5–11; text-fig. 86.

Dimensions. 38(43)48 μm; four specimens measured.

Remarks. The distal sculptural elements of this species commonly resemble small verrucae in plan view. In lateral compression, however, they prove to be commonly broad-based, blunt coni in profile (McGregor and Camfield 1982).

Occurrence. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *lindlarensis-sextantii* to *lemurata-langii* zones.

Previous records. From upper Emsian – lower Eifelian of Algeria (Moreau-Benoit *et al.* 1993); ?Emsian–Eifelian of Bolivia (McGregor 1984); upper Eifelian of the Parnaíba Basin, Brazil (Breuer and Grahn 2011); upper Eifelian – lower Givetian of Canada (McGregor and Uyeno 1972; McGregor and Camfield 1982); Emsian–lower Eifelian of Libya (Moreau-Benoit 1989); Emsian–Eifelian of Morocco (Rahmani-Antari and Lachkar 2001); and ?upper Eifelian–Givetian of Saudi Arabia (PB, pers. obs.).

Genus LOPHOZONOTRILETES Naumova, 1953

Type species. Lophozonotriletes lebedianensis Naumova, 1953.

Lophozonotriletes media Taugourdeau-Lantz, 1967
Figure 36C–D

1965 Unidentified spores types Kerr *et al.*, pl. 4, figs 9, 11.
1967 *Lophozonotriletes media* Taugourdeau-Lantz, p. 52, pl. 2, fig. 6.
1971 *Geminospora verrucosa* Owens, p. 63, pl. 19, figs 10–12.
1989 *Spinozonotriletes verrucosus* (Owens) Coquel and Moreau-Benoit, p. 93.

Dimensions. 40(65)92 μm; 18 specimens measured.

Comparison. The specimens figured by Owens (1971) of *Geminospora verrucosa* Owens, 1971 do not seem to have an inner body as alleged in the diagnosis. These specimens seem to correspond rather to *L. media*. Note that many species of *Lophozonotriletes* Naumova, 1953 were described in the literature and notably from Libya (Massa and Moreau-Benoit 1976; Moreau-Benoit 1979, 1980*b*). It is impossible to compare all because their diagnoses are inadequate. In addition, some of these species could be grouped together or be synonymous with *L. media* since the latter is a highly variable form. *Archaeozonotriletes variabilis* Naumova emend. Allen, 1965 is also finely punctate without protuberances. Some extreme variants of *L. media*, which show a much reduced ornamentation, could intergrade with *A. variabilis* in the *A. variabilis* Morphon (Table 1). As the latter includes variable and intergrading morphotypes, the concept of *L. media* may appear challenging to constrain and larger here than in the literature. *Cyrtospora tumida* sp. nov. may be infrapunctate and commonly has larger protuberances. It may also intergrade with *L. media*.

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

Previous records. From lower Givetian – upper Frasnian of Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003; Breuer and Grahn 2011); upper Eifelian–Frasnian of Canada (Owens 1971; McGregor and Camfield 1982); Frasnian of France (Loboziak *et al.* 1983, 1988); middle Givetian of Greenland (Friend *et al.* 1983; Marshall and Hemsley 2003); middle Eifelian – upper Frasnian (Streel *et al.* 1988; Moreau-Benoit 1989); Givetian of Poland (Turnau and Racki 1999); upper Givetian – lower Frasnian of Portugal (Lake *et al.* 1988); Givetian–Frasnian of Saudi Arabia (PB, pers. obs.); and uppermost Givetian – lower Frasnian of Scotland (Marshall *et al.* 1996).

Genus LYCOSPORA Schopf *et al.* emend. Potonié and Kremp, 1954

Type species. Lycospora micropapillata (Wilson and Coe) Schopf *et al.*, 1944.

FIG. 36. 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, *Lophotriletes devonicus* (Naumova ex Chibrikova) McGregor and Camfield, 1982. 1, A1-69, 1486 ft, 26977, R39. 2, A1-69, 2108–2111 ft, 26913, G44. C–D, *Lophozonotriletes media* Taugourdeau-Lantz, 1967. C, A1-69, 1174 ft, 62673, K-L32. D, A1-69, 971 ft, 62640, X-Y49. E–H, *Lycospora culpa* Allen, 1965. E, BAQA-2, 64.5 ft, 03CW132, R31. F, BAQA-2, 54.8 ft, 03CW129, R38/3. G, BAQA-2, 52.0 ft, 03CW128, N27/1. H, BAQA-2, 134.4 ft, 03CW137, H35/4. I–J, *Perotrilites caperatus* (McGregor) Steemans, 1989. I, JNDL-3, 389.0 ft, 68563, D48/3. J, JNDL-4, 120.0 ft, 68612, H50/3. K–M, *Raistrickia commutata* sp. nov. K, MG-1, 2194 m, 63013, G29/4. L, Holotype, MG-1, 2247 m, 62942, J30. M, MG-1, 2258 m, 62948, E42.


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Lycospora culpa Allen, 1965
Figure 36E–H

1965 *Lycospora culpa* Allen, p. 713, pl. 98, figs 7–8.
? 1968 *Zonotriletes* sp. 5 Jardiné and Yapaudjian, pl. 2, figs 4–5.

Dimensions. 32(40)48 μm; 15 specimens measured.

Remarks. According to Somers (1972), *Lycospora culpa* Allen, 1965 should be excluded from this genus because of the zonate nature of the equatorial flange. This statement is rejected here as the definition of the genus matches the species described here.

Comparison. The figured specimens of *Zonotriletes* sp. 5 *in* Jardiné and Yapaudjian (1968) are very similar to the present specimens, but they are not described.

Occurrence. BAQA-1 and BAQA-2; Jauf Formation (Sha'iba to Subbat members); *papillensis-baqaensis* to *ovalis* zones. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Previous record. From Pragian of Spistbergen, Norway (Allen 1965).

Genus PEROTRILITES Couper emend. Evans, 1970

Type species. Perotrilites granulatus Couper, 1953.

Perotrilites caperatus (McGregor) Steemans, 1989
Figure 36I–J

1989 *Perotrilites caperatus* (McGregor) Steemans, pp. 150–151 (*cum syn.*), pl. 42, figs 12–14; pl. 43, figs 1–2.
2006 *Camptozonotriletes? caperatus* McGregor; Wellman, p. 190, pl. 18, figs a–c.

Dimensions. 37(65)95 μm; 16 specimens measured.

Remarks. The zonate, zonate-camerate and camerate conditions are difficult to differentiate in compressed specimens.

Comparison. Camptozonotriletes aliquantus Allen, 1965 is both zonate and camerate, like *P. caperatus*. According to McGregor (1973), the radially directed muri of *C. aliquantus* are not similar to the fold-like structures of *P. caperatus*. *C. aliquantus* also differs in having prominent distal anastomosing muri. *Zonotriletes venatus* sp. nov. is larger, only zonate and does not exhibit such a distal sculpture on the central body.

Occurrence. BAQA-1, JNDL-3 and JNDL-4; Jauf Formation (Subbat to Muray members); *milleri* to *annulatus-protea* zones. MG-1, Ouan-Kasa Formation, *lindlarensis-sextantii* to *svalbardiae-eximius* zones.

Previous records. From upper Pragian – lower Emsian of Argentina (Rubinstein and Steemans 2007); upper Lochkovian–Emsian of Belgium (Steemans 1989); upper Pragian–lower Emsian of Paraná and Parnaíba basins, Brazil (Grahn *et al.* 2005; Mendlowicz Mauller *et al.* 2007); Pragian–Emsian of Canada (McGregor and Owens 1966; McGregor 1973, 1977; McGregor and Camfield 1976); upper Lochkovian–Emsian of Germany (Steemans 1989); upper Pragian of Morocco (Rahmani-Antari and Lachkar 2001); Pragian–uppermost Emsian of Poland (Turnau 1986; Turnau *et al.* 2005); upper Lochkovian of Romania (Steemans 1989); and upper Pragian – ?lowermost Emsian of Scotland (Wellman 2006).

Genus RAISTRICKIA Schopf *et al.* emend. Potonié and Kremp, 1954

Type species. Raistrickia grovensis Schopf *et al.*, 1944.

Raistrikia commutata sp. nov.
Figures 36K–M, 37A–B

? 1968 *Raistrickia* sp. Jardiné and Yapaudjian, pl. 2, fig. 7.

Derivation of name. From *commutatus* (Latin), meaning variable; refers to the proximo-equatorial and distal sculpture.

Holotype. EFC J30 (Fig. 36L), slide 62942.

Paratype. EFC G34 (Fig. 37A), slide 62746; MG-1 borehole, sample 2160.6 ft.

FIG. 37. 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, *Raistrickia commutata* sp. nov. A, Paratype, MG-1, 2160.6 m, 62746, G34. B, MG-1, 2258 m, 62948, T49. C–H, *Raistrickia jaufensis* sp. nov. C, Paratype, BAQA-1, 390.6 ft, 03CW120, N38. D, BAQA-1, 371.1 ft, 03CW118, H47. E, Holotype, BAQA-1, 366.9 ft, 03CW117, T35/2. F, BAQA-1, 222.5 ft, 03CW108, M31. G, BAQA-1, 371.1 ft, 03CW118, N26/3. H, BAQA-1, 285.5 ft, 03CW111, H31/4. I–L, *Retusotriletes atratus* sp. nov. I, JNDL-4, 272.0 ft, 68656, Q41/1. J, Paratype, WELL-4, 16273.0 ft, 62122, O34-35. K, JNDL-1, 153.8 ft, 60834, O38/2. L, Holotype, WELL-4, 16316.6 ft, 62157, T48. M–R, *Retusotriletes celatus* sp. nov. M, BAQA-1, 175.9 ft, 66778, T38/3. N, Holotype, JNDL-4, 448.6 ft, 68693, S25/4. O, WELL-3, 14195.3 ft, 66836, R53/1. P, WELL-3, 14195.2 ft, 60550, K35/1. Q, WELL-7, 13689.7 ft, 62317, J37/2. R, Paratype, WELL-7, 13689.7 ft, 62316, D-E57.


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

Diagnosis. A *Raistrickia* irregularly sculptured with a variable mixture of coni, spinae, bacula and verrucae. Sculptural elements mostly longer than wide, very variable in shape and in density.

Description. Amb is sub-circular to sub-triangular, or occasionally oval. Laesurae are straight, simple, one-half to nine-tenths of the amb radius in length. Exine is commonly 1.5–4 μm thick equatorially, homogeneous or punctate. Proximo-equatorial and distal regions are irregularly sculptured with a variable mixture of coni, spinae, bacula and verrucae with blunt, flat-topped, pointed or widened tips. Sculptural elements are 1–12 μm wide at base, 2–20 μm high, mostly longer than wide. They are very variable in shape and in density. Contact areas are laevigate or with sculpture like that of the distal face but reduced in size.

Dimensions. 55(68)96 μm; 13 specimens measured.

Comparison. Raistrickia aratra Allen, 1965 is more densely sculptured with less elongated elements. *Raistrickia* cf. *clavata* Hacquebard, 1957 *in* Richardson (1965) has few sculptural elements around the equator and these are not really elongated as in *R. commutata*. *Raistrickia* sp. *in* Jardiné and Yapaudjian (1968) could be assignable to *R. commutata*, but no diagnosis was given.

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

Previous record. Similar specimens have been reported in ?upper Eifelian–Givetian of Saudi Arabia (PB, pers. obs.).

Raistrikia jaufensis sp. nov.
Figure 37C–H

Derivation of name. From *jaufensis* (Latin); refers to the lithostratigraphic unit (formation) where this species occurs.

Holotype. EFC T35/2 (Fig. 37E), slide 03CW117.

Paratype. EFC N38 (Fig. 37C), slide 03CW120; BAQA-1 core hole, sample 390.6 ft.

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

Diagnosis. A sub-triangular to triangular *Raistrickia* usually irregularly sculptured with bacula. Base of elements generally flared. Tops of elements flat or slightly concave, with generally a bifurcate shape.

Description. Amb is sub-triangular to triangular. Laesurae are straight, simple, three-fifths to nine-tenths of the amb radius in length, but often indistinct because the proximal face seems to be usually torn. Exine is 1–2 μm thick equatorially. Equatorial and distal regions are usually irregularly sculptured with bacula, 1–3 μm wide at base, 2–5 μm high, 1–8 μm apart. The base of elements is generally flared. The tops of elements are flat or slightly concave, with generally a bifurcate shape. Contact areas are laevigate.

Dimensions. 27(36)48 μm; 26 specimens measured.

Remarks. Some of these specimens are preserved as tetrads.

Comparison. Raistrickia sp. *in* McGregor (1973) may correspond to the description of the specimens presented here, but it is subcircular and only a few specimens were recorded from the Gaspé assemblages. *Cymbosporites dammamensis* Steemans, 1995 is patinate and more densely sculptured with generally smaller bacula.

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

Genus RETUSOTRILETES Naumova emend. Streel, 1964

Type species. Retusotriletes simplex Naumova, 1953.

Retusotriletes atratus sp. nov.
Figure 37I–L

2005 *Retusotriletes* sp. A Hashemi and Playford, p. 338, pl. 2, fig. 12.

Derivation of name. From *atratus* (Latin), meaning dark; refers to the proximal interradial thickened zones.

Holotype. EFC T48 (Fig. 37L), slide 62157.

Paratype. EFC O34-35 (Fig. 37J), slide 62122; WELL-4 well, sample 16273.0 ft.

Type locality and horizon. WELL-4 well, sample 16316.6 ft; Jauf Formation at Kharma, Saudi Arabia.

Diagnosis. A *Retusotriletes* with a darker proximal zone, variable in size and shape, present in each contact area.

Description. Amb is sub-circular. Laesurae are straight, simple or accompanied by labra, up to 3 μm in overall width, three-fifths to nine-tenths of the amb radius in length, connected by curvaturae perfectae. Exine is laevigate or scabrate, 1–2 μm thick.

A darker proximal zone is present in each contact area. These thickened zones are variable in size and shape, and situated towards the proximal pole between the laesurae.

Dimensions. 45(56)77 µm; 14 specimens measured.

Comparison. Retusotriletes crassus Clayton *et al.*, 1980 is slightly different because it has simple laesurae which are also rarely seen. *R. aureoladus* Rodriguez, 1978*a* is smaller and has a paler ring around the proximal thickened zones. *Retusotriletes* sp. A *in* Hashemi and Playford (2005) is similar but slightly smaller.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-4, WELL-7 and WELL-8; Jauf (Sha'iba to Hammamiyat members) and Jubah formations; *ovalis-biornatus* to *triangulatus-catillus* zones.

Previous record. From Emsian–lower Givetian of Adavale Basin, Australia (Hashemi and Playford 2005).

Retusotriletes celatus sp. nov.
Figure 37M–R

Derivation of name. From *celatus* (Latin), meaning hidden; refers to the fact that this species may have a delicate folded outer layer and thus have a different genus and species name (see below).

Holotype. EFC S25/4 (Fig. 37N), slide 68693.

Paratype. EFC D-E57 (Fig. 37R), slide 62316; WELL-7 well, sample 13689.7 ft.

Type locality and horizon. JNDL-4 core hole, sample 448.6 ft; Jauf Formation at Domat A1–Jandal, Saudi Arabia.

Diagnosis. A *Retusotriletes* with a darker apical sub-triangular band, with sharp margins and straight, slightly concave or convex sides, that extends almost to, or to the end of, laesurae. Inner lighter sub-triangular band generally with slightly concave sides also present at the proximal pole.

Description. Amb is sub-circular. Laesurae are straight, simple or rarely accompanied by narrow labra, *c.* 1 µm in overall width, two-thirds to three-quarters of the amb radius in length, connected by curvaturae perfectae not always well developed. Exine is laevigate, commonly 1–2 µm thick. A darker apical sub-triangular band, with sharp margins and 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 exine), generally with slightly concave sides, is present proximally and surrounded by the darkened band.

Dimensions. 28(39)54 µm; 15 specimens measured.

Remarks. Retusotriletes celatus is comparable with the specimens of *Diaphanospora milleri* sp. nov. in which the outer layer is absent. The very delicate outer layer of the second species could have been torn off by sedimentary or taphonomic processes. The two form-species *R. celatus* and *D. milleri* represent thus a unique biological species with the different states of preservation between both. They are grouped in the *D. milleri* Morphon (Table 1). They sometimes co-occur and have comparable stratigraphical ranges.

Comparison. Retusotriletes tenerimedium Chibrikova, 1959 has a lighter apical area that is sub-triangular with convex sides. Moreover, the darker area is diffuse at its outer margin and does not reach the end of laesurae. *R. rotundus* (Streel) Streel emend. Lele and Streel, 1969 and *R. triangulatus* (Streel) Streel, 1967 are larger, and their thickened apical areas do not extend to the end of laesurae.

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

Retusotriletes goensis Lele and Streel, 1969
Figure 38A

1969 *Retusotriletes goensis* Lele and Streel, p. 93, pl. 1, figs 12–16.
non 1978*b* *Retusotriletes goensis* Lele and Streel; Rodriguez, p. 420, pl. 2, fig. 25.

Dimensions. 47(68)104 µm; four specimens measured.

Comparison. Retusotriletes rotundus (Streel) Streel emend. Lele and Streel, 1969 and *R. tenerimedium* Chibrikova, 1959 have a sub-triangular apical area which is differentiated into two zones. *Retusotriletes* cf. *microgranulatus* (Vigran) Streel, 1967 is sculptured with micropila.

Occurrence. BAQA-1, JNDL-4, WELL-3 and WELL-8; Jauf (Subbat and Hammamiyat members) and Jubah formations; *asymmetricus* to *lemurata-langii* zones.

Previous records. From upper Emsian (Lessuise *et al.* 1979) and the Pepinster Formation of Belgium (Lele and Streel 1969), the age of which is considered as late Eifelian by Laloux *et al.* (1996); upper Lochkovian of Solimões Basin, Brazil (Rubinstein *et al.* 2005); and lower Eifelian – lower Givetian of Libya (Moreau-Benoit 1989).