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A distinctive marginal marine palynological assemblage from the Přídolí of northwestern Saudi Arabia

Un assemblage palynologique marin marginal distinctif du Přídolí du nord-ouest d'Arabie Saoudite

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Abstract

A rare occurrence of a rich and diverse palynological assemblage from the Tawil Formation is described from well JLMD-EW-8 in northwestern Saudi Arabia. The composition of this assemblage strongly indicates a middle Přídolí age. The assemblage encountered contains very characteristic chitinozoans, acritarchs, tasmanitids, freshwater algae, scolecodonts, eurypterid cuticle and other organic remains. Land-derived miospores are also common and two new cryptospore species (*Cymbohilates jalamidensis* and *Gneudnaspora sordida*) are herein formally described. Most taxa of taxonomic interest and useful for regional and intercontinental correlation are illustrated. The palaeogeographic distribution of this assemblage is also discussed as organic-walled microphytoplankton, chitinozoans and miospores encountered in the studied samples correlate well with similar assemblages from various Algerian, Libyan, and Ibero-armorican localities (i.e. Ibarmaghian regions). This corresponds to what is considered as a transgressive middle Přídolí event in the Algerian Sahara, with non-marine intervals bracketing this brief marine sea level rise. This event is likely to have extended into all of north Gondwana, including Arabia, and can be correlated to the S50 Maximum Flooding Surface from the sequence stratigraphic framework defined in the Neflex Geodynamic Earth Model.

Résumé

Une occurrence rare d'un assemblage palynologique riche et diversifié de la Formation Tawil est décrite du sondage JLMD-EW-8 effectué dans le nord-ouest de l'Arabie Saoudite. La composition de cet assemblage indique clairement un âge Pridolí moyen. L'assemblage contient des chitinozoaires, acritarches, tasmanitides, algues d'eau douce, scolécodontes, cuticules d'euryptérides et autres restes organiques très caractéristiques. Des miospores continentales sont également fréquentes et deux nouvelles espèces de cryptospore (*Cymbohilates jalamidensis* et *Gneudnaspora sordida*) sont ici formellement décrites et proposées. La plupart des taxons d'intérêt taxonomique et utiles pour les corrélations régionales et intercontinentales sont illustrés. La distribution paléogéographique de cet assemblage est également discutée, étant donné que comme certaines formes du microphytoplancton à paroi organique, des chitinozoaires et des miospores rencontrés dans les échantillons étudiés sont trouvés dans des assemblages similaires provenant de diverses localités algériennes, libyennes, et ibéro-armoricaines (à savoir les régions ibarmaghiennes). Cet assemblage correspond à ce qui est considéré comme un événement transgressif court du Pridolí moyen dans le Sahara algérien, avec des intervalles non-marins le précédant et le succédant. Cet événement est susceptible de s'être étendu à l'ensemble du Nord Gondwana, y compris l'Arabie et peut être corrélé en stratigraphie séquentielle à la surface d'inondation maximale S50 définie par Neflex dans son modèle géodynamique de la Terre.

Keywords: Acritarchs; Chitinozoans; Spores; Biostratigraphy; Pridolí; Saudi Arabia

Mots clés : Acritarches ; Chitinozoaires ; Spores ; Biostratigraphie ; Pridolí ; Arabie Saoudite

1. Introduction

The biostratigraphy of the Tawil Formation is poorly documented especially because of its continental nature in most of Saudi Arabia and sand-dominated facies unsuitable for palynology. Only a few publications partly document the taxonomy and distribution of the palynological assemblages from the Tawil Formation (e.g. Steemans; 1995; Al-Hajri et al., 1999; Steemans et al., 2007) but these studied sections were exclusively located in proximal settings in eastern Saudi Arabia. Consequently, they only yielded miospore assemblages and lacked independent biostratigraphic control. More marine assemblages however occur in northwestern Saudi Arabia, where the Tawil deposits are more distal, allowing a better worldwide age calibration.

This study describes a rich marginal marine palynological assemblage from a well, which penetrated the Tawil Formation in northwestern Saudi Arabia. Although Al-Hajri et al. (2008) briefly described this assemblage previously, the purpose of this study is to give an exhaustive description of organic-walled microphytoplankton, chitinozoan and miospore assemblages, and integrate the palynological data. Although this study is stratigraphically limited to a single isolated core from the Tawil Formation, the palaeogeographical relationships and palaeocological implications of the described

assemblage can be drawn by comparison with other coeval sections from northern Gondwana, allowing placement of this assemblage in a sequence stratigraphic context.

2. Location and geological setting

Well JLMD-EW-8 was drilled in 1983 as a water supply well in the Jalamid area in northwestern Saudi Arabia (Fig. 1). From top to bottom, this well successively penetrated Neogene, Upper Cretaceous and Palaeozoic formations. The Palaeozoic succession includes the Jauf (268–366 m), Tawil (366–1582 m) and Qalibah (1581–1996 m) formations. The Tawil Formation stratigraphically extends between the Sharawra Member of the Qalibah Formation and the Sha'iba Member of the Jauf Formation. It was deposited after a period of uplift, which affected most of Saudi Arabia (Senalp, 2006). Unfortunately, no hydrocarbon reservoir has been yet discovered in the thick sandstone sequence of the Tawil Formation, and therefore until recently, no detailed sedimentological study has been carried out on it. Al-Laboun and Walthall (1988) stated that the Tawil Formation represents the maximum retreat of the Silurian seas and marks the beginning of a Devonian transgression.

In outcrops, the Tawil Formation can be subdivided into four or five subunits, separated by erosional surfaces, which correspond to fining- and thinning upward sequences (Janjou et al., 1996; Senalp, 2006). During deposition of the Tawil Formation, the sequence boundaries were developed corresponding to relative sea-level fall. Each systems tract, confined by sequence boundaries, shows a continuous change in depositional facies from braided fluvial system in proximal parts (landward) to open marine sediments in distal parts (seaward). The Tawil Formation is comprised of a generally eastward prograding clastic sequence that is divided into three packages: alluvial plain, coastal plain and offshore marine.

The Tawil Formation is dated in the subsurface by miospores (e.g. Steemans; 1995; Al-Hajri et al., 1999). It extends from Ludlow (late Silurian) to early Pragian (Early Devonian). Stump et al. (1995) first reported on the present assemblage discussed herein, attributing it to the Přídolí. Al-Hajri et al. (2008) then briefly illustrated the assemblage and discussed the inter-regional correlation with coeval sections.

3. Material and methods

This study concerns three samples (637.19 m, 638.43 m and 639.42 m) from core 6 in well JLMD-EW-8, northwestern Saudi Arabia. Samples were processed in the laboratory of Saudi Aramco in Dhahran. Samples were prepared using standard palynological acid maceration techniques to mount palynological microscope slides. The procedure described by Paris (1981) for the isolation and preparation of chitinozoans was also used to prepare SEM stubs. The samples were productive, yielding abundant palynomorphs that are well preserved and of low thermal maturity (T.A.I. ca. 2+). All figured material from the palynological slides is housed in the collections of the laboratory of

‘*Palaeobiogeology, Palaeobotany, Palaeopalynology*’, Liège University and ‘*Domaines Océaniques*’, Institut Universitaire Européen de la Mer. Individual specimens on palynological slides are located by providing sample, slide details and England Finder Co-ordinates (EFC). SEM stubs are stored in the Saudi Aramco collections in Dhahran.

4. Systematic palaeontology

4.1. Identified taxa

All palynomorph genera and species present in the assemblage are alphabetically listed by genera and species under their respective categories. The illustrated taxa are also indicated (Plates 1–14).

Organic-walled microphytoplankton

- Arkonion nova* Le Hérisse, 2002 (Plate 8, Figs. 16 and 17)
Arkonion paulumstriata Le Hérisse, 2002 (Plate 8, Fig. 18)
Arpylorus antiquus Calandra, 1964
Baltisphaeridium sp. 3 in Le Hérisse, 2002 (Plate 8, Fig. 4)
Cepillum puerospinoides Cramer, 1964a (Plate 12, Fig. 9)
Clypeolus tortugoides (Cramer) Miller et al., 1997 (Plate 12, Figs. 4–6)
Cymatiosphaera aff. *C. mariae* Cramer et al., 1976 (Plate 11, Fig. 9)
Cymatiosphaera nimia Le Hérisse, 2002 (Plate 11, Fig. 10)
Cymbosphaeridium pilaris typicum (Cramer) Le Hérisse, 1989 (Plate 7, Fig. 14)
Cymbosphaeridium sp. 1 in Le Hérisse, 2002 (Plate 7, Figs. 10 and 11)
Cymbosphaeridium sp. 5 in Le Hérisse, 2002 (Plate 7, Figs. 12 and 13)
Deflandrastrum colonnae Combaz, 1962 (Plate 8, Fig. 19)
Dactylofusa oblancae (Cramer and Díez) Cramer, 1968 (Plate 9, Fig. 6)
Dictyotidium aff. *D. eurydictyotum* Kiryanov, 1978 (Plate 11, Fig. 11)
Dictyotidium legionis (Cramer) Rodriguez, 1983 (Plate 11, Figs. 5 and 6)
Dictyotidium sp. (Plate 11, Figs. 7 and 8)
Dorsennidium sp. (Plate 8, Fig. 14)
Duvernaysphaera aranaides (Cramer) Le Hérisse, 1989
Elektoriskos sp. (Plate 6, Fig. 12)
Eupoikilofusa cantabrica (Cramer) Cramer, 1970 (Plate 9, Fig. 3)
Eupoikilofusa filifera (Downie) Dorning, 1981 (Plate 9, Figs. 1, 2 and 4)
Eupoikilofusa striatifera (Cramer) Cramer, 1970
Evittia cymosa Loeblich, 1970 (Plate 6, Figs. 5–7)
Evittia spp. (Plate 6, Figs. 1–4)
Geron sp. (Plate 11, Figs. 3 and 4)
Hemibaltisphaeridium dedosmuertosi (Cramer) Cramer, 1970 (Plate 7, Figs. 1 and 2)
Leiofusa banderillae Cramer, 1964b (Plate 9, Fig. 5)
Leoniella carminae Cramer, 1964a (Plate 6, Fig. 13)
Leprotolypa gordonense (Cramer) Colbath, 1979 (Plate 6, Figs. 8–10)
?Lophodiacrodium sp. (Plate 8, Figs. 1–3, 8)
Mazuelloid (Plate 8, Fig. 20)

Michrystridium stellatum Deflandre, 1945 (Plate 7, Fig. 15)
Michrystridium spp. (Plate 7, Figs. 16–19)
Multiplicisphaeridium malum (Cramer) Eisenack et al., 1973
Multiplicisphaeridium moharra Cramer et al., 1976 (Plate 6, Figs. 14–16)
Multiplicisphaeridium pardaminum Díez and Cramer, 1976
Multiplicisphaeridium sp. 4 in Le Hérisse, 2002 (Plate 7, Figs. 3–5)
Multiplicisphaeridium spp. (Plate 7, Figs. 6–9)
Nothooidium sp. in Le Hérisse, 2002
Nanocyclopia sp. (Plate 12, Fig. 19)
Onondagella asymmetrica (Deunff) Cramer, 1966 (Plate 8, Figs. 9 and 10)
Ovnia desertica Cramer and Díez, 1977 (Plate 12, Fig. 3)
Ovnia uahabita Cramer and Díez, 1977 (Plate 12, Figs. 1 and 2)
Pardaminella crassicosta Díez and Cramer, 1976 (Plate 12, Fig. 18)
Perforella perforata Díez and Cramer, 1976 (Plate 12, Figs. 7 and 8)
Polyedryxium rabians Cramer, 1964a
Proteolobus sp. (Plate 11, Fig. 20)
Pulvinosphaeridium trifidum Kiryanov, 1978 (Plate 11, Fig. 12)
Pulvinosphaeridium sp.
Quadraditum fantasticum Cramer, 1964a
Quadrisporites spp. (Plate 11, Figs. 16–19)
Saturnus? sp. (Plate 12, Figs. 17 and 20)
Schismatosphaeridium sp. 1 in Le Hérisse, 2002 (Plate 12, Figs. 10–12)
 Scolecodonts
Solisphaeridium eriza Cramer et al., 1976 (Plate 6, Fig. 11)
 Tasmanitids
Triangulina alargada Cramer, 1964a (Plate 8, Figs. 7 and 12)
Triangulina sanpetrensis (Cramer) Fensome et al., 1990
Tunisphaeridium caudatum Deunff and Evitt, 1968 (Plate 11, Figs. 1 and 2)
Umbellasphaeridium? aff. *Umbellasphaeridium?* *wicanderi* Richards and Mullins, 2003 (Plate 7, Figs. 20–25)
Veryhachium europaeum Stockmans and Willièrè, 1960 (Plate 8, Fig. 11)
Veryhachium trispinosum (Eisenack) Downie, 1959 (Plate 8, Fig. 13)
Veryhachium sp. (Plate 8, Fig. 15)
Visbysphaera albanega (Cramer et al.) Le Hérisse, 2002 (Plate 9, Figs. 7–12)
Visbysphaera bonita (Cramer) Le Hérisse, 2002 (Plate 10, Figs. 1 and 2)
Visbysphaera gotlandica (Eisenack) Lister, 1970 (Plate 9, Figs. 13–16)
Visbysphaera jardinei (Cramer) Le Hérisse, 2002 (Plate 10, Figs. 3–9)
Visbysphaera pirifera (Eisenack) Lister, 1970 (Plate 9, Fig. 17)

Chitinozoans

Ancyrochitina brevis Taugourdeau and de Jekhowsky, 1960 (Plate 13, Figs. 5–7; Plate 14, Figs. 1–3)
Ancyrochitina regularis Taugourdeau and de Jekhowsky, 1960
Cingulochitina serrata (Taugourdeau and de Jekhowsky, 1960) (Plate 13, Fig. 4; Plate 14, Fig. 4)
Eisenackitina lagenomorpha (Eisenack, 1931) (Plate 13, Fig. 8)

Eisenackitina granulata (Cramer, 1964a)
Hoegisphaera staplini Cramer, 1966 (Plate 12, Fig. 13)
Hoegisphaera testudo Cramer, 1966 (Plate 12, Fig. 14)
Margachitina elegans (Taugourdeau and de Jekhowsky, 1960) (Plate 13, Figs. 1–3; Plate 14, Fig. 6)
Pseudoclathrochitina carmenchui Cramer, 1964a (Plate 13, Fig. 9; Plate 14, Figs. 8–10)
Sphaerochitina sphaerocephala (Eisenack, 1932)
Urnochitina urna (Eisenack, 1934) (Plate 14, Fig. 5)
Vinnalochitina corinnae (Jaglin, 1986) (Plate 13, Figs. 11–12; Plate 14, Fig. 7)

Cryptospores

Artemopyra laevigata Wellman and Richardson, 1996 (Plate 1, Fig. 1)
Chelinohilates erraticus Richardson, 1996 (Plate 1, Figs. 2–9)
Cymbohilates cymosus Richardson, 1996 (Plate 1, Fig. 10)
Cymbohilates jalamidensis nov. sp. (Plate 1, Figs. 11–20)
Cymbohilates sp. B in Lavender and Wellman (2002) (Plate 1, Figs. 21–23)
Dyadospora murusattenuata Strother and Traverse, 1979 (Plate 2, Figs. 1 and 2)
Gneudnaspora divellomedia (Chibrikova) Balme, 1988 var. *minor* Breuer et al., 2007 (Plate 2, Figs. 3–7)
Gneudnaspora sordida nov. sp. (Plate 2, Figs. 8–20)
Pseudodyadospora petasus Wellman and Richardson, 1993 (Plate 2, Fig. 21)
Tetrahedraletes medinensis Strother and Traverse emend. Wellman and Richardson, 1993 (Plate 2, Figs. 22 and 23)

Trilete and monolete spores

Ambitisporites avitus Hoffmeister, 1959 (Plate 3, Fig. 1)
Aneurospora bollandensis Steemans, 1989 (Plate 3, Fig. 2)
Aneurospora cf. *A. bollandensis* Steemans, 1989 (Plate 3, Figs. 3 and 4)
Aneurospora isidori (Cramer and Díez) Richardson et al., 1982 (Plate 3, Fig. 5)
Aneurospora richardsonii (Rodríguez) Richardson et al., 2001 (Plate 3, Figs. 6–9)
Aneurospora spp.
Archaeozonotriletes chulus Richardson and Lister, 1969 (Plate 3, Fig. 10)
Archaeozonotriletes chulus var. *inframurinus* Richardson and Lister, 1969 (Plate 3, Fig. 11)
Breconisporites simplex Wellman, 1993 (Plate 3, Figs. 12 and 13)
cf. *Brochotriletes* sp. A in Richardson and Ioannides (1973) (Plate 3, Fig. 14)
Chelinospora hemiesferica (Cramer and Díez) Richardson et al., 2001 (Plate 3, Fig. 15)
Chelinospora cf. *C. hemiesferica* (Cramer and Díez) Richardson et al., 2001 (Plate 3, Figs. 16–25)
Chelinospora lavidensis Richardson et al., 2001 (Plate 3, Fig. 26)
Chelinospora sanpetrensis (Rodríguez) Richardson et al., 2001 (Plate 4, Fig. 1)
Chelinospora sp. 1 in Rubinstein and Steemans (2002) (Plate 4, Fig. 2)
Chelinospora sp. A (Plate 4, Figs. 3–9)
Chelinospora spp. (Plate 4, Figs. 10 and 11)

Concentricosporites sagittarius (Rodriguez) Rodriguez, 1983 (Plate 4, Fig. 12)
Coronaspora reticulata Richardson et al., 2001 (Plate 4, Figs. 13–16)
Coronaspora subornata (Cramer and Díez) Richardson et al., 2001 (Plate 4, Fig. 17)
Cymbosporites multiconus Steemans, 1989 (Plate 4, Fig. 18)
Cymbosporites sp. A in Richardson and Ioannides (1973) (Plate 4, Fig. 19)
Cymbosporites sp. (Plate 4, Figs. 20 and 21)
Devonomonoletes sp. (Plate 4, Fig. 22)
Emphanisporites multicostatus Rodriguez, 1978a (Plate 4, Figs. 23–25)
Emphanisporites novellus McGregor and Camfield, 1976 (Plate 4, Fig. 26)
Emphanisporites spp. (Plate 4, Figs. 27–29)
Iberoespora cantabrica Cramer and Díez, 1975 (Plate 4, Figs. 30–32)
Iberoespora glabella Cramer and Díez, 1975 (Plate 4, Fig. 33)
Iberoespora guzmani Cramer and Díez, 1975 (Plate 5, Figs. 1–4)
Iberoespora sp. 2 in Rubinstein and Steemans (2002) (Plate 5, Fig. 5)
Insolisporites anchistinus Burgess and Richardson, 1995 (Plate 5, Figs. 6 and 7)
Retusotriletes bipellis Rodriguez, 1978a (Plate 5, Figs. 8 and 9)
Retusotriletes dubius (Eisenack) Richardson, 1965 (Plate 5, Fig. 10)
Retusotriletes maculatus McGregor and Camfield, 1976 (Plate 5, Figs. 11 and 12)
Retusotriletes spp.
Retusotriletes? *saturnus* Richardson et al., 2001 (Plate 5, Figs. 13–15)
Scylaspora downiei Burgess and Richardson, 1995 (Plate 5, Fig. 16)
Scylaspora elegans Richardson et al., 2001 (Plate 5, Fig. 17)
Synorisporites cf. *S. libycus* Richardson and Ioannides, 1973 (Plate 5, Figs. 18–21)
Synorisporites verrucatus Richardson and Lister, 1969 (Plate 5, Figs. 22–25)
Synorisporites sp. (Plate 5, Figs. 26 and 27)

4.2. Systematic descriptions

New taxa of cryptospores are described below.

Genus *Cymbohilates* Richardson emend. Breuer et al., 2007

Type species: *Cymbohilates horridus* Richardson, 1996.

Cymbohilates jalamidensis nov. sp.

Plate 1, Figs. 11–20

Derivation of name: Refers to the locality where this species was found; *jalamidensis* = from Jalamid (Latin).

Holotype: Plate 1, Fig. 16, well JLMD-EW-8, sample 638.43 m, slide 53536(6), EFC O44.

Paratypes: Plate 1, Fig. 15, well JLMD-EW-8, sample 638.43 m, slide 53536(6), EFC G41. Plate 1, Fig. 17, well JLMD-EW-8, sample 638.43 m, slide 53536(6), EFC U40/1.

Diagnosis: A *Cymbohilates* with conical bacula.

Description: Amb is circular to subcircular. An undulating to regular curvatura delimits a more or less circular hilum. The smooth proximal surface shows random tears

or different types of tears such as a simple slit or pseudo-trilete mark. Exine is sculptured subequatorially and distally with evenly distributed conical bacula 0.5–2.0 µm high, 0.5–3.0 µm wide at base. The bacula are discrete (0.5–3.0 µm apart) or can sometimes be locally fused to form short, convolute ridges. The tops of elements are flat or rounded. Exine is 0.5–1.0 µm thick.

Dimensions: Amb diameter 28 (33) 36 µm, 13 specimens measured.

Comparison: *Cymbohilates bakaensis* Breuer et al., 2007 is sculptured with more delicate bacula, the tops of which can be slightly concave with a generally bifurcate shape. Sculptural elements of *Cymbohilates baculatus* Turnau et al., 2005 also possesses bacula but these are narrower at the base and parallel-sided.

Genus *Gneudnaspora* Balme emend. Breuer et al., 2007

Type species: *Gneudnaspora kernickii* Balme, 1988.

Gneudnaspora sordida nov. sp.

Plate 2, Figs. 8–20

Derivation of name: Refers to the appearance of the curvatura; *sordidus* = sordid (Latin).

Holotype: Plate 2, Fig. 12, well JLMD-EW-8, sample 637.19 m, slide 53535(6), EFC N37.

Paratypes: Plate 2, Fig. 13, well JLMD-EW-8, sample 637.19 m, slide 53535(6), EFC U43. Plate 2, Fig. 16, well JLMD-EW-8, sample 638.43 m, slide 53536(6), EFC R35/4.

Diagnosis: A *Gneudnaspora* with an irregular and complex zonal curvatural zone.

Description: Amb is circular to subcircular. The hilum is well defined by an irregular curvatura. The hilum radius commonly equals $\frac{1}{2}$ to $\frac{3}{4}$ of the amb radius. Narrow, concentric ridges and/or irregular radial muri can characterize the zone outside the curvatura. The contact face exine is thinner than the rest of the spore body. Distal exine is 0.5–1.0 µm thick. Proximal and distal surfaces are laevigate.

Dimensions: Amb diameter 26 (43) 57 µm, 14 specimens measured.

Comparison: *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988 has a hilum defined by a simple and regular curvatura and its hilum/amb radius ratio is larger as the hilum radius equals three-quarters to six-sevenths of the amb radius. *Artemopyra? scalariformis* Richardson, 1996 has also an irregular curvatura but the latter consists dominantly of short radial subequatorial muri bounded by concentric ridges. Besides the hilum radius equals at least $\frac{4}{5}$ of the amb radius.

Remarks: A second parallel curvatural ridge, generally closely appressed to the original curvatura, can be present on the hilum. This characteristic seems to suggest that this species is bi-layered.

5. Results

5.1. Organic-walled microphytoplankton

The organic-walled microphytoplankton assemblage is characterized by high species diversity, but with dominance of a few groups or genera, such as *Cymbosphaeridium*, which displays significant polymorphism. Although there are some differences between these assemblages they show similarities with other material described from the upper Silurian sequences elsewhere, in Bolivia (Cramer et al., 1974), Spain (Cramer, 1964a,b, 1970; Díez and Cramer, 1976; Cramer et al., 1976), Algeria (Jardiné et al., 1974), Libya (Richardson and Ioannides, 1973; Le Hérisse, 2002), Turkey (Erkmen and Bozdogan, 1979; Le Hérisse, personal observations) and Pomerania (Jachowicz, 2000).

The marine palynomorphs referred to as organic-walled microphytoplankton, include acritarchs (*incertae sedis*) and microalgae (prasinophyceae, hydrodictyaceae, zygnematales). Some of the most interesting species are: *Arkonina nova*, *A. paulumstriata*, *Arpylorus antiquus* (only fragments), *Baltisphaeridium* sp. 3 in Le Hérisse, 2002 (pl. III, fig.13), *Cepillum puerospinoides*, *Clypeolus tortugoides*, *Cymbosphaeridium* spp., *Deflandrastum colonnae*, *Dactylofusa oblancae*, *Duvernaysphaera aranoides*, *Eupoikilofusa cantabrica*, *Geron* sp., *Hemibaltisphaeridium dedosmuertosi*, *Leprotolypa gordonense*, *Multiplicisphaeridium moharra* (= *Estiastra* cf. *barbata* Downie in Richardson and Ioannides, 1973), *Multiplicisphaeridium* sp. 4 in Le Hérisse, 2002 (pl. IV, figs. 14 and 15), *Nothooidium* sp. in Le Hérisse, 2002 (pl. II, fig. 8), *Pulvinosphaeridium trifidum*, *Ovnia desertica*, *Pardaminella crassicosta*, *Perforella perforata*, *Schismatosphaeridium* sp. 1 in Le Hérisse, 2002 (pl. IV, fig. 9), *Triangulina sanpetrensis*, *Tunisphaeridium caudatum*, *Visbysphaera albanega*, *V. bonita* and *V. jardinei*.

The type material of two species (*Dactylofusa oblancae* and *Ovnia desertica*) mentioned herein originally came from Saudi Arabian material, described respectively by Cramer and Díez (1968) and Cramer and Díez (1977).

The systematic position of *Visbysphaera bonita* and *V. jardinei*, and their difference with *Thysanoprobolus polykion* Loeblich and Tappan, 1970, were previously discussed in Le Hérisse (2002). They are excellent markers of the upper Silurian (upper Ludfordian to Přídolí) of the North Gondwana region. However, they are cosmopolitan as well, because they are known also in the Middle East, as demonstrated herein, and are also recorded from the upper Silurian of Bolivia, South America (Cramer et al., 1974; Le Hérisse, unpublished data) and Pomerania (Jachowicz, 2000).

Some fragments of *Arpylorus antiquus* re-interpreted as eurypterid remains (Le Hérisse et al., 2012) are also represented in the material. Some fragments of mazuelloids, enigmatic phosphatized microfossils, sometimes referred to as acritarchs (Kremer, 2005), are also encountered. We postulate that they are mainly found in deep-water biofacies. They are, for example associated with acritarchs and chitinozoa at the Ludlow/Přídolí boundary of the Bohemian succession of the Prague Basin in the Czech Republic (Le Hérisse, 1992), and the Siluro-Devonian stratotype of Klonck (Brocke et al., 2006). Kremer (2005) suggest mazuelloids could be related to environments influenced by upwelling currents.

5.2. Chitinozoans

Twelve chitinozoan taxa, identified at the species level, were recovered from the investigated core samples. They belong to a single assemblage as there are no major differences in assemblage composition between the three samples. The assemblage is characterized mainly by common *Ancyrochitina brevis*, *Margachitina elegans*, *Pseudoclathrochitina carmenchui* and *Vinnalochitina corinnae*. Other species, such as *Urnochitina urna*, are much rarer. The recorded species are classical components of the late Silurian chitinozoan assemblages from northern Gondwana regions (see below). *P. carmenchui* was frequently misidentified prior to the use of SEM for routine observations (e.g. *Bursachitina lagenomorpha* in Deunff et al., 1971). *Ancyrochitina brevis* and *Ancyrochitina regularis*, originally described by Taugourdeau and de Jekowsky (1960) as “varieties” of *A. fragilis* Eisenack, 1955, were raised to the species rank by Paris (1981). The synonymy lists published by Jaglin and Paris (2002) provide a detailed review of the occurrences of *A. brevis*, *A. regularis*, *U. urna*, *M. elegans* and *P. carmenchui* in northern Gondwana localities.

5.3. Spores

The three studied samples yielded more-or-less identical assemblages comprising 52 species. Most of these species are only known from the late Silurian. The two eponymous species of the EC Biozone (Richardson et al., 2001), *Scylaspora elegans* and *Iberoespora cantabrica*, are present in the Saudi material. This biozone is middle-late Přídolí to earliest Lochkovian in age, which is in accordance with age dating based on chitinozoans and acritarchs. However, four of the reported miospores species were not previously known below the Lochkovian. They are *Aneurospora isidori*, *Cymbosporites multiconus*, *Iberoespora glabella* and *I. guzmani*. Due to the paucity of data around the Silurian/Devonian boundary, it seems most likely that the range of those four species should be extended down into the Přídolí.

6. Discussion

6.1. Biostratigraphy

The ranges of selected organic-walled microphytoplankton, chitinozoan and spore species of biostratigraphic significance are shown on Fig. 2, together with the north Gondwana chitinozoan zonation of Paris (1996) and Paris and Verniers (2004) and the miospore zonation established by Richardson et al. (2001) in Spain and Loboziak and Melo (2002) in Western Gondwana.

Within the chitinozoan assemblage, some species are moderately long ranging (e.g. *Sphaerochitina sphaerocephala* and *Cingulochitina serrata*) whereas others are of greater chronostratigraphic interest (e.g. *Margachitina elegans* and *Pseudoclathrochitina carmenchui*) due to their more limited stratigraphic ranges. The chitinozoan assemblage

illustrated here belongs to the *elegans* global chitinozoan biozone of Verniers et al. (1995) that is defined by the joint occurrence of *M. elegans* and *P. carmenchui*. A middle Přídolí age is therefore suggested for this assemblage (Fig. 2). It corresponds to Assemblage D of Jaglin and Paris (2002) recovered from the 2125.1–2141.8 m interval from the Alternances Grésos-Argileuses Formation in well A1-61, northwestern Libya. Furthermore, Assemblage D of Jaglin and Paris (2002) includes Biozone 3 of Le Hérissé (2002) as described below.

Unfortunately, no independent biostratigraphic graptolite or conodont control is available for a precise chronostratigraphical assignment of the concurrent range biozone of *M. elegans* and *P. carmenchui* within the Přídolí. However, the range of the underlying *kosovens* biozone (lowest chitinozoan biozone of the Přídolí) is chronostratigraphically well constrained in the GSSP of the Přídolí Series in the Czech Republic (co-occurrence with *Monograptus parultimus*, the index graptolite for the base of the Přídolí; see Kriz et al., 1986). *Fungochitina kosovens* occurs before the FAD of *M. elegans* in well A1-61 in Libya (Jaglin and Paris, 2002, fig. 3) and thus the association of *M. elegans* and *P. carmenchui* can be confidently regarded as representative of the middle part of the Přídolí. Indeed, they do not range through *Anthochitina superba* Eisenack, 1971, the index species of the highest chitinozoan biozone of the Přídolí (Verniers et al., 1995; Paris, 1996).

The spore assemblage here reported, belongs to the Spanish EC biozone of Richardson et al (2001). However, *Aneurospora* seems to occur here at horizons older than in Spain, as also suggested by Rubinstein and Steemans (2002) in their material from Libya.

Although the facies dependence of organic-walled microphytoplankton, variations in ecological tolerances and the employment of different trophic strategies by different organic-walled microphytoplankton have been demonstrated (e.g. Le Hérissé, 2002), the organic-walled microphytoplankton assemblage provides here a good alternative for the discussion of the biostratigraphy. The palynoflora described herein are very similar to that described in the A1-61 borehole in Libya (Le Hérissé, 2002), for which a zonation was proposed. The acritarchs *Arkonia nova* and *A. paulumstriata* are well represented, and associated with *Hemibaltisphaeridium dedosmuertosi*, *Multiplicisphaeridium moharra* (misidentified as *Estiastra* cf. *barbata* in Le Hérissé, 2002), *Nothooidium* sp., *Pulvinosphaeridium trifidum*, *Triangulina sanpetrensis*, *Visbysphaera bonita* and *V. jardinei*.

These taxa are characteristic of the top of Biozone 2 and Biozone 3 of early Přídolí to middle Přídolí age in the 2265.30–2125.1 m interval (and equivalent to Assemblages B to D in the A1-61 borehole described by Jaglin and Paris, 2002). However, the abundance of *Cymbosphaeridium* may be correlated with the second spike observed in the A1-61 borehole, in the Přídolí, between 2137.90 and 2127.30 m, after an earlier spike described in the upper Ludlow. In addition, the presence of other species observed in Libya, such as *Baltisphaeridium* sp. 3, *M. moharra* (as *E. cf. barbata*) or *Schismatosphaeridium* sp. 1, in the material from Saudi Arabia, is also significant, because they do not seem older than

the top of Biozone 2 (late early Přídolí) and are more characteristic of Biozone 3 (middle Přídolí).

6.2. Palaeogeography

6.2.1. Organic-walled microphytoplankton

Because the majority of acritarchs are probably cysts produced by marine, motile, phytoplanktonic unicellular algae (Martin, 1993), they have the potential for wide geographical distribution. Although a lot of species show a cosmopolitan distribution pattern during the Llandovery and Wenlock (García Muro et al., 2016), many others have specific tolerances in terms of paleolatitude, paleotemperature etc., thus confining them to the North Gondwanan margin, Baltica or Laurussia, during a large part of the Silurian, as previously described in a series of papers by Cramer (1968, 1969, 1970), Cramer and Díez (1972, 1974a,b, 1979), Le Hérisse and Gourvenec (1995) and Le Hérisse et al. (1997).

During the late Silurian, and particularly the late Ludfordian and Přídolí, Rubinstein (1995), Le Hérisse et al. (1997), Le Hérisse (2002), Rubinstein et al. (2008), and Rubinstein and García Muro (2011) previously reported a drop in provinciality and a notable morphological similarity of stratigraphically significant taxa with assemblages from Baltica, East European platform and Gondwana, on both sides of the Rheic Ocean. The phytoplankton assemblage from Saudi Arabia described herein are quite comparable to those from Pomerania in Poland (Jachowicz, 2000), the Netherlands (Van der Meer and Wicander, 1992), Libya and Spain. They seem to indicate significant geographic and climatic changes, and closer proximity of the North Gondwanan margin to the East European craton. This implies a requirement for an unrestricted oceanic circulation across the Rheic Ocean at this time, with implications for the refinement of the Rheic closure scenario.

6.2.2. Chitinozoans

The late Silurian chitinozoan assemblage reported herein belongs to the *Urnochitina urna* palaeobiogeographical province extending over the Northern Gondwana Domain *sensu* Paris (1998, fig. 1). *U. urna*, which is the index chitinozoan species for the Přídolí Series (Verniers et al. 1995), is widely reported (see references below) from southwestern Europe (south and southwestern France, Iberian Peninsula), Central Europe (Bohemia, Carnic Alps, Bulgaria and Romania) as well as from North Africa (Morocco, Algeria, Tunisia, Libya), Turkey, Florida and Saudi Arabia.

The *U. urna* palaeobiogeographical Province has a geographical extension similar to the *Linochitina pissotensis* and the *Armorochitina nigerica* palaeobiogeographical provinces, for the late Early and Late Ordovician, respectively. This supports the existence of a long-lived oceanic barrier preventing free pelagic exchanges between both margins of the

Rheic Ocean, from the early Darriwilian onwards up to Přídolí times. However, during the late Silurian, this oceanic barrier began declining due to the narrowing of the Rheic Ocean, which was actively closing by earliest Devonian times (Paris and Robardet, 1990) according to the coefficient of similarity (CS) calculated for Lochkovian chitinozoan populations (Paris, 1993; Paris 1998 and references therein). The Rheic Ocean did not act as a hermetic barrier for trans-oceanic chitinozoan exchanges because some species are also observed on its northern margin.

When focusing on the geographical distribution of *Margachitina elegans* and *Pseudoclathrochitina carmenchui*, two important and distinctive components of the chitinozoan assemblage recovered from well JLMD-EW-8, a more restricted palaeobiogeographical range is documented. Associated with less abundant *U. urna*, these two species are reported in most of the Ibarmaghian Domain defined by Plusquellec et al. (1997). This palaeobiogeographic province corresponds to the shallow southern margin of the Rheic Ocean, located in middle latitude along the northern margin of Gondwana during the late Silurian (see Paris, 1998). *M. elegans* and *P. carmenchui* occur in numerous North African sections. In Algeria from, they are reported from the Sbaa Basin in the west and Tindouff Basin in the east (Paris, unpublished data), the Central Sahara basins (Taugourdeau and de Jekhowsky, 1960; Magloire, 1967; Boumendjel, 1987), and the Illizi Basin (Jardiné and Yapaudjian, 1968; Azzoune et al., 1999; Paris et al., 2004; Henniche et al., 2003).

These two species are also well represented in northwestern Libya (Al-Ameri, 1989; Jaglin and Paris, 2002) and Tunisia (Grignani, 1967). Other occurrences are reported from the Cantabrian Mountains in northwestern Spain (Cramer, 1964a,b, 1967; Cramer and Díez, 1978; Priewalder, 1997; Richardson et al., 2001). The northernmost records are from northwestern France in Brittany (Deunff et al., 1971; Paris, unpublished data) and Normandy (Rauscher and Robardet, 1975). It is noteworthy that the Přídolí chitinozoan assemblages from Romania (Beju and Danet, 1962), Bulgaria (Lakova, 1995), Podolia (Tsegelnjuk, 1982; Paris and Grahn, 1996) and Florida (Goldstein et al., 1969) do not share the distinctive *P. carmenchui*/*M. elegans* association. Therefore, the co-occurrence of these two species in Saudi Arabia is of great interest because it documents free communication along the northern shallow margin of Gondwana and emphasizes the role of a bathymetric control on the distribution of the Přídolí chitinozoans. Numerous specimens of *M. elegans*, *P. carmenchui* and *Ancyrochitina brevis* are associated with rare *U. urna* in the nearshore shallow clastic environments, whereas *U. urna* may represent up to 90% of the chitinozoan assemblages in distal deep environments such as in Bohemia (see Paris et al., 1981; Kriz et al., 1986).

It must be stressed, however, that the mid Přídolí chitinozoans assemblages reported from Baltica (Tsegelnjuk, 1982; Nestor, 2011) share only a few species (e.g. *U. urna*) with the contemporaneous northern Gondwana assemblages, and especially with the assemblage from Saudi Arabia.

6.2.3. Spores

Only a few papers have been published detailing late Ludlow and Přídolí miospores. Data are mainly from Nova Scotia, Canada (Beck and Strother, 2001); Southern Britain (Burgess and Richardson, 1995; Richardson and Lister, 1969); Brittany, France (Deunff and Chateauneuf, 1976); Algeria (Hassan Kermadji, 2007); Spain (Rodriguez, 1978a,b,c, 1983); Libya (Rubinstein and Steemans, 2002); Tunisia (Spina and Vecoli, 2009); Brazil (Steenmans et al., 2008); Argentina (García Muro et al., 2013); Turkey (Steenmans et al., 1996) and South China (Wang and Li, 2000). Despite the paucity of data for the Přídolí, this time interval is rich in taxa with around 50 genera and 100 species reported.

Out of the 42 identified trilete and monolete spore species from Saudi Arabia, the present assemblage shares approximately 18 species with Spain, 17 with northwestern Gondwana (Libya, Tunisia and Algeria), 10 with Southern Britain, 6 with Turkey and Brazil and 4 with Nova Scotia and South China (Fig. 3).

One way to estimate most objectively the similarity between the miospore assemblages from different regions is the coefficient of similarity (CS) *sensu* Clark and Harteberg (1983) for bioprovincialism evaluation. Numerous Palaeozoic palynological studies have used CS (e.g. Le Hérissé et al., 1997; Samuelsson et al., 2002). This simple and straightforward approach is expressed by the formula:

$$CS = 2v/a+b$$

where v is the number of species in common between the two compared assemblages, a and b are the total number of species in each assemblage, respectively. If the CS is lower than 0.2, the similarity between the two compared assemblages is estimated as low. If the CS is between 0.2 and 0.55, the similarity is considered as moderate to high, and if the CS is higher than 0.55, the similarity is considered to be very high (Clark and Harteberg, 1983).

There appears to be a strong affinity (CS: 0.50) between the assemblages from Spain and Saudi Arabia. The affinity with northwestern Gondwana (CS: 0.21) and with UK (CS: 0.24) is apparently less. The CS values with South China and Nova Scotia are low, below 0.2. These calculated values have to be considered carefully because of the lack of data, imprecise age attributions, possible misidentifications, and the numerous taxa in open nomenclature. Despite these considerations, it seems clear there exists a high correlation with the Spanish assemblages.

According to the late Silurian palaeogeographic map of Torsvik and Cocks (2013) at 420 Ma the Iberian Plate is located between the northwestern margin of Gondwana and the southeast flank of the Baltica Plate (Fig. 3). This palaeogeographic position may explain the high CS value, and, furthermore, it is also supported by other miospore species in older and younger sediments.

For example, in the Ludlow and Přídolí, *Emphanisporites splendens* (= *Emphanisporites pseudoerraticus* Richardson and Ioannides, 1973) is only known on the northwestern flank of Gondwana (Richardson and Ioannides, 1973; Rubinstein and Steemans, 2002; Spina and Vecoli, 2009) and on the Iberian Plate (Richardson et al., 2001). On the other hand, *Streelispora newportensis* Richardson and Lister 1969, which is an important stratigraphic species defining the lower part of the Lochkovian, is only known on the Baltica Plate, except for one specimen in Tunisia (Loboziak et al., 1992) and from Spain. These two examples show influences both from Gondwana and Baltica, suggesting a central position of the Iberian Plate between these two palaeocontinents since at least the Ludlow (García Muro et al., 2013).

Nonetheless, the smallest CS value (0.21) for correlations between Saudi Arabia and northwestern Gondwana is difficult to explain with regard to the Spanish correlation and the palaeogeographical proximity. This value may be erroneous and due to the numerous taxa in open nomenclature, which make comparisons difficult.

Strangely, the CS value comparing southern Britain and Saudi Arabia is a little bit higher (0.24). There are two possible explanations: (i) the CS value is inversely proportional to the number of observers (this paper; Burgess and Richardson, 1995; Richardson and Lister, 1969) used to identify all taxa in an assemblage (Gradstein et al., 1985); (ii) the CS value reflects the proximity between Spain and UK in contrast to the plate configuration of the map published by Torsvik and Cocks (2013) (Fig. 3).

It is difficult to interpret the other CS values because of the lack of data. However, China and Brazil were far from Saudi Arabia, in equatorial and sub-polar latitudes respectively, whereas the other localities were in sub-tropical latitudes.

6.3. Sequence stratigraphy

The deposition of sediments characterized by this rich marine assemblage is penetrated not only in northwestern Saudi Arabia but also in the most distal settings of the Tawil Formation in the Arabian Gulf of eastern Saudi Arabia. This palynological assemblage corresponds to what is considered to be a transgressive middle Přídolí event in the Algerian Sahara, with non-marine intervals bracketing this brief marine sea level rise.

This event can be correlated to the S50 Maximum Flooding Surface (S50 MFS) from the Neftex Geodynamic Earth Model (Neftex Petroleum Consultant Ltd.), which occurs during the Přídolí. This event corresponds to the S20 MFS defined by Sharland et al. (2001) on the Arabian Plate and dated as late Přídolí at that time. Furthermore, it is correlated in southeast Turkey to phosphatic shales near the base of the Dadas Formation (Cater and Tunbridge, 1992), and it could also correspond to limestone beds at the top of the Khushsha Formation in northwestern Jordan (Beydoun et al., 1994).

Přídolí sediments are also recognized in Western Iraq in the Suffi Formation (Kaddouri, 1992; Al-Ameri, 2010) and are interpreted to reflect this event. In Qatar, the shales near

the base of the lower Tawil Formation (Hamam and Nasrulla, 1989) might be indicative of S50 MFS. Therefore, this maximum flooding surface, which took place during the *Margachitina elegans* chitinozoan Zone of Verniers et al. (1995), is likely to have extended into all of north Gondwana.

7. Conclusions

1. Chitinozoans and organic-walled microphytoplankton seem to be more consistently distributed during the Přídolí than miospores, making them extremely useful for inter-regional correlation.
2. The composition of this assemblage strongly indicates a Přídolí age.
3. The assemblage encountered contains very characteristic chitinozoans, organic-walled microphytoplankton, scolecodonts, eurypterid cuticle and remains, freshwater algae, mazuelloid fragments and common land-derived miospores.
4. Chitinozoans, such as *Margachitina elegans*, *Pseudochlathrochitina carmenchui* and *Urnochitina urna* suggest a middle Přídolí age assignment. This assemblage of chitinozoans correlates well with Assemblage D from the Alternances Grésos-Argileuses Formation of well A1-61 in northwestern Libya and material from many wells in Algeria.
5. The majority of organic-walled microphytoplankton taxa are recognized as being typical of the late Silurian of north Gondwana regions, with a substantial potential for correlation with the Libyan acritarch biozonation of Le Hérissé (2002).
6. The most important organic-walled microphytoplankton markers are *Cepillum puerospinoides*, *Hemibaltisphaeridium dedosmuertosi*, *Multiplicisphaeridium moharra*, *Pulvinosphaeridium trifidum*, *Visbysphaera bonita* and *V. jardinei*, but also species in open nomenclature such as *Baltisphaeridium* sp. 3, *Multiplicisphaeridium* sp. 4 and *Schismatosphaeridium* sp. 1. Together, these suggest a middle Přídolí age.
7. Přídolían assemblages of acritarchs and associated microalgae have implications for the refinement of paleogeography, because homogeneity of late Silurian assemblages from southern Baltica and the Gondwanan margin and the Middle East can be explained by an evident narrowing of the Rheic Ocean at this time.
8. The spore assemblage contains the important taxa *Aneurospora richardsonii*, *Breconisporites simplex*, *Chelinospora hemiesferica*, *C. sanpetrensis*, *Coronaspora reticulata*, *C. subornata*, *Emphanisporites novellus*, *Iberoespora cantabrica*, *Retusotriletes maculatus* and *Scylaspora elegans*. These species indicate the EC biozone of Richardson et al. (2001) defined in the Iberian Peninsula. Although the base of this biozone is in the middle Přídolí, the top lies within the lowermost Devonian.

9. The rich and diverse assemblage described herein appears to correspond to a transgressive mid Přídolí event, which is likely to have extended into all of north Gondwana including Arabia and can be correlated to the S50 Maximum Flooding Surface from the sequence stratigraphic framework defined in Neflex Geodynamic Earth Model (Neflex Petroleum Consultant Ltd.).

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Figure captions

Fig. 1. Location map of the studied section.

Fig. 2. Global Stratigraphic distribution of selected chitinozoan (CT), miospore (SP) and organic-walled microphytoplankton (OWM) species found in JLMD-EW-8 compared to the chitinozoan and miospore zonations.

Fig. 3. Palaeogeographic reconstruction after Torsvik and Cocks (2013). 1, Saudi Arabia; 2, northwestern Gondwana; 3, Turkey; 4, Spain; 5, southern Britain; 6, Nova Scotia; 7, South China; 8, Brazil.

Plate 1. Each miospore is identified by sample, slide numbers and England Finder Coordinate. Magnification $\times 1000$. Fig. 1. *Artemopyra laevigata* Wellman and Richardson, 1996. 637.19 m, 53535(6), H34/4. Figs. 2–9. *Chelinohilates erraticus* Richardson, 1996. 2, 637.19 m, 53535(6), W46; 3, 637.19 m, 53535(6), U36/1; 4, 638.43 m, 53536(6), X39/1; 5, 637.19 m, 53535(6), M50/2; 6, 638.43 m, 53536(6), M37/2; 7, 637.19 m, 53535(6), T35/2; 8, 639.42 m, 53537(6), N37/4; 9, 639.42 m, 53537(6), G39/3. Fig. 10. *Cymbohilates cymosus* Richardson, 1996. 639.42 m, 53537(6), P46. Figs. 11–20.

Cymbohilates jalamidensis nov. sp. 11, 639.42 m, 53537(6), S48/3; 12, 637.19 m, 53535(6), X43/1; 13, 639.42 m, 53537(6), U42/1; 14, 639.42 m, 53537(6), K48/1; 15, 638.43 m, 53536(6), G41, paratype; 16, 638.43 m, 53536(6), O44, holotype; 17, 638.43 m, 53536(6), U40/1, paratype; 18, 637.19 m, 53535(6), R35; 19, 638.43 m, 53536(6), U38/1; 20, 637.19 m, 53535(6), R37. Figs. 21–23. *Cymbohilates* sp. B in Lavender and Wellman (2002). 21, 637.19 m, 53535(6), W38/4; 22, 639.42 m, 53537(2), T39/2; 23, 638.43 m, 53536(6), J39.

Plate 2. Each miospore is identified by sample, slide numbers and England Finder Coordinate. Magnification $\times 1000$. Figs. 1 and 2. *Dyadospora murusattenuata* Strother and Traverse, 1979. 1, 639.42 m, 53537(6), W49; 2, 637.19 m, 53535(6), V34. Figs. 3–7. *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988 var. *minor* Breuer et al., 2007. 3, 637.19 m, 53535(6), N40/4; 4, 637.19 m, 53535(6), M39–40; 5, 639.42 m, 53537(2), V52/1; 6, 639.42, 53537(2), G52; 7, 637.19 m, 53535(6), S37. Figs. 8–20. *Gneudnaspora sordida* nov. sp. 8, 639.42 m, 53537(6), Q49/3; 9, 637.19 m, 53535(6), K38; 10, 639.42 m, 53537(6), U43; 11, 637.19 m, 53535(6), P37/2; 12, 637.19 m, 53535(6), N37, holotype; 13, 637.19 m, 53535(6), U43, paratype; 14, 637.19 m, 53535(6), L40/1; 15, 637.19 m, 53535(6), J38/4; 16, 638.43 m, 53536(6), R35/4, paratype; 17, 637.19 m, 53535(6), S36/1; 18, 639.42 m, 53537(6), V42; 19, 638.43 m, 53536(6), S51/4; 20, 638.43 m, 53536(6), M38. Fig. 21. *Pseudodyadospora petasus* Wellman and Richardson, 1993. 639.42 m, 53537(6), S42/3. Figs. 22 and 23. *Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, 1993. 22, 639.42 m, 53537(6), U40; 23, 639.42 m, 53537(6), S43.

Plate 3. Each miospore is identified by sample, slide numbers and England Finder Coordinate. Magnification $\times 1000$. Fig. 1. *Ambitisporites avitus* Hoffmeister, 1959. 638.43 m, 53536(6), O45/1. Fig. 2. *Aneurospora bollandensis* Steemans, 1989. 639.42 m, 53537(6), V52. Figs. 3 and 4. *Aneurospora* cf. *A. bollandensis* Steemans, 1989. 3, 639.42 m, 53537(6), P43/3; 4, 639.42 m, 53537(2), K44/1. Fig. 5. *Aneurospora isidori* (Cramer and Díez) Richardson et al., 1982. 639.42 m, 53537(6), S52. Figs. 6–9. *Aneurospora richardsonii* (Rodríguez) Richardson et al., 2001. 6, 637.19 m, 53535(6), M34; 7, 638.43 m, 53536(6), R47; 8, 639.42 m, 53537(6), M41/1; 9, 638.43 m, 53536(6), M42/4. Fig. 10. *Archaeozonotriletes chulus* Richardson and Lister, 1969. 639.42 m, 53537(2), L50. Fig. 11. *Archaeozonotriletes chulus* var. *inframurinus* Richardson and Lister, 1969. 638.43 m, 53536(6), Y39. Figs. 12 and 13. *Breconisporites simplex* Wellman, 1993. 12, 639.42 m, 53537(2), J38/4; 13, 639.42 m, 53537(6), L40/4. Fig. 14. cf. *Brochotriletes* sp. A in Richardson and Ioannides (1973). 637.19 m, 53535(6), L50. Fig. 15. *Chelinospora hemiesferica* (Cramer and Díez) Richardson et al., 2001. 639.42 m, 53537(6), G42. Figs. 16–25. *Chelinospora* cf. *C. hemiesferica* (Cramer and Díez) Richardson et al., 2001. 16, 639.42 m, 53537(6), N48; 17, 638.43 m, 53536(6), P45; 18, 639.42 m, 53537(6), P37/3; 19, 637.19 m, 53535(6), N38/4; 20, 639.42 m, 53537(6), R49/2; 21, 637.19 m, 53535(6), U38; 22, 637.19 m, 53535(6), W43/1; 23, 638.43 m, 53536(6), X46; 24, 637.19 m, 53535(6), R48/2; 25, 637.19 m, 53535(6), W38. Fig. 26. *Chelinospora lavidensis* Richardson et al., 2001. 638.43 m, 53536(6), H37.

Plate 4. Each miospore is identified by sample, slide numbers and England Finder Coordinate. Magnification $\times 1000$. Fig. 1. *Chelinospora sanpetrensis* (Rodríguez) Richardson et al., 2001. 637.19 m, 53535(6), O49. Fig. 2. *Chelinospora* sp. 1 in Rubinstein and Steemans (2002). 638.43 m, 53536(6), O42. Figs. 3–9. *Chelinospora* sp. A. 3, 639.42 m, 53537(6), Q50/2; 4, 53537(6), H48/1; 5, 637.19 m, 53535(6), U43/2; 6, 638.43 m, 53536(6), X50; 7, 638.43 m, 53536(6), Y51; 8, 639.42 m, 53537(6), V40/4; 9, 639.42 m, 53537(6), P43/4. Figs. 10 and 11. *Chelinospora* spp. 10, 637.19 m, 53535(6), F45; 11, 638.43 m, 53536(6), P40. Fig. 12. *Concentricosisporites sagittarius* (Rodríguez) Rodríguez, 1983. 637.19 m, 53535(6), V35/1. Figs. 13–16. *Coronaspora reticulata* Richardson et al., 2001. 13, 638.43 m, 53536(6), O53/1; 14, 639.42 m, 53537(6), S43/4; 15, 637.19 m, 53535(6), Q40/1; 16, 639.42 m, 53537(6), V46/1. Fig. 17. *Coronaspora subornata* (Cramer and Díez) Richardson et al., 2001. 637.19 m, 53535(6), R42/4. Fig. 18. *Cymbosporites multiconus* Steemans, 1989. 639.42 m, 53537(6), O45/3. Fig. 19. *Cymbosporites* sp. A in Richardson and Ioannides (1973). 637.19 m, 53535(6), M-N40. Figs. 20 and 21. *Cymbosporites* sp. 20, 638.43 m, 53536(6), O37/2; 21, 638.43 m, 53536(6), R49. Fig. 22. *Devonomonoletes* sp. 639.42 m, 53537(6), R40/4. Figs. 23–25. *Emphanisporites multicostatus* Rodríguez, 1978a. 23, 639.42 m, 53537(6), Q49; 24, 639.42 m, 53537(6), S42; 25, 639.42 m, 53537(6), Q53/2. Fig. 26. *Emphanisporites novellus* McGregor and Camfield, 1976. 639.42 m, 53537(6), N37. Figs. 27–29. *Emphanisporites* spp. 27, 637.19 m, 53535(6), O46; 28, 638.43 m, 53536(6), O42/2; 29, 637.19 m, 53535(6), W34/3. Figs. 30–32. *Iberoespora cantabrica* Cramer and Díez, 1975. 30, 637.19 m, 53535(6), S38/1; 31, 637.19 m, 53535(6), H34/3; 32, 637.19 m, 53535(6), R43/2. Fig. 33. *Iberoespora glabella* Cramer and Díez, 1975. 637.19 m, 53535(6), R36.

Plate 5. Each miospore is identified by sample, slide numbers and England Finder Coordinate. Magnification $\times 1000$. Figs. 1–4. *Iberoespora guzmani* Cramer and Díez, 1975. 1, 638.43 m, 53536(6), H40/3; 2, 639.42 m, 53537(2), V48; 3, 639.42 m, 53537(6), V46/4; 4, 637.19 m, 53535(6), L50/4. Fig. 5. *Iberoespora* sp. 2 in Rubinstein and Steemans (2002). 639.42 m, 53537(6), K54/2. Figs. 6 and 7. *Insolisporites anchistinus* Burgess and Richardson, 1995. 6, 638.43 m, 53536(6), W38; 7, 639.42 m, 53537(2), U48/3. Figs. 8–9. *Retusotriletes bipellis* Rodríguez, 1978a. 8, 638.43 m, 53536(6), V49; 9, 637.19 m, 53535(6), T41/3. Fig. 10. *Retusotriletes dubius* (Eisenack) Richardson, 1965. 638.43 m, 53536(6), Y50. Figs. 11–12. *Retusotriletes maculatus* McGregor and Camfield, 1976. 11, 637.19 m, 53535(6), J39/1; 12, 637.19 m, 53535(6), W35. Figs. 13–15. *Retusotriletes?* *saturnus* Richardson et al., 2001. 13, 639.42 m, 53537(2), N38. 14, 639.42 m, 53537(6), H41/2; 15, 639.42 m, 53537(2), S38. Fig. 16. *Scylaspora downiei* Burgess and Richardson, 1995. 639.42 m, 53537(6), G44. Fig. 17. *Scylaspora elegans* Richardson et al., 2001. 639.42 m, 53537(6), H48/1. Figs. 18–21. *Synorisporites* cf. *S. libycus* Richardson and Ioannides, 1973. 18, 639.42 m, 53537(6), S50; 19, 637.19 m, 53535(6), O41; 20, 639.42 m, 53537(2), M38; 21, 638.43 m, 53536(6), O52/4. Figs. 22–25. *Synorisporites verrucatus* Richardson and Lister, 1969. 22, 637.19 m, 53535(6), P36; 23, 639.42 m, 53537(6), W49/1; 24, 639.42 m, 53537(6), O-P36; 25, 639.42 m, 53537(6), T37. Figs. 26 and 27. *Synorisporites* sp. 637.19 m, 53535(6), R43/3. 26, proximal face; 27, distal face.

Plate 6. Each organic-walled microphytoplankton is identified by sample, slide numbers and England Finder Co-ordinate. Magnification $\times 1000$. Figs. 1–4. *Evittia* spp. 1, 637.19 m, 53535(6), R43/2; 2, 637.19 m, 53535(6), E45; 3, 637.19 m, 53535(6), R43/3, P39; 4, 637.19 m, 53535(6), Q38. Figs. 5–7. *Evittia cymosa* Loeblich, 1970. 5, 638.43 m, 53536(6), W53; 6, 638.43 m, 53536(6), P39; 7, 637.19 m, 53535(6), T34/2. Figs. 8–10. *Leptolyta gordonense* (Cramer) Colbath, 1979. 8, 639.42 m, 53537(1), K48; 9, 639.42 m, 53537(1), K38; 10, 639.42 m, 53537(2), G48. Fig. 11. *Solisphaeridium eriza* Cramer et al., 1976. 639.42 m, 53537(1), K48. Fig. 12. *Elektoriskos* sp. 639.42 m, 53537(1), W44. Fig. 13. *Leoniella carminae* Cramer, 1964a. 638.43 m, 53536(6), O37/1. Figs. 14–16. *Multiplicisphaeridium moharra* Cramer et al., 1976. 14, 639.42 m, 53537(1), L53/3; 15, 639.42 m, 53537(2), P50; 16, 639.42 m, 53537(1), L53/1.

Plate 7. Each organic-walled microphytoplankton is identified by sample, slide numbers and England Finder Co-ordinate. Magnification $\times 1000$. Figs. 1 and 2. *Hemibaltisphaeridium dedosmuertosi* (Cramer) Cramer, 1970. 1, 639.42 m, 53537(1), U45/4; 2, 639.42 m, 53537(1), P41. Figs. 3–5. *Multiplicisphaeridium* sp. 4 in Le Hérisse (2002). 3, 639.42 m, 53537(1), L46; 4, 637.19 m, 53535(6), P46; 5, 638.43 m, 53536(6), Q36/4. Figs. 6–9. *Multiplicisphaeridium* sp. 6, 637.19 m, 53535(6), T39; 7, 639.42 m, 53537(2), R46/2; 8, 637.19 m, 53535(6), W36/1; 9, 639.42 m, 53537(2), N43. Figs. 10 and 11. *Cymbosphaeridium* sp. 1 in Le Hérisse (2002). 10, 637.19 m, 53535(6), M33/3; 11, 639.42 m, 53537(1), G45/1. Figs. 12 and 13. *Cymbosphaeridium* sp. 5 in Le Hérisse (2002). 12, 637.19 m, 53535(6), V40; 13, 638.43 m, 53536(6), X39. Fig. 14. *Cymbosphaeridium pilaris typicum* (Cramer) Le Hérisse, 1989. 637.19 m, 53535(6), W40/3. Fig. 15. *Michrystridium stellatum* Deflandre, 1945. 637.19 m, 53535(6), S45. Figs. 16–19. *Michrystridium* sp. 16, 639.42 m, 53537(2), U46; 17, 638.43 m, 53536(6), M36; 18, 637.19 m, 53535(6), K37/1; 19, 639.42 m, 53537(1), N51. Figs. 20–25. *Umbellasphaeridium?* aff. *Umbellasphaeridium?* *wicanderi* Richards and Mullins, 2003. 20, 638.43 m, 53536(6), T39; 21, 637.19 m, 53535(6), U39; 22, 638.43 m, 53536(6), Y46; 23, 638.43 m, 53536(6), Q40/2; 24, 637.19 m, 53535(6), O44/3; 25, 639.42 m, 53537(2), T49/2.

Plate 8. Each organic-walled microphytoplankton is identified by sample, slide numbers and England Finder Co-ordinate. Magnification $\times 1000$. Figs. 1–3. *?Lophodiacrodium* sp. 1, 639.42 m, 53537(2), S48/1; 2, 637.19 m, 53535(6), H41/4; 3, 637.19 m, 53535(6), R34. Fig. 4. *Baltisphaeridium* sp. 3 in Le Hérisse (2002). 637.19 m, 55535, H42. Figs. 5 and 6. Indeterminate. 5, 637.19 m, 53535(6), R34; 6, 639.42 m, 53537(1), S44. Fig. 7. *Triangulina alargada* Cramer, 1964a. 639.42 m, 53537(1), H37. Fig. 8. *?Lophodiacrodium* sp. 638.43 m, 53536(6), X47. Figs. 9 and 10. *Onondagella asymmetrica* (Deunff) Cramer, 1966. 9, 638.43 m, 53536(6), G52; 10, 638.43 m, 53536(6), L36. Fig. 11. *Veryhachium europaeum* Stockmans and Willièrè, 1960. 637.19 m, 53535(6), R46/1. Fig. 12. *Triangulina alargada* Cramer, 1964a. 638.43 m, 53536(6), N52. Fig. 13. *Veryhachium trispinosum* (Eisenack) Downie, 1959. 639.42 m, 53537(2), E47. Fig. 14. *Dorsennidium* sp. 639.42 m, 53537(2), L45. Fig. 15. *Veryhachium* sp. 639.42 m, 53537(2), R49/2, abnormal form. Figs. 16 and 17. *Arkonion nova* Le Hérisse, 2002. 637.19 m, 53535(6), J38/1; 17, 639.42 m, 53537(2), S40/1. Fig. 18. *Arkonion paulumstriata* Le Hérisse, 2002. 638.43 m, 53536(6), R52. Fig. 19. *Deflandrastrum*

colonnae Combaz, 1962. 637.19 m, 53535(6), O43, fragment. Fig. 20. Mazuelloid. 639.42 m, 53537(2), E45, fragment.

Plate 9. Each organic-walled microphytoplankton is identified by sample, slide numbers and England Finder Co-ordinate. Magnification $\times 1000$. Figs. 1 and 2. *Eupoikilofusa filifera* (Downie) Dorning, 1981. 1, 639.42 m, 53537(1), S52; 2, 637.19 m, 53535(6), L36/3. Fig. 3. *Eupoikilofusa cantabrica* (Cramer) Cramer, 1970. 639.42 m, 53537(2), J37/1. Fig. 4. *Eupoikilofusa filifera* (Downie) Dorning, 1981. 638.43 m, 53536(6), X44/2. Fig. 5. *Leiofusa banderillae* Cramer, 1964b. 637.19 m, 53535(6), R46/3. Fig. 6. *Dactylofusa oblancae* Cramer and Díez, 1968. 638.43 m, 53536(6), Q52/3. Figs. 7–12. *Visbysphaera albanega* (Cramer et al.) Le Hérisse, 2002. 7, 637.19 m, 53535(6), O47; 8, 637.19 m, 53535(6), J43/2; 9, 637.19 m, 53535(6), M47/3; 10, 637.19 m, 53535(6), O46; 11, 639.42 m, 53537(2), J47/1; 12, 638.43 m, 53536(6), T49/1. Figs. 13–16. *Visbysphaera gotlandica* (Eisenack) Lister, 1970. 13, 639.42 m, 53537(2), P49; 14, 639.42 m, 53537(2), M47/4; 15, 638.43 m, 53536(6), P43/4; 16, 637.19 m, 53535(6), P33/1. Fig. 17. *Visbysphaera pirifera* (Eisenack) Lister, 1970. 637.19 m, 53535(6), G48.

Plate 10. Each organic-walled microphytoplankton is identified by sample, slide numbers and England Finder Co-ordinate. Magnification $\times 1000$. Figs. 1 and 2. *Visbysphaera bonita* (Cramer) Le Hérisse, 2002. 1, 639.42 m, 53537(1), G38; 2, 638.43 m, 53536(6), P41. Figs. 3–9. *Visbysphaera jardinei* (Cramer) Le Hérisse, 2002. 3, 637.19 m, 53535(6), P38/3; 4, 639.42 m, 53537(2), L44; 5, 639.42 m, 53537(1), O44; 6, 639.42 m, 53537(1), R36/3; 7, 639.42 m, 53537(1), H39; 8, 639.42 m, 53537(2), R52/3; 9, 639.42 m, 53537(2), R36/3.

Plate 11. Each organic-walled microphytoplankton is identified by sample, slide numbers and England Finder Co-ordinate. Magnification $\times 1000$ except where mentioned otherwise. Figs. 1 and 2. *Tunisphaeridium caudatum* Deunff and Evitt, 1968. 1, 639.42 m, 53537(1), O53/4; 2, 639.42 m, 53537(1), V54/1. Figs. 3–4. *Geron* sp. 3, 637.19 m, 53535(6), Q47/1; 4, 637.19 m, 53535(6), L37. Figs. 5 and 6. *Dictyotidium legionis* (Cramer) Rodriguez, 1983. 5, 639.42 m, 53537(2), H44/2; 6, 639.42 m, 53537(2), R46/1. Figs. 7 and 8. *Dictyotidium* sp. 7, 639.42 m, 53537(2), N47; 8, 639.42 m, 53537(2), M49/3. Fig. 9. *Cymatiosphaera* aff. *C. mariae* Cramer et al., 1976. Fig. 10. *Cymatiosphaera nimia* Le Hérisse, 2002. 639.42 m, 53537(1), S37. Fig. 11. *Dictyotidium* aff. *D. eurydictyotum* Kiryanov, 1978. 639.42 m, 53537(1), G51. Fig. 12. *Pulvinosphaeridium trifidum* Kiryanov, 1978, magnification $\times 500$. 639.42 m, 53537, G41/4. Figs. 13–15. Indeterminate. 13, 637.19 m, 53535(6), M42; 14, 637.19 m, 53535(6), T41; 15, 637.19 m, 53535(6), P38. Figs. 16–19. *Quadrisporites* spp. 16, 639.42 m, 53537(2), O50; 17, 637.19 m, 53535 (6), F42; 18, 637.19 m, 53535 (6), R39; 19, 639.42 m, 53537(1), Q42/4. Fig. 20. *Proteolobus* sp. 639.42 m, 53537(1), M36/4.

Plate 12. Each organic-walled microphytoplankton or chitinozoan is identified by sample, slide numbers and England Finder Co-ordinate. Magnification $\times 1000$. Figs. 1 and 2. *Ovnia uahabita* Cramer and Díez, 1976. 1, 639.42 m, 53537(2), H44/4; 2, 639.42 m, 53537(1), S51. Fig. 3. *Ovnia desertica* Cramer and Díez, 1976. 637.19 m, 53535(6), L37/3. Figs. 4–6. *Clypeolus tortugaides* (Cramer) Miller et al., 1997. 4, 639.42 m,

53537(2), F47; 5, 639.42 m, 53537(2), P42; 6, 638.43 m, 53536(6), W42. Figs. 7 and 8. *Perforella perforata* Díez and Cramer, 1976. 7, 639.42 m, 53537(2), Q48/1; 8, 639.42 m, 53537(2), K53. Fig. 9. *Cepillum puerospinooides* Cramer, 1964a. 639.42 m, 53537(2), H50/3. Figs. 10–12. *Schismatosphaeridium* sp. 1 in Le Hérisse (2002). 10, 638.43 m, 53536(6), Q46/4; 11, 639.42 m, 53537(1), Q51/3; 12, 639.42 m, 53537(2), P53. Fig. 13. *Hoegisphaera staplini* Cramer, 1966. 638.43 m, 53536(6), P38/3. Fig. 14. *Hoegisphaera testudo* Cramer, 1966. 639.42 m, 53537(2), O46. Figs. 15 and 16. Indeterminate. 15, 637.19 m, 53535(6), M46; 16, 639.42 m, 53537(2), J37. Fig. 17. *Saturnus?* sp. 639.42 m, 53537(1), N52. Fig. 18. *Pardaminella crassicosta* Díez and Cramer, 1976. 637.19 m, 53535, O36. Fig. 19. *Nanocyclopia* sp. 637.19 m, 53535(6), T34. Fig. 20. *Saturnus?* sp. 639.42 m, 53537(2), N45.

Plate 13. Each chitinozoan is identified by sample, slide numbers and England Finder Coordinate. Scale bar 100 μm . Figs. 1–3. *Margachitina elegans* (Taugourdeau and de Jekhowsky, 1960). 1, 637.19 m, 53535(6), L45; 2, 638.43 m, 53536(6), H42; 3, 637.19 m, 53535(6), M38/1. Fig. 4. *Cingulochitina serrata* (Taugourdeau and de Jekhowsky, 1960). 637.19 m, 53535(6), L49. Figs. 5–7. *Ancyrochitina brevis* Taugourdeau and de Jekhowsky, 1960. 5, 638.43 m, 53536(6), T46; 6, 637.19 m, 53535(6), T43; 7, 638.43 m, 53536(6), T41. Fig. 8. *Eisenackitina lagenomorpha* (Eisenack, 1931). 637.19 m, 53535(6), M38. Fig. 9. *Pseudoclathrochitina carmenchui* Cramer, 1964a. 637.19 m, 53535(6), P47. Fig. 10. *Ancyrochitina regularis* Taugourdeau and de Jekhowsky, 1960. 637.19 m, 53535(6), U35. Figs. 11 and 12. *Vinnalochitina corinnae* (Jaglin, 1986). 11, 638.43 m, 53536(6), U38/3; 12, 638.43 m, 53536(6), N40.

Plate 14. Each chitinozoan is identified by sample depth and stub number. Scales bar 100 μm for Figs. 1–9, and 5 μm for Fig. 10. Figs. 1–3. *Ancyrochitina brevis* Taugourdeau and de Jekhowsky, 1960. 1, 638.43 m, 3; 2, 638.43 m, 4; 3, 639.42 m, 3. Fig. 4. *Cingulochitina serrata* (Taugourdeau and de Jekhowsky, 1960). 639.42 m, 1. Fig. 5. *Urnochitina urna* (Eisenack, 1934). 638.43 m, 4. Fig. 6. *Margachitina elegans* (Taugourdeau and de Jekhowsky, 1960). 638.43 m, 3. Fig. 7. *Vinnalochitina corinnae* (Jaglin, 1986). 637.19 m, 7. Figs. 8–10. *Pseudoclathrochitina carmenchui* Cramer, 1964a. 8, 638.43 m, 4; 9, 638.43 m, 4; 10, 638.43 m, 4.