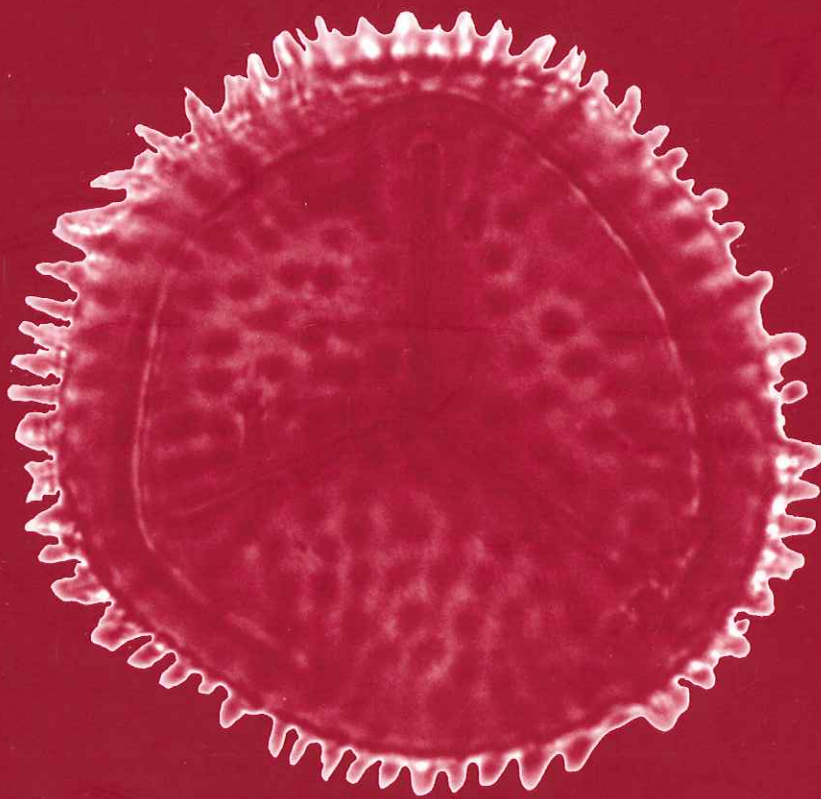


Devonian spore assemblages from northwestern Gondwana: taxonomy and biostratigraphy

by PIERRE BREUER *and* PHILIPPE STEEMANS



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Cover: The *Cymbasporites wellmanii* sp. nov., which occurs in the Sha'iba Member, Jauf Formation, Saudi Arabia.

SPECIAL PAPERS IN PALAEOLOGY NO. 89

DEVONIAN SPORE ASSEMBLAGES FROM NORTHWESTERN
GONDWANA: TAXONOMY AND BIOSTRATIGRAPHY

BY
PIERRE BREUER *and* PHILIPPE STEEMANS

with 56 figures and 1 table

THE PALAEOLOGICAL ASSOCIATION
LONDON

April 2013

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Abstract: Devonian spores from 16 subsurface successions in Saudi Arabia and North Africa are systematically documented to characterize assemblages for the northern margin of western Gondwana. The taxonomic study provides the identification and description for 205 spore taxa and forms the basis for a refined biostratigraphy and palaeogeography. Most species are illustrated by multiple specimens to document morphological variation and the effects of taphonomy. Numerous species have considerable morphological variability and require examination of larger populations to become fully understood. These spores show intergrading morphological variation and were grouped into morphons. Although a majority of spore species were previously described, many others are new and endemic to north-western Gondwana. Forty-two species (*Acinosporites tristratus*, *Alatisporites? trisacculus*, *Biornatispora elegantula*, *B. microclavata*, *Brochotriletes crameri*, *B. tenellus*, *B. tripapillatus*, *Camarozonotriletes asperulus*, *Chelinospora carnosa*, *C. condensata*, *C. densa*, *C. laxa*, *C. vulgata*, *Coronaspora inornata*, *Cristatisporites streelii*, *Cymbosporites variabilis*, *C. variegatus*, *C. wellmanii*, *Cyrtospora tumida*, *Diaphanospora milleri*, *Dibolisporites tuberculatus*, *D. verecundus*, *Dictyotriletes hemeri*, *D. marshallii*,

Elenisporis gondwanensis, *Emphanisporites laticostatus*, *E. plicatus*, *Geminospora convoluta*, *Grandispora maura*, *Granulatisporites concavus*, *Hystricosporites brevispinus*, *Raistrickia commutata*, *R. jaufensis*, *Retusotriletes atratus*, *R. celatus*, *Samarisporites tunisiensis*, *Verrucosisporites nafudensis*, *V. onustus*, *V. stictus*, *Zonotriletes brevivelatus*, *Z. rotundus* and *Z. venatus*), five varieties (*Cymbosporites stellospinosus* var. *minor*, *C. variabilis* vars *variabilis*, *densus* and *dispersus*, and *Dictyotriletes biornatus* var. *murinatus*) and seven combinations (*Ambitisporites asturicus*, *Camarozonotriletes retiformis*, *Cristatisporites reticulatus*, *Cymbosporites ocularis*, *Dibolisporites gaspiensis*, *Grandispora stolidota* and *Jhariatriletes emsiensis*) are newly proposed. As the reference spore zones usually used and defined in Euramerica are not all recognized in the Gondwanan coeval sections, a new biostratigraphical scheme based on the own characteristics of the spore assemblages described here is proposed. It consists of nine assemblage zones, nine interval zones and one acme zone spanning from the upper Pragian to lower Frasnian.

Key words: Trilete spores, cryptospores, taxonomy, biostratigraphy, Devonian, Gondwana.

THE Devonian palynology of the Arabian Plate remains incompletely known despite recent significant studies (Loboziak and Streel 1995b; Steemans 1995; Al-Hajri *et al.* 1999; Al-Hajri and Owens 2000; Loboziak 2000; Al-Ghazi 2007; Breuer *et al.* 2007c). To further document north-western Gondwanan assemblages, palynological samples from two additional boreholes from North Africa (Libya and Tunisia) were re-examined to compare with the Saudi Arabian Devonian succession (Fig. 1). The palynology of these sections was first examined by Loboziak and Streel (1989), Streel *et al.* (1990) and Loboziak *et al.* (1992a), but additional study, in the light of results from Saudi Arabian material, allows a more detailed understanding of Devonian palynology including endemic species, from the northern margin of western Gondwana.

The palynostratigraphic studies of Gondwanan spores rely mainly on biostratigraphical zonations established for Euramerica (Richardson and McGregor 1986; Streel *et al.* 1987). Endemic species, which are not useful for intercontinental correlations, were not incorporated in their zonations, but can be of a great utility for refined local

and regional biozonations. It is essential to develop a biostratigraphical zonation combining endemic spores for the local correlations and more cosmopolitan species for interregional biostratigraphy. A new biozonation based on the own characteristics of the spore assemblages described here is thus developed for more accurate local, regional and intercontinental correlations in north-western Gondwana.

GEOLOGICAL SETTING

Regional geological background

Through much of the Palaeozoic, the broad passive margin of northern Gondwana, which bordered the Rheic Ocean, included present day North Africa, Arabia, Turkey, central and north-west Iran, Afghanistan, India and some minor plates (Scotese 2000). Much of this region was intermittently covered by shallow epeiric seas that bordered lowlands, which represented the low-relief

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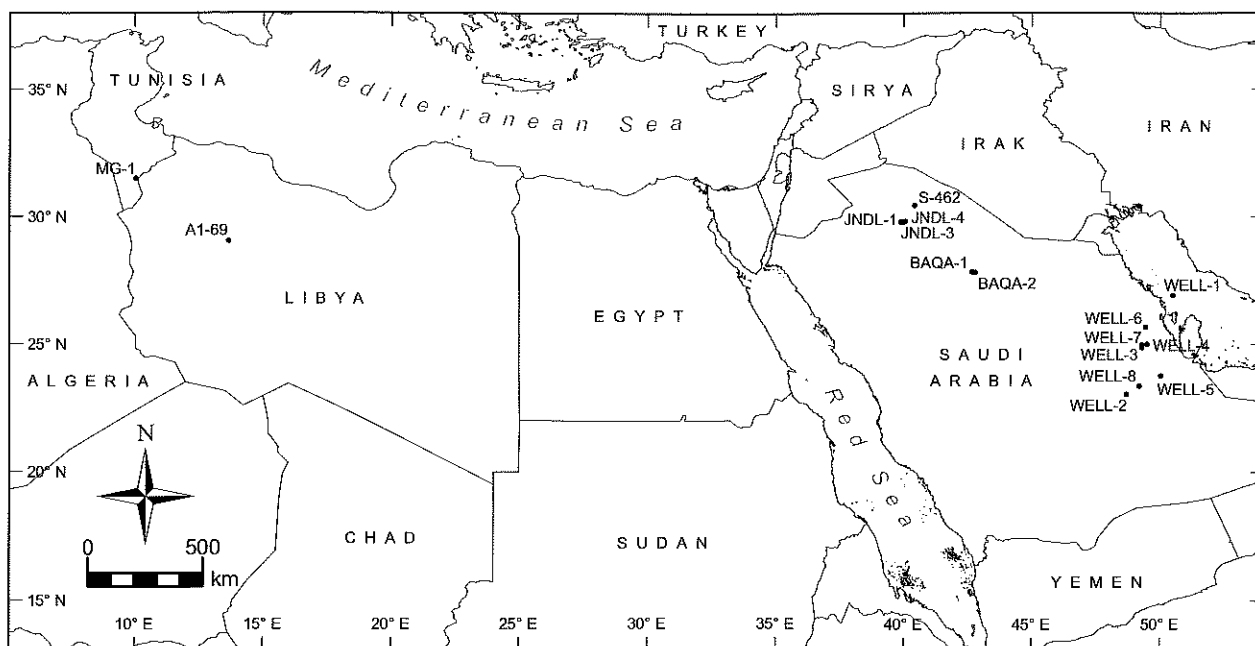


FIG. 1. Location of the studied sections.

erosion surface formed on Precambrian basement. Consequently, shallow-marine, littoral and fluvial sand, silts and muds were deposited along the margin of northern Gondwana from the end of the Neoproterozoic.

During the Devonian, the Arabian Plate lay in southern tropical latitudes (Beydoun 1991). Much of Arabia was subaerially exposed, with shallow seas extending over the remaining area. Substantial Devonian deposits accumulated, essentially as broad transgressive-regressive cycles: a Lower Devonian retrogradational cycle (fining-upward) and a progradational cycle (coarsening-upward) through much of the Middle–Upper Devonian. Thin Lower Devonian limestone intervals indicate that brief periods of limited clastic input occurred resulting in the shoreward advance of an outboard carbonate ramp in north-western Saudi Arabia (Sharland *et al.* 2001).

In North Africa, a transgressive-dominated sequence succeeded the Late Silurian hiatus with the development of a vast, regionally continuous, fluvial system notably in the Ghadames Basin, thinning to the north and locally onto intraplateau structural arches (Boote *et al.* 1998). The sediments were derived from a south-eastern source. Epeirogenic activity, reflecting the initial collision between Gondwana and Laurussia, increased in Middle to Late Devonian causing increased stratigraphical complexity. Eifelian–earliest Givetian uplift and erosion terminated the previous sequence. It was followed by a widespread marine transgression, grading up into a series of stacked depositional cycles, each strongly influenced by intraplateau highs. The Middle and Late Devonian cycles are made up of regressive, fluvial-dominated delta systems each with an

erosional upper surface, in places incised and capped by extensive transgressive marine shales, limestones and iron oolites (Boote *et al.* 1998).

Lithostratigraphy

Saudi Arabia. The Devonian strata of Saudi Arabia occur within a more or less conformable package of Upper Silurian – Lower Carboniferous deposits, which are subdivided into the Tawil, Jauf and Jubah formations (Fig. 2; Steineke *et al.* 1958; Powers *et al.* 1966; Powers 1968; Meissner *et al.* 1988). Below a regional disconformity, Silurian deposits of the underlying Qalibah Formation are present (Al-Hajri *et al.* 1999). Several regional unconformities separate the Upper Silurian – Lower Carboniferous package from higher strata: either the sub-Unayzah Unconformity (from the Permo–Carboniferous Unayzah Formation) or the sub-Khuff Unconformity (from the Middle Permian Khuff Formation), particularly on structural highs such as the Central Arabian Arch and the Ghawar structure. Current age calibrations of these deposits suggest that the sediments of the Tawil Formation, occurring directly above the disconformity, were deposited during the Ludlow (late Silurian) to early Pragian (Early Devonian; Stump *et al.* 1995; Al-Hajri and Paris 1998; Al-Hajri *et al.* 1999). Breuer *et al.* (2005b, 2007c) referred the Jauf Formation to upper Pragian – upper Emsian stages. The overlying Jubah Formation extends up into the lower Tournaisian (Al-Hajri *et al.* 1999; Clayton *et al.* 2000) where it is not removed by the

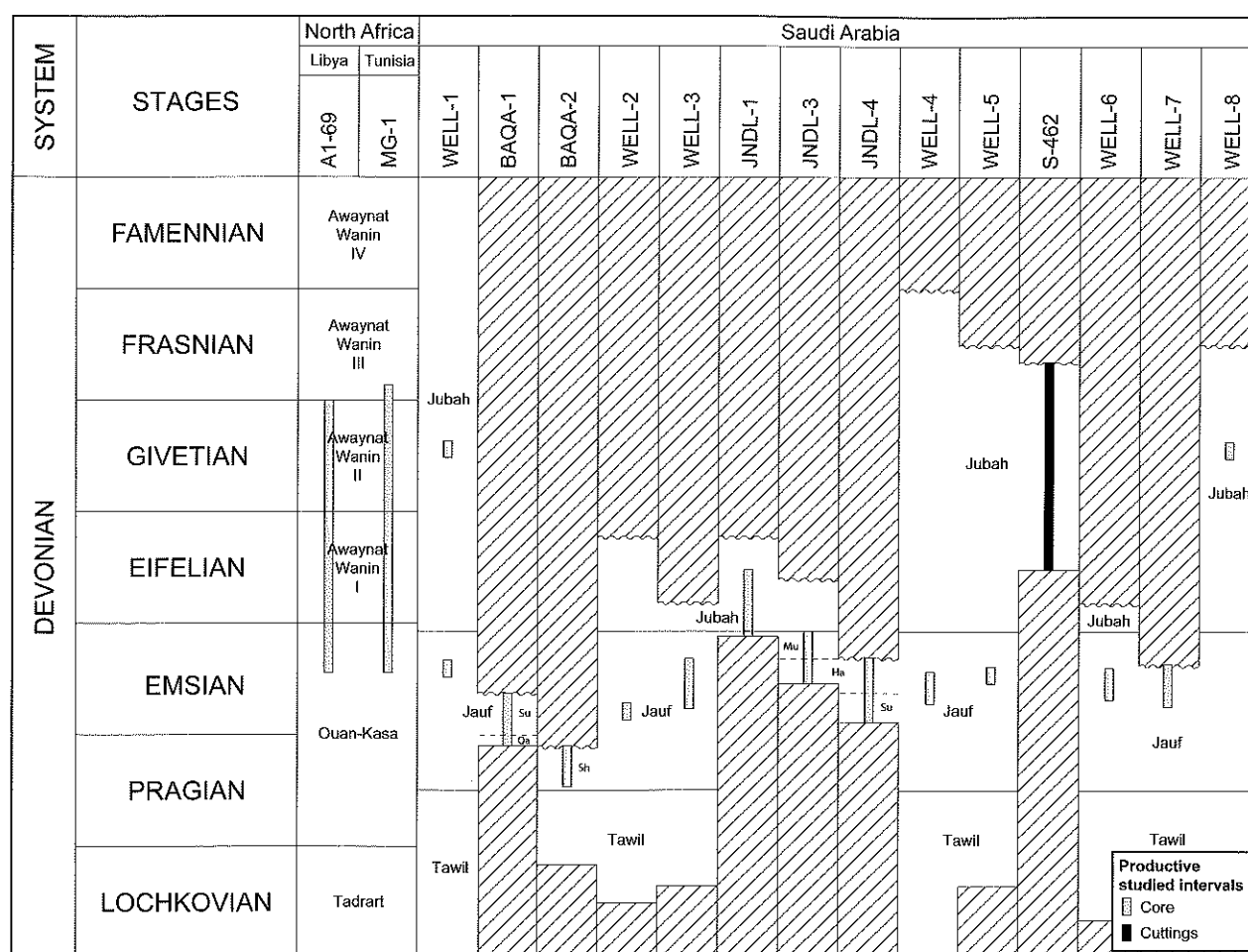


FIG. 2. Stratigraphical successions of the studied sections. Ha, Hammamiyat Member; Mu, Murayr Member; Qa, Qasr Member; Sh, Sha'iba Member; Su, Subbat Member.

Hercynian erosion. Additional biostratigraphical evidence is provided by different macrofossils groups collected at surface exposures (Boucot *et al.* 1989; Forey *et al.* 1992). Trilobites and conodonts indicate that the uppermost Sha'iba and Qasr members (lower Jauf Formation) are Pragian to lower Emsian, and brachiopods suggest that the Hammamiyat Member (upper Jauf Formation) is upper Emsian (Boucot *et al.* 1989). In Saudi Arabia, Devonian sedimentary rocks are only known to be exposed in the type outcrop area of north-western Saudi Arabia (Nafud Basin) and in the south-west (e.g. Wajid outcrop), adjacent to the exposed Precambrian Arabian Shield. Devonian deposits occur extensively in the subsurface, not only in the north-west but also in eastern Saudi Arabia.

These formations reflect, in order of succession, shifts in sedimentation from siliciclastics (Tawil Formation) to mixed siliciclastics and carbonates (Jauf Formation) and a return to siliciclastics (Jubah Formation). The Upper Silurian – lowest Carboniferous package is generally conti-

nental to near-shore shallow marine but there are regional-scale facies changes. The Jauf Formation changes from marine in north-western Saudi Arabia to marginal marine/continental in eastern, central and southern regions (Al-Hajri *et al.* 1999; Al-Hajri and Owens 2000). The alternating siliciclastics and carbonates of the Jauf Formation only in north-western Saudi Arabia are used to subdivide this formation into five members in ascending stratigraphical order: the Sha'iba, Qasr, Subbat, Hammamiyat and Murayr members. The five members constitute a conformable succession according to Wallace *et al.* (1996, 1997); their lithological descriptions and sedimentary interpretations are summarized in Al-Husseini and Matthews (2006).

North Africa. The Devonian strata present in the subsurface of Ghadames Basin occur within a more or less conformable package that is subdivided into the Tadrart, Ouan-Kasa, Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations (Fig. 2). From outcrops,

these lithological units were recently redescribed by Ben Rahuma *et al.* (2008) and interpreted in terms of sequence stratigraphy. Massa (1988) studied these formations and discussed their age assignment from numerous wells. The Tadrart and Ouan-Kasa formations are Lower Devonian according to macrofauna, although Streeel *et al.* (1990) demonstrated diachronism for these units. The Awaynat Wanin I to IV formations are considered as being Eifelian, Givetian, Frasnian and Famennian, respectively, on the basis of faunal assemblages (Fig. 2). The rich spore assemblages from the Ghadames Basin allowed establishing a detailed palynostratigraphic zonation (Massa and Moreau-Benoit 1976; Moreau-Benoit 1988, 1989; Loboziak and Streeel 1989; Loboziak *et al.* 1992a) and partially confirmed the age stated by Massa (1988; see below).

These lithological units are dominated by siliciclastic sediments. North-westward, along a structural dip section, correlation shows an overall thinning of the sandstone units and thickening and deepening of the shaly units. Marine limestones are mainly known along the northern flank of the Ghadames Basin. The environments of the Devonian deposits show a wide range of facies from continental, fluvial, lagoonal and intertidal to open marine facies. These deposits relate to the transgressive-dominated sequence that succeeded the uplifting and erosion of the southern flank of the basin by Caledonian tectonic activity during the Late Silurian (Boote *et al.* 1998).

REVIEW OF DEVONIAN SPORE PALYNOLOGICAL STUDIES

Saudi Arabia

Hemer and Nygreen (1967) were the first to report on Devonian spore assemblages from Saudi Arabia. These assemblages were isolated from cuttings samples of a 1341-ft-thick Devonian succession in the S-462 borehole, northern Saudi Arabia (Fig. 1), that were re-examined here. They interpreted this interval to represent a non-marine extension of the Jauf Formation present in outcrops approximately 70 km away (but which is now considered correlative with the Jubah Formation). Based on spore assemblages, they subdivided the strata into four zones, interpreted to range from Middle (probably Givetian) to Upper Devonian. Figure 3 compares and summarizes Devonian spore biozonations defined and/or applied in the different palynostratigraphic studies in Saudi Arabia.

Loboziak and Streeel (1995b) examined Devonian age cuttings from TRBH-1 borehole also in northern Saudi Arabia, with additional data from the DMMM-45 and SDGM-211 wells from eastern Saudi Arabia. Based on taxa common to Euramerica, they applied the Devonian

spore zonation developed for Western Europe by Streeel *et al.* (1987). In all three wells, they assigned the spore assemblages from the uppermost Tawil and lower Jauf formations to the Emsian. Higher in the sequence, in the Jauf Formation in DMMM-45 and the Subbat Member in TRBH-1, they recognized an upper Emsian spore assemblage. As few characteristic spore taxa occurred above this assemblage in the lower Jubah Formation, Loboziak and Streeel (1995b) considered these strata to be late Emsian – early Givetian in age. Stratigraphically above this, in TRBH-1, they assigned assemblages to Givetian biozones already known in Western Europe.

Steemans (1995) published reports of Devonian spore assemblages from cuttings in the DMMM-45 and UDYN-1 wells. In DMMM-45, the spores were recovered from the lower part of the Tawil Formation and assigned to Lochkovian–Pragian (Lower Devonian). Those recovered from the Jauf Formation were dated as Emsian. In UDYN-1, Steemans (1995) reported Lochkovian spore assemblages from the Tawil Formation and Givetian–Frasnian spore assemblages from the upper Tawil to lower Jauf formations, which are now understood to be the result from downhole caving.

Al-Hajri *et al.* (1999) published an operational palynological zonation developed by Saudi Aramco for Devonian strata of Saudi Arabia. Because it was developed for oil industry application, and based largely on cuttings samples, this zonation is based primarily on first downhole occurrences of taxa (i.e. extinctions), although it also incorporates first common downhole occurrences/co-occurrences and acme zones. The biozonation was age-calibrated based on comparisons with the established spore zonations of Richardson and McGregor (1986) and Streeel *et al.* (1987).

From the Devonian succession studied by Hemer and Nygreen (1967; see above), Loboziak (2000) described spore assemblages from Jubah Formation cuttings of S-462 over the interval 1465–2806 ft, also restudied here. The oldest assemblages were interpreted as lower lower Eifelian and the youngest upper lower Frasnian, based on comparisons with the spore biostratigraphy of Streeel *et al.* (1987).

Clayton *et al.* (2000) recognized uppermost Devonian – lowermost Carboniferous spore assemblages from the uppermost Jubah Formation in wells of eastern Saudi Arabia. In HRML-51, 'Strunian' (latest Famennian) assemblages characterized by *Retispora lepidophyta* (Kedo) Playford, 1976 were recovered. Latest Famennian and earliest Tournaisian assemblages occurred in ABSF-29 typified by common representatives of *Verruciretusispora famennensis* (Kedo) Massa *et al.*, 1980 and *Indotriradites explanatus* (Luber) Playford, 1991, respectively. This work clearly demonstrated that in some locations the Jubah Formation extended into the Carboniferous.

AUTHORS	Hemer and Nygreen (1967)	Loboziak and Streel (1995b)	Steemans (1995)	Al-Hajri <i>et al.</i> (1999)	Loboziak (2000)	Loboziak (2000)	Clayton <i>et al.</i> (2000)	Breuer <i>et al.</i> (2007c)	Al-Ghazi (2007)
STAGES									
FAMENNIAN				D0			<i>R. lepidophyta</i> Assemblage <i>V. famennensis</i> Assemblage		
FRASNIAN	Zone I ? Zone II ?		Frasnian - Givetian	D1					
	Zone III ?	TA			TA-BJ/BM	<i>ovalis-bulliferus</i> <i>optivus-triangulatus</i>			
GIVETIAN	Zone IV ?	AD-Lem		D2	Lem AD	<i>lemurata-magnificus</i> <i>devonicus-naumovii</i>		AD-Lem (pars)	
					Mac				
EIFELIAN		AP			AP (pars)	<i>velata-langii</i> (pars)			
				D3	A			AP-Pro (pars)	
EMSIAN		FD-Min			B			FD-Min	<i>annulatus</i> <i>sextantii</i>
		AB	AB	D3/D4				AB or FD	
PRAGIAN			Pa W PoW		A			PoW-Su	
			BZ-E	D4					
LOCHKOVIAN			MN-Si to Z MN-R		B				

FIG. 3. Chart comparing biozonation from the main studies on Devonian from Saudi Arabia.

More recently, Breuer *et al.* (2005b, 2007c) described spore assemblages and introduced new species from the Jauf and Jubah formations in five fully cored shallow core holes (BAQA-1, BAQA-2, JNDL-1, JNDL-3 and JNDL-4) from northern Saudi Arabia (Fig. 1). Based on cosmopolitan index species, the stratigraphical distribution of these new taxa was compared to the Devonian West European zonation of Streel *et al.* (1987). Although a late Pragian–Givetian age was suggested for this sequence by Breuer *et al.* (2005b, 2007c), it appears, in the light of these new results, that the top of the sequence is not younger than lower upper Eifelian. From an exploration borehole in northern Saudi Arabia, Al-Ghazi (2007) referred the partly cored Jauf Formation to the Emsian Stage by correlating with the spore zonations of Richardson and McGregor (1986) and Streel *et al.* (1987).

Finally, Marshall *et al.* (2007) described for the first time two Givetian megaspore species from the Jubah Formation quite similar to the species found in Arctic Canada. This study demonstrated that plants producing megaspores were able to achieve dispersal over a wide range.

North Africa

The most significant Devonian palynological studies of North African Palaeozoic basins are summarized herein. Figure 4 compares Devonian spore biozonations defined and/or applied in the different studies. Jardiné and Yapaudjian (1968) and Magloire (1968) first reported on spore assemblages from the Devonian of North Africa; these were from core samples of petroleum wells drilled in the Illizi (Polignac) Basin (western Algeria) and in the Bechar Basin (eastern Algeria), respectively. These authors established local biozonations based on acritarch, chitinozoan and spore assemblages in ‘Gedinnian’ (Lochkovian) to Givetian strata (Jardiné and Yapaudjian 1968) and in Lochkovian and ‘Siegenian’ (Pragian) strata (Magloire 1968). The two papers provided stratigraphical ranges and illustrations of spore species, but no formal taxonomy was proposed.

Subsequently, Massa and Moreau-Benoit (1976) published a palynological synthesis of the Devonian of the western Libyan portion of the Ghadames Basin. Samples

AUTHORS	Magloire (1968)	Jardiné and Yapaudjian (1968)	Massa and Moreau-Benoit (1976)	Streel <i>et al.</i> (1988)	Boumendjel <i>et al.</i> (1988)	Loboziak and Streel (1989)	Moreau-Benoit (1989)	Moreau-Benoit <i>et al.</i> (1993)	Rahmani-Antari and Lachkar (2001)
STAGES									
FAMENNIAN			Palynozone 11	D-VII	Assemblage 4		Palynozone 11	<i>pusillites-lepidophytus</i>	ST1
			Palynozone 10				?	<i>flexuosa-cornuta</i>	DS3
			Palynozone 9				Palynozones 9-10		DS2
FRASNIAN			Palynozone 8	D-VI		IV	Palynozone 8	<i>ovalis-bulliferus</i>	DS1
			Palynozone 7			BM			DS1
GIVETIAN		d	Palynozone 6	D-V		TCO-BJ(?)	?	<i>optivus-triangularis</i>	
			Palynozone 5			TA		<i>lemurata-magnificus (pars)</i>	DM2
EIFELIAN		c	Palynozone 4	D-IV		Lem	Palynozone 7		
				D-III		Mac	Palynozone 6		DM1
				D-II		Vel	Palynozone 5		
EMSIAN		a	Palynozone 3	D-I		Pro	Palynozone 4	<i>douglasowense-eurypterota</i>	
							Palynozone 3	<i>annulatus-sextantii</i>	DI2
							Palynozone 2		DI1
PRAGIAN	Biozone J	Zone VII	Palynozone 2		Assemblage 2		Palynozone 2		
LOCHKOVIAN	Biozone I	Zone V	Palynozone 1				Palynozone 1	?	
							Palynozone 0		

FIG. 4. Chart comparing biozonation from the main studies on Devonian from North Africa.

from numerous deep boreholes drilled during oil prospecting provided the study material. They assigned a Pragian-late Famennian age to the 11 spore assemblages that were recognized from the Tadrart Formation to the Tahara Formation. Moreau-Benoit (1979, 1980b) formally described the spore species from the 1976 synthesis. Further data about the systematics and stratigraphical distribution of Middle and Late Devonian spore species appeared later in Massa and Moreau-Benoit (1985) and Moreau-Benoit (1988, 1989). Moreau-Benoit (1989) reinterpreted the age of the biozonation previously proposed in Massa and Moreau-Benoit (1976). This synthesis, which is comprised of a series of publications by the same authors, constitutes the most important record of Devonian spores from North Africa.

Paris *et al.* (1985) presented preliminary results from a project, which illustrated all of the stratigraphically significant species encountered in a comprehensive study, on the Ordovician to Late Cretaceous palynology of north-eastern Libya. They recorded Emsian-Famennian spore assemblages from cuttings and core samples from exploration wells situated in Cyrenaica (north-eastern Libya).

This first publication gave only brief documentation of the different assemblages without presenting the stratigraphical ranges of the spores. In the final phase of this project, Streel *et al.* (1988) correlated these assemblages with the well-established Devonian Western European zonation of Streel *et al.* (1987). In addition, they proposed a recalibration of the western Libyan Palynozones 4–8 of Massa and Moreau-Benoit (1976) with emphasis on the significance of the evolutionary appearance of *Geminospora lemurata*. Palynozones 4–6 were restricted to the Eifelian by Streel *et al.* (1988). These zones were previously dated as Eifelian to upper Givetian. Palynozones 7–8, initially interpreted to be Frasnian by Massa and Moreau-Benoit (1976), were also reassigned by Streel *et al.* (1988) but to the lower Givetian.

Boumendjel *et al.* (1988) examined core samples of TRN-3 borehole drilled in the Illizi Basin. Only 'Siegenian' (Pragian) and early Givetian spore assemblages were recognized. Other data from the Illizi Basin were published on the Emsian to uppermost Famennian stratigraphical interval (Coquel and Latrèche 1989; Moreau-Benoit *et al.* 1993). Moreau-Benoit *et al.* (1993) applied the biozonation

developed by Richardson and McGregor (1986) to the spore succession from the Illizi Basin.

Loboziak and Streel (1989) systematically studied the most important species encountered in four boreholes from the Ghadames Basin. Their results were compared with the zonation of Streel *et al.* (1987). In the A1-69 borehole (Fig. 1), the first appearances of characteristic spores showed the same stratigraphical succession as in the Ardenne-Rhenish biozonation. Chronostratigraphic correlations made using this biozonation gave an Emsian to latest Frasnian age for the studied Libyan samples. From the 55 recorded species, almost 90 per cent were also found in Western Europe according to Loboziak and Streel (1989).

Streel *et al.* (1990) reviewed the relationship between spores, faunas (i.e. brachiopods and conodonts) and megaflores for the Lower and Middle Devonian in Libya. They demonstrated the diachronism of the Tadrart and Ouan-Kasa formations across the Ghadames Basin. At the northern margin of the basin, the lower part of the Tadrart Formation in MG-1 borehole (Fig. 1) is within the lowermost part of the Lochkovian, not at its base. At the southern margin, the Tadrart and Ouan-Kasa formations are probably no older than upper Emsian or possibly lower Eifelian. The Awaynat Wanin I Formation is often absent in the south or strongly reduced in thickness.

Devonian spores from the Tunisian MG-1 well on the northern margin of the Ghadames Basin were compared to available faunal data in Loboziak *et al.* (1992a). The age of the various formations drilled was revised. The authors concluded that the Emsian and the Eifelian are represented by an increased sedimentation rate, resulting in thicker sections, than present for the other stages.

Rahmani-Antari and Lachkar (2001) is the only palynological study on Devonian material from Morocco. The authors studied four wells and one outcrop section in order to document palynomorphs from the Devonian. Spores, acritarchs as well as chitinozoans allowed the subdivision of the Devonian into eight palynozones despite some stratigraphical gaps in the succession.

A most recent significant palynological study was carried out by Rubinstein and Steemans (2002). It concerned A1-61 borehole situated on the northern margin of the Ghadames Basin. The Silurian/Devonian boundary was recognized in the Tadrart Formation. Ludlow to early Lochkovian spore assemblages were described, compared and correlated with spore zonations established for the type sequences of the Welsh Borderland, and those previously described from Libya.

Finally, de Ville de Goyet *et al.* (2007) and Steemans *et al.* (2011b) studied a rich and diverse Middle Devonian megaspore assemblages from the A1-69 borehole (Fig. 1). Seventeen megaspore taxa were elaborately described, illustrated and compared to coeval Euramerican assemblages.

MATERIAL AND METHODS

Location of studied sections

The reference core holes for the Jauf-Jubah succession are located in north-western Saudi Arabia (Fig. 1). They are BAQA-1, BAQA-2, JNDL-1, JNDL-3 and JNDL-4 and S-462 borehole that in combination give a nearly complete section through the Jauf and Jubah formations (Fig. 2). The preliminary palynological results from the five core holes were published by Breuer *et al.* (2005b, 2007c). Also in the same general area is the S-462 borehole, which was previously studied by Hemer and Nygreen (1967) and then by Loboziak (2000; see above). The second study area is located in eastern Saudi Arabia and comprises cores from eight deep exploration wells (WELL-1, WELL-3, WELL-2, WELL-4, WELL-5, WELL-6, WELL-7 and WELL-8; Fig. 1). The studied intervals are also from the Jauf and Jubah formations but were not previously published (Fig. 2).

Palynology preparations from the two boreholes from the Ghadames Basin in North Africa were re-examined. A1-69 borehole was drilled on the southern flank of the basin (Libya) while MG-1 borehole is located on the northern flank in Tunisia (Fig. 1). Formations studied in ascending stratigraphical order are the Ouan-Kasa, Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations (Fig. 2). Previous Devonian palynological results of these boreholes were published in Loboziak and Streel (1989) and Loboziak *et al.* (1992a; see above).

Material

Saudi Aramco provided 440 samples from various Saudi Arabian core holes and exploration wells. Among these, 295 were fossiliferous and were used for palynological analysis. The remaining 145 were either barren or contained very few biostratigraphically significant palynomorphs. The Laboratory of Palaeontology of the University of Lille (France) provided the North African samples. Of the 96 available samples from North Africa, 84 samples yielded palynomorphs and were usable for palynological study. In total, 350 core samples and 29 cutting samples (S-462) were productive and used in this study. All samples were collected from dark-coloured, fine-grained, shaly sandstones, siltstones and shales.

Palynological processing

The samples from BAQA-1, BAQA-2, JNDL-3 and JNDL-4 were processed by the Centre for Palynology of the University of Sheffield (UK). Samples from A1-69, JNDL-1, MG-1, S-462, WELL-1, WELL-2, WELL-4,

WELL-5, WELL-6, WELL-7 and WELL-8 and most of the samples from WELL-3 were processed in the Laboratory of 'Palaeobiogeologie, Palaeobotanique et Palaeopalynologie' at the University of Liège (Belgium). Saudi Aramco processed the remainder of the WELL-3 samples and some additional samples from BAQA-1, BAQA-2, JNDL-3 and JNDL-4. New palynological slides from the residues of MG-1, dating from the previous studies (see above), were prepared for this study in Liège.

All samples were processed according to standard palynological laboratory methods (Streel 1965). Each sample was crushed, and 10–25 g were demineralized in 10 per cent HCl and 40 per cent HF. The residue of the most thermally mature samples was oxidized in 65 per cent HNO₃ and KClO₃ (Schultze solution) and sieved through a 10-µm mesh. Subsequently, a hot bath in 25 per cent HCl eliminated the remaining fine neoformed fluorided particles. The residue of all samples was sieved through a 10-µm mesh. The final residue was mounted on palynological slides using Euparal or Eukit resin. One to four slides were made for each productive sample.

Taxonomy

The term 'spore' is used throughout the following text as all propagule produced by embryophytes. They include cryptospores, monolete spores, trilete spores and megaspores. Some spore species were previously described; others are new and endemic to north-western Gondwana and consequently defined herein.

For stratigraphical correlation, it is essential to consistently identify spores; but differences between taxa may be so slight that intermediates can often be found between varieties, species or even genera, usually regarded as distinct. Many cases of intergradations are common in Devonian spores (Playford 1983; Steemans and Gerrienne 1984; Richardson *et al.* 1993; Marshall 1996; Breuer *et al.* 2005a, b, 2007a, b). The variability in spore morphology often obscures the taxonomic limits that were originally defined. The concept of the morphon was introduced by Van der Zwan (1979) to address this taxonomic issue. A morphon is defined as '...a group of species united by continuous variation of morphological characters' (Van der Zwan 1979, p. 11). The main idea of the morphon concept can be refined as follows: the apparent morphological continua may represent spore variation in a particular known or hypothetical natural plant species or group of related species. Evolutionary convergence may, however, cause morphological similarities between spores that do not necessarily reflect links between their parent plants. During Palaeozoic times, different plant groups often produced spores of similar morphology (Gensel 1980; Fanning *et al.* 1992; Wellman 2009). In contrast,

and further complicating the problem, cases where a single sporangium can produce two different genera of trilete spores were recognized (Habgood *et al.* 2002).

The present taxonomic study of large populations reveals that many defined spore species have considerable overlap in their morphologies. The morphological variations of spores can be attributed to phylogenetic evolution, ontogeny (maturation of sporangia) or taphonomic factors (Breuer *et al.* 2007a). This occurs at a time of explosive evolution of early land plant floras (Steemans *et al.* 2012). Some species show continuous morphological intergradations with other genera/species and, therefore, are grouped into morphons (Table 1). Morphons centred on the following nominal species are introduced herein: *Apiculiretusispora brandtii*, *Archaeozonotrites variabilis*, *Chelinospora vulgata*, *Cristatisporites reticulatus*, *Cymbosporites catillus*, *Diaphanospora milleri*, *Grandispora incognita*, *G. protea*, *Samarisporites eximius*, *Synorisporites papillensis* and *Verrucosisorites scurrus*. They are briefly discussed in the systematic descriptions, and Table 1 summarizes the morphological features used to characterize the morphons introduced herein. Morphons are regarded as informal groupings of taxa under the Botanical Code; their circumscribing characters and the lists of their constituent taxa are subject to emendation as work continues to further understand these and other morphologically intergrading forms.

The morphon concept is considered complementary to the typological approach of traditional binomial nomenclature in palynology. It emphasizes the similarity of the morphological characters more than the differences and integrates morphological trends, which are space and/or time dependent, but also sensitive to various environmental conditions. The morphon may facilitate the interpretation of species with similar morphological characters in terms of a more natural grouping (Breuer *et al.* 2007a). The morphological variability presented by spores may reflect intraspecific variability or biological evolution. Indeed, it may be influenced locally by other parameters such as state of preservation (e.g. *Diaphanospora milleri* Morphon), sedimentary sorting (Jäger 2004) and/or reworking of simpler and older morphotypes into assemblages containing more complex and younger ones (Breuer *et al.* 2005a).

Systematic descriptions

The spore populations of 205 rare-to-common species are described and measured in detail in this contribution. Their morphological variability is illustrated in Figures 5–52 by several specimens for each species when possible and synonymies are listed for each species. The terminology used to describe the morphology of spores is defined in Wellman and Richardson (1993), Richardson (1996) and Punt *et al.* (2007). The Erdtman's (1952) wall stratification

TABLE 1. Spore morphons and their characterizing features referred to in the text.

Morphon name	Constituent taxa	Morphological characters
<i>Apiculiretusispora brandtii</i>	<i>Apiculiretusispora brandtii</i> <i>Cymbosporites asymmetricus</i> <i>Rhabdosporites minutus</i>	Densely spaced, small coni, grana and spinae; exine partially or completely detached from nexine at the equator.
<i>Archaeozonotriletes variabilis</i>	<i>Archaeozonotriletes variabilis</i> <i>Cyrtospora tumida</i> <i>Lophozonotriletes media</i>	Patinate spores; laevigate to variably sculptured with scattered coarse, rounded protuberances and flat-topped verrucae.
<i>Chelinospora vulgata</i>	<i>Chelinospora condensata</i> <i>Chelinospora densa</i> <i>Chelinospora laxa</i> <i>Chelinospora vulgata</i>	Patinate spores; distal region sculptured with loosely distributed or brain-like convoluted muri; laesurae simple; subcircular to triangular amb.
<i>Cristatisporites reticulatus</i>	<i>Cristatisporites reticulatus</i> <i>Cristatisporites streelii</i>	Zonate spores; distal region sculptured with fold-like ridges, bearing spinae.
<i>Cymbosporites catillus</i>	<i>Cymbosporites catillus</i> <i>Cymbosporites cyathus</i>	Patinate spores; distal region sculptured with densely packed grana, coni or spinae.
<i>Dictyotriletes biornatus</i>	<i>Cymbosporites variabilis</i> var. <i>densus</i> <i>Cymbosporites variabilis</i> var. <i>dispersus</i> <i>Cymbosporites variabilis</i> var. <i>variabilis</i> <i>Dictyotriletes biornatus</i> var. <i>biornatus</i> <i>Dictyotriletes biornatus</i> var. <i>murinatus</i>	Patinate spores; distal region sculptured of coni, discrete or partly fused in elongate elements, evenly distributed to organized in a reticulum pattern; simple laesurae; subcircular to subtriangular amb.
<i>Diaphanospora milleri</i>	<i>Diaphanospora milleri</i> <i>Retusotriletes celatus</i>	Strongly folded sexine possible; dark subtriangular apical area; subcircular amb.
<i>Grandispora incognita</i>	<i>Grandispora incognita</i> <i>Grandispora naumovae</i>	Camerate spores; distal region sculptured with slender spinae with flared bases.
<i>Grandispora protea</i>	<i>Grandispora douglstownensis</i> <i>Grandispora protea</i>	Camerate spores; distal region sculptured with biform or parallel-sided spinae.
<i>Samarisporites eximius</i>	<i>Samarisporites angulatus</i> <i>Samarisporites eximius</i> <i>Samarisporites praetervisus</i>	Zonate spores; distal region sculptured with discrete spinae, sometimes arranged in rugulae; sub-circular to triangular amb.
<i>Synorisporites papillensis</i>	? <i>Knoxisporites riondae</i> <i>Synorisporites papillensis</i>	Proximal papillae; distal region, laevigate, irregularly verrucate or showing an annulus.
<i>Verrucosisporites scurrus</i>	<i>Dibolisporites farraginis</i> <i>Dibolisporites uncatus</i> <i>Verrucosisporites premnus</i> <i>Verrucosisporites scurrus</i>	Varied, spaced or partially fused, evenly or asymmetrically distributed, coni/spinae/bacula/verrucae; simple laesurae; subcircular amb.

based on purely morphological criteria is more appropriate for Palaeozoic palynology and consequently applied here to identify the layers of the exine. The comparison of each described species with possible similar forms is discussed. The stratigraphical and geographical distribution of species are summarized almost exclusively from the major part of Devonian literature. Although the age of the spore assemblages, where the species described here also occur, are cited according to the Epochs and Ages defined by the International Commission on Stratigraphy, they were not reappraised. Genera and species are arranged in the artificial morphographic system of suprageneric categories (*anteturmae* and *turmae*) devised by Potonié (1956, 1970) and modified by others, but within these categories, genera, species and varieties are arranged in alphabetical order for ease of use.

As sample depths are expressed in metres for the previous studies on MG-1 (Streel *et al.* 1990; Loboziak *et al.* 1992a), this convention is kept herein to allow easy comparisons between the different studies. Samples from other studied sections (A1-69 and Saudi Aramco sections) were originally measured in feet.

Repository of material. All material from JNDL-1, MG-1, S-462, WELL-1, WELL-2, WELL-3, WELL-4, WELL-5, WELL-6, WELL-7 and WELL-8 is housed in the collections of Laboratory of 'Palaeobiogeologie, Palaeobotanique et Palaeopalynologie' of the University of Liège. All these palynological slides have a five-digit reference number, except the third palynological slide of samples from JNDL-1, which have a three-digit reference number preceded by 'PPM'. From BAQA-1, BAQA-2, JNDL-3 and JNDL-4, one set of palynological slides is stored

in the collections of the Laboratory of 'Palaeobiogeologie, Palaeobotanique et Palaeopalynologie', and each has a five-digit reference number. A second set of slides for these four core holes is housed in the Centre for Palynology of the University of Sheffield, and the slides have a three-digit reference number preceded by '03CW'. The palynological slides from A1-69 are from the collections of the Laboratory of Palaeontology of the University of Lille and are referenced by a five-digit number. These were previously studied by Loboziak and Streef (1989).

SYSTEMATIC PALAEOONTOLOGY

Anteturma CRYPTOSPORITES (Richardson *et al.*) Richardson, 1988 emend. Steemans, 2000

Genus ARTEMOPYRA Burgess and Richardson, 1991 emend. Richardson, 1996

Type species. *Artemopyra brevicosta* Burgess and Richardson, 1991.

Artemopyra inconspicua Breuer *et al.*, 2007c
Figure 5A–B

2007c *Artemopyra inconspicua* Breuer *et al.*, p. 42, pl. 1, figs 1–5.

Dimensions. 36(48)57 µm; 20 specimens measured.

Occurrence. BAQA-1, JNDL-1, JNDL-3 and JNDL-4; Jauf (Subbat to Murayr members) and Jubah formations; *ovalis-biornatus* to *svalbardiae-eximius* zones. A1-69; Awaynat Wanin II Formation; *lemurata* Zone. MG-1; Awaynat Wanin I Formation; *incognita* Zone.

Artemopyra recticosta Breuer *et al.*, 2007c
Figure 5C–D

2006 *Artemopyra?* spp. Wellman, pl. 20, fig. i.
2007c *Artemopyra recticosta* Breuer *et al.*, p. 43, pl. 1, figs 6–12.

Dimensions. 34(51)70 µm; 36 specimens measured.

Occurrence. BAQA-1, JNDL-1, JNDL-3, JNDL-4, S-462, WELL-2, WELL-3, WELL-4, WELL-7 and WELL-8; Jauf (Subbat to Murayr members) and Jubah formations; *ovalis-biornatus* to *triangulatus-catillus* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *lindlarensis-sextantii* to *triangulatus-catillus* zones. MG-1; Ouan-Kasa, Awaynat Wanin I, Awaynat Wanin II and Awaynat Wanin III formations; *annulatus-protea* to *langii-concinna* zones.

Previous records. From upper Pragian – lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller *et al.* 2007); upper Eifelian – middle Givetian of Parnaíba Basin, Brazil (Breuer and Grahn 2011); Emsian from Saudi Arabia (Al-Ghazi, 2007); and upper Pragian – ?lowermost Emsian of Scotland (Wellman 2006).

Genus CYMBOHILATES Richardson emend. Breuer *et al.*, 2007c

Type species. *Cymbohilates horridus* Richardson, 1996.

Cymbohilates baqaensis Breuer *et al.*, 2007c
Figure 5E–F

2007c *Cymbohilates baqaensis* Breuer *et al.*, p. 43, pl. 1, figs 13–19.

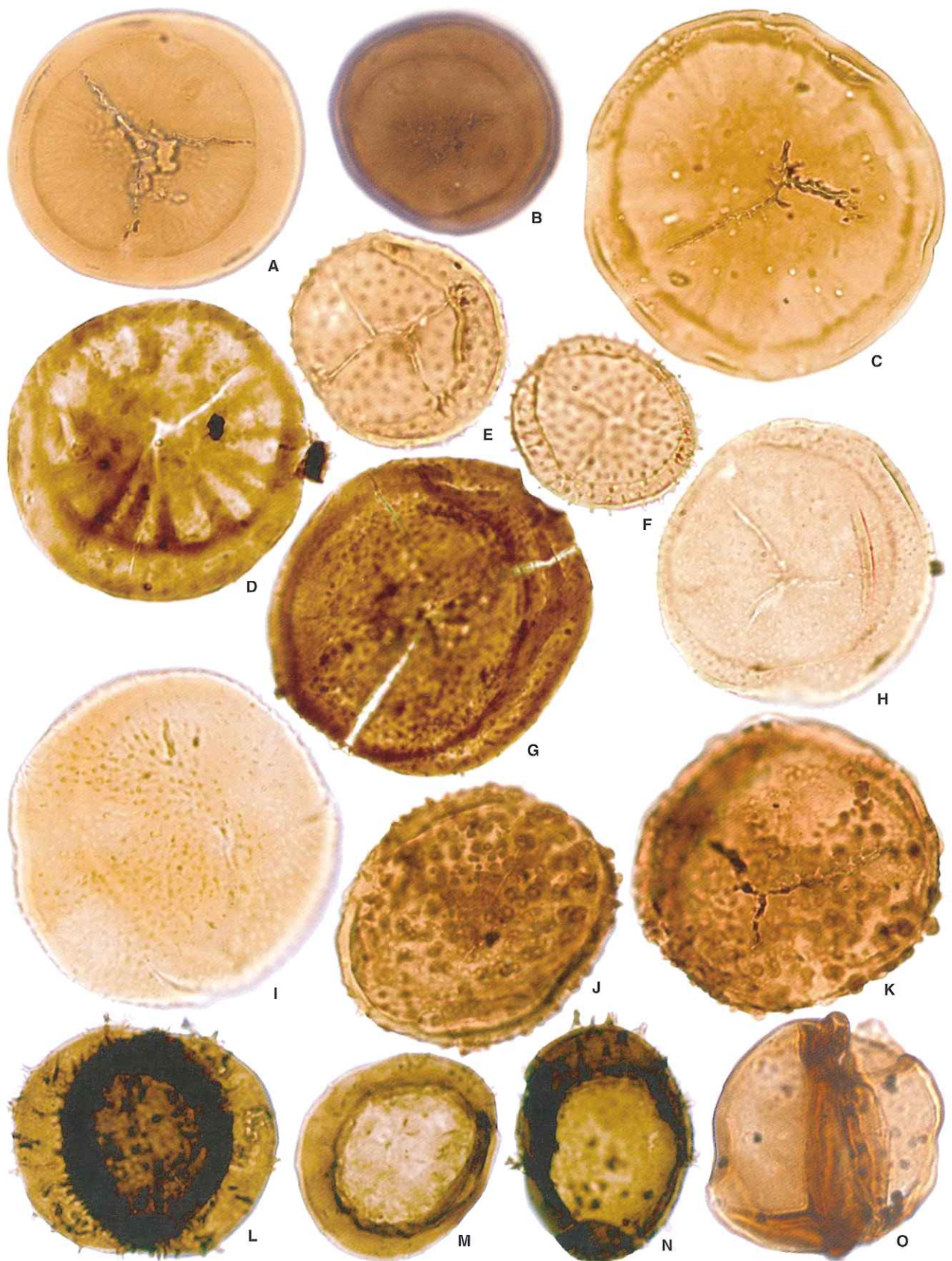
Dimensions. 30(36)40 µm, 16 specimens measured.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-3, WELL-4, WELL-6 and WELL-7; Jauf and Jubah formations; *papillensis-baqaensis* to *svalbardiae-eximius* zones. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Cymbohilates comptulus Breuer *et al.*, 2007c
Figure 5G–I

? 1988 *Gneudnaspora* sp. (Chibrikova) Balme, p. 17, pl. 3, fig. 15.
? 1996 *Cymbohilates amplius* Wellman and Richardson, p. 55, pl. 10, figs 1–3.

FIG. 5. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification $\times 1000$ except where mentioned otherwise. A–B, *Artemopyra inconspicua* Breuer *et al.*, 2007c. A, JNDL-4, 182.5 ft, 68636, H45; hilum exhibits a pseudotrite mark. B, BAQA-1, 227.1 ft, 66784, D34. C–D, *Artemopyra recticosta* Breuer *et al.*, 2007c. C, WELL-7, 13689.7 ft, 62319, L51/4. D, JNDL-1, 172.7 ft, 60845, T-U36. E–F, *Cymbohilates baqaensis* Breuer *et al.*, 2007c. E, BAQA-2, 134.4 ft, 03CW137, P40/1. F, BAQA-2, 133.0 ft, 03CW136, T29. G–I, *Cymbohilates comptulus* Breuer *et al.*, 2007c. G, WELL-3, 14214.1 ft, 66839, O57/2. H, BAQA-1, 376.4 ft, 03CW119, U25/1. I, MG-1, 2258 m, 62948, S48/2. J–K, *Cymbohilates heteroverrucosus* Breuer *et al.*, 2007c. J, JNDL-1, 162.3 ft, 60841, G32/4. K, 167.8 ft, 60843, X29/1. L–N, *Cymbohilates* sp. 1. L, MG-1, 2631.2 m, 62551, K29/2. M, MG-1, 2631.2 m, 62552, N45. N, MG-1, 2631.2 m, 62552, T43/1. O, *Dyadaspora murusattenuata* Strother and Traverse, 1979. BAQA-2, 57.2 ft, 66817, H40.



2007c *Cymbohilates comptulus* Breuer *et al.*, p. 43, pl. 2, figs 1–7.

Dimensions. 48(58)70 µm; 28 specimens measured.

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

Cymbohilates cymosus Richardson, 1996

1996 *Cymbohilates cymosus* Richardson, p. 34, pl. 6, figs 3–6; pl. 7, figs 1–4.

Dimensions. 62 µm; one specimen measured.

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

Previous record. From lower-middle Lochkovian of England (Richardson, 1996).

Cymbohilates heteroverrucosus Breuer *et al.*, 2007c
Figure 5J–K

2007c *Cymbohilates heteroverrucosus* Breuer *et al.*, p. 47, pl. 2, figs 9–12; pl. 3, figs 1–2.

Dimensions. 45(53)62 µm; 34 specimens measured.

Comparison. *Hispanaedisca? irregularis* Wellman and Richardson, 1996 has less variation in the size of the verrucae and is only sculptured outside the contact surface. It does not show tears on the proximal face.

Occurrence. JNDL-1, JNDL-3, JNDL-4 and WELL-7; Jauf (Hammamiyat and Murayr members) and Jubah formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones.

Cymbohilates sp. 1
Figure 5L–N

Description. Amb is sub-circular. A curvatura 0.5–1 µm wide delimits a circular to sub-circular, smooth hilum. The hilum radius either equals or is approximately seven-tenths of the amb radius. Exine is sculptured subequatorially and distally with widely spaced and irregularly distributed spines 1–3.5 µm high, 0.75–2.5 µm wide at base. In some specimens, spines are very few in number.

Dimensions. 37(39)42 µm; five specimens measured.

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

Genus DYADASPORA Strother and Traverse, 1979

Type species. *Dyadaspora murusattenuata* Strother and Traverse, 1979.

Dyadaspora murusattenuata Strother and Traverse, 1979
Figure 5O

1979 *Dyadaspora murusattenuata* Strother and Traverse, p. 15, pl. 3, figs 9–10.

Dimensions. 45–52 µm; two specimens measured.

Occurrence. BAQA-2 and WELL-3; Jauf Formation (Sha'iba Member); *papillensis-baqensis* to *lindlarensis-sextantii* zones.

Previous records. Widely reported from Silurian through Lochkovian assemblages; e.g. Argentina (Rubinstein and Toro 2006); Brazil (Stemans *et al.* 2008), North Africa (Rubinstein and Stemans 2002; Spina and Vecoli 2009); Pennsylvania, USA (Strother and Traverse 1979; Beck and Strother 2008); Saudi Arabia (Stemans *et al.* 2000b; Wellman *et al.* 2000a); Sweden (Hagström 1997; Mehlgvist 2009); and UK (Wellman 1993; Wellman *et al.* 2000b).

Genus GNEUDNASPORA Balme, 1988 emend.
Breuer *et al.*, 2007c

Type species. *Gneudnaspora kernickii* Balme, 1988.

Gneudnaspora divellomedia (Chibrikova) Balme, 1988 var.
divellomedia Breuer *et al.*, 2007c
Figure 6A–B

1988 *Gneudnaspora divellomedium* (Chibrikova) Balme, p. 125, pl. 3, figs 1–7.

non 1991 *Laevolancis divellomedia* (Chibrikova) Burgess and Richardson, p. 607, pl. 2, figs 4, 6.

2007c *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988 var. *divellomedia* Breuer *et al.*, p. 48, pl. 3, figs 3–9.

Dimensions. 32(54)82 µm; 17 specimens measured.

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

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

Previous records. From Emsian – lower Frasnian of Australia (Balme 1988; Hashemi and Playford 2005); upper Eifelian – middle Givetian of Parnaíba Basin, Brazil (Breuer and Grahn 2011); upper Pragian – lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller *et al.* 2007); upper Emsian – lower Eifelian of Russian Platform (Avkhimovitch *et al.* 1993); and Emsian of Saudi Arabia (Al-Ghazi 2007).

Remarks. Contrary to the *G. divellomedia* (Chibrikova) Balme, 1988 var. *minor* Breuer *et al.*, 2007c, *G. divellomedia* var. *divellomedia* only occurs in Devonian strata.

Gneudnaspora divellomedia (Chibrikova) Balme, 1988 var.
minor Breuer *et al.*, 2007c
Figure 6C–E

- 1973 *Archaeozonotrites* cf. *divellomedium* Chibrikova; Richardson and Ioannides, p. 280, pl. 8, fig. 10–11.
- 1978 *Hispanaedisca* sp.; McGregor and Narbonne, p. 1296, pl. 1, figs 20–22.
- 1979 *Archaeozonotrites* cf. *chulus nanus* Richardson and Lister; Holland and Smith, pl. 2, figs 7–9.
- 1979 'smooth-walled inaperturate spore'; Strother and Traverse, p. 14, pl. 3, fig. 5.
- 1993 *Archaeozonotrites* cf. *divellomedium* Chibrikova; Moreau-Benoit *et al.*, pl. 1, fig. 2.
- 2007c *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988 var. *minor* Breuer *et al.*, p. 48 (*cum syn.*), pl. 3, figs 10–16.

Dimensions. 28(31)34 µm; 21 specimens measured.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-3, WELL-5, WELL-6 and WELL-7; Jauf and Jubah formations; *papillensis-baqaensis* to *svalbardiae-eximius* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Previous records. *Gneudnaspora divellomedia* var. *minor* has been reported in Ordovician (Vecoli *et al.* 2011), widely in the Silurian through Middle Devonian palynofloras from many parts of the world.

Genus TETRAHEDRALETES Strother and Traverse emend.
Wellman and Richardson, 1993

Type species. *Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, 1993.

Tetrahedraletes medinensis Strother and Traverse emend.
Wellman and Richardson, 1993

- 1993 *Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, p. 165 (*cum syn.*), pl. 2, figs 8, 10–12.

Dimensions. 40(50)58 µm; 14 specimens measured.

Comparison. In *Cheilotetras caledonica* Wellman and Richardson, 1993, the equatorial crassitude of individual spores is drawn out into distinct extended flanges, and there are no discernible lines of attachment between adjacent spores. *Rimosotetras problematica* Burgess, 1991 encompasses tetrads composed of loosely attached, frequently partially separated, laevigate, alete or indistinctly tri-lete spores.

Occurrence. BAQA-2, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4 and WELL-7; Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqaensis* to *lindlarensis-sextantii* zones but most of occurrences are probably reworked.

Previous record. *Tetrahedraletes medinensis* has been reported worldwide in Ordovician through Lower Devonian.

Anteturma SPORITES Potonié, 1893
Turma MONOLETES Ibrahim, 1933

Genus ARCHAEOOPERISACCUS Naumova emend. McGregor,
1969

Type species. *Archaeoperisaccus menneri* Naumova, 1953.

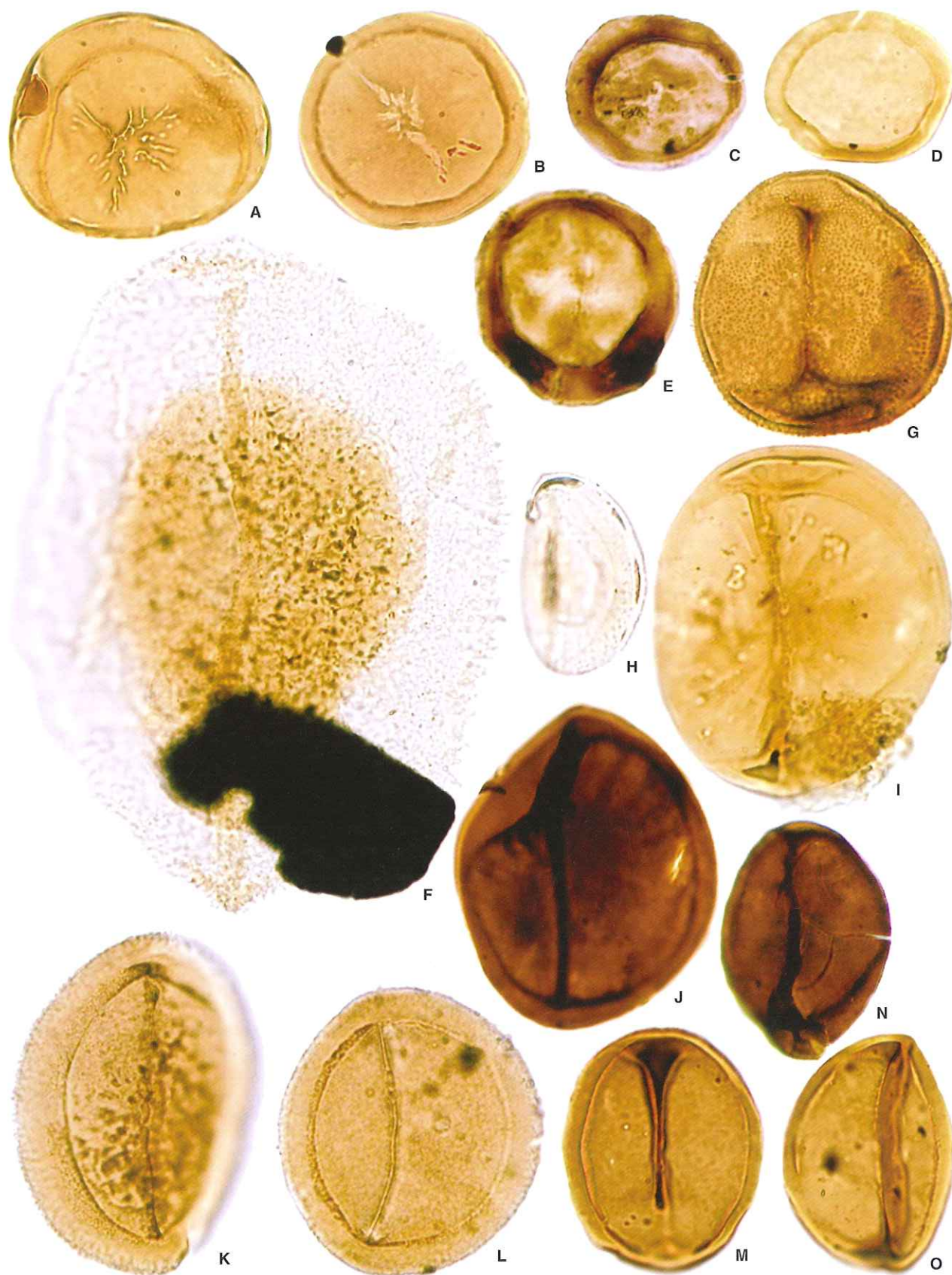
Archaeoperisaccus cf. *A. rhacodes* Hashemi and Playford,
2005
Figure 6F

- cf. 2005 *Archaeoperisaccus rhacodes* Hashemi and Playford, p. 388, pl. 13, figs 10–11; pl. 14, figs 4, 7–8.

Description. Amb is generally oval to irregular. The length of the short axis is equal to three-quarters of the long axis. Laesura is marked by fold-like labra c. 2–4 µm thick. Central body radius equals about three-fifths to three-quarters of the amb radius. Ornamentation is closely and regularly distributed, consisting of coni and spines, up to 3 µm high and 2 µm in basal diameter.

Dimensions. 74–115 µm; two specimens measured.

Remarks. *Archaeoperisaccus rhacodes* Hashemi and Playford, 2005 is slightly different than the specimens figured here; it is larger (108–136 µm) and has conate elements, which can be loosely distributed. A larger population of



the form described here is needed to correctly place this taxonomically.

Comparison. *Archaeoperisaccus verrucosus* Pashkevich, 1964 is verrucate and therefore sculpturally distinct from *Archaeoperisaccus* cf. *A. rhacodes* Hashemi and Playford, 2005. *A. opiparus* Owens, 1971 has a greater overall length, a strongly elevated fold-like labra, thicker nexine and bifurm sculptural elements. *A. oblongus* Owens, 1971 has a more elongate amb and a coarser sculpture. *A. indistinctus* Lu Lichang, 1980 is scabrate.

Occurrence. MG-1; Awaynat Wanin II Formation; *undulatus* to *langii-concinna* zones.

Genus DEVONOMOLETEs Arkhangel'skaya, 1985

Type species. *Devonomoletes microtuberculatus* (Chibrikova) Arkhangel'skaya, 1985.

Devonomoletes sp. 1

Figure 6G

Description. Amb is sub-circular. Contact faces are laevigate. Laesura equals one-half to three-quarters of the amb radius. Laesura is distinct, straight to slightly curved, terminating in well-defined curvaturae. Sculptured outside of the contact area with evenly distributed spines 0.5–1.5 µm high and 0.5–1 µm apart.

Dimensions. 36(49)58 µm; five specimens measured.

Comparison. *Devonomoletes microtuberculatus* (Chibrikova) Arkhangel'skaya, 1985 is clearly oval-shaped and is sculptured with small tubercles. Furthermore, indistinctly outlined darkened muri are present where the distal and proximal sides meet.

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

Genus LATOSPORITES Potonié and Kremp, 1954

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

Latosporites ovalis Breuer et al., 2007c

Figure 6M–O

2006 ?monoete spore; Wellman, pl. 19, fig. h.

2007c *Latosporites ovalis* Breuer et al., p. 52, pl. 12, figs 8–12.

Dimensions. 32(48)62 µm; 22 specimens measured.

Comparison. *Laevigatosporites* sp. A in Hashemi and Playford (2005) has laesura equal to two-fifths to one-half of the long axis. Wellman (2006) found a monoete spore similar to *L. ovalis* in the Rhynie Outlier, Scotland.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-1, WELL-2, WELL-3, WELL-4, WELL-5, WELL-6 and WELL-7; Jauf and Jubah formations; *ovalis-biornatus* to *svalbardiae-eximius* zones but specimens recovered from the Jubah Formation are probably reworked.

Previous records. From upper Pragian – lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller et al. 2007); Emsian from Saudi Arabia (Al-Ghazi 2007); and upper Pragian – ?lowermost Emsian of Scotland (Wellman 2006).

Latosporites sp. 1

Figure 7A–B

Description. Amb is oval. The length of the short axis equals eight-tenths to nine-tenths of the long axis. Laesura is distinct, simple and straight, and generally equals to more or less eight-tenths of the long axis and is terminated by well-defined curvaturae. Exine entirely laevigate, 0.5–1.5 µm thick.

Dimensions. 38(43)49 µm; three specimens measured.

Comparison. *Latosporites ovalis* Breuer et al., 2007c is labrate, more elliptical and thicker, resulting in a sturdy appearance.

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

FIG. 6. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification $\times 1000$ except where mentioned otherwise. A–B, *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988 var. *divellomedia* Breuer et al. 2007c. A, BAQA-2, 50.8 ft, 03CW127, V35/2. B, BAQA-2, 50.2 ft, 03CW126, V24. C–E, *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988 var. *minor* Breuer et al., 2007c. C, WELL-7, 13614.6 ft, 62379, E28/1. D, JNDL-1, 172.7 ft, PPM007, M49/3. E, WELL-7, 13613.2 ft, 62370, J33/1. F, *Archaeoperisaccus* cf. *A. rhacodes* Hashemi and Playford, 2005. MG-1, 2264 m, 62950, G41/3. G, *Devonomoletes* sp. 1. BAQA-2, 133.0 ft, 03CW136, E29. H, *Devonomoletes* spp. MG-1, 2212.5 m, 62530, Q27. I–J, *Emphanisporites rotatus* McGregor emend. McGregor, 1973. I, MG-1, 2693 m, 62961, L37. J, WELL-3, 14188.5 ft, 60547, N35/1. K–L, *Geminispora lemurata* Balme emend. Playford, 1983. K, MG-1, 2180 m, 62972, U-V32. L, MG-1, 2160.6 m, 62746, V41. M–O, *Latosporites ovalis* Breuer et al., 2007c. M, BAQA-2, 50.8 ft, 03CW127, T30/2. N, WELL-3, 14195.3 ft, 66837, R61. O, BAQA-2, 50.2 ft, 03CW126, H26/1.

Genus RETICULOIDOSPORITES Pflug in Thomson and Pflug,
1953

Type species. *Reticuloidosporites dentatus* Pflug in Thomson and Pflug, 1953.

Reticuloidosporites antarcticus Kemp, 1972

Figure 7C–E

1972 *Reticuloidosporites antarcticus* Kemp, p. 117, pl. 56, figs 1–13.

Dimensions. 37(47)60 µm; 13 specimens measured.

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

Previous records. From the Horlick Formation of Antarctica (Kemp 1972), the age of which is considered as Pragian by Troth *et al.* (2011) based on correlation of chitinozoans and spore assemblages from South America.

Turma TRILETES Reinsch, 1881 emend. Dettmann, 1963

Genus ACINOSPORITES Richardson, 1965

Type species. *Acinosporites acanthomammillatus* Richardson, 1965.

Acinosporites acanthomammillatus Richardson, 1965

Figure 7F–G

1925 Type I Lang, pl. 1, fig. 21.

1965 *Acinosporites acanthomammillatus* Richardson, p. 577, pl. 91, figs 1–2; text-fig. 6.

Dimensions. 63(71)80 µm; eight specimens measured.

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

Previous records. *Acinosporites acanthomammillatus* is eponymous for the upper Eifelian – lower Givetian AD Oppel Zone of Western Europe (Streel *et al.* 1987). *A. acanthomammillatus* occurs from Eifelian into Frasnian and has been widely reported, e.g. Argentina (Amenábar 2009), Australia (Hashemi and Playford 2005), Bolivia (Perez-Leyton 1990), Brazil (Loboziak *et al.* 1988; Loboziak *et al.* 1992b; Breuer and Grahn 2011), Canada (Owens 1971; McGregor and Uyeno 1972; McGregor and Camfield 1976, 1982), China (Gao Lianda 1981), Germany (Riegel 1968, 1973; Loboziak *et al.* 1990), Iran (Ghavidel-Syooki 2003), Libya (Paris *et al.* 1985; Streel *et al.* 1988; Moreau-Benoit 1989), Poland (Turnau 1996), Russian Platform (Avkhimovitch *et al.* 1993) and Scotland.

Acinosporites apiculatus (Streel) Streel, 1967

Figure 7H

1964 *Verrucosporites apiculatus* Streel, pl. 1, fig. 13.

1967 *Acinosporites* cf. *apiculatus* (Streel); Streel, p. 36, pl. 3, figs 38–39.

Dimensions. 57(85)125 µm; seven specimens measured.

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

Previous records. *Acinosporites apiculatus* is eponymous for the upper Emsian – upper Eifelian AP Oppel Zone of Western Europe (Streel *et al.* 1987). *A. apiculatus* has been reported from upper Emsian through lower Givetian from Belgium (Streel 1964, 1967), Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003; Breuer and Grahn 2011), Germany (Riegel 1968, 1973; Tiwari and Schaarschmidt 1975; Loboziak *et al.* 1990), Luxembourg (Steemans *et al.* 2000a) and Morocco (Rahmani-Antari and Lachkar 2001).

Acinosporites eumammillatus Loboziak *et al.*, 1988

Figure 7I–K

1966 *Acinosporites* sp. McGregor and Owens, pl. 3, figs 9–10.

FIG. 7. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification $\times 1000$ except where mentioned otherwise. A–B, *Latosporites* sp. 1. A, MG-1, 2241 m, 62964, V41/2. B, MG-1, 2639 m, 62779, X47. C–E, *Reticuloidosporites antarcticus* Kemp, 1972. C, BAQA-1, 308.3 ft, 62246, L29. D, BAQA-1, 308.3 ft, 62247, K46. E, BAQA-1, 308.3 ft, 62246, N44. F–G, *Acinosporites acanthomammillatus* Richardson, 1965. F, JNDL-1, 162.3 ft, 60841, M33. G, JNDL-1, 156.0 ft, 60839, F31. H, *Acinosporites apiculatus* (Streel) Streel, 1967. A1-69, 1850 ft, 26967, U32/2. I–K, *Acinosporites eumammillatus* Loboziak *et al.*, 1988. I, MG-1, 2520 m, 62594, H27/4. K, MG-1, 2520 m, 62593, H47. 11, MG-1, 2520 m, 62593, T49/1. L, *Acinosporites lindlarensis* Riegel, 1968. JNDL-4, 182.5 ft, 03CW220, M-N42.



- 1968 *Acinosporites* sp. B Riegel, p. 89, pl. 19, figs 8–10.
 1987 *Acinosporites* sp. Burjack *et al.*, pl. 1, fig. 6.
 1988 *Acinosporites eumammillatus* Loboziak *et al.*, p. 354, pl. 1, figs 4–11.

Dimensions. 36(41)44 μm ; seven specimens measured.

Comparison. *Acinosporites acanthomammillatus* Richardson, 1965 is clearly more massive. Its ornamentation is higher and wider (2–8 μm) and surmounted by spines, 1–3 μm high and 1 μm wide at base. They are very closely distributed to anastomosed. Other species of *Acinosporites* Richardson, 1965 have commonly biform ornamentation, but they do not show, in general, this typical feature of mammae.

Occurrence. MG-1; Awaynat Wanin I Formation; *rugulatus* Zone.

Previous records. From upper Givetian – lower Frasnian of Argentina (Ottone 1996); upper Frasnian of Paraná Basin, Brazil (Loboziak *et al.* 1988); Emsian of Canada (McGregor and Owens 1966); and Eifelian of Germany (Riegel 1968).

Acinosporites lindlarensis Riegel, 1968

Figure 7L

- 1966 Unidentified spore McGregor and Owens, pl. 5, fig. 17.
 1968 *Acinosporites lindlarensis* Riegel, p. 89, pl. 19, figs 11–16.
 ? 1969 Indeterminate Cramer, pl. 2, fig. 27.
 1972 *Aneurospora* cf. *heterodonta* (Naumova); Streel, p. 206, pl. 2, figs 1–7.
 1973 *Geminospora treverica* Riegel, p. 97, pl. 16, figs 4–7.
 ? 1975 *Cymbosporites cyathus* Allen; Tiwari and Schaarschmidt, pl. 15, fig. 4.
 1976 *Acinosporites lindlarensis* Riegel var. *lindlarensis*; McGregor and Camfield, p. 6, pl. 5, figs 2–3.
 1976 *Acinosporites lindlarensis* Riegel var. *minor* McGregor and Camfield, p. 8, pl. 5, figs 4–5.
 ? 1991 *Dibolisporites* sp. cf. *echinaceus* (Eisenack) Richardson; Grey, pl. 1, fig. 9.

Dimensions. 63(75)91 μm ; 20 specimens measured.

Remarks. A separated inner body (probably only attached proximally) is regarded by some authors (McGregor and Camfield 1976) of doubtful significance at the generic level. This feature is not mentioned as a criterion circumscribing *Acinosporites* by Richardson (1965). Indeed, some *A. acanthomammillatus* described by Richardson (1965) occasionally have a discernible central body. Therefore, the presence of this feature in *A. lindlarensis* is not considered sufficient to exclude it from the genus.

Acinosporites lindlarensis shows continuous morphological variation of the distribution, size and shape of the ornamentation. Morphotypes with widely distributed sculpture intergrade with others characterized by more crowded distal sculpture. Richardson *et al.* (1993) addressed this issue by defining the *A. lindlarensis* Morphon. It contains different types and subtypes that are difficult to recognize in the present material.

Comparison. McGregor and Camfield (1976) have shown that *Geminospora treverica* Riegel, 1973, characterized by a completely separated inner body, cannot be separated from *A. lindlarensis*. *A. acanthomammillatus* Richardson, 1965 has close similarities (Richardson *et al.* 1993), but it is distinguished from *A. lindlarensis* by a more massive appearance due to commonly coarser ridges.

Occurrence. BAQA-1, JNDL-1, JNDL-3, JNDL-4, S-462, WELL-1, WELL-3, WELL-4, WELL-6, WELL-7 and WELL-8; Jauf (Subbat to Murayr members) and Jubah formations; *lindlarensis-sexantii* to *triangulatus-catillus* zones. A1-69; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *lemurata-langii* zones. MG-1; Ouan-Kasa, Awaynat Wanin I and Awaynat Wanin II formations; *annulatus-protea* to *langii-concinna* zones.

Previous records. *Acinosporites lindlarensis* has an almost world-wide distribution and has been widely reported from Emsian through Frasnian palynofloras; e.g. Algeria (Moreau-Benoit *et al.* 1993), Argentina (Le Hérisse *et al.* 1997; Amenábar 2009), Belgium (Lessuise *et al.* 1979; Gerrienne *et al.* 2004), Bolivia (Perez-Leyton 1990), Brazil (Loboziak *et al.* 1988; Melo and Loboziak 2003; Breuer and Grahn 2011), Canada (McGregor and Owens 1966; McGregor and Uyeno 1972; McGregor 1973; McGregor and Camfield 1976, 1982), Germany (Riegel 1968, 1973; Loboziak *et al.* 1990), Iran (Ghavidel-Syooki 2003), Libya (Streel *et al.* 1988; Moreau-Benoit 1989), Poland (Turnau 1986, 1996; Turnau *et al.* 2005), Scotland (Marshall and Allen 1982; Marshall and Fletcher 2002) and Georgia, USA (Ravn and Benson 1988).

Acinosporites tristratus sp. nov.

Figure 8A–C

Derivation of name. From *tristratus* (Latin), meaning three-layered; refers to the structure of the spore wall.

Holotype. EFC N43/2 (Fig. 8A), slide 60849.

Paratype. EFC J30/1 (Fig. 8C), slide 60845; JNDL-1 core hole, sample 177.0 ft.

Type locality and horizon. JNDL-1 core hole, sample 172.7 ft; Jubah Formation, Domat Al-Jandal, Saudi Arabia.

Diagnosis. An *Acinosporites* with three layers visible. Distal surface sculptured with coarse biform elements joined to form ridges of varied length.

Description. Amb is sub-circular to sub-triangular. Three wall layers are visible. Laesurae are straight, simple or bordered by labra up to 4 μm in total thickness and extending generally to the outer margin of the second layer. Endonexine is (c. 1 μm) not always discernible, ectonexine 1–2.5 μm thick, laevigate, sexine 1.5–3.5 μm thick, sculptured proximo-equatorially and distally with biform processes (bulbous base with apical spine). Sculptural elements on the distal hemisphere are round in plan view, 3–7 μm wide at their base, 2–8 μm high, joined to form ridges of varied length. The longest elements occur subequatorially at the outer limit of the contact area. Proximal surface granular.

Dimensions. 59(71)85 μm ; nine specimens measured.

Remarks. According to Richardson (1965), an inner body is not a feature circumscribing *Acinosporites* (see above). Therefore, the assignment of this new species to this genus is legitimate on the basis of the characteristics of ornamentation.

Comparison. *Acinosporites acanthomammillatus* Richardson, 1965 is single-layered and has ornamentation that is a more closely distributed than that *A. tristratus*. The three wall layers distinguish *A. tristratus* from all the other species of *Acinosporites* Richardson, 1965.

Occurrence. JNDL-1; Jauf (Murray Member) and Jubah Formation; *annulatus-protea* to *svalbardiae-eximius* zones.

Genus ALATISPORITES Ibrahim, 1933

Type species. *Alatisporites pustulatus* Ibrahim, 1933.

Alatisporites? trisacculus sp. nov.

Figure 8D–E

Derivation of name. From *trisacculus* (Latin) meaning three small sacci; refers to the size of the sacci.

Holotype. EFC W40/4 (Fig. 8E), slide 03CW195.

Paratype. EFC E52/4 (Fig. 8D), slide 03CW159; JNDL-3 core hole, sample 353.8 ft.

Type locality and horizon. JNDL-4 core hole, sample 87.2 ft; Jauf Formation, Domat Al-Jandal, Saudi Arabia.

Diagnosis. An *Alatisporites* bearing three individual proximo-equatorial sacci opposite the laesurae. Sacci thin and often folded.

Description. Amb is circular to sub-circular. Laesurae are distinct, straight, simple and equal one-half to two-thirds of the

amb radius. Curvaturae are sometimes visible. Central body diameter equals commonly three-fifths to fourth-fifths of the total amb diameter. Exine of the central body is 1.5–3 μm thick equatorially. Zona is divided entirely or partially into three individual proximo-equatorial sacci, the maximum width (commonly 14–25 μm) of which is opposite the laesurae. Sacci are thin and often folded radially and can be folded back on the spore body. Thin generally sinuous attachment lines of the sacci on the central body can be distinguished on the proximal face. Proximal and distal surfaces are entirely laevigate.

Dimensions. 64(88)103 μm ; five specimens measured.

Remarks. There is some doubt about the allocation of this species to the genus *Alatisporites* Ibrahim, 1933 because the sacci are opposite the laesurae sacci, whereas they are interrally arranged in the other species. Besides, representatives of *Alatisporites* usually first occur in Carboniferous age strata.

Comparison. *Alatisporites trialatus* Kosanke, 1950 has interrally granulate sacci and a sub-triangular to triangular central body. *A. pustulatus* Ibrahim, 1933 and *A. punctatus* Kosanke, 1950 differ by having a distal central body densely sculptured with fine rugulae and verrucae which may impart a microreticulate appearance. *A. hoffmeisteri* Morgan, 1955 possesses a verrucate ornament on the distal central body. *Zonotriletes* sp. 1 has a more sub-triangular amb is only zonate and thus possess an entire flange, which can appear tri-lobed, surrounding the central body.

Occurrence. JNDL-3 and JNDL-4; Jauf Formation (Hammamiyat Member); *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *annulatus-protea* to *rugulatalibensis* zones.

Genus AMBITISPORITES Hoffmeister, 1959

Type species. *Ambitisporites avitus* Hoffmeister, 1959.

Remarks. The genus *Archaicusporites* Rodriguez, 1983 is considered here as a junior synonym of *Ambitisporites* Hoffmeister, 1959. Indeed the diagnosis of *Archaicusporites* describes cingulate spores characterized by folds that are disposed parallel and concentrically with respect to the curvaturae. As folds are probably due to polar compression, this genus can be included in the circumscription of *Ambitisporites*.

Ambitisporites (Archaicusporites) asturicus (Rodriguez) comb. nov.

Figure 9A–D

1978b *Retusotriletes rotundus* (Streel) Streel emend. Lele and Streel; Rodriguez, p. 420, pl. 4, fig. 2.

- 1978b *Retusotriletes triangulatus* (Streel) Streel; Rodriguez, p. 421, pl. 3, fig. 1.
 1983 *Archaicopores asturicus* Rodriguez, p. 32, pl. 6, fig. 5; pl. 7, fig. 3; text-fig. 3: 54.

Dimensions. 30(39)47 µm; 14 specimens measured.

Comparison. *Retusotriletes tenerimedium* Chibrikova, 1959 has a more pronounced wider darker sub-triangular apical zone and does not have elevated curvatures.

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

Previous record. From Přídolí-lower Pragian of Spain (Rodriguez 1978b).

Ambitisporites avitus Hoffmeister, 1959

Figure 9E-F

- 1959 *Ambitisporites avitus* Hoffmeister, p. 332, pl. 1, figs 1-8.
 1969 *Ambitisporites* cf. *avitus* Hoffmeister; Richardson and Lister, p. 228, pl. 40, fig. 2.

Dimensions. 31(38)67 µm; 13 specimens measured.

Comparison. As *A. avitus* and *A. dilutus* (Hoffmeister) Richardson and Lister, 1969 may intergrade, Steemans *et al.* (1996) defined the *A. avitus* Morphon to include them. *A. avitus* may be distinguished from *A. dilutus* by its larger diameter and thicker cingulum.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-3 and WELL-7; Jauf and Jubah formations; *papillensis-baqaensis* to *svalbardiae-eximius* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *lindlarensis-sextantii* to *rugulata-libyensis* zones.

Previous record. *Ambitisporites avitus* has a worldwide distribution and has been widely reported from Early Silurian through Early Devonian assemblages.

Ambitisporites eslae (Cramer and Díez)

Richardson *et al.*, 2001

Figure 9G-I

- ? 1968 Spore no. 2513 Magloire, pl. 1, fig. 13.
 1973 *Ambitisporites* sp. B Richardson and Ioannides, p. 277 (pars), pl. 6, fig. 8 (*non* figs 7, 9).
 1975 *Retusotriletes eslae* Cramer and Díez, p. 343, pl. 1, figs 11-12.
 1976 *Ambitisporites tripapillatus* Moreau-Benoit, p. 37, pl. 7, fig. 2-4.
 2001 *Ambitisporites eslae* (Cramer and Díez) Richardson *et al.*, p. 142, pl. 5, fig. 1.

Dimensions. 28(44)62 µm; 13 specimens measured.

Comparison. *Ambitisporites tripapillatus* Moreau-Benoit, 1976 is considered as a junior synonym of *A. eslae* (Cramer and Díez) Richardson *et al.*, 2001. *Scylaspora elegans* Richardson *et al.*, 2001 has a large darkened apical area and proximal rugulate sculpture. *Retusotriletes maculatus* McGregor and Camfield, 1976 and, in part, *Ambitisporites* sp. B in McGregor and Camfield (1976) appear to have an equatorially thinner exine, but are otherwise similar to *A. eslae*. *Synorisporites papillensis* McGregor, 1973 has smaller proximal papillae. Its distal face is commonly verrucate and its cingulum is irregular.

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

Previous records. From lower Lochkovian - lower Pragian of Spain (Cramer and Díez 1975; Rodriguez 1978b; Richardson *et al.* 2001); Pragian of Armorican Massif, France (Le Hérisse 1983); middle Přídolí of Libya (Rubinstein and Steemans 2002); upper Pragian - lower Emsian of Argentina (Rubinstein and Steemans 2007); and lower Lochkovian of Brazil (Steemans *et al.* 2008).

Genus AMICOSPORITES Cramer, 1966a

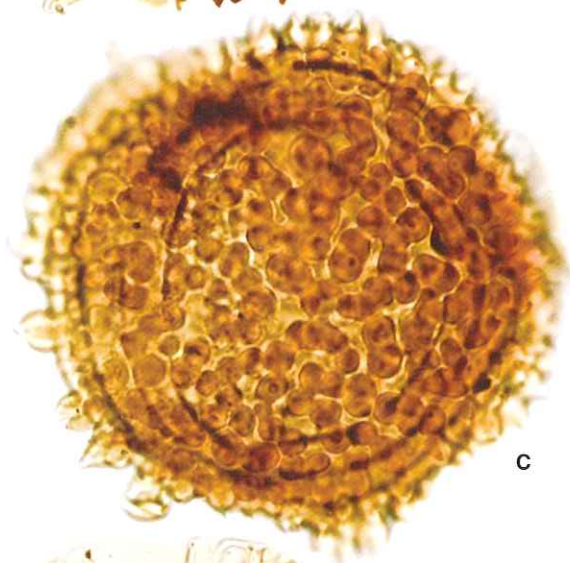
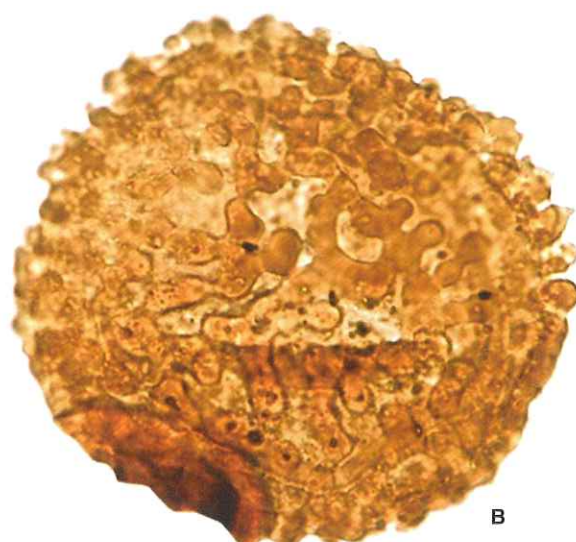
Type species. *Amicosporites splendidus* Cramer, 1966a.

Amicosporites jonkeri (Riegel) Steemans, 1989

Figure 9J-L

- 1989 *Amicosporites jonkeri* (Riegel) Steemans, p. 91 (*cum syn.*), pl. 19, figs 9-11.

FIG. 8. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification $\times 1000$ except where mentioned otherwise. A-C, *Acinosporites tristratus* sp. nov. A, Holotype, JNDL-1, 177.0 ft, 60849, N43/2. B, JNDL-1, 177.0 ft, 60849, F35/1. C, Paratype, JNDL-1, 172.7 ft, 60845, J30/1. D-F, *Alatisporites? trisacculus* sp. nov. D, Paratype, JNDL-3, 353.8 ft, 03CW159, E52/4. E, Holotype, JNDL-4, 87.2 ft, 03CW195, W40/4. F, MG-1, 2713 m, 62810, M34.



Dimensions. 32(40)46 µm; 11 specimens measured.

Comparison. *Amicosporites splendidus* Cramer, 1966a has a narrower annulus close to the equator. *A. streelii* Steemans, 1989 has an annulus formed by verrucae resulting in an irregular appearance. Moreover, other verrucae are present in the centre of the annulus. *Concentricosporites barbulatus* (Rodríguez) Rodríguez, 1983 has a similar appearance except that the author interpreted the annulus to be in a proximal position. The smooth specimens of *Coronaspora* sp. in Le Hérisse (1983) are synonymous with *A. jonkeri* whereas those sculptured with verrucae are synonymous with *A. streelii*.

Occurrence. BAQA-1, BAQA-2, JNDL-3 and JNDL-4, Jauf Formation (Sha'iba to Hammamiyat members); *papillensis-baqensis* to *lindlarensis-sextantii* zones. A1-69; Ouan-Kasa Formation; *lindlarensis-sextantii* Zone. MG-1; Ouan-Kasa and Awaynat Wanin I formations; *lindlarensis-sextantii* to *svalbardiae-eximius* zones but the youngest occurrences are probably due to reworking.

Previous records. From upper Lochkovian–Emsian of Belgium (Steemans 1989); Pragian–lower Emsian of Armorican Massif, France (Le Hérisse 1983); upper Lochkovian – lower Eifelian of Germany (Riegel 1973; Steemans 1989); and Pragian–Emsian of Poland (Turnau 1986; Turnau *et al.* 2005).

Amicosporites streelii Steemans, 1989
Figure 9M–O

- 1967 *Cirratriadites* sp. F Strel, pl. 5, fig. 59.
1981 *Coronaspora mariae* Rodríguez; Strel *et al.*, p. 184, pl. 3, figs 1–4.
1983 *Coronaspora* sp. Le Hérisse, p. 41 (*pars*), pl. 7, fig. 16–17; pl. 8, figs 1–2 (*non* fig. 3).
1989 *Amicosporites streelii* Steemans, p. 92, pl. 19, figs 15–17; pl. 20, figs 1–2.
2006 *Amicosporites* spp. Wellman, pl. 19, fig. m.

Dimensions. 30(38)45 µm; 18 specimens measured.

Remarks. In Steemans (1989), *A. streelii* does not often show a single sub-circular verruca in the centre of the

annulus; the specimens are generally sculptured with irregularly distributed verrucae. The varied verrucae organization in the centre of the annulus could represent different varieties (PS, pers. obs.).

Comparison. Although some specimens of *Coronospora* sp. in Le Hérisse (1983, pl. 7, figs 16–17; pl. 8, figs 1–2) are synonymous with *A. streelii*, others (pl. 8, fig. 3) have no ornamentation other than the annulus. The latter are consequently placed in synonymy with *A. jonkeri* (Riegel) Steemans, 1989.

Occurrence. BAQA-1, BAQA-2, JNDL-3, JNDL-4, WELL-2, WELL-3, WELL-4 and WELL-7; Jauf Formation; *papillensis-baqensis* to *annulatus-protea* zones. MG-1; Ouan-Kasa Formation; *svalbardiae-eximius* Zone but occurrences are probably reworked.

Previous records. From upper Lochkovian – ?Emsian of Belgium (Strel 1967; Steemans 1989); lower Lochkovian of Amazon Basin, Brazil (Steemans *et al.* 2008); Pragian–lower Emsian of Armorican Massif, France (Le Hérisse 1983); Lochkovian–Pragian of Saudi Arabia (Steemans, 1995); and upper Pragian – ? lowermost Emsian of Scotland (Wellman 2006).

Genus *ANCYROSPORA* Richardson, 1960 emend. Richardson,
1962

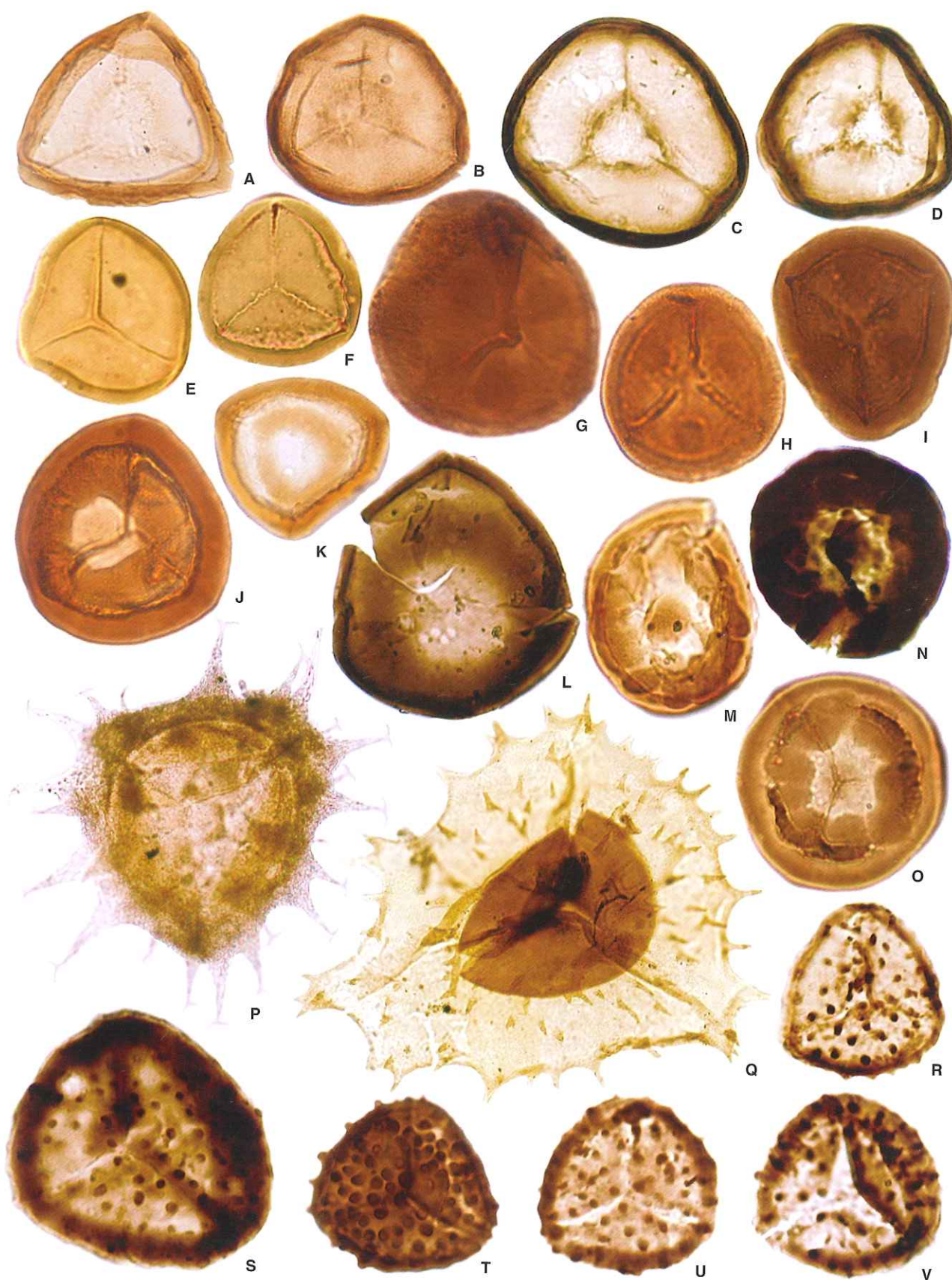
Type species. *Ancyrospora grandispinosa* Richardson emend. Richardson, 1962.

Remarks. Morphology and wall ultrastructure of *Ancyrospora* are discussed in details in Wellman (2002).

Ancyrospora langii (Taugourdeau-Lantz) Allen, 1965
Figure 9P

- ? 1953 *Hymenozonotriletes incisus* Naumova, p. 68, pl. 9, fig. 11.
1960 *Archaeotriletes langii* Taugourdeau-Lantz, p. 145, pl. 3, fig. 33–34, 39.
1965 *Ancyrospora langii* (Taugourdeau-Lantz) Allen, p. 743, pl. 106, figs 5–7.

FIG. 9. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification $\times 1000$ except where mentioned otherwise. A–D, *Ambitisporites* (*Archaicisporites*) *asturicus* (Rodríguez) comb. nov. A, JNDL-4, 495.2 ft, 68702, G37. B, BAQA-1, 308.3 ft, 66791, Q41. C, MG-1, 2631.2 m, 62553, V49/1. D, MG-1, 2631.2 m, 62552, K39/4. E–F, *Ambitisporites avitus* Hoffmeister, 1959. E, BAQA-2, 54.8 ft, 03CW129, N28. F, BAQA-2, 52.0 ft, 03CW128, O27/1. G–I, *Ambitisporites eslae* (Cramer and Díez) Richardson *et al.*, 2001. G, BAQA-2, 57.2 ft, 66817, F31. H, BAQA-1, 395.2 ft, 66807, P26. I, BAQA-2, 50.8 ft, 66813, L23/1. J–L, *Amicosporites jonkeri* (Riegel) Steemans, 1989. J, BAQA-2, 134.4 ft, 66826, U38/3. K, JNDL-4, 120.0 ft, 68612, E53/2. L, MG-1, 2741.4 m, 62611, L41. M–O, *Amicosporites streelii* Steemans, 1989. M, BAQA-1, 371.1 ft, 03CW118, F28/2. N, WELL-3, 14195.3 ft, 66838, F62/2. O, BAQA-2, 133.0 ft, 03CW136, F40/4. P, *Ancyrospora langii* (Taugourdeau-Lantz) Allen, 1965, magnification $\times 500$. S-462, 1470–1475 ft, 63212, U30/4. Q, *Ancyrospora nettersheimensis* Riegel, 1973, magnification $\times 500$. A1-69, 1540 ft, 26988, K35. R–V, *Aneurospora* cf. *A. bollandensis* Steemans, 1989. R, WELL-7, 13689.7 ft, 62319, Q43. S, WELL-7, 13614.6 ft, 62377, L27. T, BAQA-1, 285.5 ft, 03CW111, E31. U, WELL-7, 13689.7 ft, 62316, C37. V, WELL-7, 13689.7 ft, 62317, J36/2.



- 1966 *Ancyrospora* sp.; de Jersey, p. 21, pl. 9, figs 5, 7.
 1968 *Ancyrospora amadei* Hodgson, p. 74, pl. 8, fig. 8.
 1968 *Ancyrospora* cf. *A. simplex* Guennel; Hodgson,
 p. 75, pl. 8, figs 9–11; text-fig. 1.
 1975 *Ancyrospora* sp. A; Grey, fig. 61b.

Dimensions. 83(103)128 μm ; 10 specimens measured.

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

Previous records. From Frasnian–Famennian of Algeria (Boumendjel *et al.* 1988; Moreau-Benoit *et al.* 1993); upper Givetian – lower Frasnian of Argentina (Ottone 1996); middle Givetian – lower Frasnian of Australia (Balme 1988; Grey 1991; Hashemi and Playford 2005); ?Givetian–Famennian of Belgium (Becker *et al.* 1974; Streel and Loboziak 1987); upper Givetian–Famennian of Bolivia (Perez-Leyton 1990); Givetian of China (Gao Lianda 1981); upper Givetian – upper Frasnian of France (Brice *et al.* 1979; Loboziak and Streel 1980, 1988); uppermost Eifelian – Givetian of Germany (Loboziak *et al.* 1990); middle Givetian – ?early Famennian of Libya (Paris *et al.* 1985; Coquel and Moreau-Benoit 1986; Streel *et al.* 1988; Moreau-Benoit 1989); Givetian of Spitsbergen, Norway (Allen 1965); and uppermost Givetian – lower Frasnian (Marshall *et al.* 1996).

Ancyrospora nettersheimensis Riegel, 1973

Figure 9Q

- 1973 *Ancyrospora nettersheimensis* Riegel, p. 100, pl. 17, figs 6–8.

Dimensions. 128(140)155 μm ; nine specimens measured.

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

Previous records. From upper Emsian – lower Eifelian of Algeria (Moreau-Benoit *et al.* 1993); upper Emsian–Eifelian of Germany (Riegel 1973; Loboziak *et al.* 1990); lower Eifelian – lower Givetian of Libya (Paris *et al.* 1985; Streel *et al.* 1988; Moreau-Benoit 1989); uppermost Emsian – ?lowermost Eifelian of Poland (Turnau 1986; Turnau *et al.* 2005); and ?late Emsian–Eifelian of Saudi Arabia (PB, pers. obs.).

Genus ANEUROSPORA Streel, 1964 emend. Richardson *et al.*, 1982

Type species. *Aneurospora goensis* Streel, 1964.

Comparison. *Synorisporites* Richardson and Lister, 1969 has distal sculpture of verrucae and/or muri. *Ambitisporites* Hoffmeister, 1959 has a uniform cingulum and is very often laevigate.

Aneurospora cf. *A. bollandensis* Steemans, 1989

Figure 9R–V

- 1983 *Cymbosporites echinatus* Richardson and Lister; Le Hérisse, p. 50, pl. 7, fig. 10.
 cf. 1989 *Aneurospora bollandensis* Steemans, p. 96, pl. 20, figs 14–19, 46.
 2008 *Aneurospora* cf. *A. bollandensis* Steemans; Steemans *et al.*, pl. 6, fig. 6.

Description. Amb is sub-circular to sub-triangular. Laesurae are straight, accompanied by labra, 1–3 μm wide individually, approximately three-quarters of the amb radius in length. Equatorial crassitude is 2–5 μm wide. Proximal region is laevigate. Distal and equatorial regions are sculptured with evenly distributed conical bacula, 1–2.5 μm wide and high, 0.5–3 μm apart. The tops of elements are flat or slightly rounded and can be slightly flared.

Dimensions. 30(36)49 μm ; nine specimens measured.

Comparison. *Aneurospora bollandensis* Steemans, 1989 is distinguished by the presence of proximal inspissations or papillae. *Cymbosporites echinatus* Richardson and Lister, 1969 in Le Hérisse (1983) is similar to *A. bollandensis* except for the absence of proximal inspissations or papillae. The specimen figured by Le Hérisse (1983, pl. 7, fig. 10) is thus considered to be synonymous with the specimens described here. *C. echinatus* is patinate and bears larger, not always parallel-sided, sculptural elements. *C. dammamensis* Steemans, 1995 is also patinate, with simple laesurae and the tops of elements are generally bifurcate.

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

Previous records. From Pragian of Armorican Massif (France; Le Hérisse 1983); and lower Lochkovian of Brazil (Steemans *et al.* 2008).

Genus APICULIRETUSISPORIA (Streel) Streel, 1967

Type species. *Apiculiretusispora brandtii* Streel, 1964.

Apiculiretusispora arabiensis Al-Ghazi, 2009

Figure 10A–B

- ? 1986 Unidentified; Turnau, pl. 8, fig. 4.
 2007 *Apiculiretusispora densa* Al-Ghazi, p. 68, pl. 1, figs 1–6; text-fig. 5 (*nom. nud.*).
 2009 *Apiculiretusispora arabiensis* Al-Ghazi, p. 193.

Dimensions. 35(53)70 μm ; 21 specimens measured.

Remarks. *Apiculiretusispora densa* Al-Ghazi, 2007 was renamed as *A. arabiensis*, because the first species name was preoccupied by *A. densa* Lu Lichang, 1988.

Comparison. *Apiculiretusispora arabiensis*, differs from all published species of the genus *Apiculiretusispora* (Streel) Streel, 1967 by its characteristic dark-coloured, rounded interrarial thickenings on the proximal face. *A. brandtii* Streel, 1964 possesses a more densely distributed conate sculpture. Turnau (1986) illustrated an unnamed specimen resembling *A. arabiensis* but no description was given.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4 and WELL-4; Jauf and Jubah formations; *papillensis-baqensis* to *svalbardiae-eximius* zones.

Previous record. From Emsian of Saudi Arabia (Al-Ghazi 2007).

Apiculiretusispora brandtii Streel, 1964

Figure 10C–D

- 1963 *Cyclogranisporites* sp. Chaloner, fig. 8.
- 1964 *Apiculiretusispora brandtii* Streel, p. 8, pl. 1, figs 6–10.
- 1966 *Cyclogranisporites* sp. McGregor and Owens, pl. 2, fig. 7, 17–19.
- 1966 ?*Perotrilites* sp. McGregor and Owens, pl. 5, fig. 13.
- 1967 *Cyclogranisporites* sp. McGregor, pl. 1, fig. 1.

Dimensions. 50(69)95 μm , 15 specimens measured.

Remarks. The specimens of *Apiculiretusispora brandtii* Streel, 1964 which show local detachment of sexine could be transitional with those of *Rhabdosporites minutus* Tiwari and Schaarschmidt, 1975 that has a completely detached sexine. The two species have a very similar fine ornamentation. In addition, they appear to intergrade with *Cymbosporites asymmetricus* Breuer *et al.*, 2007c that has the same type of ornamentation but is patinate and with an oval shape. To accommodate the morphological intergradation between these genera and species, the *A. brandtii* Morphon is defined here (Table 1). Wellman (2009) concluded that there is a smooth evolutionary transition between spores belonging to *Apiculiretusispora* (Streel) Streel, 1967 and those related to *Rhabdosporites* Richardson emend. Marshall and Allen, 1982.

Comparison. *Cymbosporites asymmetricus* Breuer *et al.*, 2007c is patinate. *A. plicata* (Allen) Streel, 1967 is smaller and does not show partial detachment of the sexine.

Occurrence. BAQA-1, BAQA-2, JNDL-1, JNDL-3, JNDL-4, WELL-1, WELL-3, WELL-4, WELL-6 and WELL-7; Jauf and

Jubah formations; *papillensis-baqensis* to *lemurata-langii* zones. A1-69; Ouan-Kasa Formation; *annulatus-protea* Zone. MG-1; Ouan-Kasa Formation; *annulatus-protea* Zone.

Previous records. *Apiculiretusispora brandtii* has an almost worldwide distribution and has been reported from Pragian through Givetian assemblages from many parts of the world; e.g. Emsian–lower Eifelian of Algeria (Moreau-Benoit *et al.* 1993); upper Emsian–upper Eifelian of Belgium (Streel 1964; Lele and Streel 1969; Lessuise *et al.*, 1979; Laloux *et al.* 1996); upper Pragian–lower Emsian of Paraná Basin, Brazil (Mendlowicz Mauller *et al.* 2007); Emsian–Eifelian of Canada (McGregor and Owens 1966; McGregor 1973); Pragian–lower Emsian of Armorican Massif, France (Le Hérissé 1983); upper Emsian–lower Givetian of Germany (Riegel, 1968; Tiwari and Schaarschmidt 1975); middle Emsian–lower Givetian of Libya (Paris *et al.* 1985; Streel *et al.* 1988; Moreau-Benoit 1989); upper Emsian of Luxembourg (Steevens *et al.* 2000a); upper Pragian–Emsian of Morocco (Rahmani-Antari and Lachkar 2001); Pragian–middle Eifelian of Poland (Turnau and Matyja 2001; Turnau *et al.* 2005); Emsian of Saudi Arabia (Al-Ghazi 2007); upper Pragian–?lowermost Emsian of Scotland (Wellman 2006); and ?Emsian–Eifelian of Georgia, USA (Ravn and Benson 1988).

Apiculiretusispora plicata (Allen) Streel, 1967

Figure 10E–F

- 1965 *Cyclogranisporites plicatus* Allen, p. 695, pl. 94, figs 6–9.
- 1966 ?*Perotrilites* sp.; McGregor and Owens, pl. 5, fig. 13.
- 1967 *Apiculiretusispora plicata* (Allen) Streel, p. 33, pl. 2, figs 31, 34.
- 1968 *Cyclogranisporites plicatus* Allen; Lanninger, p. 120, pl. 22, fig. 3.
- 1972 *Granulatisporites* sp.; Kemp, p. 110, pl. 52, figs 4–5, 7.
- 1974 ?*Apiculiretusispora plicata* (Allen) Streel; McGregor, pl. 1, fig. 39.

Description. Amb is sub-circular to more rarely sub-triangular. Laesurae are simple, straight, c. 1 μm wide and equals three-fifths or almost extends to the amb radius. Curvaturae are visible. Distal and equatorial regions are ornamented with small conical or spinous, up to 1 μm high, rarely up to 1 μm wide and 0.5–1 μm apart. proximal surface laevigate. Exine is 0.5–2 μm thick.

Dimensions. 41(49)73 μm ; 39 specimens measured.

Comparison. *Apiculiretusispora plicata* is distinguished from *A. brandtii* Streel, 1964 by its smaller size and does not show partial detachment of the sexine. In addition, ornamentation of the former is more regular and slightly less packed. *A. microconus* (Richardson) Streel, 1967 has an ornamentation similar to *A. plicata* but is much larger.

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

Previous record. *Apiculiretusispora plicata* has a worldwide distribution and has been widely reported from Lower Devonian through Middle Devonian assemblages.

Genus ARCHAEOZONOTRILETES Naumova emend. Allen,
1965

Type species. *Archaeozonotriletes variabilis* Naumova emend. Allen, 1965.

Comparison. *Cymbosporites* Allen, 1965 has a variably sculptured patina. *Cyrtospora* Winslow, 1962 has a laevigate distal surface with a large irregular intumescent or glebous mass and tubercles.

Archaeozonotriletes chulus (Cramer) Richardson and Lister,
1969

Figure 10G–H

- 1966b *Retusotriletes chulus* Cramer, p. 74, pl. 2, fig. 14.
1969 *Archaeozonotriletes chulus* var. *chulus* (Cramer)
Richardson and Lister, p. 234, pl. 43,
figs 1–6; text-fig. 4.
1969 *Archaeozonotriletes chulus* (Cramer) var. *nanus*
Richardson and Lister, p. 238, pl. 43, figs 10–11;
text-fig. 4.
1973 *Tholisporites chulus* var. *chulus* (Cramer) McGre-
gor, p. 56, pl. 7, figs 13–15.

Dimensions. 27(31)37 μ m; 14 specimens measured.

Remarks. The specimens encountered here are included in the *A. chulus* Morphon introduced by Steemans *et al.* (1996). It includes two varieties: *chulus* and *nanus* Richardson and Lister (1969), which collectively extend over a large size range. As these varieties closely intergrade, they are not distinguished here. In polar compression, some *Archaeozonotriletes* Naumova emend. Allen, 1965 resemble spores of the genus *Ambitisporites* Hoffmeister, 1959

except that the former have very thin contact areas. However, some tetrads and obliquely compressed specimens show clearly that the exine is much thicker at the equator and over the distal surface (Richardson and Lister 1969).

Comparison. *Ambitisporites avitus* Hoffmeister, 1959 and *A. dilutus* (Hoffmeister) Richardson and Lister, 1969 appear to have a more or less similar equatorial thickening. They can be distinguished from *Archaeozonotriletes chulus* since these species show an equatorial thickening that clearly narrows opposite the laesurae. They lack the thin proximal face and thick distal wall. *Retusotriletes semizonalis* McGregor, 1964 does not have the pronounced differential thickening between the proximal and distal surfaces of the spores described above and has minute sculpture.

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

Previous records. *Archaeozonotriletes chulus* has a worldwide distribution and has been widely reported from Silurian through Lower Devonian palynofloras. Locally it seems to reach rarely the Eifelian (Ravn and Benson 1988).

Archaeozonotriletes variabilis Naumova emend. Allen, 1965
Figure 10I–J

- 1953 *Archaeozonotriletes variabilis* Naumova, p. 30, 83,
pl. 2, figs 12–13; pl. 12, figs 8–11; pl. 13, figs 7–9.
1965 *Archaeozonotriletes variabilis* Naumova emend.
Allen, p. 721, pl. 100, figs 3–6.

Dimensions. 46(58)71 μ m; 12 specimens measured.

Remarks. As *A. variabilis* has a very thick distal patina, it is therefore frequently preserved in oblique compression, thus giving the impression of an irregular cingulum. The thickness of the patina may comprise as much as two-fifths of the amb diameter.

FIG. 10. Each figured specimen is identified by borehole, sample, slide number and England Finder Co-ordinate location. All figured specimens are at magnification $\times 1000$ except where mentioned otherwise. A–B, *Apiculiretusispora arabiensis* Al-Ghazi, 2009. A, JNDL-1, 174.6 ft, 60848, V29. B, BAQA-1, 308.3 ft, 03CW112, E43. C–D, *Apiculiretusispora brandtii* Strel, 1964. C, JNDL-4, 182.5 ft, 03CW220, T31. D, BAQA-1, 227.1 ft, 03CW110, L-M25. E–F, *Apiculiretusispora plicata* (Allen) Strel, 1967. E, WELL-3, 14186.3 ft, 66833, W44. F, BAQA-1, 169.1 ft, 03CW103, V24. G–H, *Archaeozonotriletes chulus* (Cramer) Richardson and Lister, 1969. G, JNDL-1, 172.7 ft, PPM007, U40/1. H, JNDL-1, 172.7 ft, 60845, L47/4. I–J, *Archaeozonotriletes variabilis* Naumova emend. Allen, 1965. I, MG-1, 2292 m, 63025, H32. J, MG-1, 2241 m, 62964, F34/1. K, *Auroraspora macromanifesta* (Hacquebard) Richardson, 1960, magnification $\times 750$. MG-1, 2241 m, 62966, U46. L–M, *Auroraspora minuta* Richardson, 1965, magnification $\times 750$. L, MG-1, 2258 m, 62948, U28/4. M, MG-1, 2264 m, 62951, F34.

