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AN ENDEMIC FLORA OF DISPERSED SPORES FROM THE MIDDLE DEVONIAN OF IBERIA

by ALEXANDER J. ASKEW  and CHARLES H. WELLMAN

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Abstract: Diverse assemblages of dispersed spores have been recovered from Middle Devonian rocks in northern Spain, revealing a significant endemism in the flora. Middle Devonian Iberia was part of a relatively isolated island complex (Armorican Terrane Assemblage), separated by considerable tracts of ocean from Laurussia to the north-west and Gondwana to the south-east. The Middle Devonian deposits of the Cantabrian Zone of northern Spain are entirely marine and comprise a thick clastic unit sandwiched between extensive carbonate units. The clastic unit, the laterally equivalent Naranco, Huergas and Gustalapedra formations of Asturias, León and Palencia provinces, represents a nearshore-offshore transect across a marine shelf. This unit is also believed to encompass the Kačák Event, an important global extinction event. The recovered palynomorphs include marine (phytoplankton, chitinozoans, scolecodonts) and terrestrial (spores) assemblages. These are abundant and well preserved, although

of variable thermal maturity. Here, we describe the dispersed spores and consider their significance as regards biostratigraphy, palaeophytogeography and Kačák Event interpretation. The dispersed spores represent a single assemblage assignable to the *lemurata-langii* Assemblage Zone (*lemurata* Subzone) indicating a probable early (but not earliest) Givetian age. Signs of endemism include various taxa known only from this region, some taxa appearing to have discordant ranges compared with elsewhere, and the absence from Iberia of certain prominent taxa characteristic of coeval assemblages elsewhere, such as those with grapnel-tipped processes. The abrupt interruption of carbonate deposition, with a change to rapid deposition of thick clastic deposits, provides support for a monsoonal cause of the Kačák Event.

Key words: endemism, Spain, Eifelian, Givetian, Kačák Event, Iberia.

DISPERSED spore assemblages from Middle Devonian deposits of northern Spain have previously been relatively neglected and briefly considered in only three publications (Cramer 1966, 1969; Fombella Blanco 1988). This is unfortunate as these deposits are otherwise well studied and exhibit a number of extremely interesting features. They represent an entirely marine onshore-offshore transect, represented by a clastic unit sandwiched between thick carbonate sequences, securely age-constrained by conodonts and sedimentologically/palaeontologically well characterized. The sequence is of particular interest because: (1) it accumulated around a small group of islands in a palaeogeographically isolated location situated between the large continents of Laurussia and Gondwana (Torsvik & Cocks 2013); and (2) the clastic unit is believed to incorporate the Kačák Event (García-Alcalde 1998). This extinction event has been identified globally (House 2002) although its characteristics and causes remain the subject of much debate (Marshall *et al.* 2007; Becker *et al.* 2016). The aim of this study is to describe the composition and distribution of dispersed spore

assemblages from throughout this sequence and use them to test and refine previously erected spore biostratigraphical schemes, identify palaeophytogeographical differentiation on this isolated island group, and shed light on the nature of the Kačák Event.

GEOLOGICAL SETTING

Devonian sediments crop out in the Cantabrian Zone in northern Spain in a large partial arc from the northern coast near Gijón, south through Asturias and in an east-west orientation across León and Palencia provinces (García-Alcalde *et al.* 2002). They are interpreted as having been deposited in a transect across the shelf from nearshore (Asturias) to offshore (Palencia) (García-Alcalde *et al.* 2002). Details of the stratigraphic sequence are given in Figure 1. The sedimentary sequence broadly alternates between calcareous and clastic in character. This paper concerns the Middle Devonian clastic unit classified as the laterally equivalent Naranco, Huergas and Gustalapedra

formations located in Asturias, León and Palencia, respectively. They are bounded by thick limestone sequences below (the laterally equivalent Moniello, Santa Lucía and Polentinos formations) and above (the laterally equivalent Candás, Portilla and Cardaño formations).

The age of the Naranco, Huergas and Gustalapedra formations is Eifelian–Givetian, supported directly by biostratigraphical analysis based on various marine macrofaunal groups (García-López *et al.* 2002). Conodonts from the bounding limestone formations provide a refined age constraint. Those from the underlying Santa Lucía Formation (and possibly lowermost Huergas and Naranco formations) belong to the *Polygnathus costatus* Zone of middle Eifelian age (*c.* 391–392 Ma based on Becker *et al.* 2012). Those from the overlying Portilla and Candás formations belong to the lower *Polygnathus varcus* zone of early, but not earliest, Givetian age (*c.* 386–387 Ma based on Becker *et al.* 2012) (García-López & Sanz-López 2002; García-López *et al.* 2002).

The sediments of the Naranco, Huergas and Gustalapedra formations are in excess of 500 m in thickness

in Asturias but reduced to only 50 m in thickness in Palencia. The deposits are characterized by a lower and an upper unit. The lower unit is coarser in character, dominated by thick sandstone layers, and represents a more abundant terrigenous clastic supply. The upper unit has a more mixed character, with rapid alternations between sandstones and siltstones (and occasional limestones) and represents a combination of coarse terrigenous and finer basinal deposits. In León, it includes euxinic nodular black shales that are pelagic-like in character. García-Ramos (1978) details the wide range of facies present in the Naranco Formation and its equivalents that represent varied marine and transitional depositional environments associated with large deltas (García-Alcalde *et al.* 2002).

For this project, 30 localities were examined and samples collected for palynological analysis. The location of each site is indicated in Figure 2. Details of the sites' location and precise geological setting, as well as samples taken, are provided in Askew & Wellman (2018).

Stage	Asturias		León		Palencia	
Famennian	C/B \ V		B/LE \ V		Vidrieros	
	Ermita		Ermita		Murcia	
	Piñeres		conglomerate \ Fueyo	Cardaño		
Frasnian			Crémenes \ Nocedo			
Givetian	Candás		Portilla		Man member \ Gustalapedra	
Eifelian	Naranco		Huergas		Polentinos	
Emsian	Moniello		Santa Lucía		Abadía	
	Rafieces Group	Aguión	La Vid Group	Coladilla		
		La Ladrona		Valporquero		
Pragian	Rafieces Group	Bañugues	La Vid Group	La Pedrosa	Lebanza	
		Nieva		Felmin		
Lochkovian	Furada		Nieva		Carazo	
					Cortés–Cardaño Group	

FIG. 1. Age and correlation of Devonian units in several Iberian areas. Dashed lines indicate uncertainly placed boundaries. Diagram not to scale. Abbreviations for uppermost Famennian units: B, Balears; C, Candamo; LE, Las Ermitas; V, Vegamián. Redrawn from García-Alcalde *et al.* (2002).

PREVIOUS PALYNOLOGICAL STUDIES

Previous palynological studies of the Naranco and Huergas formations are limited to three papers. Cramer (1966) described an assemblage from one sampled site of the Naranco Formation, believed to be the '120' site of Cramer (1969) and this study. Cramer (1969) expanded the earlier work with four additional sites from the same general area. These studies described a spore assemblage containing many new species, with others mostly showing an affinity with Russian and European floras known at the time, relatively early in the history of Devonian spore studies. Cramer interpreted the spore assemblage as supporting the Eifelian–Givetian age the Naranco Formation had previously been assigned based on invertebrate macrofossil evidence. Fombella Blanco (1988) described an assemblage of spores (including one newly described species) and phytoplankton from a single site in the Huergas Formation, relocated during the present study and described in Askew & Wellman (2018), but made no comment on the formation's age. Table 1 lists the species named in these studies, along with a correlation with the species identified and taxonomy utilized in the present study.

SAMPLING AND METHODS

A total of 130 samples were collected for palynological analysis from across the outcrop area of the Naranco, Huergas and Gustalapedra formations during two field-trips in January and August–September 2015. Sampling focused on beds of dark, fine-grained material, predominantly mudstones and siltstones, interspersed within the mostly sandstone formations (Fig. 3). As outlined in Askew & Wellman (2018), three relatively long sections, two incomplete and one nearly complete, were sampled with the remaining localities representing either spot samples or relatively short sections. It is important to note that during the extensive folding and thrusting of the Spanish sequence the clastic sediments of the Naranco, Huergas and Gustalapedra formations often acted as a slip plane between the more rigid limestone formations above and below. Furthermore, compared to the bounding limestones they are often deeply weathered, with surface exposures vegetated. As a consequence: (1) long sections are rare (see above); (2) good upper and lower boundary sections are rare and difficult to identify; and (3) short exposed sections are difficult to place in stratigraphical context.

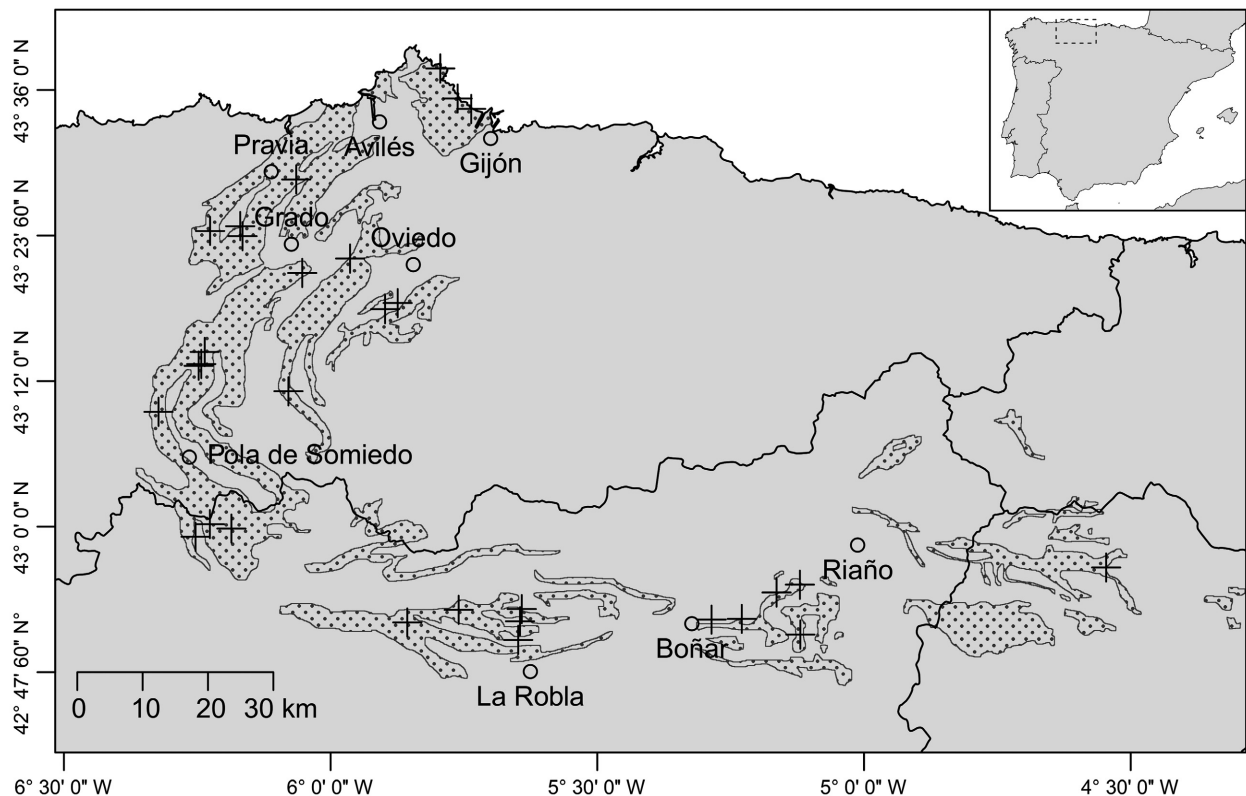


FIG. 2. Outline map of northern Spain. Sites surveyed in this study are marked with crosses. Outlined areas marked with dots indicate the outcrop area of Devonian sediments.

TABLE 1. Comparison of the spore taxa found in this study with those previously reported.

Identifications used in this study and comments on previously identified species not synonymized here	Species reported in previous studies
<i>Acinosporites acanthomammillatus?</i>	
<i>A. lindlarensis</i>	
<i>Ambitisporites avitus</i>	
<i>A. dilutus</i>	
<i>A. sp. A</i>	
<i>A. sp. B</i>	
<i>A. sp. C</i>	
<i>Anapiculatisporites abrepunius</i>	
<i>A. carminae</i>	<i>Anapiculatisporites carminae</i> (Cramer 1966) <i>A. carminae</i> Cramer (Cramer 1969)
<i>A. picantus</i>	
<i>Apiculatasporites perpusillus</i>	
<i>Apiculatisporis cf. elegans</i>	
<i>Apiculiretusispora cf. brandtii</i>	<i>cf. Apiculiretusispora cf. brandtii</i> Strel (Fombella Blanco 1988)
<i>A. plicata</i>	<i>Cyclogranisporites plicatus</i> Allen (Cramer 1969) ? <i>Aneurospora gregsii</i> Clayton <i>et al.</i> (Fombella Blanco 1988) ? <i>Apiculiretusispora arenorugosa</i> McGregor (Fombella Blanco 1988)
<i>A. sp. A</i>	
<i>A.? sp. B</i>	
<i>Brochotriletes foveolatus?</i>	
<i>Camazonotriletes? concavus</i>	
<i>C. parvus</i>	
<i>Concavisporites? sp. A</i>	
<i>Corystisporites cf. sp.</i>	
<i>Deltoidospora priddyi</i>	
<i>Devonomonoletes cf. sp. 1</i>	
<i>Diatomozonotriletes cf. franklinii</i>	
<i>Dibolisporites tuberculatus</i>	? <i>Dibolisporites echinaceous</i> (Eisenack) Richardson (Fombella Blanco 1988)
<i>D. sp. A</i>	
<i>Dictyotriletes cf. hemeri</i>	? <i>Cymatiosphaera magnata</i> Pilchler (Fombella Blanco 1988)
<i>D. gorgoneus</i>	
<i>Emphanisporites annulatus</i>	<i>Emphanisporites annulatus</i> McGregor (Cramer 1966) <i>E. annulatus</i> McGregor (Cramer 1969) <i>E. cf. anulatus</i> McGregor (Fombella Blanco 1988)
<i>E. cf. annulatus</i>	
<i>E. annulatus?</i>	
<i>E. augusta</i>	
<i>E. cf. laticostatus</i>	
<i>E. mcgregorii</i>	<i>Emphanisporites mcgregorii</i> Cramer (Cramer 1969)
<i>E. micronatus</i>	
<i>E. orbicularis</i>	? <i>Emphanisporites erraticus</i> (Eisenack) (Cramer 1966)
<i>E. cf. orbicularis</i>	
<i>E. protoannulatus</i>	
<i>E. rotatus</i>	<i>Emphanisporites rotatus</i> McGregor (Cramer 1966) <i>E. obscurus</i> McGregor (Cramer 1969) <i>E. robustus</i> McGregor (Cramer 1969) <i>E. rotatus</i> McGregor (Cramer 1969) <i>E. rotatus</i> McGregor (Fombella Blanco 1988)
<i>E. cf. rotatus</i>	
<i>E. sp. A</i>	

(continued)

TABLE 1. (Continued)

Identifications used in this study and comments on previously identified species not synonymized here	Species reported in previous studies
<i>Geminospora lemurata</i>	? <i>Geminospora</i> cf. <i>tuberculata</i> (Kedo) Allen (Fombella Blanco 1988)
<i>G. cf. svalbardiae</i>	<i>Hymenozonotriletes argutus</i> 'II' Naumova (Cramer 1966)
<i>Grandispora argutus</i>	p. <i>Calyptosporites</i> cf. <i>deliquescens</i> (Naumova) New Combination (Cramer 1969)
<i>G. douglastownensis?</i>	? <i>Hymenozonotriletes</i> cf. <i>eximius?</i> Naumova (Cramer 1966)
	<i>H. cf. deliquescens?</i> Naumova (Cramer 1966)
	? <i>Calyptosporites argutus</i> (Naumova) New Combination (Cramer 1969)
	p. <i>C. cf. deliquescens</i> (Naumova) New Combination (Cramer 1969)
<i>G. cf. inculta</i>	? <i>Hymenozonotriletes argutus</i> 'I' Naumova (Cramer 1966)
	<i>H. narancae</i> Cramer (Cramer 1966)
	p. <i>Calyptosporites microspinosus</i> (Richardson) Richardson (Cramer 1966)
	cf. <i>C. optivus</i> (Chibrikova) Allen; (Cramer 1969)
	p. <i>C. (?) narancae</i> (Cramer) New Combination (Cramer 1969)
	? <i>Grandispora sp.C</i> Paris <i>et al.</i> (Fombella Blanco 1988)
<i>G. permulta</i>	<i>Grandispora</i> sp. A, Paris <i>et al.</i> (Fombella Blanco 1988)
<i>G. protea</i>	? <i>Calyptosporites</i> cf. <i>domanicus</i> (Naumova) New Combination (Cramer 1969)
<i>G. cf. stolidota</i>	
<i>G. velata</i>	p. <i>Calyptosporites microspinosus</i> (Richardson) Richardson (Cramer 1969)
	<i>C. velatus</i> (Eisenack) Richardson (Cramer 1969)
<i>Granulatisporites concavus</i>	? <i>Leiotriletes bonitus</i> Cramer (Cramer 1969)
<i>G. cf. muninensis</i>	
<i>Latosporites</i> sp. 1	
<i>Planisporites</i> cf. <i>minimus</i>	<i>Cyclogranisporites rosendae</i> Cramer (Cramer 1966)
	<i>Rhabdosporites prosperus</i> (Cramer) New Combination (Cramer 1969)
	? <i>Acanthotriletes</i> sp. (Fombella Blanco 1988)
<i>Retusotriletes atratus</i>	
<i>R. goensis</i>	
<i>R. rotundus</i>	<i>Retusotriletes barbatus</i> Cramer (Cramer 1969)
	<i>R. rotundus</i> (Streel) Streel (Cramer 1969)
	<i>Retusotriletes pychovii</i> Naumova <i>major</i> Naumova (Cramer 1969)
<i>R. semizonalis</i>	
<i>R. triangulatus</i>	? <i>Retusotriletes triangulatus</i> (Streel) Streel (Fombella Blanco 1988)
<i>R. sp. A</i>	
<i>R. spp.</i>	
<i>Rhabdosporites minutus</i>	
<i>Samarisporites</i> cf. <i>praetervisus</i>	
<i>Verrucosporites scurrus</i>	<i>Raistrickia aratra</i> Allen (Fombella Blanco 1988)
<i>V. tumulentus</i>	
<i>Zonotriletes armillatus</i>	
<i>Z. simplicissimus</i>	
Spore type A	
A phytoplankton specimen	<i>Acanthotriletes espinositus</i> Cramer (Cramer 1969)
Too poorly figured to identify	<i>A. heterodontus</i> (Fombella Blanco 1988)
A phytoplankton specimen	<i>A. tenuispinosus tenuispinosus</i> Naumova (Cramer 1969)
Too poorly figured to identify;	<i>Camptotriletes araneosus</i> Cramer (Cramer 1966)
probably <i>Dictyotriletes</i>	
Too poorly figured to identify	<i>Grandispora</i> sp. B Paris <i>et al.</i> (Fombella Blanco 1988)
Too poorly figured to identify;	<i>G. sp. B</i> (Fombella Blanco 1988)
potentially <i>Apiculiretusispora</i>	

(continued)

TABLE 1. (Continued)

Identifications used in this study and comments on previously identified species not synonymized here	Species reported in previous studies
Too poorly figured to identify; potentially <i>Apiculiretusispora</i>	cf. <i>Hymenozonotriletes discors</i> Chibrikova (Fombella Blanco 1988)
Not described or figured	<i>Hystichosporites delectabilis</i> McGregor (Cramer 1969)
Too poorly figured to identify; probably <i>Apiculiretusispora</i>	<i>Retusotriletes</i> sp. Paris <i>et al.</i> (Fombella Blanco 1988)
Not described or figured	<i>Rhabdosporites butifarrus</i> (Cramer) New Combination (Cramer 1969)
Too poorly figured to identify	<i>Samarisporites</i> sp. B Paris <i>et al.</i> (Fombella Blanco 1988)
Poorly figured; possibly a megaspore	<i>Verrucosisporites</i> cf. <i>tuberosus</i> (Loose) Smith & Butterworth (Fombella Blanco 1988)

Previously reported species are reproduced as cited and followed in parenthesis by the reference in which they were reported. Previously reported species synonymized with species found in this investigation are listed against them.

Rock samples were processed at the University of Sheffield using standard HCl–HF–HCl acid maceration, followed by sieving using a 15 µm mesh to remove the finest mineral matter. Remaining mineral residue was removed using heavy liquid centrifugation with ZnCl₂. The organic residue was then assessed, with three barren samples and one with very poor preservation not being processed further. The remaining kerogen samples were evaluated by strew mounting on microscope slides and viewing using a light microscope.

The palynomorph assemblages are mostly well preserved but of variable thermal maturity, between 2– and 4 on the TAI scale (Traverse 2008). All samples were oxidized in Schulze's solution for between 5 and 60 min, except for four extremely mature samples that were oxidized for around 19 h. At this stage, the samples were spiked with *Lycopodium* tablets at a ratio of one tablet per millilitre of solid yield. Two to four strew mounts were made of these final preparations. From these, 113 samples were counted to 200 identifiable palynomorph specimens or the end of the slide in the occasional samples with less than 200 palynomorphs per slide. A note was kept of the number of modern *Lycopodium* spores encountered to enable quantitative assessment of the fossil material using an equation derived from one given by Stockmarr (1971). Slides were examined using standard light microscopy techniques and photographed using a Meiji Techno Infinity 1-5C camera mounted on a Meiji Techno MT5300H transmitted light microscope.

SYSTEMATIC PALAEOLOGY

Taxa are organized alphabetically by genera and species. Species with an uncertain identification are signified cf. or ?, after Matthews (1973). A limited synonymy is provided

for species previously recorded from the Naranco and Huergas formations. Dimensions are given for each species as diameters and where three numbers are given these correspond to the minimum value (arithmetic mean) and maximum values. Species occurrences are given as locality code characters for brevity (for an explanation see Askew & Wellman 2018). Previous records are taken from consultation of the John Williams Index of Palaeopalynology (for details see Riding *et al.* 2012). Materials (rock samples, residues and slides) are housed in the collections of the Centre for Palynology, Department of Animal and Plant Sciences, University of Sheffield, UK. Figured specimens are located using an England Finder.

Genus ACINOSPORITES Richardson, 1965

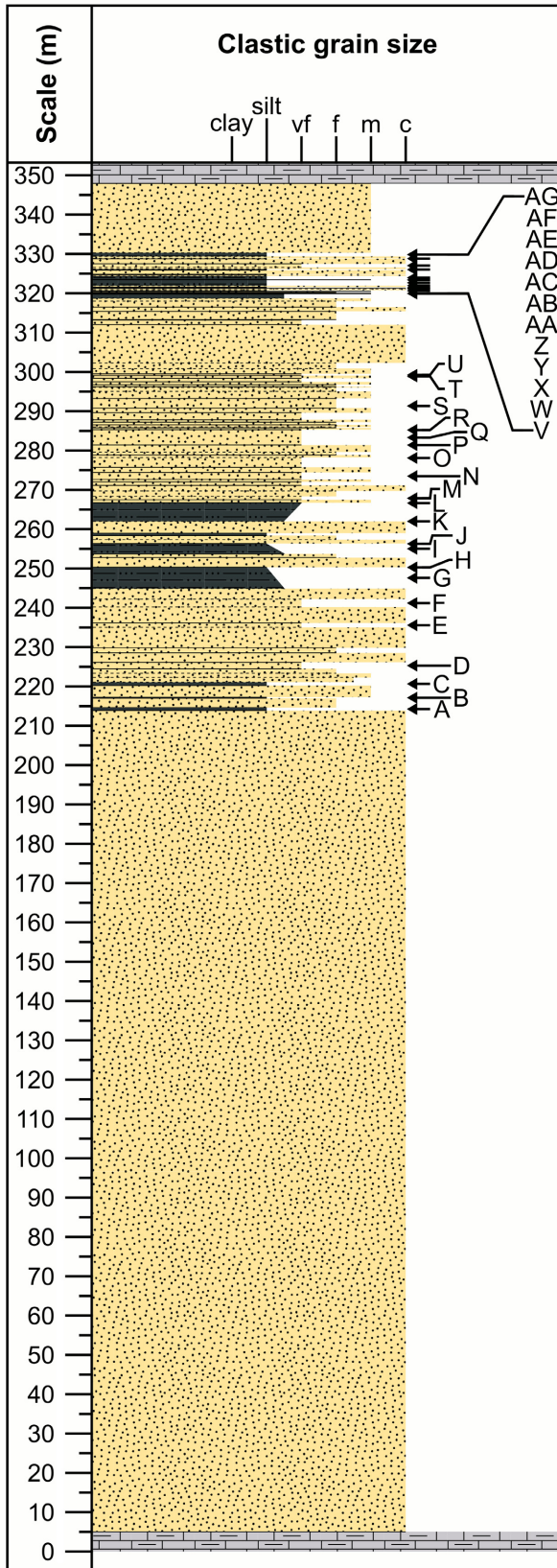
Type species. *Acinosporites acanthomammillatus* Richardson, 1965.

Acinosporites acanthomammillatus? Richardson, 1965 Figure 4A, L

Description. Amb shape uncertain. Laesurae not observed. Exine appears quite thick, ornamented with bifurcated processes. Sculptural elements are rounded, up to 6 µm wide, often joined to form ridges and surmounted by apical spines up to 4 µm high.

Dimensions. 55 (70) 85 µm (5 specimens measured).

Remarks. Identification is highly questionable, as it is based entirely on the characteristic ornament of rounded ridges topped by spines, in a low number of incomplete and very poorly preserved specimens.



Occurrence. Sites 3, 11, G.

Previous records. Reported from Eifelian–Frasnian strata with a worldwide distribution (Breuer & Steemans 2013).

Acinosporites lindlarensis Riegel, 1968

Figure 5A

Description. Amb circular to subcircular. Laesurae straight, extending one-half to the whole amb radius. Equatorial thickening of 2–4 µm observed, with some minor separation of the exoexine from a possible inner body. Proximal surface laevigate. Distal surface bears an ornament of microgranulae, large conate elements up to 3 µm high and wide as well as more irregular, parallel sided, sometimes biform elements up to 5 µm high.

Dimensions. 49 (79) 153 µm (8 specimens measured).

Remarks. This genus is distinguished by bearing its ornament atop anastomosing ridges. These ridges are not visible in these specimens except for some small joining of ornament bases. However, this species has been repeatedly recorded as having an extremely variable morphology, including a lack of obvious ridges (McGregor & Camfield 1976; Richardson *et al.* 1993).

Occurrence. Sites 3, 7, G.

Previous records. Reported from Emsian to Frasnian strata and with an almost worldwide distribution (although absent from Australia) (Breuer & Steemans 2013; Xu *et al.* 2014), as well as an unusual specimen from the Lochkovian of Belgium (Steemans 1989).

Genus *AMBITISPORITES* Hoffmeister, 1959

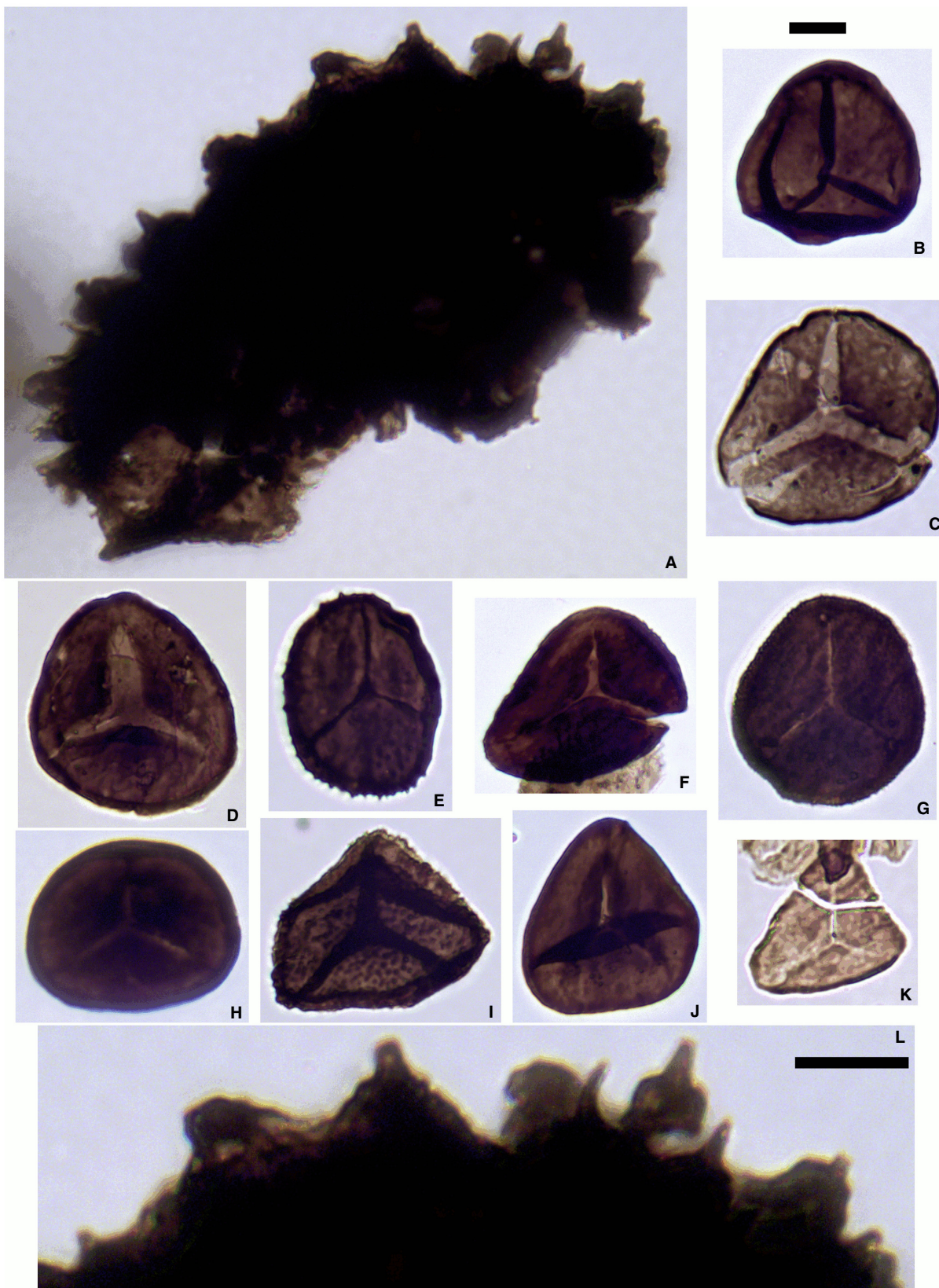
Type species. *Ambitisporites avitus* Hoffmeister, 1959.

Ambitisporites avitus Hoffmeister, 1959

Figure 4B

Dimensions. 26 (37) 67 µm (10 specimens measured).

FIG. 3. Stratigraphic log of the Playa del Tranqueru (3) site, including locations of samples taken (see Askew & Wellman (2018, chart S1) for detailed information on sample positions). Colour online.



Occurrence. Sites 2, 3, 7, 11, 19, 120, 598, G.

Previous records. Reported from Lower Silurian to Lower Devonian strata and with a worldwide distribution (Breuer & Steemans 2013).

Ambitisporites dilutus (Hoffmeister) Richardson & Lister,
1969
Figure 4C

Dimensions. 21 (35) 54 µm (43 specimens measured).

Occurrence. Sites 2, 3, 4, 7, 10, 11, 13, 15, 19, 22, 120, 598, 599, G, P.

Previous records. Reported from Upper Ordovician to Eifelian strata and with an almost worldwide distribution (although absent from Australia).

Ambitisporites sp. A
Figure 4D

Description. Amb circular to subcircular. Laesurae straight, extending from one-third to five-sixths of the amb radius. Tips of the laesurae may be slightly spatulate. Wall 1–2 µm thick. Surface laevigate.

Dimensions. 18 (36) 65 µm (142 specimens measured).

Remarks. This taxon is distinguished from *A. dilutus* by its shorter laesurae.

Occurrence. Sites 2, 3, 4, 5, 7, 10, 11, 15, 19, 120, 598, 599, G, P.

Ambitisporites sp. B
Figure 4H

Description. Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from one-half to two-thirds of the amb radius. Wall c. 1 µm thick. Surface laevigate.

Dimensions. 24 (35) 55 µm (35 specimens measured).

Remarks. This taxon is distinguished from *A. sp. A* by its possession of labra.

Occurrence. Sites 2, 3, 4, 5, 7, 10, 11, 22, 120, 598, 599, G, P.

Ambitisporites sp. C
Figure 4G

Description. Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from three-quarters to the whole amb radius. Wall c. 1 µm thick. Surface laevigate to occasionally scabrate.

Dimensions. 22 (35) 48 µm (26 specimens measured).

Remarks. This taxon is distinguished from *A. sp. B* by its longer laesurae and from *A. dilutus* by its distal ornament.

Occurrence. Sites 2, 3, 5, 7, 10, 11, 13, 19, 20, 22, 120, 598, 599, G, P.

Genus ANAPICULATISPORITES Potonié & Kremp, 1954

Type species. *Anapiculatisporites isselburgensis* Potonié & Kremp, 1954.

Anapiculatisporites abrepunius Cramer, 1966
Figure 5F

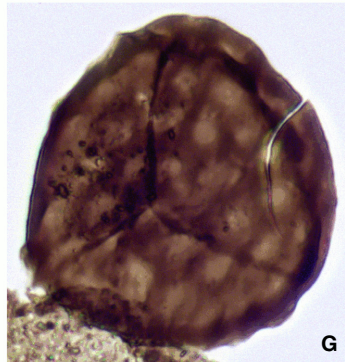
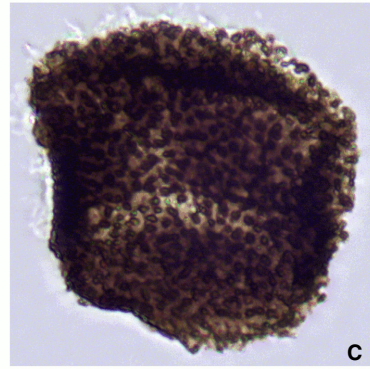
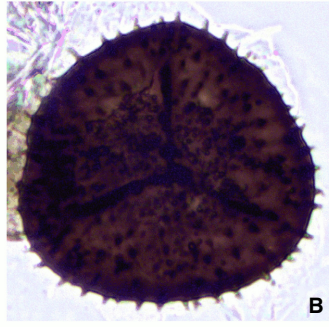
Description. Amb circular to subcircular. Laesurae straight, extending from one-half to the whole amb radius. Equatorial thickening of 1–4 µm observed. Proximal surface laevigate. Distal surface bears a sparse ornament of microgranulae and small spines separated by at least 2 µm.

Dimensions. 25 (38) 61 µm (9 specimens measured).

Remarks. Some of the specimens have shorter trilete rays than specified in the original description, though this was considered to be insufficient to justify an alternative identification.

Occurrence. Sites 2, 3, 4, 5, 7, 10, 15, 120, 598.

FIG. 4. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A, L, *Acinospirites acanthomammillatus?*; AJA2-GZ-O1, R31; L, detail of ornament. B, *Ambitisporites avitus*; AJA3A-O1; X34/3. C, *Ambitisporites dilutus*; AJA2-PC-O1; G46/3 (open trilete form). D, *Ambitisporites* sp. A; AJA598C-O1; N39/1 (open trilete form). E, *Anapiculatisporites carminae*; AJA598C-O1; D46/4. F, *Camarozonotriletes parvus*; AJA2-7G-O1; W30/2 (open trilete form). G, *Ambitisporites* sp. C; AJA11A-O1; M33/1. H, *Ambitisporites* sp. B; AJA3A-O1; Y34/2. I, *Anapiculatisporites picantus*; AJA598C-O1; D26. J, *Concavisporites* sp. A; AJA7A-O1; Y37/2. K, *Deltoidospora priddyi*; AJA2-7B-O1; V44/4. Scale bars represent: 10 µm (A–K); 10 µm (L). Colour online.



Previous records. Reported from the Pragian–Emsian of Spain (Cramer 1966).

Anapiculatisporites carminae Cramer, 1966

Figure 4E

1966 *Anapiculatisporites carminae* Cramer, p. 261; pl. 3, figs 51, 52.

1969 *Anapiculatisporites carminae* Cramer; Cramer, p. 435; pl. 2, fig. 19.

Description. Amb circular to subcircular. Laesurae straight, extending from three-quarters to the whole amb radius. Equatorial thickening of 1–4 µm observed. Proximal surface laevigate. Distal surface bears an ornament of microgranulae and granulae above 1 µm in size.

Dimensions. 21 (36) 65 µm (26 specimens measured).

Remarks. The specimens reported by Cramer (1966) from the Naranco Formation are often larger than the specimens seen here.

Occurrence. Sites 2, 3, 4, 5, 7, 10, 11, 13, 14, 19, 20, 22, G.

Previous records. Reported from the upper Eifelian to lower Frasnian of Spain (Cramer 1966, 1969).

Anapiculatisporites picantus Cramer, 1966

Figure 4I

Description. Amb circular to subcircular. Laesurae straight, extending from two-fifths to the whole amb radius. Equatorial thickening of 1–3 µm observed. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

Dimensions. 25 (39) 83 µm (25 specimens measured).

Remarks. Distinguished from *A. abrepunius* by its denser ornament. Specimens seen here may have shorter laesurae than originally described.

Occurrence. Sites 2, 3, 4, 5, 7, 10, 11, 13, 14, 16, 19, 20, 22, 120, 598, G.

Previous records. Reported from the Pragian of Belgium (Stemans 1989) and the Pragian–Emsian of Spain (Cramer 1966).

Genus APICULATASPORITES Potonié & Kremp, 1956

Type species. *Apiculatasporites spinulistratus* (Loose) Ibrahim, 1933.

Apiculatasporites perpusillus (Naumova ex Chibrikova)

McGregor, 1973

Figure 5B

Dimensions. 25 (38) 55 µm (12 specimens measured).

Occurrence. Sites 3, 7, 13, 19, 22, G.

Previous records. Reported from Upper Silurian to Famennian strata and with an almost worldwide distribution (although absent from Australia).

Genus APICULATISPORIS Potonié & Kremp, 1956

Type species. *Apiculatisporis aculeatus* (Ibrahim) Potonié, 1956.

Apiculatisporis cf. *elegans* McGregor, 1960

Figure 5C

Description. Amb circular to subcircular. Laesurae straight, usually open, extending from one-half to three-quarters of the amb radius. Proximal surface laevigate. Distal surface bears a dense ornament of large microgranulae up to 1 µm in size.

Dimensions. 34 (48) 63 µm (6 specimens measured).

Remarks. The species as originally described has a less variable trilete size and slightly larger ornament than the specimens found here. Owens (1971) considered *A. elegans* to be one end member of a morphological series, with *Planisporites minimus* McGregor, 1960 as the other extreme. This series shows an increase in ornament size with amb dimensions. This study recovered both end members of the series

FIG. 5. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A, *Acinospores lindlarensis*; AJA2-7A-O1; W40/4. B, *Apiculatasporites perpusillus*; AJA3A-O1; R34/2. C, *Apiculatisporis* cf. *elegans*; AJA598C-O1; L33/1 (open trilete form). D, *Apiculiretusispora plicata*; AJA10B-O1; V37/4. E, *Apiculiretusispora* cf. *brandtii*; AJA7A-O1; C33/3. F, *Anapiculatisporites abrepunius*; AJA598C-O1; J27 (open trilete form). G, *Brochotriletes foveolatus?*; AJA2-7E-O1; O33. H, *Devonomonolites* cf. sp. 1; AJA2-7E-O1; H46/3. Scale bar represents 10 µm. Colour online.

but no intermediate forms. The decision was taken to preserve them as separate, tentatively assigned species, as *P. minimus* is not formally included under synonymy with *A. elegans* by Owens (1971) or McGregor (1964) and *A. elegans* has only ever been synonymized with a tentatively identified assemblage of *Apiculatasporites dilucidus* (McGregor) McGregor, 1964 (Owens 1971), which does not resemble the specimens found here.

Occurrence. Sites 3, 7, G.

Previous records. Reported from the upper Eifelian to lower Givetian of the USA (Urban 1968), the middle to upper Givetian of Greenland (Friend *et al.* 1983), the Frasnian of Canada (McGregor 1960) and the Upper Devonian of Romania (Venkatachala *et al.* 1968).

Genus APICULIRETUSISPORIA (Stree) Stree, 1967

Type species. *Apiculiretusispora brandtii* Stree, 1964.

Apiculiretusispora cf. brandtii Stree, 1964

Figure 5E

cf. 1988 *Apiculiretusispora cf. brandtii* Stree; Fombella Blanco, pl. 4, figs 3, 5.

Dimensions. 32 (46) 61 μm (15 specimens measured).

Remarks. The species as originally described is markedly larger than the specimens described here, while the ornament seen here occasionally exceeds 1 μm in height, hence the uncertain identification.

Occurrence. Sites 2, 3, 4, 5, 7, 10, 11, 13, 14, 20, 22, 598, G.

Previous records. Reported from Pragian–Givetian strata and with a worldwide distribution (Breuer & Steemans 2013).

Apiculiretusispora plicata (Allen) Stree, 1967

Figure 5D

1969 *Cyclogranisporites plicatus* Allen; Cramer, p. 435; pl. 1, figs 15, 17.

? 1988 *Apiculiretusispora arenorugosa* McGregor; Fombella Blanco, pl. 2, fig. 6.

? 1988 *Aneurospora gregisii* Clayton *et al.*; Fombella Blanco, pl. 4, figs 2, 6.

Dimensions. 20 (52) 100 μm (45 specimens measured).

Occurrence. Sites 2, 3, 4, 5, 7, 10, 11, 13, 14, 15, 19, 20, 22, 120, 598, G, P.

Previous records. Reported from Lower–Middle Devonian strata with a worldwide distribution (Breuer & Steemans 2013).

Apiculiretusispora? sp. A

Figure 6G–H

Description. Amb circular to subcircular. Laesurae straight, extending to the equator. Possible 2–3 μm wide equatorial thickening observed. Proximal face bears subcircular thickened region extending from two-thirds to three-quarters of the distance to the equator. Distal surface bears an ornament of microgranulae.

Dimensions. 50 (61) 92 μm (4 specimens measured).

Remarks. These specimens are doubtfully assigned to this genus owing to their lack of obvious curvaturae, although these could be incorporated in the thickened wall. Some previously figured specimens of *Apiculiretusispora* do not show obvious curvaturae, such as Breuer & Steemans (2013, fig. 10F). This species' interrational thickenings are reminiscent of the structures seen in *A. arabensis* Al-Ghazi, 2009 although they are not of such a clear rounded shape.

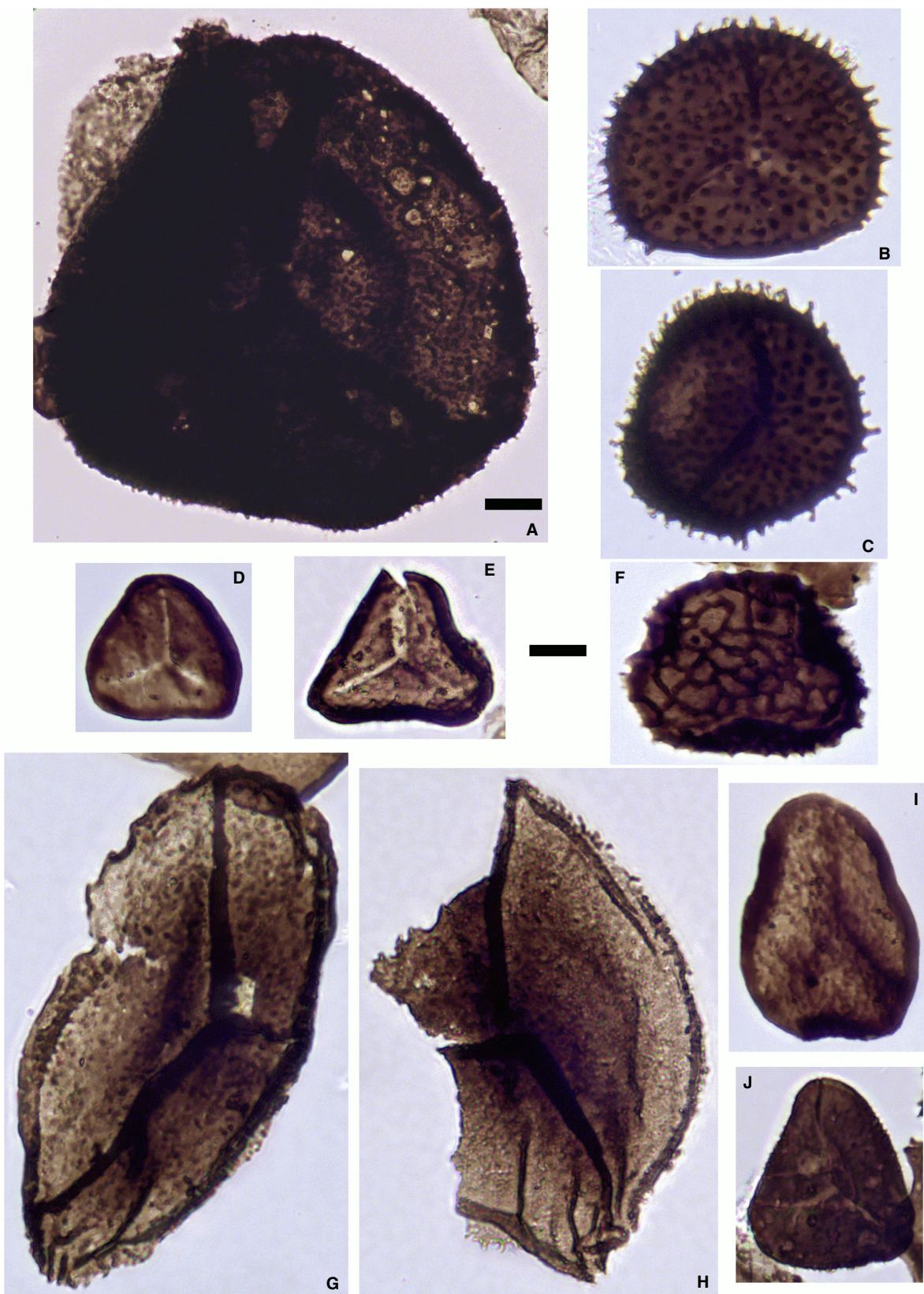
Occurrence. Site G.

cf. *Apiculiretusispora* sp. B

Figure 6A

Description. Amb circular to subcircular. Laesurae straight, extending almost to the equator. Laesurae connected by curvaturae perfectae delimiting obvious proximal contact areas, up to 15 μm away from the equator. Distal surface bears an ornament of microgranulae and granulae together with a prominent,

FIG. 6. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A, cf. *Apiculiretusispora* sp. B; AJA2-GP-O2; S37. B–C, *Dibolisporites tuberculatus*: B, AJA3A-O1, P40; C, AJA3A-O1, V28. D–E, I, *Camaronotriletes? concavus*: D, AJA2-7Q-O1, W41/2; E, AJA2-7J-O1, W43/3; I, AJA2-7B-O1, X35/3. F, *Dictyotriletes gorgoneus*; AJA2-3R-O1; X41/4. G–H, *Apiculiretusispora?* sp. A: G, AJA2-GZ-O1, U44; H, AJA2-GA-O1, X33. J, *Diatomozonotriletes cf. franklinii*; AJA598C-O1; J33/1. Scale bars represent: 20 μm (A); 10 μm (B–J). Colour online.



10 µm wide annulus, positioned one-half of the distance of the equator.

Dimensions. 147 (198) 268 µm (2 specimens measured).

Remarks. This taxon could be accommodated by the genus *Apiculiretusispora* except that it is outside the normal size range for the genus, with the larger specimen being of megaspore size.

Occurrence. Site G.

Genus BROCHOTRILETES Naumova ex Ishchenko, 1952

Type species. *Brochotriletes magnus* Ishchenko, 1952.

Brochotriletes foveolatus? Naumova, 1953
Figure 5G

Dimensions. 39 (51) 64 µm (3 specimens measured).

Remarks. The identification of this species is doubtful for similar reasons cited in McGregor (1973); the original description and figures are inadequate for confident identification of modern material. In addition, the specimens seen here have slightly larger luminae than the specimens in McGregor (1973).

Occurrence. Sites 3, 7, G.

Previous records. Reported from Upper Silurian to upper Famennian strata with a worldwide distribution.

Genus CAMARAZONOTRILETES Naumova ex Naumova, 1953

Type species. *Camarazonotriletes devonicus* Naumova, 1953.

Camarazonotriletes? concavus Loboziak & Streel, 1989
Figure 6D–E, I

Description. Amb subtriangular with slightly concave to slightly convex interradial margins. Laesurae straight, may be accompanied by narrow labra along their length, extending from two-thirds to the whole amb radius. Equatorial thickening of 1–4 µm observed, wider in the interradial areas though this is not always obvious. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

Dimensions. 24 (31) 39 µm (11 specimens measured).

Remarks. The generic assignment of this species is dubious owing to only a slight thinning of the equatorial thickening opposite the laesurae (Breuer & Steemans 2013). Distinguished from *C. parvus* by its concave interradial margins.

Occurrence. Sites 3, 7, G.

Previous records. Reported from the middle Eifelian to lower Frasnian of Tunisia (Breuer & Steemans 2013), the upper Eifelian to Frasnian of Brazil (Loboziak *et al.* 1988; Melo & Loboziak 2003; Breuer & Grahn 2011), the lower–middle Givetian of Libya and the lower–upper Givetian of Saudi Arabia (Breuer & Steemans 2013).

Camarazonotriletes parvus Owens, 1971
Figure 4F

Dimensions. 24 (32) 41 µm (5 specimens measured).

Occurrence. Sites 7, G.

Previous records. Reported from the lower Eifelian to upper Frasnian of Libya (Moreau-Benoit 1989), the upper Eifelian to Frasnian of Canada (McGregor & Owens 1966; Owens 1971; McGregor & Uyeno 1972; McGregor & Camfield 1982), the lower Givetian of Saudi Arabia (Breuer & Steemans 2013), the Givetian of Morocco (Rahmani-Antari & Lachkar 2001), Algeria (Moreau-Benoit *et al.* 1993), Brazil (Breuer & Grahn 2011) and Libya (Breuer & Steemans 2013), and the Frasnian of Tunisia (Breuer & Steemans 2013).

Genus CONCAVISPORITES Pflug in Thomson & Pflug, 1953

Type species. *Concavisporites rugulatus* Pflug in Thomson & Pflug, 1953.

Concavisporites? sp. A
Figure 4J

Description. Amb subtriangular with straight to slightly convex interradial margins. Laesurae straight, simple or accompanied by narrow labra along their length, extending from one-half to two-thirds of the amb radius. Proximal surface bears thickened kytotomes in the interradial areas, reaching the tips of the laesurae. Surface otherwise laevigate.

Dimensions. 29 (31) 33 µm (3 specimens measured).

Remarks. This species meets the generic criteria for *Concavisporites*, although this genus has not previously been used in the Palaeozoic.

Occurrence. Site 7.

Genus *CORYSTISPORITES* Richardson, 1965

Type species. Corystisporites multispinosus Richardson, 1965.

Corystisporites cf. sp. Turnau, 1996
Figure 7A

Description. Amb subcircular to vaguely subtriangular. Laesurae not easily discerned, believed to extend to the equator. Proximal surface presumed to be laevigate. Distal surface bears an ornament of densely packed, tapering spines up to 19 µm high. Spines often have wide bases with marked shoulders at around one-third to one-half of their height, before a thinner tapering portion begins. Large, rounded granulae are also seen, though these are probably broken spine bases.

Dimensions. 70 (98) 139 µm (5 specimens measured).

Remarks. The specimens seen here are sometimes smaller than those of Turnau (1996) and with less variation in the length of the spines. Aside from this we draw similar conclusions: the species resembles *Acinosporites macrospinosus* Richardson, 1965 except for having more densely distributed spines not clearly superimposed on convolute ridges.

Occurrence. Site G.

Previous records. The study of Turnau (1996) was carried out on Middle Devonian strata from Poland. *A. macrospinosus*, which the species has been compared to, is reported from upper Pragian to Lower Carboniferous strata and has a worldwide distribution.

Genus *DELTOIDOSPORA* Miner, 1935

Type species. Deltoidospora hallii Miner, 1935.

Deltoidospora priddyi (Berry) McGregor, 1973
Figure 4K

Dimensions. 23 (32) 48 µm (8 specimens measured).

Occurrence. Sites 3, 7, 11, 599.

Previous records. Reported from the upper Pragian to lower Emsian of France (Le Hérisse 1983), the Emsian to lower

Eifelian of Bolivia (McGregor 1984), the Emsian to middle Eifelian of Canada (McGregor 1973), the Eifelian of Russia (Chibrikova & Olli 1992) and the Emsian–Eifelian (Andrews *et al.* 1977) and Pennsylvanian of the USA (Ravn 1986; Willard 1992; Gennett & Ravn 1993; Peppers 1993; Eble 1996).

Genus *DEVONOMONOLETES* Arkhangelskaya, 1985

Type species. Devonomonoletes microtuberculatus (Chibrikova) Arkhangelskaya, 1985.

Devonomonoletes cf. sp. 1 Breuer & Steemans, 2013
Figure 5H

Description. Amb circular to subcircular. Monolete mark observed, extending from one-half to the whole amb radius. Curvaturae perfectae may be observed at the laesurae tips. Equatorial thickening of 1–2 µm observed. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

Dimensions. 32 (42) 49 µm (4 specimens measured).

Remarks. The specimens described here do not show obvious curvaturae as seen in the original figured specimens. These specimens resemble *Latosporites* sp. B Owens, 1971, though *Latosporites* is a laevigate genus.

Occurrence. Sites 2, 3, 4, 5, 7, 10, 13, 14, G.

Previous records. Reported from the Pragian to middle Emsian of Saudi Arabia (Breuer & Steemans 2013).

Genus *DIATOMOZONOTRILETES* (Naumova) emend.
Playford, 1963

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

Diatomozonotriletes cf. *franklinii* McGregor & Camfield,
1982
Figure 6J

Description. Amb subtriangular with straight to slightly convex interrational margins. Laesurae straight, extending from two-thirds to the whole amb radius. Proximal surface laevigate. Distal surface bears an ornament of microgranulae, with a prominent row of spines around 1 µm high in the interrational regions. The areas opposite the laesurae are laevigate to very finely scabrate.

Dimensions. 26 (29) 30 µm (3 specimens measured).



Remarks. The specimens seen here have shorter interradial spines than the species as originally described, possibly attributable to damage.

Occurrence. Sites 3, 7, G.

Previous records. Reported from the Emsian–Eifelian of Morocco (Rahmani-Antari & Lachkar 2001), the middle Emsian of Saudi Arabia (Breuer & Steemans 2013), the upper Emsian to lower Eifelian of Algeria (Moreau-Benoit *et al.* 1993), the upper Emsian to Givetian of Brazil (Loboziak *et al.* 1988; Melo & Loboziak 2003), the upper Emsian to middle Givetian of Libya (Breuer & Steemans 2013), the upper Emsian to lower Frasnian of Tunisia (Breuer & Steemans 2013), the upper Eifelian of Russia (Avkhimovitch *et al.* 1993) and the upper Eifelian to lower Givetian of Canada (McGregor & Uyeno 1972).

Genus DIBOLISPORITES Richardson, 1965

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

Dibolisporites tuberculatus Breuer & Steemans, 2013 Figure 6B–C

? 1988 *Dibolisporites echinaceus* (sic) (Eisenack) Richardson; Fombella Blanco, p. 35; pl. 3, fig. 3.

Description. Amb circular to subcircular. Laesurae straight, extending from three-quarters to the whole amb radius. An equatorial thickening up to 4 µm is sometimes observed. Curvaturae perfectae joining the tips of the laesurae are sometimes observed, often coincident with equator. Proximal surface laevigate. Distal surface bears an ornament of rounded granules and pointed spines. Well-preserved specimens may show slightly bulbous tips on the spines. These ornamental units are 2–3 µm high and separated by at least 1–2 µm.

Dimensions. 35 (46) 77 µm (18 specimens measured).

Remarks. This species is distinguished from *D. eifeliensis* by its original authors by having a coarser ornament. The stated ornament dimensions in the original descriptions of the two species are almost identical, however, and we consider this species' much greater wall thickness to be a more useful diagnostic feature.

Occurrence. Sites 2, 3, 7, 11, 20, 120, 598.

Previous records. Reported from the Emsian–Eifelian of the USA (Ravn & Benson 1988), the Emsian to lower Givetian of Saudi Arabia (Breuer & Steemans 2013; Breuer *et al.* 2015), the upper Eifelian of Brazil (Breuer & Grahn 2011) and Tunisia (Breuer & Steemans 2013) and the Givetian of Libya (Breuer & Steemans 2013).

Dibolisporites sp. A Figure 7F

Description. Amb circular to subcircular. Laesurae not observed. Equatorial thickening of 5 µm observed. Surface (probably distal) bears a dense ornament of clavate elements, with narrow bases c. 1 µm wide and widened heads up to 3 µm wide. Elements have rounded tips and are up to 10 µm high.

Dimensions. 70 µm (one specimen measured).

Remarks. The sculptural elements on this species closely resemble those of *D. pilatus* Breuer *et al.*, 2007, except for being slightly narrower, often taller and distributed much more densely, in contrast to the sparse, irregular ornament of *D. pilatus*. The specimen also resembles a small example of the megaspore *Jhariatrilletes emsiensis* Moreau-Benoit, 1979. Only a single specimen was found.

Occurrence. Site 10.

Genus DICTYOTRILETES Naumova ex Ishchenko, 1952

Type species. *Dictyotrilletes bireticulatus* (Ibrahim) Potonié & Kremp, 1955.

Dictyotrilletes gorgoneus Cramer, 1966 Figure 6F

Dimensions. 40 µm (one specimen measured).

Remarks. Distinguished from *D. cf. hemeri* in this study by its rather more substantial looking muri and more irregularly shaped luminae. The figured specimen could be interpreted as having an interradially thickened wall, in the fashion of *Camarozonotrilletes*, but we interpret this

FIG. 7. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A, *Corytisporites* cf. sp.; AJA2-GD-O1; R45/3. B, *Emphanisporites annulatus*; AJA2-20B-2-O2; O42/4. C, *Emphanisporites* cf. *annulatus*; AJA7A-O1; X42/4. D, *Emphanisporites annulatus*?; AJA598C-O1; L32/1. E, *Emphanisporites* cf. *orbicularis*; AJA2-PC-O1; N41. F, *Dibolisporites* sp. A; AJA10B-O2; W42/3. G–H, *Dictyotrilletes* cf. *hemeri*: G, AJA2-7D-O1, W33/2 (open trilete form); H, AJA598C-O1, H31/4 (open trilete form). Scale bar represents 10 µm. Colour online.

specimen as having a widely opened trilete mark, leaving the proximal exine gathered around the margins. Though known primarily from earlier sediments this species is known from the Givetian, through a taxon known from the Givetian of Spitsbergen and placed in open nomenclature by Allen (1965), later referred to *D. gorgoneus* by Breuer & Steemans (2013). Only a single specimen was found in this study.

Occurrence. Site 3.

Previous records. Reported from the upper Lochkovian to upper Emsian of Belgium (Lessuise *et al.* 1979; Steemans 1989), the lower Pragian to Emsian of Germany (Steemans 1989), the Pragian–Emsian of Spain (Cramer 1966) and Saudi Arabia (Breuer & Steemans 2013), the Emsian of Canada (McGregor & Owens 1966; McGregor 1973) and the Emsian–Givetian of Spitsbergen (Allen 1965).

Dictyotriletes cf. hemeri Breuer & Steemans, 2013

Figure 7G–H

? 1988 *Cymatiosphaera magnata* Pilchler; Fombella Blanco, pl. 3, fig. 1.

Description. Amb circular to subcircular or ovoid. Laesurae straight, sometimes accompanied by narrow labra along their length, extending from one-half to the whole amb radius. Proximal surface laevigate. Distal surface bears a reticulate ornament with muri, *c.* 1–2 µm high and wide, enclosing mostly polygonal luminae 2–6 µm wide. Small projections may occur at muri junctions.

Dimensions. 33 (43) 53 µm (4 specimens measured).

Remarks. The species as originally described is rather larger and with larger sculptural elements than the specimens described here. In addition, the bifurcated elements at muri junction are not obvious in these specimens, though this is also the case on some of the original figured specimens.

Occurrence. Sites 3, 7, 11, 598, G, P.

Previous records. Reported from the Eifelian–Givetian of Spain (Cramer 1969) and the upper Eifelian to middle Givetian of Saudi Arabia (Breuer & Steemans 2013).

Genus EMPHANISPORITES McGregor, 1961

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

Emphanisporites annulatus McGregor, 1961

Figure 7B

1966 *Emphanisporites annulatus* McGregor; Cramer, p. 263; pl. 3, fig. 63.

1969 *Emphanisporites annulatus* McGregor; Cramer, p. 432; pl. 1, fig. 12.

1988 *Emphanisporites cf. annulatus* McGregor; Fombella Blanco, pl. 2, fig. 4.

Dimensions. 28 (38) 62 µm (15 specimens measured).

Occurrence. Sites 3, 7, 10, 19, 20, 22, G.

Remarks. Specimens questionably assigned to *E. annulatus* owing to their poor state of preservation are called *E. annulatus?* (e.g. Fig. 7D).

Previous records. Reported from Emsian–Tournaisian strata with a worldwide distribution (Taylor *et al.* 2011).

Emphanisporites cf. annulatus McGregor, 1961

Figure 7C

Description. Amb circular to subcircular. Monolete mark observed, extending to the equator. Equatorial thickening of 3 µm observed. Proximal face bears interradial muri, six in each half. Distal surface bears an annulus, otherwise laevigate.

Dimensions. 35 (40) 51 µm (3 specimens measured).

Remarks. Monolete specimens attributed to various *Emphanisporites* species have been recorded previously (Breuer & Steemans 2013).

Occurrence. Site 7.

Emphanisporites augusta Fombella Blanco, 1988

Figure 8A

Description. Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from one-half to the whole amb radius. Equatorial thickening of 1–2 µm observed. Proximal face bears interradial muri, 2–3 per sector. Distal surface bears an ornament of microgranulae.

Dimensions. 25 (38) 52 µm (32 specimens measured).

Remarks. The species as originally described is larger than the specimens seen here, with a wider cingulum.

Occurrence. Sites 2, 4, 5, 7, 10, 11, 13, 14, 19, 20, 22, G.

Previous records. Reported from the Middle Devonian of Spain (Fombella Blanco 1988).

Emphanisporites cf. laticostatus Breuer & Steemans, 2013

Figure 8B

Description. Amb circular to subcircular. Laesurae straight, accompanied by narrow labra, extending from two-thirds to three-quarters of the amb radius. Equatorial thickening of 1–3 µm observed. Proximal face bears interradial muri, 2–4 per sector. Distal surface laevigate.

Dimensions. 26 (37) 57 µm (5 specimens measured).

Remarks. The species as originally described is larger than the specimens reported here and these specimens do not show fading muri towards the equator.

Occurrence. Sites 3, 7.

Previous records. Reported from the middle Givetian of Brazil (Breuer & Grahn 2011) and the upper Givetian to Frasnian of Tunisia and Saudi Arabia (Breuer & Steemans 2013).

Emphanisporites mcgregorii Cramer, 1966

Figure 8E–F

1969 *Emphanisporites Mcgregorii* (sic) Cramer; Cramer, p. 432; pl. 1, fig. 13.

Description. Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra, extending from one-third to the whole amb radius. Equatorial thickening of 1–2 µm observed. Proximal face bears interradial muri, 4–12 per sector and arranged parallel to one another, producing a distinct heringbone pattern. Distal surface laevigate.

Dimensions. 23 (36) 53 µm (22 specimens measured).

Remarks. The description of McGregor (1961), restated by Cramer (1966), does not specify the number of interradial ridges this species should possess. We have included specimens with laesurae shorter than the radius in this species as this measurement varies in other members of the genus. The descriptions of this species and *E. spinaeformis* Schultz, 1968 do not differ in their important characteristics and the synonymization of the two by Breuer & Steemans (2013) is followed here. Care should be taken not to confuse this species with *E. mcgregorii* Schultz in Lanninger, 1968, rendered a *nomen nudum* by

McGregor (1973) as a later homonym (orthographic variant) of the species used here.

Occurrence. Sites 3, 5, 7, 10, 16, 19, 22, 598, G.

Previous records. Reported from the Lochkovian to Eifelian of Germany (Lanninger 1968; Riegel 1968; Schultz 1968; Edalat 1974; Steemans 1989; Pflug & Prössl 1991), the upper Lochkovian to Emsian of France (Steemans 1989; Moreau-Benoit 1994) and Belgium (Steemans 1989), the Pragian to upper Givetian of Libya (Massa & Moreau-Benoit 1976; Moreau-Benoit 1979, 1989; Paris *et al.* 1985; Moreau-Benoit & Massa 1988; Strel *et al.* 1988; Breuer & Steemans 2013), the Pragian to middle Emsian of Poland (Turnau 1986; Turnau & Jakubowska 1989), the Pragian–Givetian of Spain (Cramer 1966, 1969), the upper Pragian to lower Emsian of Brazil (Mendlowicz Mauller *et al.* 2007), the upper Pragian to upper Givetian of Saudi Arabia (Breuer & Steemans 2013), the Emsian to lower Eifelian of Bolivia (McGregor 1984), the Emsian–Famennian of Algeria (Abdesselam-Rouighi 1986; Moreau-Benoit *et al.* 1993), the upper Emsian to lower Frasnian of Tunisia (Breuer & Steemans 2013), the lower Givetian of Egypt (Schrank 1987) and the Upper Devonian to Tournaisian of Ireland (Naylor *et al.* 1977; Sleeman *et al.* 1978).

Emphanisporites micrornatus Richardson & Lister, 1969

Figure 8C

Description. Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra, extending from one-half to the whole amb radius. Proximal face bears interradial muri, 4–8 per sector. Distal surface bears an ornament of microgranulae.

Dimensions. 26 (37) 45 µm (23 specimens measured).

Remarks. These specimens possess more interradial muri than the species as originally described.

Occurrence. Sites 2, 4, 7, 10, 13, 14, 19, 20, 22, G.

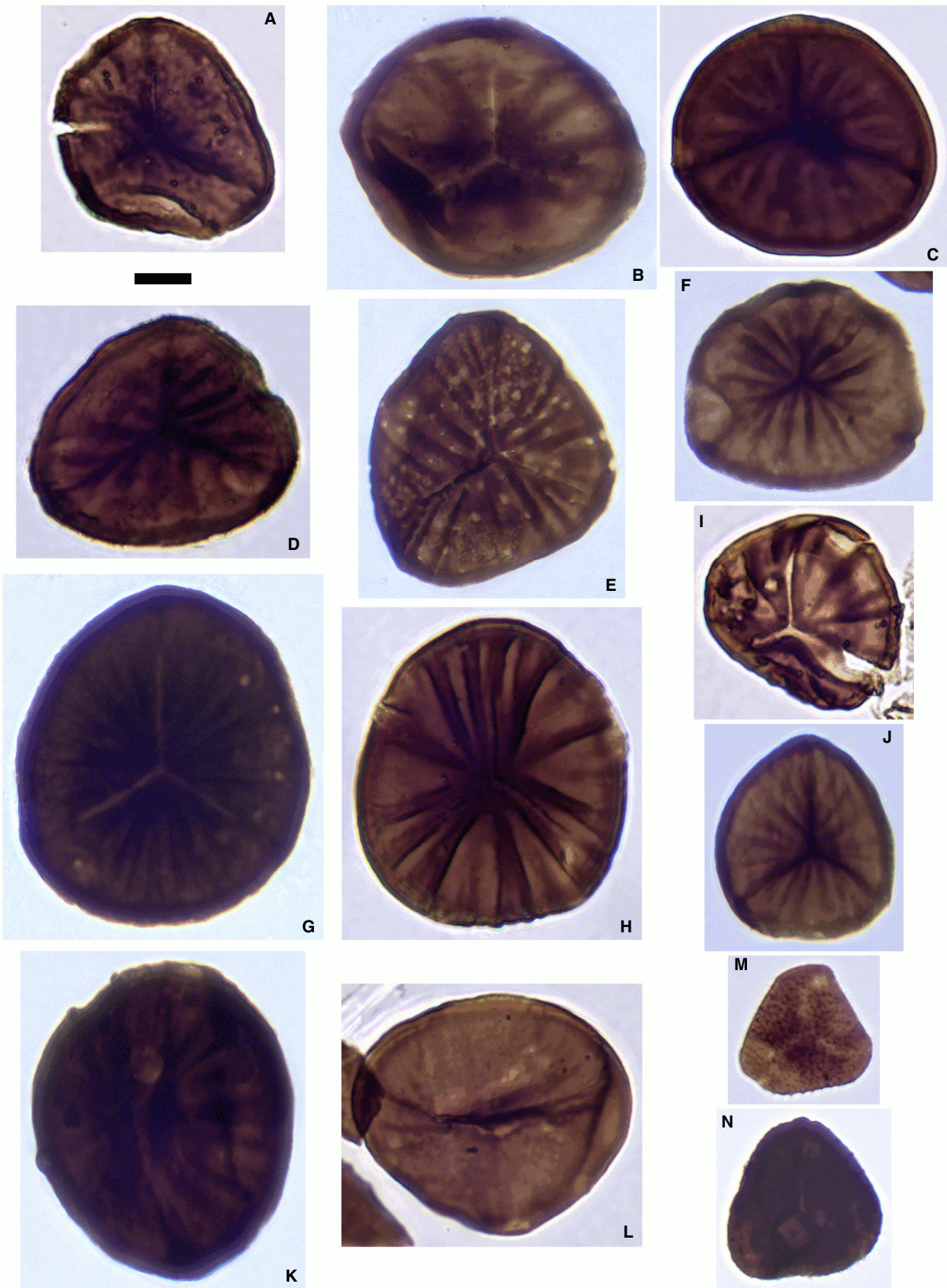
Previous records. Reported from Lochkovian–Emsian strata with a worldwide distribution (Taylor *et al.* 2011).

Emphanisporites orbicularis Turnau, 1986

Figure 8G–H

? 1966 *Emphanisporites erraticus* (Eisenack); Cramer, p. 263; pl. 3, figs 60, 61.

Description. Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending



from one-third to three-quarters of the amb radius. Equatorial thickening of 1–5 μm observed. Proximal face bears interradial muri, 3–10 per sector. Distal surface laevigate.

Dimensions. 22 (33) 58 μm (70 specimens measured).

Remarks. The original description for this species does not specify how many interradial muri it should possess and does not mention labra, though they may be visible on one of the figured specimens (pl. 4, fig. 9).

Occurrence. Sites 3, 7, 10, 11, 13, 19, 22, 120, 598, G, P.

Previous records. Reported from the upper Lochkovian to Emsian of Poland (Turnau 1986; Turnau & Jakubowska 1989), the upper Givetian to Frasnian of Iran (Ghavidel-Syooki 1994) and the upper Famennian to lower Tournaisian of Canada (Playford & McGregor 1993).

Emphanisporites cf. orbicularis Turnau, 1986

Figure 7E

Description. Amb circular to subcircular. Monolete mark observed, extending from one-half to three-quarters of the amb radius. Proximal face bears interradial muri, 8–15 in each half. Distal surface laevigate.

Dimensions. 25 (33) 40 μm (15 specimens measured).

Remarks. Monolete specimens attributed to various *Emphanisporites* species have been recorded previously (Breuer & Steemans 2013).

Occurrence. Sites 3, P.

Emphanisporites protoannulatus Rodríguez, 1978

Figure 8I

Description. Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending two-thirds of the amb radius. Proximal face bears interradial muri, 3–4 per sector. Distal surface bears a 3–4 μm annulus, otherwise laevigate.

Dimensions. 31 (35) 39 μm (3 specimens measured).

Remarks. Distinguished from *E. annulatus* in this study by its shorter trilete rays.

Occurrence. Sites 3, G.

Previous records. Reported from the Ludlow to Lower Devonian of Spain (Rodríguez 1978a, 1983).

Emphanisporites rotatus McGregor emend. McGregor, 1973
Figure 8J

- 1966 *Emphanisporites rotatus* McGregor; Cramer, p. 262; pl. 3, figs 57, 58, 62.
- 1969 *Emphanisporites rotatus* McGregor; Cramer, p. 431.
- 1969 *Emphanisporites obscurus* McGregor; Cramer, p. 432.
- 1969 *Emphanisporites robustus* McGregor; Cramer, p. 434; pl. 1, fig. 11.
- 1988 *Emphanisporites rotatus* McGregor; Fombella Blanco, pl. 2, fig. 3.

Dimensions. 21 (34) 52 μm (165 specimens measured).

Occurrence. Sites 2, 3, 4, 5, 7, 10, 11, 13, 14, 19, 20, 22, 120, 598, 599, G, P.

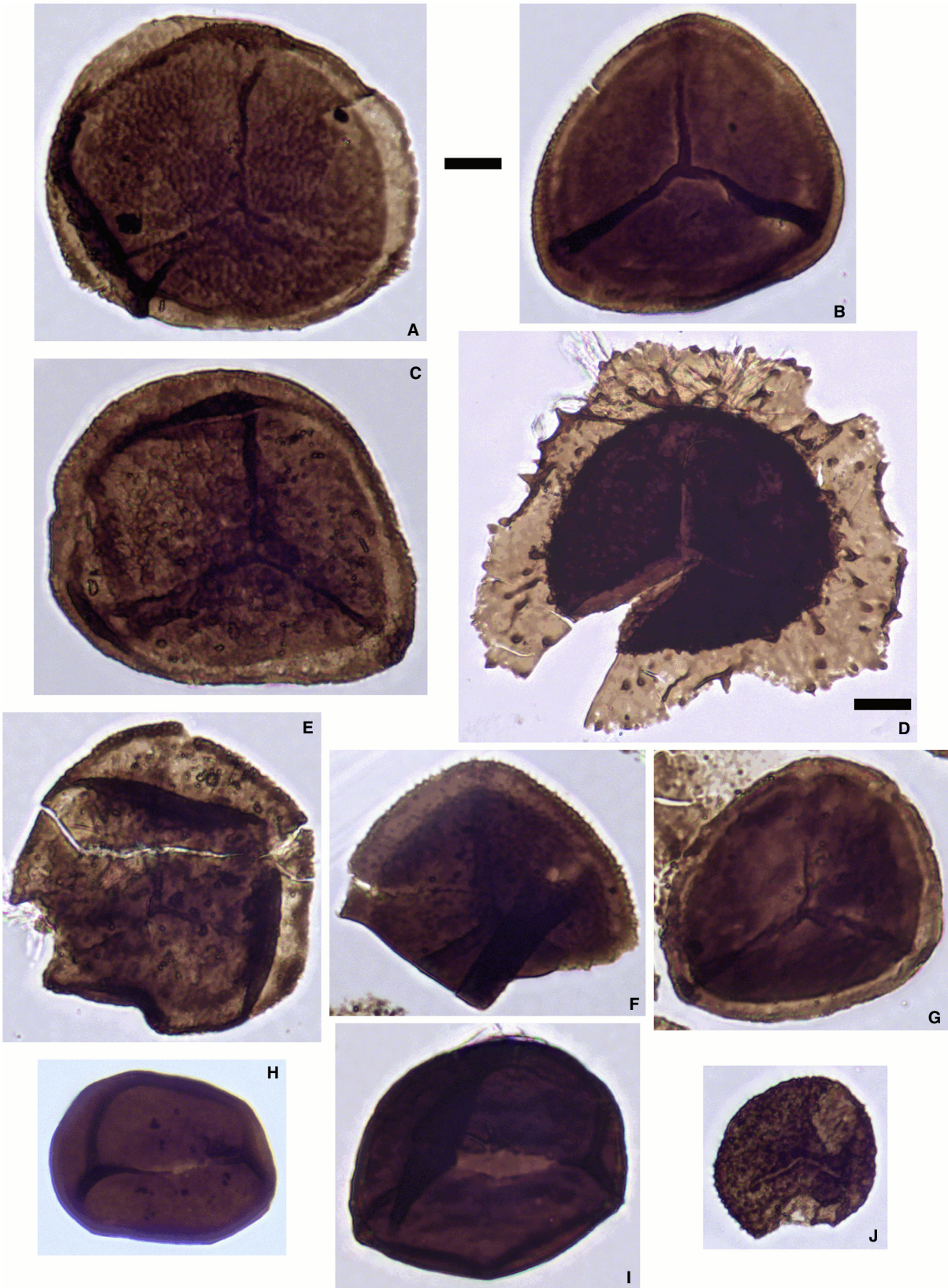
Previous records. Reported from Upper Silurian to Tournaisian strata with a worldwide distribution (Taylor *et al.* 2011; Breuer & Steemans 2013).

Emphanisporites cf. rotatus McGregor emend. McGregor,
1973
Figure 8K–L

Description. Amb circular to subcircular. Monolete mark observed, extending to the equator. Equatorial thickening of 1–3 μm observed. Proximal face bears interradial muri, 3–12 in each half. Distal surface laevigate.

Dimensions. 23 (36) 48 μm (6 specimens measured).

FIG. 8. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A, *Emphanisporites augusta*; AJA2-7F-O1; W39/1. B, *Emphanisporites cf. laticostatus*; AJA120A-O2; L35/4. C, *Emphanisporites microranatus*; AJA2-GE-O1; T30. D, *Emphanisporites* sp. A; AJA2-7C-O1; H29. E–F, *Emphanisporites mcgregorii*: E, AJA7A-O1, S28/3; F, AJA11A-O1, C38/2. G–H, *Emphanisporites orbicularis*: G, AJA3A-O1, Q46; H, AJA2-GE-O1, S43/2. I, *Emphanisporites protoannulatus*; AJA2-GH-O1; S33/3. J, *Emphanisporites rotatus*; AJA7A-O1; C42/3. K–L, *Emphanisporites cf. rotatus*: K, AJA7A-O1, U42/1; L, AJA2-GF-O1, S40. M, *Granulatisporites concavus*; AJA10B-O1; O38. N, *Granulatisporites cf. muninensis*; AJA7A-O1; W39/2. Scale bar represents 10 μm . Colour online.



Remarks. Monolete specimens attributed to various *Emphanisporites* species have been recorded previously (Breuer & Steemans 2013).

Occurrence. Sites 3, 7, 11, 13, G.

Emphanisporites sp. A
Figure 8D

Description. Amb circular to subcircular. Laesurae straight, extending to the equator. Equatorial thickening of 2–3 µm observed. Proximal face bears interrational muri, 5–7 per sector and arranged parallel to one another, producing a distinct herringbone pattern. Distal surface bears an ornament of microgranulae.

Dimensions. 33 (41) 50 µm (7 specimens measured).

Remarks. This species has the herringbone muri pattern of *E. mcgregorii* but possesses a distal ornament.

Occurrence. Sites 7, 10, 13, 14, G.

Genus GEMINOSPORA Balme, 1962

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

Geminospora lemurata Balme emend. Playford, 1983
Figure 9A–C, E–G

Description. Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to perimeter of intexine. Exoexine extends past intexine perimeter by one-quarter to one-third the radius of the intexine. Exoexine markedly thick, always over 1 µm. Proximal surface laevigate. Exoexine distally sculptured with densely distributed grana and apiculate elements up to 1 µm high.

Dimensions. Intexine: 23 (40) 53 µm; exoexine: 30 (52) 76 µm (10 specimens measured).

Remarks. The specimens described here correspond to the specific designation in all respects. Distinguished

from species of *Grandispora* in the thickness of the exoexine and in the laesurae not extending past the intexine.

Occurrence. Sites 3, 7, G.

Previous records. Reported from Givetian–Frasnian strata with a worldwide distribution (Breuer & Steemans 2013).

Geminospora cf. *svalbardiae* (Vigran) Allen, 1965
Figure 10A–D

? 1988 *Geminospora* cf. *tuberculata* (Kedo) Allen; Fombella Blanco, pl. 2, fig. 7.

Description. Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to perimeter of intexine. Exoexine extends past intexine perimeter by one-quarter to one-third the radius of the intexine. Exoexine markedly thick, always over 1 µm. Proximal surface laevigate. Exoexine distally sculptured with densely distributed grana and apiculate elements 1–4 µm high.

Dimensions. Intexine: 33 (38) 48 µm; exoexine: 39 (46) 58 µm (5 specimens measured).

Remarks. The specimens described here differ from those assigned to *G. lemurata* primarily in having a larger ornament and sometimes a somewhat thinner exoexine, though still thicker than in *Grandispora*. The specimens described here are rather smaller than those originally described for the species.

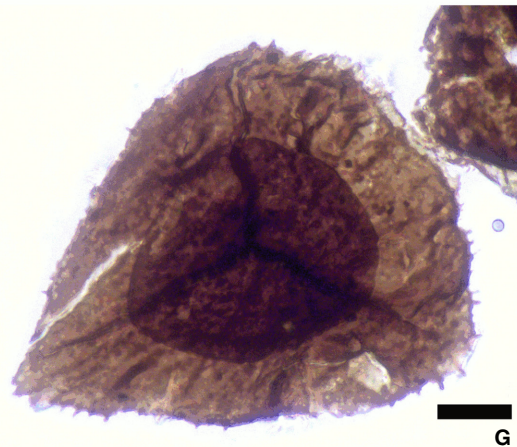
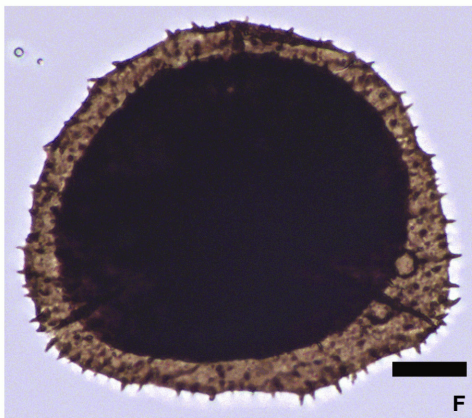
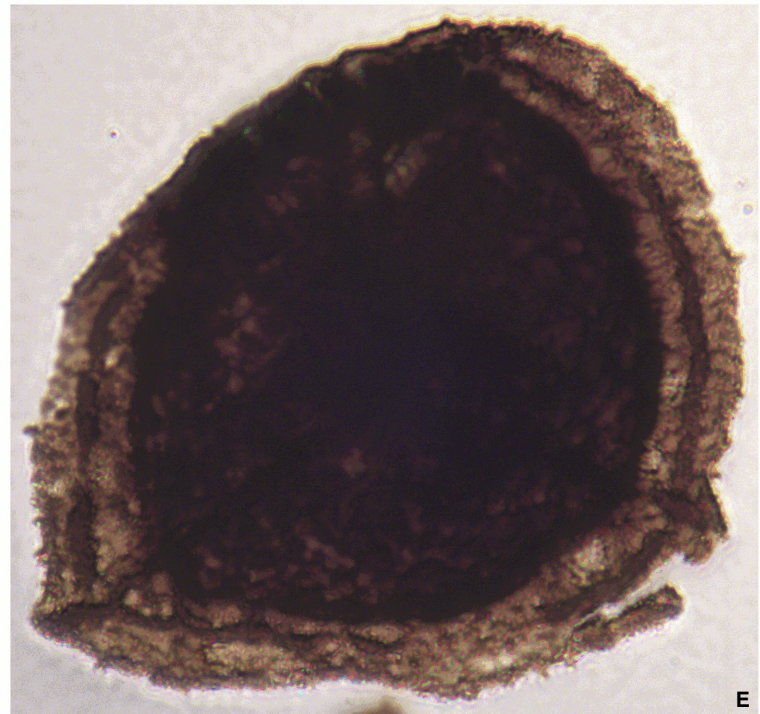
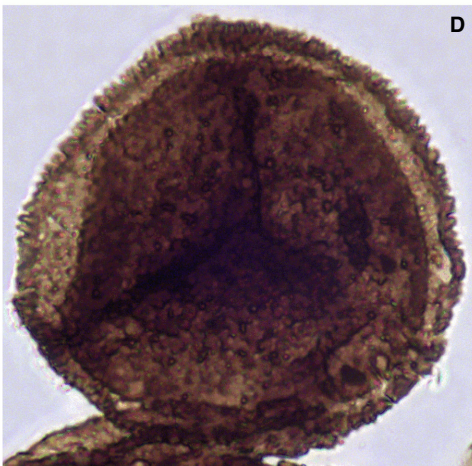
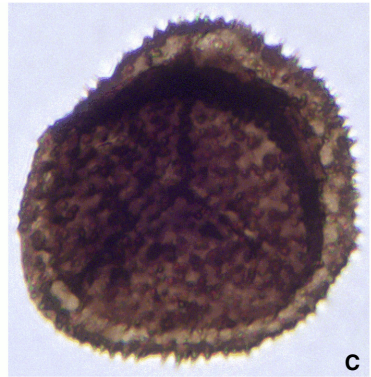
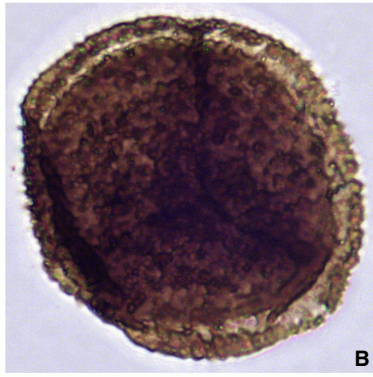
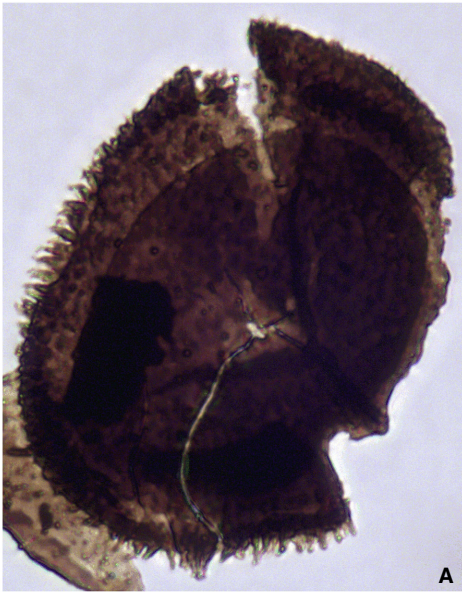
Occurrence. Sites 2, 3, 7, 10.

Previous records. Reported from Pragian to upper Famennian strata with an almost worldwide distribution (although absent from Australia).

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

Type species. *Grandispora spinosa* (Hoffmeister *et al.* 1955).

FIG. 9. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A–C, *Geminospora lemurata*: A, AJA2-3C-O2, E43/3; B, AJA2-GE-O1, R49/2; C, AJA2-7A-O1, O49/3. D, *Grandispora douglstownensis*?; AJA2-GE-O1; M49/4. E–G, *Geminospora lemurata*: E, AJA2-7Q-O1, V50; F, AJA2-GAB-O2, P29/3; G, AJA2-7A-O1, N39/2. H–I, *Latosporites* sp. 1: H, AJA10B-O1, R28; I, AJA2-7D-O1, P46/1 (open monolete form). J, *Planisporites* cf. *minimus*; AJA598C-O1; K34. Scale bars represent: 10 µm (A–C, E–J); 20 µm (D). Colour online.



'*Grandispora*' (*Hymenozonotriletes*) *argutus* Naumova, 1953
sensu Cramer, 1969

Figure 12C

- 1953 *Hymenozonotriletes argutus* Naum. Sp. n.; Naumova, pl. 9, fig. 9.
 1966 *Hymenozonotriletes argutus* 'II' Naumova; Cramer, p. 46; pl. 3, fig. 73.
non. 1969 *Calyptosporites argutus* (Naumova) New Combination; Cramer, p. 436; pl. 3, fig. 33.
 p. 1969 *Calyptosporites cf. deliquescens* (Naumova) New Combination; Cramer, p. 438; pl. 3, fig. 32.

Description. Amb subcircular to vaguely subtriangular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae not obvious, may extend to the spore equator. Exoexine extends past intexine perimeter by a distance equal to the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with an ornament of large ridges and spines up to 15 µm long. These spines have a broad base, often drawing up the exoexine around them. This produces a 'pinched' appearance and a prominent scalloped margin to the exoexine.

Dimensions. Intexine: 39 (58) 75 µm (6 specimens measured); exoexine: 75 (104) 135 µm (5 specimens measured).

Remarks. This taxon has a complicated taxonomic history. Naumova (1953) described and illustrated two new species, which are very different in structure and morphology, but called both of them *Hymenozonotriletes argutus* sp. n. These were described as spore number 73 (p. 41) and spore number 169 (p. 67) illustrated as line figures in her plate 4, figure 10 and plate 9, figure 9, respectively. Cramer (1966) identified both species in the Spanish Middle Devonian and called them *Hymenozonotriletes argutus* 'I' Naumova, 1953 and *Hymenozonotriletes argutus* 'II' Naumova, 1953 with I referring to spore number 73 and II referring to spore number 169. Subsequently Cramer (1969) placed *Hymenozonotriletes argutus* 'II' Naumova, 1953 in the genus *Calyptosporites* as a new combination: *Calyptosporites (Hymenozonotriletes) argutus* (Naumova) Cramer, 1969 (although it should be noted that Cramer appears to have inadvertently mislabelled his plates and pl. 3 fig. 32 almost certainly represents this taxon rather than pl. 3 fig. 33). In this paper, we have included Cramer's (1966) *Hymenozonotriletes argutus* 'I' Naumova, 1953 in synonymy with *Grandispora cf. inculta* Allen, 1965 (see below). We have identified

Cramer's (1966) *Hymenozonotriletes argutus* 'II' Naumova, 1953 (*Calyptosporites (Hymenozonotriletes) argutus* (Naumova) Cramer, 1969) but have placed it with the genus *Grandispora*. This follows recent taxonomic practise for Devonian spores that considers the genus *Calyptosporites* to be a junior synonym of *Grandispora* (Playford 1971; Breuer & Steemans 2013). We have named the species '*Grandispora*' (*Hymenozonotriletes*) *argutus* Naumova, 1953 *sensu* Cramer (1969) because we are not in a position to propose a formal comb. nov. This is because: (1) comparison with Naumova's material is tentative because she provided only line drawings of spores (as also noted by Cramer 1969); and (2) Naumova's (1953) first described species has priority but we are concerned with the second described species of the same name.

Comparison. The characteristic ornament of this species is similar to that of *G. douglstownensis* and *Ancyrospora nettersheimensis* Riegel, 1973 but is far more pronounced and also lacks the bifurcate ornament of *Ancyrospora*.

Occurrence. Sites 2, 3, 5, 7, 10, 11, 13, 20, 120, 598, G.

Previous records. An often-reported taxon reported from upper Emsian to upper Frasnian strata from Canada, China and Europe, particularly the former USSR, though often referred to a different genus.

Grandispora douglstownensis? McGregor, 1973

Figure 9D

- ? 1966 *Hymenozonotriletes cf. eximius*? Naumova; Cramer, p. 268; pl. 6, fig. 1.
 1966 *Hymenozonotriletes cf. deliquescens*? Naumova; Cramer, p. 269; pl. 4, fig. 77.
 ? 1969 *Calyptosporites argutus* (Naumova) New Combination; Cramer, p. 436; pl. 3, fig. 33.
 p. 1969 *Calyptosporites cf. deliquescens* (Naumova) New Combination; Cramer, p. 438; pl. 2, fig. 26.

Description. Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending from two-thirds to the whole radius of intexine. Exoexine extends past intexine perimeter by one-third to two-thirds the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with faint microgranulae and occasional, isolated, large granulate

FIG. 10. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A–D, *Geminospira cf. svalbardiae*: A, AJA2A-O1, V42; B, AJA2-7A-O1, U32/1; C, AJA11A-O1, T46/4; D, AJA2-7A-O1, N32. E, *Grandispora permulta*; AJA2-GI-O1; U46/4. F, *Grandispora cf. inculta*; AJA7A-O1; C28/4. G, *Grandispora velata*; AJA10B-O1; D28/2. Scale bars represent: 10 µm (A–E); 20 µm (F–G). Colour online.

and spinose elements with some distortion of the exoexine around them.

Dimensions. Intexine: 58 (76) 90 μm ; exoexine: 131 (142) 168 μm (3 specimens measured).

Remarks. The species as originally described has folds that accompany the laesurae and may extend to the spore equator, features not seen here. As the few specimens found of this species are poorly preserved this is attributed to a preservational deficiency.

Occurrence. Sites 3, G.

Previous records. Reported from the Emsian–Givetian of Canada (McGregor 1973; McGregor & Camfield 1976, 1982), the Emsian to middle Givetian of Libya (Moreau-Benoit 1989; Ghavidel-Syooki 2003), the upper Emsian to lower Eifelian of Algeria (Moreau-Benoit *et al.* 1993), the upper Emsian to Eifelian of Libya (Breuer & Steemans 2013), the upper Emsian to lower Givetian of Brazil (Loboziak *et al.* 1992; Melo & Loboziak 2003), the Eifelian of Germany (Loboziak *et al.* 1991) and Tunisia (Breuer & Steemans 2013), the Givetian of France (Loboziak & Strel 1980), the Eifelian to upper Givetian of Saudi Arabia (Breuer & Steemans 2013) and the Frasnian of Bolivia (Perez-Leyton 1990).

Grandispora cf. inculta Allen, 1965

Figure 10F

- ? 1966 *Hymenozonotriletes argutus* 'I' Naumova; Cramer, p. 268; pl. 4, fig. 74.
 1966 *Hymenozonotriletes narancae*, Cramer, p. 269; pl. 3, fig. 70.
 cf. 1969 *Calyptosporites optivus* (Chibrikova) Allen; Cramer, p. 440; pl. 4, fig. 38.
 p. 1969 *Calyptosporites microspinosus* (Richardson) Richardson; Cramer, p. 439; pl. 3, figs 35, 36.
 p. 1969 *Calyptosporites (?) narancae* (Cramer) New Combination; Cramer, p. 439.
 ? 1988 *Grandispora* sp. C Paris *et al.*; Fombella Blanco, pl. 1, fig. 5; pl. 2, fig. 1.

Description. Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, may be accompanied by labra or triradiate folds, extending from two-thirds the radius of the intexine to the spore equator. Exoexine extends past intexine perimeter by one-fifth to three-quarters the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with microgranulae, larger granulae and small spines.

Dimensions. Intexine: 26 (60) 94 μm (33 specimens measured); exoexine: 31 (76) 133 μm (31 specimens measured).

Remarks. This species has a very broad original description. As a result a wide variety of forms, with a relatively small, simple ornament but widely ranging exoexine:intexine ratios, can be placed in this species. The specimens in this study have a larger size range than the species as originally described but show a continuous spread.

Occurrence. Sites 2, 3, 4, 7, 10, 11, 13, 14, 20, 22, 120, 598, G.

Previous records. Reported from the Emsian to middle Givetian of Libya (Paris *et al.* 1985; Strel *et al.* 1988; Moreau-Benoit 1989), the Emsian–Frasnian of Algeria (Boumendjel *et al.* 1988; Moreau-Benoit *et al.* 1993), the Eifelian–Givetian of Morocco (Rahmani-Antari & Lachkar 2001), the upper Eifelian of Scotland (Marshall 1988), the upper Eifelian of Russia (Avkhimovitch *et al.* 1993), the upper Eifelian to lower Givetian of Canada (McGregor & Camfield 1982), the upper Eifelian to Givetian of Poland (Turnau 1996; Turnau & Racki 1999), the Givetian of Spitsbergen (Allen 1965), the Givetian to lower Frasnian of Brazil (Loboziak *et al.* 1988), the lower Givetian of Libya, the upper Givetian of Saudi Arabia (Breuer & Steemans 2013), the upper Givetian to upper Frasnian of France (Brice *et al.* 1979; Loboziak & Strel 1980, 1988; Loboziak *et al.* 1983) and the Frasnian of Bolivia (Perez-Leyton 1990).

Grandispora permulta (Daemon) Loboziak *et al.*, 1999

Figure 10E

- 1988 *Grandispora* sp. A, Paris *et al.*; Fombella Blanco, pl. 1, fig. 1.

Description. Amb subcircular to slightly subtriangular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to the spore equator. Exoexine extends past intexine perimeter by one-third the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with microgranulae.

Dimensions. Intexine: 47 (74) 93 μm ; exoexine: 72 (99) 120 μm (4 specimens measured).

Remarks. This species is distinguished from *G. inculta* in this study by its slightly subtriangular shape. A pronounced, though often discontinuous, ring is observed in the middle of the exoexine offlap, potentially representing curvaturae. A similar structure is visible in Breuer & Steemans (2013, fig. 33B).

Occurrence. Sites 2, G.

Previous records. Reported from the upper Emsian to lower Frasnian of Tunisia (Breuer & Steemans 2013), lower Eifelian to lower Givetian of Libya (Paris *et al.* 1985; Streeb *et al.* 1988), the Eifelian–Frasnian of Brazil (Loboziak *et al.* 1988; Melo & Loboziak 2003), the upper Eifelian to upper Givetian of Libya (Breuer & Steemans 2013), the upper Eifelian to lower Frasnian of Bolivia (Perez-Leyton 1990) and Saudi Arabia (Breuer & Steemans 2013), the middle Givetian of Algeria (Moreau-Benoit *et al.* 1993) and the upper Givetian to lower Frasnian of Argentina (Ottone 1996).

Grandispora protea (Naumova) Moreau-Benoit, 1980
Figure 11A

non 1966 *Hymenozonotrillates cf. domanicus* Naumova; Cramer, p. 268; pl. 3, fig. 71.

? 1969 *Calyptosporites cf. domanicus* (Naumova) New Combination; Cramer, p. 438; pl. 4, fig. 39.

Description. Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to the spore equator. Exoexine extends past intexine perimeter by two-thirds to the whole of the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with very widely separated granulae and spines up to 3 µm high.

Dimensions. Intexine: 48 (60) 77 µm; exoexine: 72 (97) 136 µm (4 specimens measured).

Remarks. This species is distinguished from the other *Grandispora* species in this study by its characteristic ornament.

Occurrence. Sites 7, 11, 20.

Previous records. Reported from upper Emsian to Frasnian strata, with an almost worldwide distribution (although absent from Asia and Australia) (Breuer & Steemans 2013).

Grandispora cf. stolidota (Balme) Breuer & Steemans, 2013
Figure 12A

Description. Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to the spore equator. Exoexine extends past intexine perimeter by a

distance equal 1 to 1.5 times the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with microgranulae.

Dimensions. Intexine: 35 (45) 52 µm; exoexine: 68 (91) 99 µm (3 specimens measured).

Remarks. This species is distinguished from the other *Grandispora* species in this study by its much larger exoexine:intexine ratio. We use this to refer the specimens provisionally to *G. stolidota*, though no intexine measurement is given in the original description and the complex, biform sculptural elements could not be seen in these specimens.

Occurrence. Sites 7, G.

Previous records. Reported from the upper Eifelian to lower Frasnian of Tunisia, Libya and Saudi Arabia (Breuer & Steemans 2013) and the middle Givetian to lower Frasnian of Australia (Balme 1988; Grey 1991).

Grandispora velata (Richardson) McGregor, 1973
Figure 10G

p. 1969 *Calyptosporites microspinosus* (Richardson) Richardson; Cramer, p. 439; pl. 3, fig. 37.

1969 *Calyptosporites velatus* (Eisenack) Richardson; Cramer, p. 440.

Description. Amb subtriangular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to the spore equator. Exoexine extends past intexine perimeter by three-quarters the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with microgranulae and small spinose ornament.

Dimensions. Intexine: 44 (51) 60 µm; exoexine: 68 (88) 116 µm (4 specimens measured).

Remarks. This species is distinguished from the other *Grandispora* species in this study by its subtriangular shape, large exoexine:intexine ratio and spinose ornament.

Occurrence. Sites 3, 7, 10, 20, G.

Previous records. Reported from upper Emsian to Frasnian strata and with a worldwide distribution (Breuer & Steemans 2013).

Genus GRANULATISPORITES Ibrahim emend. Potonié & Kremp, 1954

Type species. *Granulatisporites granulatus* Ibrahim, 1933.

Granulatisporites concavus Breuer & Steemans, 2013

Figure 8M

? 1969 *Leiotriletes bonitus* Cramer; Cramer, p. 430; pl. 1, fig. 9.

Dimensions. 20 (29) 47 µm (8 specimens measured).

Remarks. The specimens seen here meet the specific characteristics in all respects.

Occurrence. Sites 3, 4, 7, 11, 19, G.

Previous records. Reported from the middle Emsian to lower Givetian of Libya and the upper Emsian to upper Eifelian of Saudi Arabia (Breuer & Steemans 2013).

Granulatisporites cf. muninensis Allen, 1965

Figure 8N

Description. Amb subtriangular with straight or slightly convex interradian margins. Laesurae straight, extending to the equator. Proximal surface laevigate. Distal surface bears an ornament of fine microgranulae.

Dimensions. 24 (34) 44 µm (2 specimens measured).

Remarks. These specimens are doubtfully assigned to *G. muninensis* as the presence of labra could not be determined with certainty.

Occurrence. Sites 3, 22, P.

Previous records. Reported from Upper Silurian to middle Tournaisian strata with a worldwide distribution.

Genus LATOSPORITES Potonié & Kremp, 1954

Type species. *Latosporites latus* Potonié & Kremp, 1954.

Latosporites sp. 1 Breuer & Steemans, 2013

Figure 9H–I

Description. Amb subcircular to ovoid. Monolete mark observed, extending from one-half to the whole amb radius.

Curvaturae perfectae often observed at the laesurae tips. Surface laevigate.

Dimensions. 24 (36) 62 µm (20 specimens measured).

Remarks. The specimens found here have a greater size range than originally described for the species.

Occurrence. Sites 3, 4, 7, 10, 11, 120, G, P.

Previous records. Reported from the Eifelian of Libya, the Eifelian to middle Givetian of Tunisia and the middle Givetian of Saudi Arabia (Breuer & Steemans 2013).

Genus PLANISPORITES (Knox) Potonié & Kremp, 1954

Type species. *Planisporites granifer* (Ibrahim) Knox, 1950.

Planisporites cf. minimus McGregor, 1960

Figure 9J

1966 *Cyclogranisporites rosendae*, Cramer, p. 264; pl. 3, fig. 55.

1969 *Rhabdosporites prosperus* (Cramer) New Combination; Cramer, p. 443; pl. 2, figs 21, 23–25.

? 1988 *Acanthotriletes* sp.; Fombella Blanco, pl. 3, fig. 2.

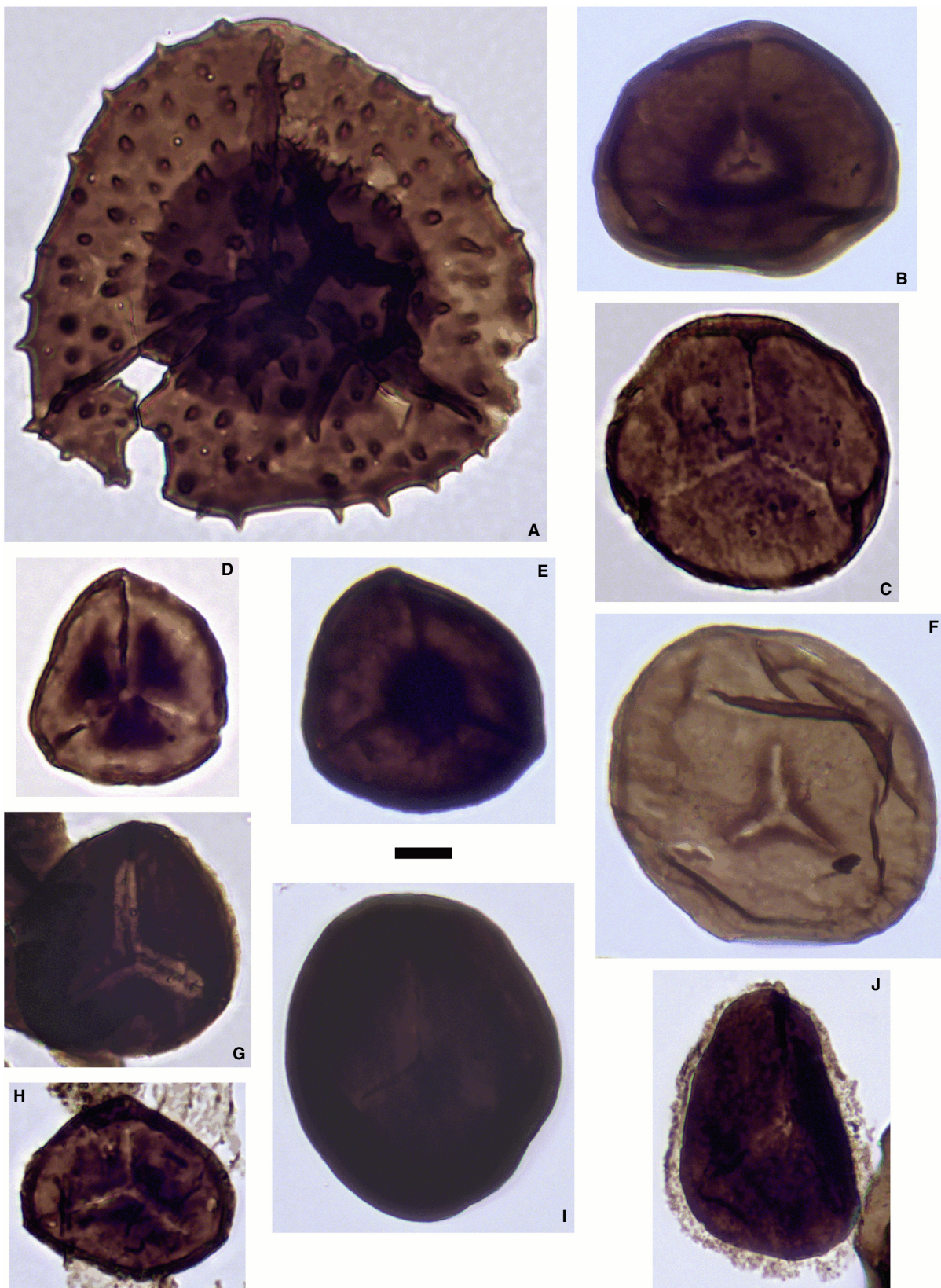
Description. Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending from one-third to the whole amb radius. Equatorial thickening of 1–3 µm observed. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

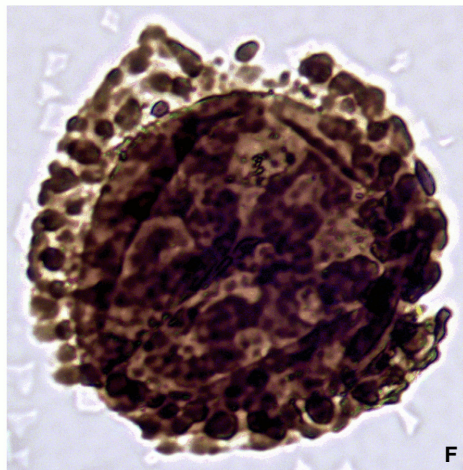
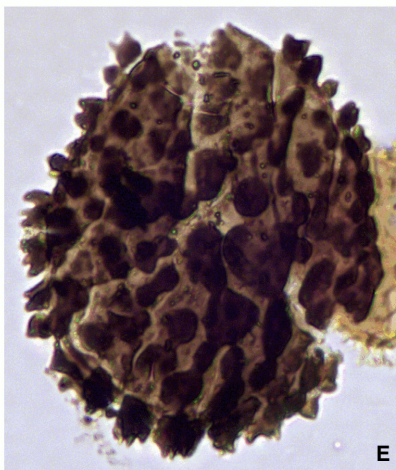
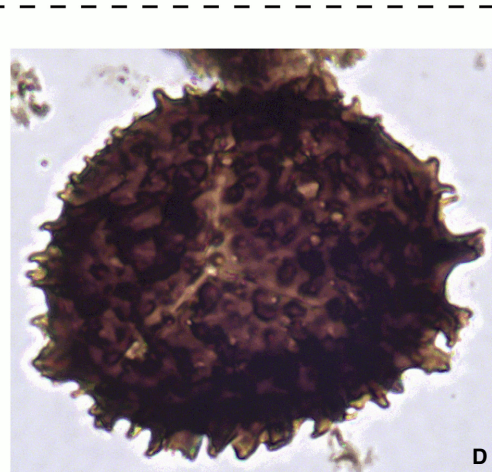
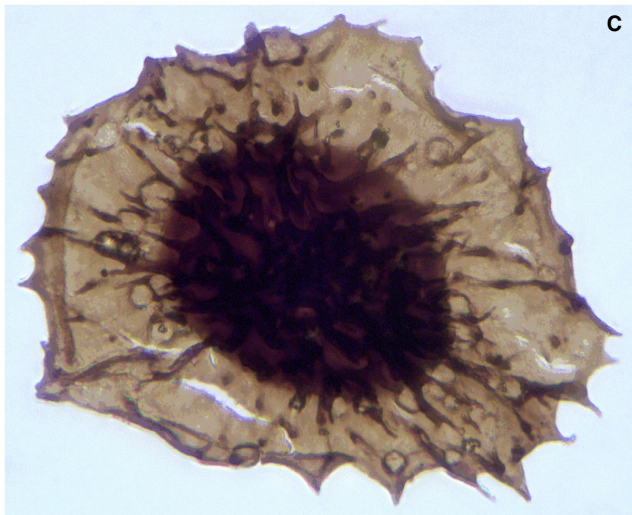
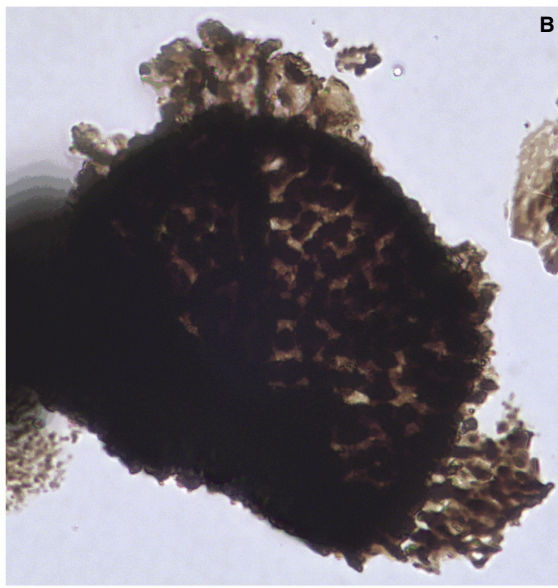
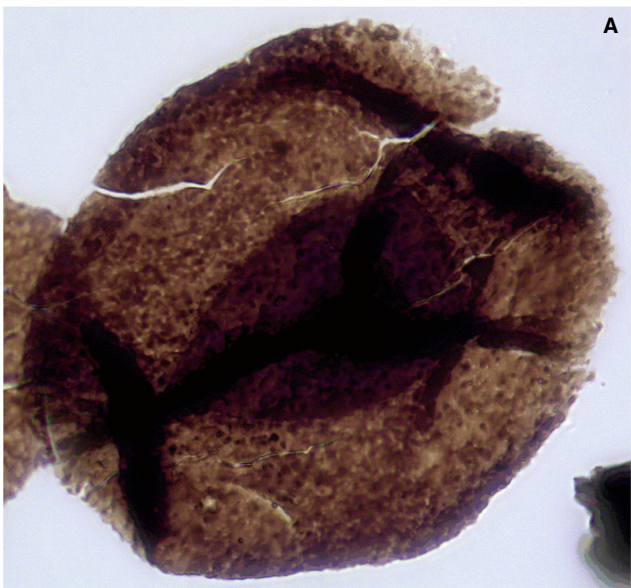
Dimensions. 15 (40) 70 µm (80 specimens measured).

Remarks. The specimens found here show a greater range of variation in the length of the trilete rays than the species as originally described, though no meaningful division of the population could be made. This species may form one end member of a morphological series with *A. elegans* at the other extreme (Owens 1971); see remarks above pertaining to that species for a fuller explanation.

Occurrence. Sites 2, 3, 4, 5, 7, 10, 11, 13, 14, 19, 20, 22, 120, 598, 599, 600, G, P.

FIG. 11. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A, *Grandidispora protea*; AJA2-20A-O1; P48. B, *Retusotriletes rotundus*; AJA7A-O1; T33/3. C, *Retusotriletes semizonalis*; AJA2-7H-O1; O39. D, *Retusotriletes atratus*; AJA2-3R-O1; E42/1. E, *Retusotriletes goensis*; AJA11A-O1; W39/4. F, *Retusotriletes triangulatus*; AJA11A-O1; M36. G, *Retusotriletes* sp. A; AJA2A-O1; L39/2. H–I, *Retusotriletes* spp.: H, AJA11A-O1, M37; I, AJA3A-O1, D34/4. J, *Rhabdosporites minutus*; AJA11A-O1; B45/4. Scale bar represents 10 µm. Colour online.





Previous records. Reported from the upper Emsian of Germany (Edalat 1974), the Frasnian of Canada (McGregor 1960) and the Mississippian of England (Lele & Walton 1962) with an additional record from the former USSR of uncertain age (Bezák & Planderova 1981).

Genus *RETUSOTRILETES* Naumova emend. Strel, 1964

Type species. *Retusotriletes simplex* Naumova, 1953.

Retusotriletes atratus Breuer & Steemans, 2013

Figure 11D

Description. Amb circular to subcircular. Laesurae straight, extending from one-half to the whole amb radius. Possible 2–3 µm wide equatorial thickening sometimes observed. Proximal face bears subtriangular, thickened regions in each interradial area, not touching the laesurae and extending up to two-thirds of the distance to the equator. Distal surface laevigate.

Dimensions. 33 (40) 54 µm (5 specimens measured).

Remarks. The species as originally described is somewhat larger than the specimens found here.

Occurrence. Sites 3, 7, 120, 598.

Previous records. Reported from the upper Pragian to upper Givetian of Saudi Arabia (Breuer & Steemans 2013) and the Emsian to lower Givetian of Australia (Hashemi & Playford 2005).

Retusotriletes goensis Lele & Strel, 1969

Figure 11E

Description. Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending from one-half to the whole amb radius. *Curvaturae perfectae* sometimes observed joining the laesurae tips. Proximal surface bears an apical, subcircular to subtriangular thickened area extending from *c.* one-third to one-half of the distance to the equator. Distal surface laevigate.

Dimensions. 23 (36) 52 µm (10 specimens measured).

Remarks. Labra accompanying the laesurae are not always mentioned in descriptions of this species, though they

have been figured (Breuer 2008; Breuer & Steemans 2013). These specimens bear a resemblance to *Concentricosporites sagittarius* (Rodríguez) Rodríguez, 1983, though they have no obvious crassitude and a diffuse outer margin to their thickened area, as opposed to the hard edge seen in *C. sagittarius*.

Occurrence. Sites 3, 4, 7, 10, 11, 598, G, P.

Previous records. Reported from the upper Lochkovian of Brazil (Rubinstein *et al.* 2005), the middle Emsian to lower Givetian of Saudi Arabia (Breuer & Steemans 2013), the upper Emsian (Lessuise *et al.* 1979) and probable upper Eifelian of Belgium (Lele & Strel 1969; Breuer & Steemans 2013) and the lower Eifelian to lower Givetian of Libya (Moreau-Benoit 1989).

Retusotriletes rotundus (Strel) Strel emend. Lele & Strel, 1969

Figure 11B

1969 *Retusotriletes barbatus* Cramer; Cramer, p. 430.

1969 *Retusotriletes psychovii* Naumova *major* Naumova; Cramer, p. 430; pl. 1, figs 3, 7.

1969 *Retusotriletes rotundus* (Strel) Strel; Cramer, p. 431; pl. 1, figs 1, 2.

Dimensions. 23 (44) 63 µm (29 specimens measured).

Remarks. The specimens found here meet the specific description for *R. rotundus* in all respects. The species is sometimes considered as part of a continuous morphological series with *R. goensis* and *R. triangulatus* (McGregor 1973).

Occurrence. Sites 2, 3, 5, 7, 10, 11, 13, 19, 20, 22, G.

Previous records. Reported from Devonian, especially Lower to Middle Devonian, strata and with a worldwide distribution (Breuer & Steemans 2013).

Retusotriletes semizonalis McGregor, 1964

Figure 11C

Description. Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from two-thirds to three-quarters of the amb radius. Prominent

FIG. 12. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A, *Grandispora* cf. *stolidota*; AJA2-7O-O1; W37. B, *Samarisporites* cf. *praetervisus*; AJA2-7K-O1; U33/3. C, ‘*Grandispora*’ (*Hymenozonotriletes*) *argutus*; AJA10B-O1; U33/3. D, *Verrucosiporites scurrus*; AJA2-GAB-O2; P44/2. E–F, *Verrucosiporites tumultentus*: E, AJA2-3N-O1, Q41; F, AJA2-3E-O2, E33/2. Scale bars represent: 20 µm (A–C); 10 µm (D–F). Colour online.

curvaturae perfectae observed joining the tips of the laesurae. Proximal surface laevigate. Distal surface bears an ornament of fine microgranulae.

Dimensions. 30 (46) 64 µm (6 specimens measured).

Remarks. These specimens meet the specific description for *R. semizonalis* in all respects.

Occurrence. Sites 2, 7, 11, 13, 19, G.

Previous records. An often-reported taxon reported from upper Pragian to lower Famennian strata from North America, China and Europe.

Retusotriletes triangulatus (Streel) Streel, 1967
Figure 11F

? 1988 *Retusotriletes triangulatus* (Streel) Streel; Fombella Blanco, pl. 2, fig. 2.

Dimensions. 25 (44) 80 µm (70 specimens measured).

Remarks. The specimens found here meet the specific description for *R. triangulatus* in all respects.

Occurrence. Sites 2, 3, 4, 7, 10, 11, 19, 120, 598, 599, G, P.

Previous records. Reported from Devonian, especially Lower to Middle Devonian, strata and with a worldwide distribution (Breuer & Steemans 2013).

Retusotriletes sp. A
Figure 11G

Description. Amb circular to subcircular. Laesurae straight, extending to the equator. Curvaturae observed at the tips of the laesurae. An area of thinner exine surrounds the laesurae with concave sides and rounded ends, extending three-quarters of the distance to the equator. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

Dimensions. 28 (38) 45 µm (4 specimens measured).

Remarks. This simple species of *Retusotriletes* lacks diagnostic characters that enable identification with previously described species of this genus. No established species could be found with a similar thinned exinal structure.

Occurrence. Sites 2, 3, 598.

Retusotriletes spp.

Figure 11H-I

Description. Various forms referable to *Retusotriletes* but lacking diagnostic characters at the species level.

Occurrence. Sites 3, 7, G.

Genus RHABDOSPORITES Richardson emend. Marshall & Allen, 1982

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

Rhabdosporites minutus Tiwari & Schaarschmidt, 1975
Figure 11J

Description. Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, may be accompanied by narrow labra along their length, extending from one-half to the whole radius of the intexine. Exoexine just extends past intexine perimeter by 2–8 µm. Proximal surface laevigate. Exoexine distally sculptured with microgranulae.

Dimensions. Exoexine: 25 (48) 91 µm (15 specimens measured).

Remarks. Some specimens found here may have a rather coarser ornament than previously described for the species but no meaningful distinction or alternative identification was forthcoming. The species can bear a resemblance to *Apiculiretusispora brandtii*, though it has a completely detached exoexine. The taxonomic history and validity of this species is complex and disputed, indeed Troth *et al.* (2011) described it as invalid, choosing to synonymize it with *G. lemurata*. Despite this, the species is widely used in biostratigraphy, including by Breuer & Steemans (2013) who reported it as occurring across a wide stratigraphical range encompassing that of the sediments studied here. We have chosen to retain this species in light of this wide usage.

Occurrence. Sites 2, 3, 7, 10, 11, 13, 19, 20, 22, 120, 598, G, P.

Previous records. Reported from the Emsian–Eifelian of Saudi Arabia (Al-Ghazi 2007; Breuer & Steemans 2013), the middle–upper Emsian of Luxembourg (Steemans *et al.* 2000), the middle Emsian to lower Givetian of Libya, the upper Emsian to lower Frasnian of Tunisia (Breuer & Steemans 2013) and the lower Eifelian to lower Givetian of Germany (Tiwari & Schaarschmidt 1975).

Genus SAMARISPORITES Richardson, 1965

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

Samarisporites cf. praetervisus (Naumova) Allen, 1965

Figure 12B

Description. Amb circular to subcircular. Laesurae often obscured, may extend to the equator. Equatorial thickening of 3–5 μm observed. Proximal surface laevigate. Distal surface bears a pattern of convolute ridges around 2–3 μm wide and high, separated by 1 μm at most. Ridges occasionally topped by small spines around 1 μm in size. A separated exoexinal layer may sometimes be seen, though poor preservation precludes a more confident identification of this structure.

Dimensions. 55 (81) 104 μm (8 specimens measured).

Remarks. The assignation of these specimens to *S. praetervisus* is difficult due to their poor preservation and rare preservation of exine remnants. The distal ornament and size range is the basis of their identification.

Occurrence. Sites 3, 7, 14, G.

Previous records. Reported from the Eifelian to middle Givetian of Libya (Paris *et al.* 1985; Strel *et al.* 1988; Moreau-Benoit 1989; Breuer & Steemans 2013) and Tunisia (Breuer & Steemans 2013), the upper Eifelian to lower Givetian of Brazil (Melo & Loboziak 2003), the lower Givetian of Algeria (Boumendjel *et al.* 1988) and the Givetian of Saudi Arabia (Breuer & Steemans 2013) and Spitsbergen (Allen 1965).

Genus VERRUCOSISPORITES Ibrahim emend. Smith, 1971

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

Verrucosisporites scurrus (Naumova) McGregor & Camfield, 1982

Figure 12D

1988 *Raistrickia aratra* Allen; Fombella Blanco, pl. 2, fig. 5; pl. 4, fig. 4.

Description. Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending from two-thirds to the whole amb radius. Equatorial thickening

of 1–2 μm observed. Proximal surface laevigate. Distal surface bears an ornament of microgranulae and larger granulae up to 7 μm high, usually narrower than they are high, with rounded or flat tops. Some of these flattened tips develop into a short bifurcation.

Dimensions. 43 (60) 76 μm (4 specimens measured).

Remarks. The species as originally described often has somewhat wider ornament than the specimens described here, usually being as wide as it is high, though with considerable variation in size.

Occurrence. Sites 3, 10, 14, G.

Previous records. Reported from lower Eifelian to lower Famennian strata, with an almost worldwide distribution (although absent from Asia) (Breuer & Steemans 2013).

Verrucosisporites tumultentus Clayton & Graham, 1974

Figure 12E–F

Description. Amb circular to subcircular. Laesurae straight, extending to the equator. Proximal surface laevigate. Distal surface bears an ornament of microgranulae and wide granulae up to 8 μm wide but of low relief, only around 1–2 μm high. Granulae sometimes topped by minute spines and a small number may be joined at their bases.

Dimensions. 44 (55) 69 μm (4 specimens measured).

Remarks. The exoexine of the specimens seen here is sometimes detached, though this is interpreted as due to damage. A comparison can be drawn between these specimens and *Acinosporites tristratus* Breuer & Steemans 2013, but these specimens have a primarily granule-based ornament rather than consisting primarily of ridges as in *Acinosporites*. It should be noted that biform ornament is not mentioned in Clayton & Graham's original description of the species, though it does appear in the specimens assigned to this species by McGregor & Camfield (1982) and in the present study.

Occurrence. Site 3.

Previous records. Reported from the Eifelian to middle Givetian (McGregor & Camfield 1982) and upper Famennian to lower Tournaisian (Braman & Hills 1992) of Canada, the Givetian–Frasnian of Ireland (Clayton & Graham 1974) and the upper Givetian to lower Frasnian of the USA (Traverse & Schuyler 1994) and Argentina (Ottone 1996).

Genus ZONOTRILETES Luber & Waltz, 1938

Type species. None designated (Breuer & Steemans 2013).

Zonotriletes armillatus Breuer *et al.*, 2007

Figure 13A–C

Description. Amb subcircular to subtriangular. Laesurae straight, extending from one-quarter to the whole amb radius. Equatorial thickening of 3–9 µm observed. Proximal surface laevigate. Distal surface bears a 4–7 µm wide subcircular to subtriangular annulus, positioned around one-half to $\frac{3}{5}$ of the distance to the equator, otherwise laevigate. A thin flange is present at the equatorial margin, extending by one-quarter to one-half the radius of the main body of the spore interradially but narrowing opposite the trilete rays so as to disappear entirely.

Dimensions. 37 (66) 104 µm (9 specimens measured).

Remarks. The equatorial thickening of the specimens seen here can be somewhat larger than originally described. Some specimens seem to possess a very fine, irregular distal ornament, though this is interpreted as a preservational effect.

Occurrence. Sites 3, 7, 13, 120, 598, G.

Previous records. Reported from the Eifelian of Saudi Arabia, the upper Eifelian of Tunisia (Breuer & Steemans 2013) and upper Eifelian to lower Givetian of Brazil (Breuer & Grahn 2011).

Zonotriletes simplicissimus Breuer *et al.*, 2007

Figure 13F

Description. Amb subtriangular. Laesurae straight, extending to the equator. Equatorial thickening of 5–10 µm observed. Surface laevigate. A thin flange is present at the equatorial margin, extending by one-quarter to one-third the radius of the main body of the spore interradially but narrowing opposite the trilete rays.

Dimensions. Main body: 41–43 µm; flange: 51–54 µm (one specimen measured).

Remarks. This species lacks the annulus of *Z. armillatus* and its equatorial flange does not disappear entirely opposite the trilete rays. Only a single specimen was found.

Occurrence. Site 120.

Previous records. Reported from the upper Emsian to lower Givetian of Saudi Arabia, the lower Givetian of Libya (Breuer & Steemans 2013) and upper Eifelian to lower Givetian of Brazil (Breuer & Grahn 2011).

OTHER FORMS

Spore type A

Figure 13D–E, G–H

Description. Amb ovoid. Laesurae observed, in an arrangement reminiscent of a monolete mark with ends that bifurcate around one-third of the distance to the equator. These secondary branches terminate a little over halfway between their point of branching and the equator. The entire laesural structure is surrounded by narrow labra. A structure at the perimeter of the spore may be an equatorial thickening of 2–6 µm thickness or a separated exoexine. Surface laevigate.

Dimensions. 42 (49) 57 µm (4 specimens measured).

Remarks. This taxon bears some resemblance to *Gneudnaspota divellomedia* (Chibrikova) Balme, 1988. However, the specimens seen here show a pronounced regularity in their monolete-like/trilete-like haptotypic structure, unlike the inherently irregular scars seen in cryptospores like *G. divellomedia*.

Occurrence. Sites 3, 7, G.

DESCRIPTION OF THE SPORE ASSEMBLAGE

The spore assemblages comprise 68 spore taxa (55 identified species belonging to 27 genera) of which 10 taxa are known only from this assemblage. Count data is presented in Askew & Wellman (2018). The spore assemblages recovered from the various sites do not differ significantly in their taxonomic composition and can be considered as essentially representing a single spore assemblage. The ranges of some important taxa within the Playa del Tranqueru section are displayed in Figure 14 (the remaining short sections are not sufficiently stratigraphically controlled to be correlated with this long section).

The spore assemblage is not particularly variable, as is evident from analysis of the three sections of significant length measured through the formations. These sections include almost all taxa found in this study, with only *Dibolisporites* sp. A, *Retusotriletes* cf. *microgranulatus*? and *Zonotriletes simplicissimus* being absent. None of these taxa are stratigraphically important, as they are either not

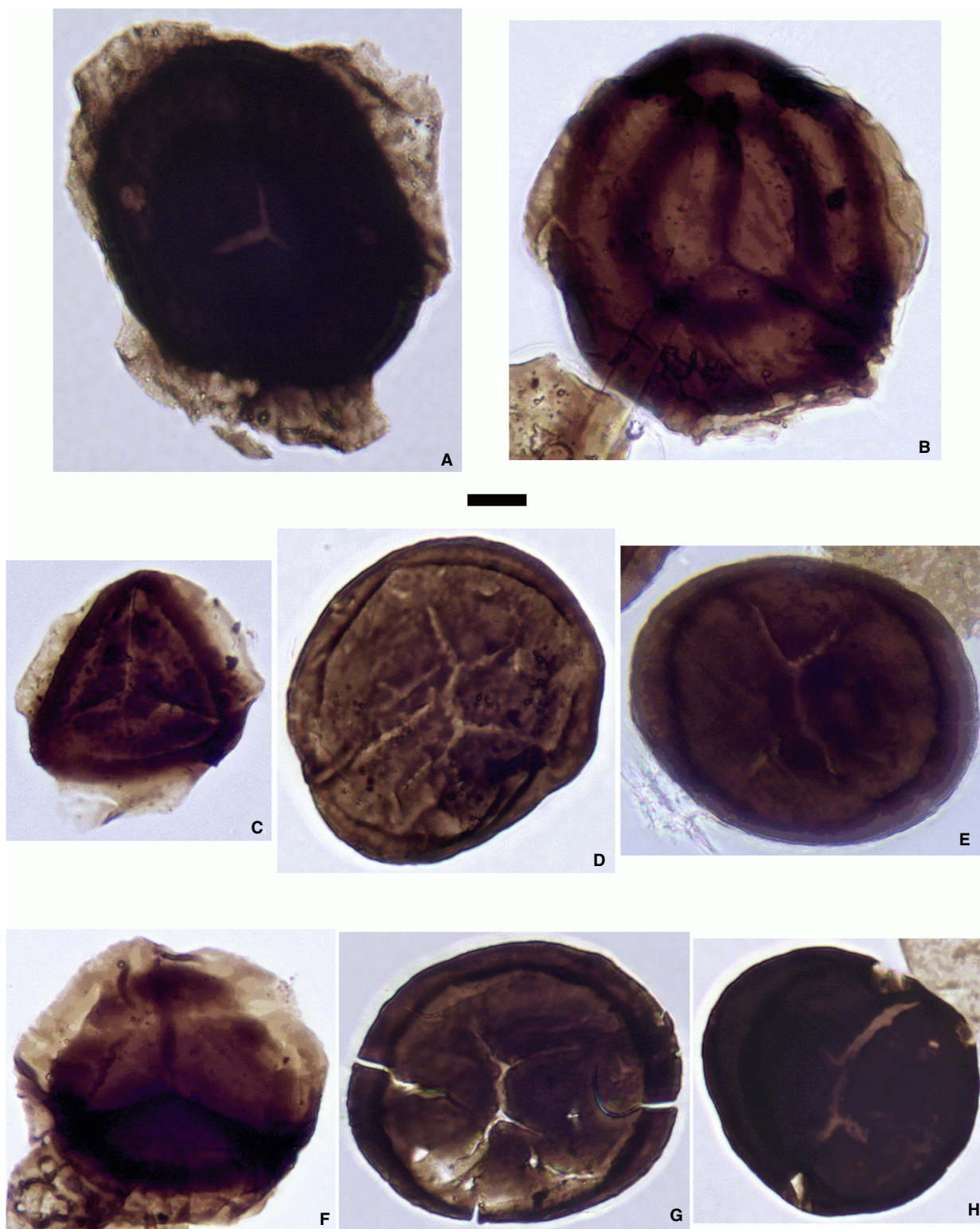


FIG. 13. Each figured specimen is identified by slide including the sample code, followed by its England Finder reference. A–C, *Zonotriletes armillatus*: A, AJA598C-O1, L28/3; B, AJA120A-O2, M40/4; C, AJA120A-O1, Q38. D–E, Spore type A: D, AJA2-3C-O2, L46/2; E, AJA7A-O1, N37/3. F, *Zonotriletes simplicissimus*; AJA120A-O1; U29. G–H, Spore type A: G, AJA2-7R-O2, K49; H, AJA2-GO-O2, O43. Scale bar represents 10 μm . Colour online.

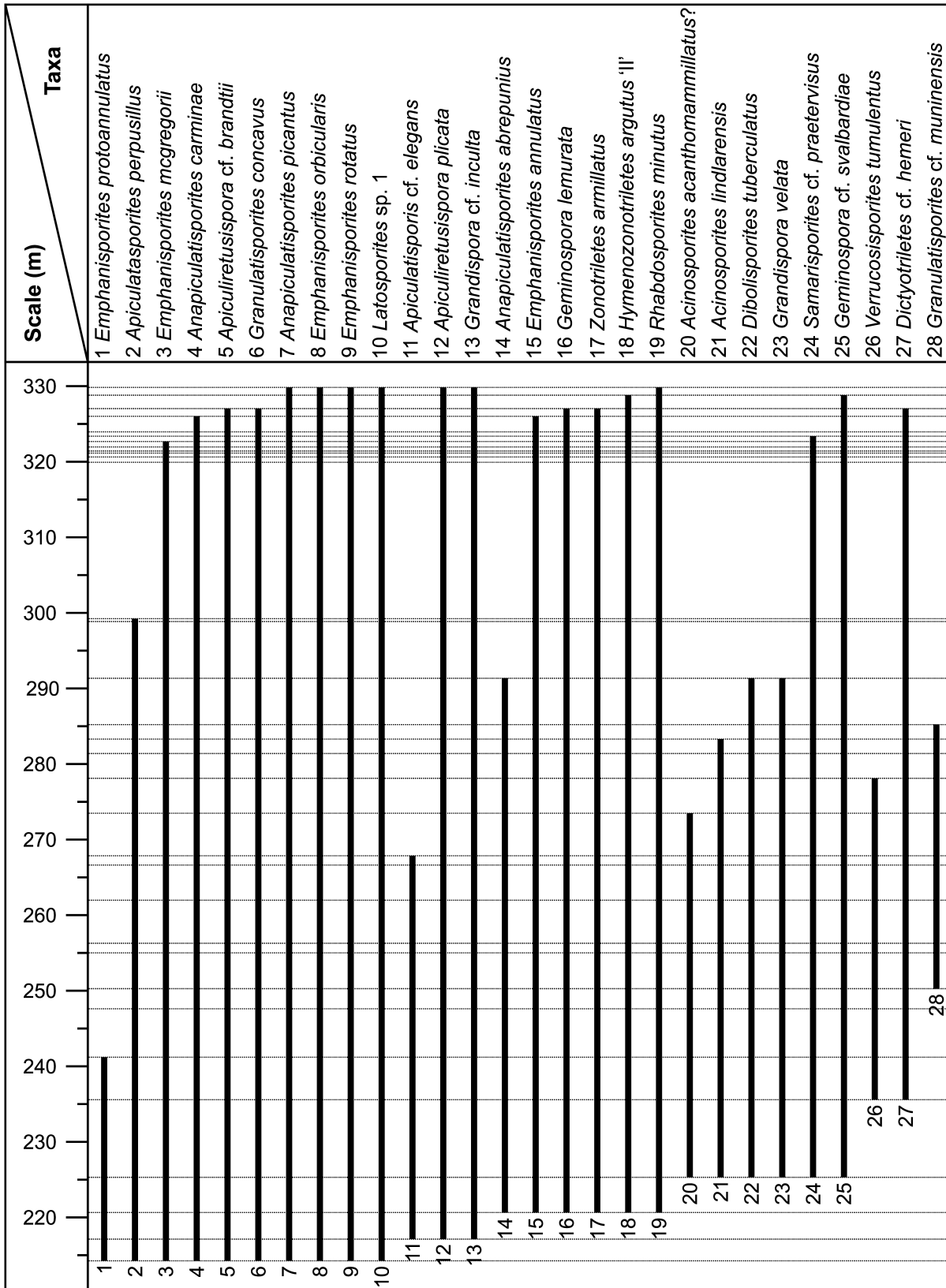


FIG. 14. Stratigraphic ranges of selected spore taxa from the Playa del Tranqueru (3) section. Dotted horizontal lines indicate sample locations, ordered from A (lowest) to AG (highest), as also indicated on Figure 3.

reported from elsewhere or are known to occur across the stratigraphical range of the formations (Breuer & Steemans 2013). The three long sections exhibit few taxon inceptions, with the vast majority occurring at the base of the sections. Those taxa that do appear higher up the sections rarely become significant components of the assemblage, with the exceptions of *Devonomonoletes* cf. sp. 1 and three species of *Emphanisporites* in the San Pedro de Nora section, and none are considered to be of stratigraphical importance.

The spore assemblage is dominated by laevigate crassitate spores that can be accommodated in the genus *Ambitisporites* spp. (20% of the assemblage), similar simple trilete spores with a distal ornament (31%), retusoid forms including *Apiculiretusispora* (17%) and *Emphanisporites* (15%). The taxon *Grandispora* cf. *inculta* is also important, as it constitutes a significant component of the spore assemblage (8%).

It seems very unlikely that reworking or sorting of spores has seriously skewed spore assemblage composition. The underlying Upper Silurian to Lower Devonian San Pedro Formation and La Vid Group spore assemblages (Cramer 1966) contain many distinctive taxa that are not found in the Middle Devonian spore assemblage, suggesting there was no large scale reworking of taxa. The fact that the range of spore sizes in the Middle Devonian spore assemblage is large, including very small simple spores as well as very large, complex spores such as *Grandispora* spp., suggests that size sorting is limited.

COMPARISON WITH PREVIOUSLY DESCRIBED SPORE ASSEMBLAGES: BIOSTRATIGRAPHICAL AND PALAEOPHYTOGEOGRAPHICAL IMPLICATIONS

The distinctive biostratigraphical marker species *Geminospora lemurata* occurs in the lowest sample of the two incomplete sections and in the third-lowest sample of the nearly complete Playa del Tranqueru section, although the two lower samples are very poor, with very few preserved palynomorphs of any kind (see Fig. 14 and Askew & Wellman (2018, charts 1–3) for details). Based on the presence of *G. lemurata*, and in the absence of younger species, the assemblage described here can be correlated with the following spore zones erected for the Old Red Sandstone continent (Euramerica): the *lemurata–magnificus* Spore Assemblage Biozone of Richardson & McGregor (1986) and the AD Opper Zone (Lem Interval Zone) of Strel *et al.* (1987). Both of these have been attributed an early to ?middle Givetian age. Beyond Euramerica there are few spore zonation schemes, although Breuer & Steemans (2013) developed a scheme for northern Gondwana

based on material from Arabia and North Africa. In their scheme, *G. lemurata* appears at the base of the *lemurata–langii* Assemblage Zone (*Geminospora lemurata* Interval Zone) which is considered to be of early (but not earliest) Givetian age (ranging from c. 385.5–387.7 Ma; Loboziak & Melo 2002; Marshall *et al.* 2007; Turnau & Narkiewicz 2011; Becker *et al.* 2012).

Previous work on conodonts recovered from the limestones that sandwich these formations provide a tight age bracket for their deposition: middle Eifelian to early Givetian. This represents a period of between 386–387 and 391–392 Ma, representing between 4 and 6 million years (based on Becker *et al.* 2012), depending on which part of each conodont zone is represented. Correlation with the *lemurata–langii* Assemblage Zone (*Geminospora lemurata* Interval Zone) would suggest that the strata yielding the spore assemblages were deposited in the upper part of this range in a period of only a little over 1.5 million years between 386 and 387.7 Ma, represented diagrammatically in Figure 15.

The scheme of Richardson & McGregor (1986) reports taxa other than the nominal ones that are considered characteristic of the *lemurata–magnificus* Zone, many of which are also present in the Spanish assemblage, namely *Acinosporites acanthomammillatus*, *Apiculiretusispora brandtii*, *Emphanisporites annulatus*, *Grandispora protea*, *G. velata*, *G. inculta* and *Verrucosporites scurrus*. However, the Spanish assemblage also includes other taxa, such as *Ambitisporites avitus*, *A. plicata*, *Dictyotriletes gorgoneus*, *E. microronatus*, and *G. douglstownensis*, which are considered to have gone extinct much earlier in Euramerica according to Richardson & McGregor (1986). The absence of *Contagisporites optivus* and *Samarisporites triangulatus*, the nominal species of the overlying *optivus–triangulatus* Spore Assemblage Biozone of Richardson & McGregor (1986), would seem to preclude the Spanish assemblage from belonging to this zone.

The AD Opper Zone of Strel *et al.* (1987) is based on the work of Riegel (1975) from Eifel, summarized by Riegel (1982). This summary reports *A. acanthomammillatus*, *A. lindlarensis*, *A. brandtii*, *E. annulatus*, *E. rotatus* and *G. velata* as occurring on the Eifelian–Givetian boundary. However, *Brochotriletes* cf. *foveolatus*, also present in the Spanish assemblage, is reported as becoming extinct earlier, in the upper Emsian. The occurrence in the Spanish assemblage of *A. acanthomammillatus*, *E. annulatus*, *G. protea*, *G. velata* and *Rhabdosporites minutus* support this assemblage's placement in the AD Opper Zone (Lem Interval Zone) of Strel *et al.* (1987). The absence of the distinctive and widespread spore *Samarisporites triangulatus*, the nominal species of the overlying TA Opper Zone of Strel *et al.* (1987), would seem to preclude the Spanish assemblage from belonging to this zone.

Scale (Ma)	Stage	Conodont Zonation	Spore Zonation		
385	Givetian	<i>Skeletognathus norrisi</i>	<i>langii–concinna</i>		
		<i>Klapperina disparilis</i>			
		<i>Schmidtnognathus hermanni</i>			
		U	<i>triangulatus–catillus</i>		
		M			
		<i>Polygnathus varcus</i>	<i>lemurata–langii</i>		
		L			
		<i>Polygnathus hemiansatus</i>			
		390	Eifelian	<i>Polygnathus ensensis</i>	<i>rugulata–libyensis</i>
				<i>Tortodus kockelianus</i>	
<i>Tortodus kockelianus</i>					
<i>Polygnathus costatus costatus</i>	<i>svalbardiae–eximius</i>				
<i>Polygnathus costatus partitus</i>					

The placement of the Spanish assemblage in the *lemurata–langii* Assemblage Zone (*lemurata* Interval Zone) of Breuer & Steemans (2013) is supported by 29 shared species including *A. acanthomammillatus*, *A. lindlarensis*, *A. brandtii*, *Camarozonotriletes? concavus*, *E. annulatus*, *G. douglastownensis*, *G. permulta*, *G. stolidota*, *G. velata*, *R. minutus* and *V. scurrus*. However, 50 taxa Breuer & Steemans (2013) reported from the *lemurata–langii* Assemblage Zone are not found in Spain and 39 taxa identified in the Spanish assemblage were not reported by Breuer & Steemans (2013), including common forms such as *A. avitus*, *A. picantus*, *A. plicata*, *E. cf. orbicularis* and *Planisporites cf. minimus*. Various taxa found in the Spanish assemblage also occur at a different stratigraphic level than they do in Breuer & Steemans (2013). For instance, *A. plicata* and *Retusotriletes tenerimedium* do not persist beyond the Emsian in this scheme while *C. parvus* occurs later in the Givetian and *E. laticostatus* does not appear until the Frasnian. Again, the absence of *Samarisporites triangulatus*, the nominal species of the overlying *triangulatus–catillus* Assemblage Zone (*triangulatus* Interval Zone), would seem to preclude the Spanish assemblage from belonging to this zone.

It is clear from the above observations that the Spanish assemblage contains a number of taxa that appear either earlier or later than expected based on their occurrence on the continents of Euramerica or Gondwana. Furthermore, it is evident that certain taxa that often dominate coeval spore assemblages from Euramerica and/or Gondwana are absent from Iberia. The absence of spores with grapnel-tipped processes (*Ancyrospora* spp.) and *Rhabdosporites langii* is particularly noteworthy.

Numerous species of *Ancyrospora* are present and often dominate Middle Devonian spore assemblages from Euramerica (Richardson & McGregor 1986). However, it is interesting that Breuer & Steemans (2013) do not report *Ancyrospora* spp. from the *lemurata–langii* Assemblage Zone of northern Gondwana. Cramer (1966) reports *Ancyrospora* spp. as only appearing in the Spanish sequences after the '*Emphanisporites annulatus* suite' he described from the Naranco Formation. *Ancyrospora* is considered to be produced by lycopsid plants based on

FIG. 15. Correlated biostratigraphy of the Middle Devonian. Conodont zonation reproduced from Becker *et al.* (2012). Spore zonation reproduced from Breuer & Steemans (2013). Note the *langii–concinna* zone continues into the Frasnian. Shaded region indicates the time range in which the studied formations were deposited. The arrow indicates the first occurrence of *Geminospora lemurata*. Spore biozone boundary ages are approximate, positioned correctly relative to conodont zones but not accurately by time. Correlation with conodont zonation based on Streef *et al.* (1987), Loboziak & Melo (2002), Marshall *et al.* (2007) and Turnau & Narkiewicz (2011).

analysis of spore wall ultrastructure (Wellman 2002), but it is not entirely clear if the plants were homosporous and/or heterosporous or whether they were trees, shrubs or herbs.

Likewise, *Rhabdosporites langii* often dominates Middle Devonian spore assemblages from Euramerica (Richardson & McGregor 1986) but this taxon is also common in spore assemblages from the *lemurata–langii* Assemblage Zone of northern Gondwana (Breuer & Steemans 2013). Its presence both north and south of Iberia makes its absence all the more puzzling. *R. langii* was produced by aneurophytalean progymnosperms (reviewed in Wellman 2009). Interestingly, Marshall (1996) proposed an evolutionary hypothesis whereby the microspore (*Geminospora lemurata*) and megaspore (*Contagisporites optivus*) of heterosporous archaeopteridalean progymnosperms evolve from *Rhabdosporites* spores, indicating a close phylogenetic relationship between these taxa.

The endemic nature of the Spanish assemblage makes biostratigraphical age assessment based on spore zonation/ranges erected elsewhere problematic. Taxa may not be appearing at the same time as elsewhere, preventing accurate correlation with other assemblages. However, a number of factors lend credence to the age determination suggested herein. Implying that *G. lemurata* appears earlier in Spain is contrary to its very well defined inception in the lowermost Givetian around the world (Loboziak *et al.* 1991). In addition, the conodont data indicate deposition of the formations had ceased before the inception of *S. triangulatus* (Fig. 15), precluding the possibility of the Spanish spore assemblage being much younger than is stated here.

In conclusion, the flora of the isolated islands of Iberia has various interesting features. There are clear differences with the spore floras from both the large continent to the north-west (Euramerica) and the large continent to the south-east (Gondwana) with: (1) some taxa endemic to Iberia; (2) taxa that are present in Euramerica and Gondwana (including some extremely common forms) entirely absent; (3) some taxa persisting for longer in Iberia than elsewhere; and (4) some taxa possibly appearing earlier in Iberia than elsewhere.

GEOLOGICAL AND PALAEOENVIRONMENTAL INTERPRETATION

The new biostratigraphical information provided by the spore assemblages has implications for the timing of deposition of the Naranco, Huergas and Gustalapedra formations. These formations are essentially divided into a lower part, dominated by thick sandstone units, and an upper part, dominated by siltstone/sandstone

intercalations. Unfortunately, good palynomorph assemblages were not recovered from the lower sandy part. They are, however, abundant in siltstones throughout the upper part. Interestingly, all of the upper part belongs to a single spore biozone of early Givetian age. In conjunction with the conodont evidence, this indicates the upper part of the formation probably represents a period estimated to be a little over 1.5 million years (*c.* 386–387.7 Ma) with the lower, sandier part accumulated within a time frame of no more than 3–4.5 million years (Fig. 15).

The deposits of the Naranco and Huergas formations are interpreted as representing large deltas prograding from the land across the marine shelf. It seems likely that this onset of clastic sedimentation terminated the previous carbonate deposition, which only resumed later when the clastic source ceased. The thick sandstone units of the lower part probably represent periods of rapid deposition with numerous unconformities in a nearshore shallow environment. However, at no time was there a long enough break in clastic deposition for significant carbonate deposition to resume. The mixed sandstone/siltstone of the upper part probably represents further offshore, deeper facies with a combination of terrigenous sands and more oceanic siltstone deposits, including euxinic black shales. The Palencia sequences consist largely of calcareous siltstones and are likely to represent offshore environments far from land, although there is an interesting interruption where a thin (<10 m) sandstone known as the Man Member is deposited (see below).

Detailed results of palynofacies analysis will be reported in a subsequent publication. However, a cursory scan of the results of these analyses indicates that the proportion of land-derived spores within palynomorph assemblages clearly decreases offshore across the shelf as terrigenous input diminishes.

THE KAČÁK EVENT

The nature of the Kačák Event is hotly debated with very little consensus in terms of its timing, duration, causes and effects (García-Alcalde 1998; Becker *et al.* 2016). It is generally considered to have occurred at or near to the Eifelian–Givetian boundary. Some authors suggest a relatively short time interval with a single marine anoxic event, whilst others prefer a more extended time interval possibly with numerous anoxic events. Recently Becker *et al.* (2016) suggested that the Kačák Event was a third-order global event with globally elevated extinction rates (at the lower taxonomic level of species and genera) within many taxonomic clades and several ecosystems. They illustrated the event as being more-or-less confined

to the lower *ensensis* conodont zone and pulsed with a lower and upper event.

The Kačák Event has previously been identified in northern Spain (House 1996; García-Alcalde 1998; García-Alcalde *et al.* 2002). It has been reported to be represented by a thin (1 m) black siltstone unit in the Naranco Formation of Asturias (House 1996), a much thicker unit of euxinic black siltstones in the Huergas Formation of León (House 1996; García-Alcalde *et al.* 2002) and a thin (5–7 m) sandstone unit (Man Member) in the Gustalapedra Formation of Palencia (García-Alcalde 1998; García-Alcalde *et al.* 2002). García-Alcalde *et al.* (2002) suggested that it occurs at the start of the upper sedimentary cycle of the Naranco and Huergas formations and the top of the Man Member.

According to Marshall *et al.* (2007), the series of events comprising the Kačák took place from the uppermost *Tortodus kockelianus* conodont zone to the very lowermost *Polygnathus hemiansatus* zone (latest Eifelian to earliest Givetian). Interestingly this is considered to be just before the inception of *Geminospora lemurata* (Troth *et al.* 2011; Marshall 2016). In this study, spore assemblages were recovered from strata above this level. These belong with the *lemurata–langii* Assemblage Zone (*lemurata* Interval Zone), indicating an age of early (but not earliest) Givetian. This places the spore-bearing strata above the Eifelian–Givetian boundary and therefore somewhat later than the Kačák Event if it is considered to be of only very short duration. Instead the lower, palynologically barren deposits must span the event. Of course, these observations may simply reflect incorrect application or inaccuracies/coarseness of the spore biozonation scheme or misplacement of the Kačák Event in the Spanish sequences. Alternatively, it may be that the Kačák Event was a drawn-out affair rather than a discrete event of short duration.

Considered as a whole, it is clear that the deposits of the Naranco, Huergas and Gustalapedra formations represent a relatively long period of clastic sedimentation that interrupted background carbonate sedimentation. Presumably, this was the result of increased terrigenous (predominantly sandy) input from the land. Either the Kačák Event is a rapid, discrete event that lies somewhere within this sequence, or it can be considered to be a more prolonged, possibly episodic, event representing a period of environmental perturbation that is manifested in increased terrigenous input from the land. A possible cause for the Kačák Event, outlined by Marshall *et al.* (2007), based on work in the Orcadian Basin of Scotland, was a switch to an increasingly monsoonal climate due to increased insolation. This would have led to increased freshwater runoff from the land, which not only increased terrigenous input, but may also have resulted in ocean stratification and the spread of hypoxia. The Spanish

sequences clearly attest to a significant period of increased terrigenous runoff that may indeed have resulted from a switch to monsoonal climates. Perhaps the Kačák Event as a whole represents a prolonged climatic event with the black shales reported elsewhere simply representing discrete horizons/locations when oceanic anoxia occurred.

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REFERENCES

- ABDESSELAM-ROUIGHI, F.-F. 1986. Premiers-resultats biostratigraphiques (Miospores, Acritarchs et Chitinozoaires) concernant le Devonien Moyen et Supérieur de Mole d'Ahara (Bassin d'Illizi, Algérie). *Revue de Micropaléontologie*, **29**, 87–92.
- AL-GHAZI, A. 2007. New evidence for the Early Devonian age of the Jauf Formation in northern Saudi Arabia. *Revue de Micropaléontologie*, **50**, 59–72.
- 2009. *Apiculiretusispora arabensis*, new name for *Apiculiretusispora densa* Al-Ghazi, 2007 (preoccupied). *Revue de Micropaléontologie*, **52**, 193.
- ALLEN, K. C. 1965. Lower and Middle Devonian spores of north and central Vestspitsbergen. *Palaentology*, **8**, 687–748.
- ANDREWS, H. N., KASPER, A. E., FORBES, W. H., GENSEL, P. G. and CHALONER, W. G. 1977. Early Devonian flora of the Trout Valley Formation of northern Maine. *Review of Palaeobotany & Palynology*, **23**, 255–285.
- ARKHANGELSKAYA, A. D. 1985. Zonal spore assemblages and stratigraphy of the Lower and Middle Devonian in the Russian Plate. 5–21. In MENNER, V. V. and BYVSHEVA, T. V. (eds). *Atlas of spores and pollen from the Phanerozoic petroleum formations in the Russian and Turanian plates*. Trudy Vsesoiuznogo Nauchno-Issledovatel'skogo Geologo-razvedoch-nogo Neftianogo Institute (VNIGNI), Moscow.
- ASKEW, A. J. and WELLMAN, C. H. 2018. Data from: An endemic flora of dispersed spores from the Middle Devonian of Iberia. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.cs44q29>
- AVKHIMOVITCH, V. I., TCHIBRIKOVA, E. V., OBUKHOVSKAYA, T. G., NAZARENKO, A. M., UMNOVA, V. T., RASKATOVA, L. G., MANTSUROVA, V. N., LOBOZIAK, S. and STREEL, M. 1993. Middle and Upper Devonian spore zonation of Eastern

- Europe. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine*, **17**, 79–147.
- BALME, B. E. 1962. Upper Devonian (Frasnian) spores from the Carnarvon basin, Western Australia. *The Palaeobotanist*, **9**, 1–10.
- 1988. Miospores from Late Devonian (early Frasnian) strata, Carnarvon Basin, Western Australia. *Palaeontographica Abteilung B Paläophytologie*, **209**, 109–166.
- BECKER, R. T., GRADSTEIN, F. M. and HAMMER, O. 2012. The Devonian period. 559–602. In GRADSTEIN, F. M., OGG, J. G., SCHMITZ, M. D. and OGG, G. M. (eds). *The geologic time scale 2012*. Elsevier.
- KÖNIGSHOF, P. and BRETT, C. E. 2016. Devonian climate, sea level and evolutionary events: an introduction. *Geological Society, London, Special Publications*, **423**, 1–10.
- BEZAK, V. and PLANDEROVA, E. 1981. Nove Poznatky o Veku Metamorfitov v Kohutstkom Pasmе Veporidov. *Geologické Práce, Správy*, **75**, 183–184.
- BOUMENDJEL, K., LOBOZIAK, S., PARIS, F., STEEMANS, P. and STREEL, M. 1988. Biostratigraphie des Miospores et des Chitinozoaires du Silurien supérieur et du Dévonien dans le bassin d'Illizi (S.E. du Sahara algérien). *Geobios*, **21**, 329–357.
- BRAMAN, D. R. and HILLS, L. V. 1992. Upper Devonian and Lower Carboniferous miospores, Western District of MacKenzie and Yukon Territory, Canada. *Palaeontographica Canadiana*, **8**, 1–97.
- BREUER, P. 2008. *Devonian Miospore Palynology in Western Gondwana: an application to oil exploration*. PhD thesis. Université de Liège, 734 pp.
- and GRAHN, Y. 2011. Middle Devonian spore stratigraphy in the eastern outcrop belt of the Parnaíba Basin, northeastern Brazil. *Revista Española de Micropaleontología*, **43**, 1–21.
- and STEEMANS, P. 2013. Devonian spore assemblages from northwestern Gondwana: taxonomy and biostratigraphy. *Special Papers in Palaeontology*, **89**, 1–163.
- AL-GHAZI, A., AL-RUWAILI, M., HIGGS, K. T., STEEMANS, P. and WELLMAN, C. H. 2007. Early to Middle Devonian miospores from northern Saudi Arabia. *Revue de Micropaléontologie*, **50**, 27–57.
- MILLER, M. A., LESZCZYŃSKI, S. and STEEMANS, P. 2015. Climate-controlled palynofacies and miospore stratigraphy of the Jauf Formation, Lower Devonian, northern Saudi Arabia. *Review of Palaeobotany & Palynology*, **212**, 187–213.
- BRICE, D., BULTYNCK, P., DEUNFF, J., LOBOZIAK, S. and STREEL, M. 1979. Données biostratigraphiques nouvelles sur le Givetien et le Frasnien de Ferques (Boulonnais, France). *Annales de la Société Géologique du Nord*, **98**, 325–344.
- CHIBRIKOVA, E. V. 1959. Spory iz Devonskikh; Boleye Drevnikh otlozheni Bashkirii. *Bashkirskii Filnal, Institut Geologii, Akademiya Nauk SSR*, 3–116.
- and OLLI, V. A. 1992. Eifelskie otlozheniya Peredovogo Khehta Severnogo Kavkaza. *Sovetskaya Geologiya*, **3**, 45–50.
- CLAYTON, G. and GRAHAM, J. R. 1974. Miospore assemblages from the Devonian Sherkin Formation of southwest County Cork, Republic of Ireland. *Pollen et Spores*, **16**, 565–588.
- CRAMER, F. H. 1966. Palynology of Silurian and Devonian rocks in Northwest Spain. *Boletín del Instituto Geológico y Minero de España*, **77**, 223–286.
- 1969. Plant spores from the Eifelian to Givetian Gosseletia Sandstone Formation near Candás, Asturias, Spain. *Pollen et Spores*, **11**, 425–447.
- EBLE, C. F. 1996. Lower and lower Middle Pennsylvanian coal palynofloras, southwestern Virginia. *International Journal of Coal Geology*, **31**, 67–113.
- EDALAT, B. 1974. Sporenvergesellschaftungen und Acritarchen aus dem Unterdevon (Ems) des südlichen Bergischen Landes (Rheinisches Schiefergebirge). *Kölner Geologische Hefte*, **24**, 1–75.
- FOMBELLA BLANCO, M. A. 1988. Miosporas de la formación Huergas, edad Devónico medio, Provincia de León, NO. de España. *Acta Salmanticensia: Biblioteca de las Ciencias*, **65**, 299–305.
- FRIEND, P. F., ALEXANDER-MARRACK, P. D., ALLEN, K. C., NICHOLSON, J. and YEATS, A. K. 1983. Devonian Sediments of East Greenland: review of results. VI. *Meddelelser om Grønland*, **206**, 1–96.
- GARCÍA-ALCALDE, J. L. 1998. Devonian events in northern Spain. *Newsletters on Stratigraphy*, **36**, 157–175.
- CARLS, P., ALONSO, M. V. P., LÓPEZ, J. S., SOTO, F., TRUYÓLS-MASSONI, M. and VALENZUELA-RÍOS, J. I. 2002. Devonian. 67–91. In GIBBONS, W. and MORENO, T. (eds). *The geology of Spain*. The Geological Society, London.
- GARCÍA-LÓPEZ, S. and SANZ-LÓPEZ, J. 2002. Devonian to Lower Carboniferous conodont biostratigraphy of the Bernesga Valley section (Cantabrian Zone, NW Spain). 163–205. In GARCÍA-LÓPEZ, S. and BASTIDA, F. (eds). *Palaeozoic conodonts from northern Spain: 8th international conodont symposium held in Europe*. Publicaciones del Instituto Geológico y Minero de España, Madrid.
- — and SARMIENTO G. N. 2002. The Palaeozoic succession and conodont biostratigraphy of the section between Cape Peñas and Cape Torres (Cantabrian coast, NW Spain). 125–161. In GARCÍA-LÓPEZ, S. and BASTIDA, F. (eds). *Palaeozoic conodonts from northern Spain: eighth International Conodont Symposium Held in Europe*. Publicaciones del Instituto Geológico y Minero de España, Madrid.
- GARCÍA-RAMOS, J. C. 1978. Estudio e interpretación de las principales facies sedimentarias comprendidas en las Formaciones Naranco y Huergas (Devónico medio) en la Cordillera Cantábrica. *Trabajos de Geología*, **10**, 195–266.
- GENNETT, J. A. and RAVN, R. L. 1993. Palynology of the Upper Pennsylvanian Dalton Coal, Palo Pinto County, Texas, U.S.A. *Palynology*, **17**, 115–122.
- GHAVIDEL-SYOOKI, M. 1994. Biostratigraphy and paleobiogeography of some Paleozoic rocks at Zagros and Alborz Mountains. *Geological Survey of Iran. Treatise on the Geology of Iran*, **18**, 1–168.
- 2003. Palynostratigraphy of Devonian sediments in the Zagros Basin, southern Iran. *Review of Palaeobotany & Palynology*, **127**, 241–268.
- GREY, K. 1991. A mid-Givetian miospore age for the onset of reef development on the Lennard Shelf, Canning Basin,

- Western Australia. *Review of Palaeobotany & Palynology*, **68**, 37–48.
- HASHEMI, H. and PLAYFORD, G. 2005. Devonian spore assemblages of the Adavale Basin, Queensland (Australia): descriptive systematics and stratigraphic significance. *Revista Española de Micropaleontología*, **37**, 317–417.
- LE HÉRISSÉ, A. 1983. Les spores du Dévonien inférieur du Synclinorium de Laval (Massif Armoricain). *Palaeontographica Abteilung B Paläophytologie*, **188**, 1–81.
- HOFFMEISTER, W. S. 1959. Lower Silurian plant spores from Libya. *Micropaleontology*, **5**, 331–334.
- STAPLIN, F. L. and MALLOY, R. E. 1955. Mississippian plant spores from the Hardinsburg formation of Illinois and Kentucky. *Journal of Paleontology*, **29**, 372–399.
- HOUSE, M. R. 1996. The middle Devonian Kačák event. *Proceedings of the Ussher Society*, **9**, 79–84.
- 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **181**, 5–25.
- HUGHES, N. F. and PLAYFORD, G. 1961. Palynological reconnaissance of the lower Carboniferous of Spitsbergen. *Micropaleontology*, **7**, 27–44.
- IBRAHIM, A. C. 1933. *Sporenformen des Ägirhorizontes des Ruhrreviers*. Dissertation. Universität Berlin, 46 pp.
- ISHCHENKO, A. M. 1952. *Atlas mikrospor i pyl'tsy Srednego Karbona Zapadno y Chasti Donets Kogo Basseyina*. Trudy Instituta Geologicheskikh, Akademiyi Nauk Ukrainskoy SSR, Kiev.
- KNOX, E. M. 1950. The spores of *Lycopodium*, *Phylloglossum*, *Selaginella* and *Isoetes*, and their value in the study of microfossils of Paleozoic age. *Transactions of the Botanical Society of Edinburgh*, **35**, 209–357.
- LANNINGER, E.-P. 1968. Sporen-Gesellschaften aus dem Ems der SW-Eifel (Rheinisches Schiefergebirge). *Palaeontographica Abteilung B Paläophytologie*, **122**, 95–170.
- LELE, K. M. and STREEL, M. 1969. Middle Devonian (Givetian) plant microfossils from Goé (Belgium). *Annales de la Société Géologique de Belgique*, **92**, 89–121.
- and WALTON, J. 1962. Fossil flora of the Drybrook Sandstone in the Forest of Dean, Gloucestershire. *British Museum (Natural History) Geology, Bulletin*, **7**, 137–152.
- LESSUISE, A., STREEL, M. and VANGUESTAINE, M. 1979. Observations palynologiques dans le Couvinien (Emsien terminal et Eifelien) du bord oriental du Synclinorium de Dinant, Belgique. *Annales de la Société Géologique de Belgique*, **102**, 325–355.
- LOBOZIAK, S. and MELO, J. H. G. 2002. Devonian miospore successions of Western Gondwana: update and correlation with Southern Euramerican miospore zones. *Review of Palaeobotany & Palynology*, **121**, 133–148.
- and STREEL, M. 1980. Miospores in Givetian to Lower Frasnian sediments dated by conodonts from the Boulonnais, France. *Review of Palaeobotany & Palynology*, **29**, 285–299.
- 1988. Synthèse palynostratigraphique de l'intervalle Givétien-Famennien du Boulonnais (France). *Biostratigraphie du Paléozoïque*, **7**, 71–77.
- 1989. Middle-Upper Devonian miospores from the Ghadamis Basin (Tunisia-Libya): systematics and stratigraphy. *Review of Palaeobotany & Palynology*, **58**, 173–196.
- — and VANGUESTAINE M. 1983. Spores et acritarches de la Formation d'Hydrequent (Frasnien supérieur à Famennien inférieur, Boulonnais, France). *Annales de la Société Géologique de Belgique*, **106**, 173–183.
- — and BURJACK M. I. A. 1988. Miospores du Dévonien Moyen et Supérieur du bassin du Parana, Brésil: systématique et stratigraphie. *Sciences Géologiques, Bulletin*, **41**, 351–377.
- — and WEDDIGE K. 1991. Miospores, the *lemurata* and *triangulatus* levels and their faunal indices near the Eifelian/Givetian boundary in the Eifel (F.R.G.). *Annales de la Société Géologique de Belgique*, **113**, 299–313.
- — CAPUTO, M. V. and MELO, J. H. G. 1992. Middle Devonian to Lower Carboniferous spore stratigraphy in the Central Parnaíba Basin (Brazil). *Annales de la Société Géologique de Belgique*, **115**, 215–226.
- — and MELO J. H. G. 1999. *Grandispora* (al. *Contagisporites*) *permulta* (Daemon, 1974) Loboziak, Streel et Melo, comb. nov., a senior synonym of *Grandispora riegelii* Loboziak et Streel, 1989 – nomenclature and stratigraphic distribution. *Review of Palaeobotany & Palynology*, **106**, 97–102.
- LUBER, A. A. and WALTZ, I. E. 1938. Classification and stratigraphic value of spores of some Carboniferous coal deposits in the U.S.S.R. *Trudy Tsentral'nogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta*, **105**, 1–43.
- MARSHALL, J. E. A. 1988. Devonian miospores from Papa Stour, Shetland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **79**, 13–18.
- 1996. *Rhabdosporites langii*, *Geminispora lemurata* and *Contagisporites optivus*: an origin for heterospory within the progymnosperms. *Review of Palaeobotany & Palynology*, **93**, 159–189.
- 2016. Palynological calibration of Devonian events at near-polar palaeolatitudes in the Falkland Islands, South Atlantic. *Geological Society, London, Special Publications*, **423**, 25–44.
- and ALLEN, K. C. 1982. Devonian miospore assemblages from Fair Isle, Shetland. *Palaeontology*, **25**, 277–312.
- ASTIN, T. R., BROWN, J. F., MARK-KURIK, E. and LAZAUSKIENE, J. 2007. Recognizing the Kačák Event in the Devonian terrestrial environment and its implications for understanding land-sea interactions. *Geological Society, London, Special Publications*, **278**, 133–155.
- MASSA, D. and MOREAU-BENOIT, A. 1976. Essai de synthèse stratigraphique et palynologique du système dévonien en Lybie occidentale. *Revue de L'Institut Français du Pétrole*, **31**, 287–334.
- MATTHEWS, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, **16** (4), 713–719.
- MCGREGOR, D. C. 1960. Devonian spores from Melville Island, Canadian Arctic Archipelago. *Palaeontology*, **3**, 26–44.
- 1961. Spores with proximal radial pattern from the Devonian of Canada. *Bulletin of the Geological Survey of Canada*, **76**, 1–11.
- 1964. Devonian miospores from the Ghost River formation, Alberta. *Geological Survey of Canada, Bulletin*, **109**, 1–31.
- 1973. Lower and Middle Devonian spores of Eastern Gaspé, Canada. I. Systematics. *Palaeontographica Abteilung B Paläophytologie*, **142**, 1–77.

- 1984. Late Silurian and Devonian spores from Bolivia. *Academia Nacional de Ciencias, Córdoba, Argentina, Miscelánea*, **67**, 1–43.
- and CAMFIELD, M. 1976. Upper Silurian? to Middle Devonian spores of the Moose River Basin, Ontario. *Geological Survey of Canada, Bulletin*, **263**, 1–63.
- — 1982. Middle Devonian miospores from the Cape de Bray, Weatherall, and Hecla Bay formations of northeastern Melville Island, Canadian Arctic. *Geological Survey of Canada, Bulletin*, **348**, 1–105.
- and OWENS, B. 1966. Devonian spores of eastern and northern Canada. *Geological Survey of Canada, Paper*, **66**, 1–66.
- and UYENO, T. T. 1972. Devonian spores and conodonts of Melville and Bathurst Islands, District of Franklin. *Geological Survey of Canada, Paper*, **71**, 1–37.
- MELO, J. H. G. and LOBOZIAK, S. 2003. Devonian-Early Carboniferous miospore biostratigraphy of the Amazon Basin, Northern Brazil. *Review of Palaeobotany & Palynology*, **124**, 131–202.
- MENDLOWICZ MAULLER, P., MACHADO CARDOSO, T. R., PEREIRA, T. R. and STEEMANS, P. 2007. Resultados Palinoestratigráficos do Devoniano da Sub-bacia de Alto Garças (Bacia do Paraná-Brasil). 607–619. In CARVALHO, I. S., CASSAB, R. C. T., SCHWANKE, C., CARVALHO, M. A., FERNANDES, A. C. S., RODRIGUES, M. A. C., CARVALHO, M. S. S., ARAI, M. and OLIVEIRA, M. E. Q. (eds). *Paleontologia: Cenários de Vida*, Vol. 2, Interciência, Rio de Janeiro. 632 pp.
- MINER, E. L. 1935. Paleobotanical examinations of cretaceous and tertiary coals. *The American Midland Naturalist*, **16**, 585–628.
- MOREAU-BENOIT, A. 1979. Les spores du Dévonien de Libye. Première partie. *Cahiers de Micropaléontologie*, **4**, 1–58.
- 1980. Les spores du Dévonien de Libye. Deuxième partie. *Cahiers de Micropaléontologie*, **1**, 1–53.
- 1989. Les spores du Dévonien moyen et supérieur de Libye occidentale: compléments-système-répartition stratigraphique. *Cahiers de Micropaléontologie*, **4**, 1–32.
- 1994. Les spores des Grès de Landevennec, dans la coupe de Lanvéoc, Lochkovien du Massif Armoricaïn, France. *Revue de Micropaléontologie*, **37**, 75–93.
- and MASSA, D. 1988. Palynologie et stratigraphie d'une Coupe-Type du Devonien Inferieur au Sahara Oriental (Bassin de Rhadames, Libye). *Comptes Rendus de l'Académie des Sciences, Série II*, **306**, 451–454.
- COQUEL, R. and LATRÈCHE, S. 1993. Étude palynologique du Dévonien du bassin d'Ilizi (Sahara Oriental Algérien). Approche Biostratigraphique. *Geobios*, **26**, 3–31.
- NAUMOVA, S. N. 1953. Spore-pollen assemblages of the Upper Devonian of the Russian Platform and their stratigraphic value. *Akademiya Nauk SSSR, Institut Geologii Nauk*, **143**, 204 pp. [In Russian]
- NAYLOR, D., HIGGS, K. T. and BOLAND, M. A. 1977. Stratigraphy on the North Flank of the Dunmanus Syncline, west Cork. *Geological Survey of Ireland, Bulletin*, **2**, 143–157.
- NEVES, R. and OWENS, B. 1966. Some Namurian camerate miospores from the English Pennines. *Pollen et Spores*, **8**, 337–360.
- OTTONE, G. E. 1996. Devonian palynomorphs from the Los Monos formation, Tarija Basin, Argentina. *Palynology*, **20**, 105–155.
- OWENS, B. 1971. Miospores from the Middle and Early Upper Devonian rocks of the western Queen Elizabeth Islands, Arctic Archipelago. *Geological Survey of Canada, Paper*, **70–38**, 1–157.
- PARIS, F., RICHARDSON, J. B., RIEGEL, W., STREEL, M. and VANGUESTAINE, M. 1985. Devonian (Emsian-Famennian) palynomorphs. *Journal of Micropalaeontology*, **4**, 49–82.
- PEPPERS, R. A. 1993. Correlation of the 'Boskydell Sandstone' and other sandstone containing marine fossils in Southern Illinois using palynology of adjacent coal beds. *Illinois State Geological Survey, Circular*, **553**, 1–18.
- PEREZ-LEYTON, M. 1990. Miospores du Dévonien Moyen et supérieur de la coupe de Bermejo-La Angostura (Sud-Est de la Bolivie). *Annales de la Société Géologique de Belgique*, **113**, 373–389.
- PFLUG, H. D. and PRÖSSL, K. F. 1991. Palynostratigraphical and paleobotanical studies in the pilot hole of the German continental deep drilling program; results and implications. *Scientific Drilling*, **2**, 13–33.
- PLAYFORD, G. 1963. Lower Carboniferous microfloras of Spitsbergen. Part Two. *Palaeontology*, **5**, 619–678.
- 1971. Lower Carboniferous spores from the Bonaparte Gulf Basin, Western Australia and Northern Territory. *Bureau of Mineral Resources, Geology & Geophysics, Bulletin*, **115**, 1–102.
- 1983. The Devonian miospore genus *Geminospora* Balme 1962: a reappraisal based upon topotypic *G. lemurata* (type species). *Memoirs of the Association of Australasian Palaeontologists*, **1**, 311–325.
- and MCGREGOR, D. C. 1993. Miospores and organic-walled microphytoplankton of Devonian-Carboniferous boundary beds, (Bakken Formation), southern Saskatchewan: a systematic and stratigraphic appraisal. *Geological Survey of Canada, Bulletin*, **445**, 1–107.
- POTONIÉ, R. 1956. Synopsis der Gattungen der Sporae Dispersae. Teil 1: Sporites. *Beihefte zum Geologischen Jahrbuch*, **23**, 1–103.
- and KREMP, G. 1954. Die Gattungen der paläozoischen Sporae dispersae und ihre Stratigraphie. *Geologisches Jahrbuch*, **69**, 111–194.
- — 1955. Die Sporae Dispersae des Ruhrkarbons, ihre Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte. *Palaeontographica Abteilung B Paläophytologie*, **98**, 1–136.
- — 1956. Die Sporae Dispersae des Ruhrkarbons, ihre Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte. Teil III. *Palaeontographica Abteilung B Paläophytologie*, **100**, 65–121.
- RAHMANI-ANTARI, K. and LACHKAR, G. 2001. Contribution à l'étude biostratigraphique du Dévonien et du Carbonifère de la plate-forme marocaine. Datation et corrélations. *Revue de Micropaléontologie*, **44**, 159–183.
- RAVN, R. L. 1986. Palynostratigraphy of the Lower and Middle Pennsylvanian Coals of Iowa. *Iowa Geological Survey, Technical Paper*, **7**, 1–244.

- and BENSON, D. G. 1988. Devonian miospores and reworked acritarchs from Southeastern Georgia, U.S.A. *Palynology*, **12**, 179–200.
- RICHARDSON, J. B. 1960. Spores from the Middle Old Red Sandstone of Cromarty, Scotland. *Palaeontology*, **3**, 45–63.
- 1965. Middle Old Red Sandstone spore assemblages from the Orcadian basin, north-east Scotland. *Palaeontology*, **7**, 559–605.
- and LISTER, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology*, **12**, 201–252.
- and MCGREGOR, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geological Survey of Canada, Bulletin*, **364**, 1–79.
- BONAMO, P. M. and MCGREGOR, D. C. 1993. The spores of *Leclercqia* and the dispersed spore morphon *Acinosporites lindlarensis* Riegel: a case of gradualistic evolution. *Bulletin of the Natural History Museum Geology Series*, **49**, 121–155.
- RIDING, J. B., POUND, M. J., HILL, T. C. B., STUKINS, S. and FEIST-BURKHARDT, S. 2012. The John Williams Index of Palaeopalynology. *Palynology*, **36**, 224–233.
- RIEGEL, W. 1968. Die Mitteldevon-Flora von Lindlar (Rheinland) 2. Sporae dispersae. *Palaeontographica Abteilung B*, **123**, 76–96.
- 1973. Sporenformen aus dem Heisdorf-, Lauch- und Nohn-Schichten (Emsium und Eifelium) der Eifel, Rheinland. *Palaeontographica Abteilung B Paläophytologie*, **142**, 78–104.
- 1975. *Die dispersen Sporen der Ems-, Eifel- und Givet-Stufe der Eifel (Rheinisches Schiefergebirge) und ihre stratigraphische und Paläofloristische Bedeutung*. Habilitation thesis. Universität Göttingen, 282 pp.
- 1982. Palynological aspects of the Lower/Middle Devonian transition in the Eifel region. *Courier Forschungsinstitut Senckenberg*, **55**, 279–292.
- RODRÍGUEZ, R. M. 1978. Mioesporas de la Formación San Pedro/Furada (Silúrico Superior-Devónico Inferior), Cordillera Cantábrica, NO de España. *Palinología, Número Extraordinario*, **1**, 407–433.
- 1983. *Palinología de las Formaciones del Silúrico Superior-Devónico Inferior de la Cordillera Cantábrica, Noroeste de España*. Institución Fray Bernardino de Sahagún de la Excelentísima Diputación Provincial de León y del Servicio de Publicaciones de la Universidad de León.
- RUBINSTEIN, C., MELO, J. H. G. and STEEMANS, P. 2005. Lochkovian (earliest Devonian) miospores from the Solimões Basin, northwestern Brazil. *Review of Palaeobotany & Palynology*, **133**, 91–113.
- SCHRANK, E. 1987. Palaeozoic and Mesozoic palynomorphs from northeast Africa (Egypt and Sudan) with special reference to Late Cretaceous pollen and dinoflagellates. *Berliner Geowissenschaftliche Abhandlungen. Reihe A, Geologie und Paläontologie*, **75**, 249–310.
- SCHULTZ, G. 1968. Eine unterdevonische Mikroflora aus den Klerfer Schichten der Eifel (Rheinisches Schiefergebirge). *Palaeontographica Abteilung B Paläophytologie*, **123**, 5–42.
- SLEEMAN, A. G., REILLY, T. A. and HIGGS, K. T. 1978. Preliminary stratigraphy and palynology of five sections through the Old Head Sandstone and Kinsale Formations, (Upper Devonian-Lower Carboniferous), on the west side of Cork Harbour. *Geological Survey of Ireland, Bulletin*, **2**, 167–186.
- SMITH, A. H. V. 1971. Le genre *Verrucosiporites* Ibrahim 1933 emend. 35–87. In POTONIE, R. and ALPERN, B. (eds). *Microfossiles organiques du Paléozoïque. Vol. 4: Les spores*. Commission Internationale de Microflore Du Paléozoïque Éditions du Centre National de la Recherche Scientifique, Paris.
- STEEMANS, P. 1989. Etude palynostratigraphique du Dévonien inférieur dans l'Ouest de l'Europe. *Service Géologique de Belgique, Mémoires pour servir à l'Explication des Cartes Géologiques et Minières de la Belgique*, **27**, 1–453.
- DEBBAUT, V. and FABER, A. 2000. Preliminary survey of the palynological content of the Lower Devonian in the Oesling, Luxembourg. *Bulletin de la Société des Naturalistes Luxembourgeois*, **100**, 171–186.
- STOCKMARR, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores*, **13**, 615–621.
- STREEL, M. 1964. Une association de spores du Givétien inférieur de la Vesdre, à Goé (Belgique). *Annales de la Société Géologique de Belgique*, **87**, 1–30.
- 1967. Associations de spores du Dévonien inférieur belge et leur signification stratigraphique. *Annales de la Société Géologique de Belgique*, **90**, 11–53.
- HIGGS, K., LOBOZIAK, S., RIEGEL, W. and STEEMANS, P. 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne-Rhenish regions. *Review of Palaeobotany & Palynology*, **50**, 211–229.
- PARIS, F., RIEGEL, W. and VANGUESTAINE, M. 1988. Acritarch, chitinozoan and spore stratigraphy from the Middle and Late Devonian of northeast Libya. 111–128. In EL ARNAUTI, A., OWENS, B. and THUSU, B. (eds). *Sub-surface palynostratigraphy of Northeast Libya*. Garyounis University Publications, Benghazi.
- TAYLOR, W. A., GENSEL, P. G. and WELLMAN, C. H. 2011. Wall ultrastructure in three species of the dispersed spore *Emphanisporites* from the Early Devonian. *Review of Palaeobotany & Palynology*, **163**, 264–280.
- THOMSON, P. W. and PFLUG, H. D. 1953. Pollen und Sporen des Mitteleuropäischen Tertiärs. *Palaeontographica Abteilung B Paläophytologie*, **94**, 1–138.
- TIWARI, R. S. and SCHAARSCHMIDT, F. 1975. Palynological studies in the Lower and Middle Devonian of the Prüm Syncline, Eifel (Germany). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **534**, 1–129.
- TORSVIK, T. H. and COCKS, L. R. M. 2013. Gondwana from top to base in space and time. *Gondwana Research*, **24**, 999–1030.
- TRAVERSE, A. 2008. *Paleopalynology*. Springer.
- and SCHUYLER, A. 1994. Palynostratigraphy of the Catskill and part of the Chemung Magnafacies, Southern New York State, USA. *Courier Forschungsinstitut Senckenberg*, **169**, 261–274.

- TROTH, I., MARSHALL, J. E. A., RACEY, A. and BECKER, R. T. 2011. Devonian sea-level change in Bolivia: a high palaeolatitude biostratigraphical calibration of the global sea-level curve. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **304**, 3–20.
- TURNAU, E. 1986. Lower to Middle Devonian spores from the vicinity of Pionki (Central Poland). *Review of Palaeobotany & Palynology*, **46**, 311–354.
- 1996. Miospore stratigraphy of Middle Devonian deposits from Western Pomerania. *Review of Palaeobotany & Palynology*, **93**, 107–125.
- and JAKUBOWSKA, L. 1989. Early Devonian miospores and age of the Zwolen Formation (Old Red Sandstone facies) from Ciepielów IG-1 borehole. *Annales Societatis Geologorum Poloniae*, **59**, 391–416.
- and NARKIEWICZ, K. 2011. Biostratigraphical correlation of spore and conodont zonations within Givetian and ? Frasnian of the Lublin area (SE Poland). *Review of Palaeobotany & Palynology*, **164**, 30–38.
- and RACKI, G. 1999. Givetian palynostratigraphy and palynofacies: new data from the Bodzentyn Syncline (Holy Cross Mountains, central Poland). *Review of Palaeobotany & Palynology*, **106**, 237–271.
- URBAN, J. B. 1968. Palynologic studies of the Devonian. *Southwest Center for Advanced Studies, Annual Report. Geoscience Division*, **1967–1968**, 42–46.
- VENKATACHALA, B. S., BEJU, D. and KAR, R. K. 1968. Devonian microfossils from the Calarasi Zone of the Moesian Platform, Rumania. *The Palaeobotanist*, **17**, 65–67.
- WELLMAN, C. H. 2002. Morphology and wall ultrastructure in Devonian spores with bifurcate-tipped processes. *International Journal of Plant Sciences*, **163**, 451–474.
- 2009. Ultrastructure of dispersed and *in situ* specimens of the Devonian spore *Rhabdosporites langii*: evidence for the evolutionary relationships of progymnosperms. *Palaeontology*, **52**, 139–167.
- WILLARD, D. A. 1992. Early Virgilian palynofloras from the Kinney Quarry, Manzanita Mountains, New Mexico. *New Mexico Bureau of Mines & Mineral Resources, Bulletin*, **138**, 49–60.
- XU, H.-H., MARSHALL, J. E. A., WANG, Y., ZHU, H.-C., BERRY, C. M. and WELLMAN, C. H. 2014. Devonian spores from an intra-oceanic volcanic arc, West Junggar (Xinjiang, China) and the palaeogeographical significance of the associated fossil plant beds. *Review of Palaeobotany & Palynology*, **206**, 10–22.