The Middle Devonian palynology and biostratigraphy of northern Spain

By:

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Abstract

The Naranco, Huergas and Gustalapiedra formations of the Asturias, León and Palencia provinces of northern Spain represent a nearshore marine clastic sequence deposited during the Mid Devonian. The formations are laterally equivalent, becoming more offshore in character through León and Palencia but representing the same stratigraphic interval. They have received limited palynological study, despite previous reports of their palynological assemblage and their important stratigraphic interval at the onset of early forests. A palynomorph assemblage from these formations is described here, comprising acritarchs, prasinophytes, chitinozoans and dispersed spores, with additional comment on the formations' lithology. The sampled rock was processed using standard palynological procedures and yielded a well-preserved assemblage, though thermal maturity was variable. A quantitative count of the palynomorph assemblage was undertaken using a *Lycopodium* spike. The assemblage is an early Givetian one, as evidenced by the presence of *Geminospora lemurata*, with some evidence of diachronism in the further offshore locations. The formations' biostratigraphy, in conjunction with lithological evidence, indicates that deposition was rapid. The assemblage presents various unexpected features, with some important taxa absent and others present at an unusual time. The palynomorph assemblage is significantly endemic to Iberia, and this is interpreted as indicating significant palaeogeographic isolation of northern Spain during the Middle Devonian. Terrestrial spores were prevented from dispersing here by a large geographic separation, while marine plankton may have been stopped by ocean currents running past these isolated islands, also indicating an open Rheic Ocean able to support such currents. This deposition also took place just after the Kačák Event, a major extinction event in the marine realm. The results presented here support an existing, monsoonal hypothesis for the origin of the Kačák Event, as this would also create the rapid nearshore deposition observed here, however this raises questions over how the event would be expected to manifest around the world. As an environmental event, the anoxia usually used to mark the event may have been sporadic or localised, not necessarily occurring in all areas, especially the nearshore location studied here. These results lend support to the existing idea of the Kačák Event as a longer, possibly polyphased event extending into the earliest Givetian.

Contents

Acknowledgements

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I mustn't forget the many other students who have joined me in the Sheffield Paly lab and ACCE in my time here. Sam, Steph, Chloe, Martha, Emma, Alysha, Matt, (other) Sam and everyone else whose names escape me, you've all helped make this past 4 years an unforgettable experience!

My parents have put up with me admirably while I've slaved away over bottles of acid and racks of microscope slides, being alternately excited and infuriated. Also, I mustn't forget Tina, a well-rounded individual and a great listener.

Final tally: 19,753 counted specimens, 213 taxa, 147 samples, 400 slides, 298 pages, 80,403 words

1 - Introduction

The environment of the distant past cannot, of course, be directly observed, therefore preserved sediment must be used to study this palaeoenvironment. Lithology and fossil content are invaluable in this endeavour and will be utilised in the present study of the Middle Devonian of northern Spain. This area has a well-known geological character, but its palynology is poorly described, greatly reducing its utility in the study of this important interval. This study seeks to address this deficit and present a comprehensive synthesis of the Naranco, Huergas and Gustalapiedra formations of Asturias, León and Palencia.

In addition, an important extinction event, the Kačák, is known to occur in various parts of the world during the Middle Devonian interval (House, 2002). This study will also present comment on this event's characteristics in northern Spain. Previous research has identified the event lithologically and using various marine macrofossils (García-Alcalde, 1998) but no information on the accompanying palynomorph assemblage has been presented.

2 - Geological Setting

2.1 - Introduction to the Middle Devonian world

2.1.1 - Timescale

The Middle Devonian epoch is defined as encompassing the Eifelian and the succeeding Givetian stages (Cohen et al., 2014) between approximately 390 and 380 Ma. Figure 1 depicts these stages within the Devonian Period, together with various biostratigraphic schemes. All the stage boundaries today have associated Global Stratotype Sections and Points (GSSPs), determined and defined using lithological and biostratigraphic indicators over and above the biostratigraphical zones depicted in figure 1 (Ziegler & Klapper, 1985; Klapper et al., 1987; Walliser et al., 1995).

2.1.2 - Palaeogeography

The palaeogeography of this period has received considerable attention, as it was during this time that the continents of Laurussia and Gondwana began to move closer together, allowing some flora and fauna to migrate across the rapidly narrowing seaways, before fusing into the supercontinent Pangaea (Scotese, 2001) (see Fig. 2). Various reconstructions of this changing palaeogeography have been made using a variety of methods. They generally concur on the position of Iberia, although there are some exceptions. It should be noted Iberia is made up of at least five different terranes (García-Alcalde et al., 2002) which were not necessarily close to one another during the Devonian period. The ambiguity surrounding their exact position means that for convenience most reconstructions consider Iberia as a single entity, without attempting to place its terranes (Torsvik & Cocks, 2016).

It is agreed that Iberia was originally part of Gondwana, positioned adjacent to South America (Torsvik & Cocks, 2013a, 2016), North Africa (Torsvik & Cocks, 2004; Cocks & Torsvik, 2006) or slightly further east (Stampfli et al., 2002; Torsvik et al., 2012). This particular disagreement is mostly associated with the rotational position of Gondwana. Iberia separated from Gondwana due to the opening of the Palaeotethys ocean (Stampfli et al., 2002). However, reconstructions differ greatly as to when this occurred, with different authors claiming any time from the Cambrian onwards (Torsvik & Cocks, 2004). Torsvik & Cocks (2004) simply depict it as having separated sometime before 400 Ma. Cocks & Torsvik (2006) refine this view with Iberia, as part of the Armorican Terrane Assemblage (ATA), remaining part of Gondwana until the end of the Silurian, as evidenced by its fauna, and breaking away sometime between 420

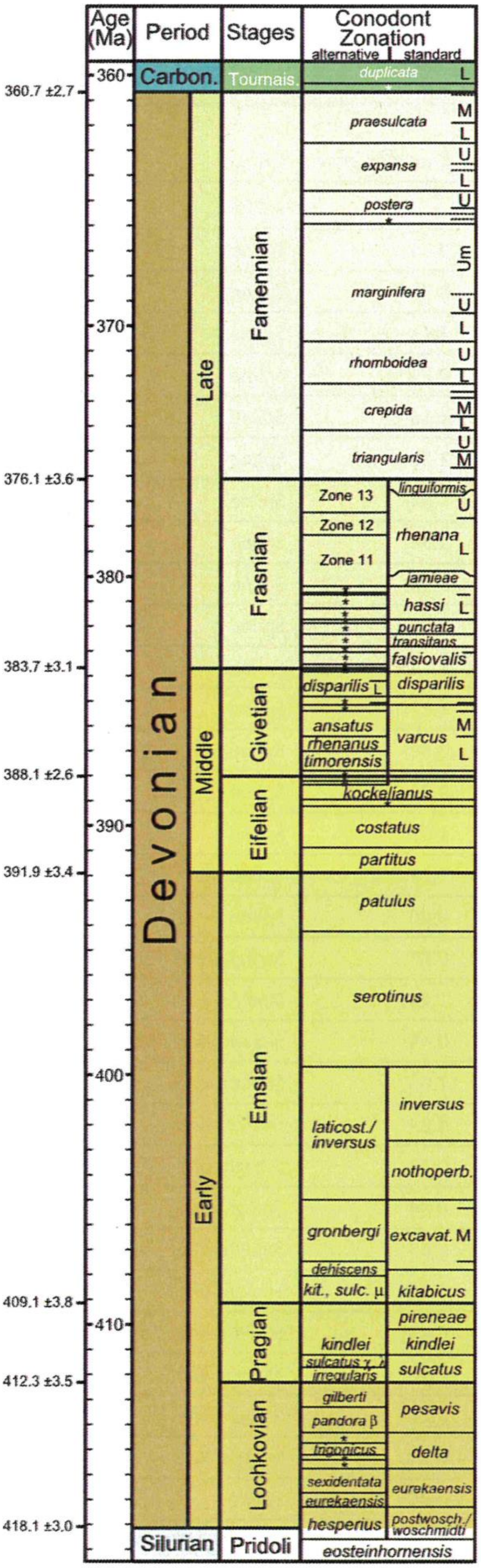


Figure 1. Devonian chronostratigraphy and conodont biostratigraphy (Becker et al., 2012).

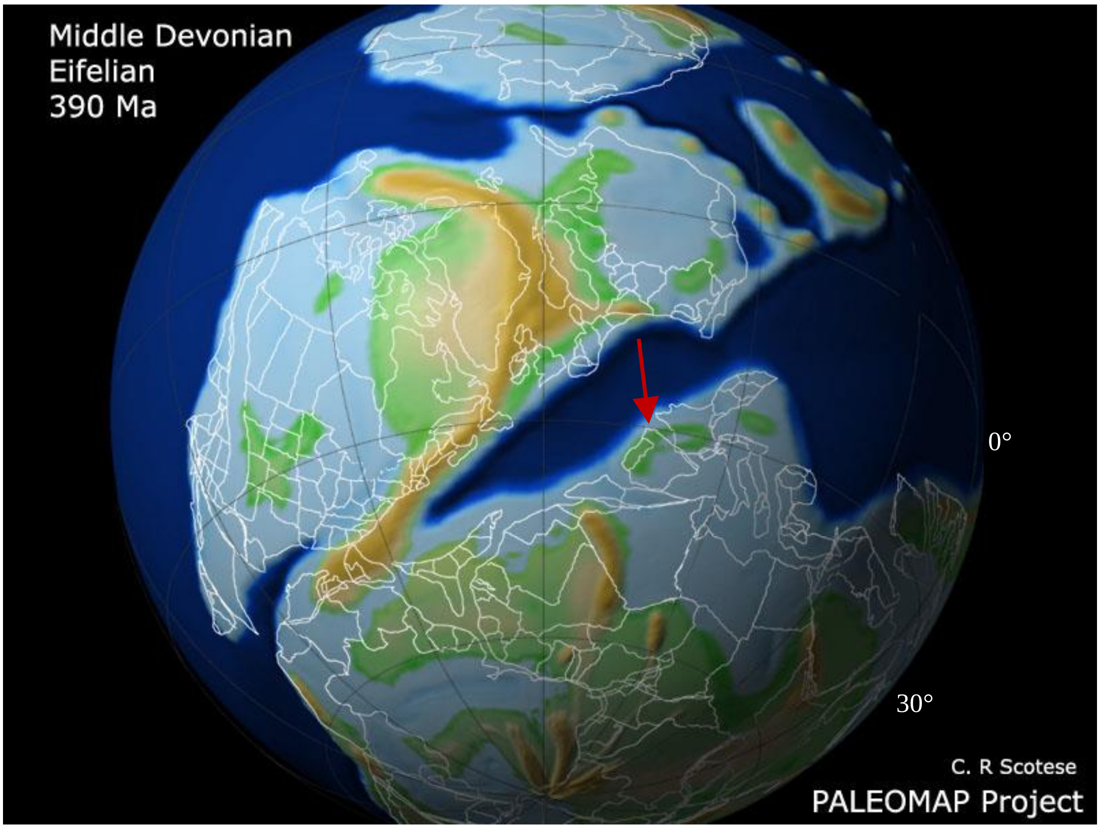


Figure 2. The palaeogeography of the Middle Devonian. The position of Iberia is marked by the arrow. The white outlines depict modern political boundaries, while colours indicate relief (adapted from Scotese (2001)).

and 400 Ma. This study also claims that at this time the Rheic Ocean was no longer wide enough to prevent faunal interchange between Gondwana and Laurussia. This view is supported by Torsvik et al. (2012) and Torsvik & Cocks (2013a), though Torsvik & Cocks (2013b) illustrate an additional landmass joining Iberia to North Africa. As this landmass is not mentioned in the key it is difficult to compare to the other descriptions. Stampfli et al. (2002) suggest separation occurred somewhat earlier during the Silurian, while Torsvik & Cocks (2016) suggest separation during the Ordovician.

By the Middle Devonian, the focus of the present study, Iberia had certainly become a separate entity bounded by the widening Palaeotethys to the south and the narrowing Rheic Ocean to the north. Various studies (Torsvik & Cocks, 2004, 2013a, 2016; Cocks & Torsvik, 2006; Torsvik et al., 2012) depict the ATA as an elongate chain of landmasses, positioned at around 30°S by 400 Ma, which subsequently moved westwards, at least in relation to Laurussia and Gondwana, to approach Laurussia by 370 Ma and to collide with Laurussia and Gondwana shortly afterwards as Pangaea formed. Stampfli et al. (2002), however, present a differing reconstruction. They depict southern Europe as being extremely fragmented and elongated into a group of landmasses named the Hun superterrane. Cantabria is its own terrane within this, positioned quite far eastwards of Armorica and other parts of Iberia. It reaches 30°

S by 400 Ma, before continuing northwards and reaching almost 10° S by 380 Ma. It then travels westwards, colliding with Laurussia followed by Gondwana over a 40 million year period, which is a much greater period of time than that given in the studies cited earlier. Cantabria is depicted in this study as being much further away from major land masses and further into the tropical zone than others suggest, which should presumably affect the character and degree of endemism of its flora and fauna.

The above descriptions are summarised in figures 3-6, taken from the reports in question and illustrating the differences between reconstructions.

2.1.3 - Palaeoenvironment

Numerous studies of the environmental conditions prevalent during the Middle Devonian have been conducted. These are summarised in the following section.

The atmospheric concentration of CO_2 has varied widely through time. This has been estimated in the various GEOCARB models of Berner (1991, 1994). The latest iterations of this model, GEOCARB-III (Berner & Kothavala, 2001) and GEOCARBSULF (Berner, 2006a) both indicate that atmospheric CO_2 concentrations dropped quite significantly to a low of 10 times today's concentrations by the Late Silurian and were increasing again to a high of about 15 times today's levels by the end of the Middle Devonian (see Fig. 7). This is as high as CO_2 concentrations have been since that time and possibly contributed to the rapid expansion of vascular plants which occurred around the Middle Devonian (Willis & McElwain, 2002). It should be noted that the addition of variable volcanic weathering to this model removes the rise in CO_2 concentrations during the Middle Devonian and depicts the level actually dropping slightly (Berner, 2006a, 2006b). This result is based on a number of assumptions concerning the erosion of silicates but it should still be taken into consideration as evidence of the uncertainty inherent in modelling studies of this kind.

Atmospheric oxygen levels in the Devonian are subject to some debate. Many models agree on a fall in atmospheric oxygen concentration during the Silurian to a low in the Middle Devonian. There followed a more or less rapid increase, depending on the model, through the Late Devonian and Carboniferous. Models disagree over the magnitude of the Middle Devonian low point. The models of Berner (1999, 2006a) indicate a low of around 13-18% O_2 concentration, somewhat lower than today's level of 21%. However, a model (Algeo & Ingall, 2007) based on the ratio of organic carbon to phosphorus in organic-rich sediments indicates a low point in the region of 5% (see Fig. 8). This is markedly lower than other models and represents a low point for the entire Phanerozoic Eon. As the authors state, this model does explain the purported charcoal gap, a time during the Middle Devonian in which fossil

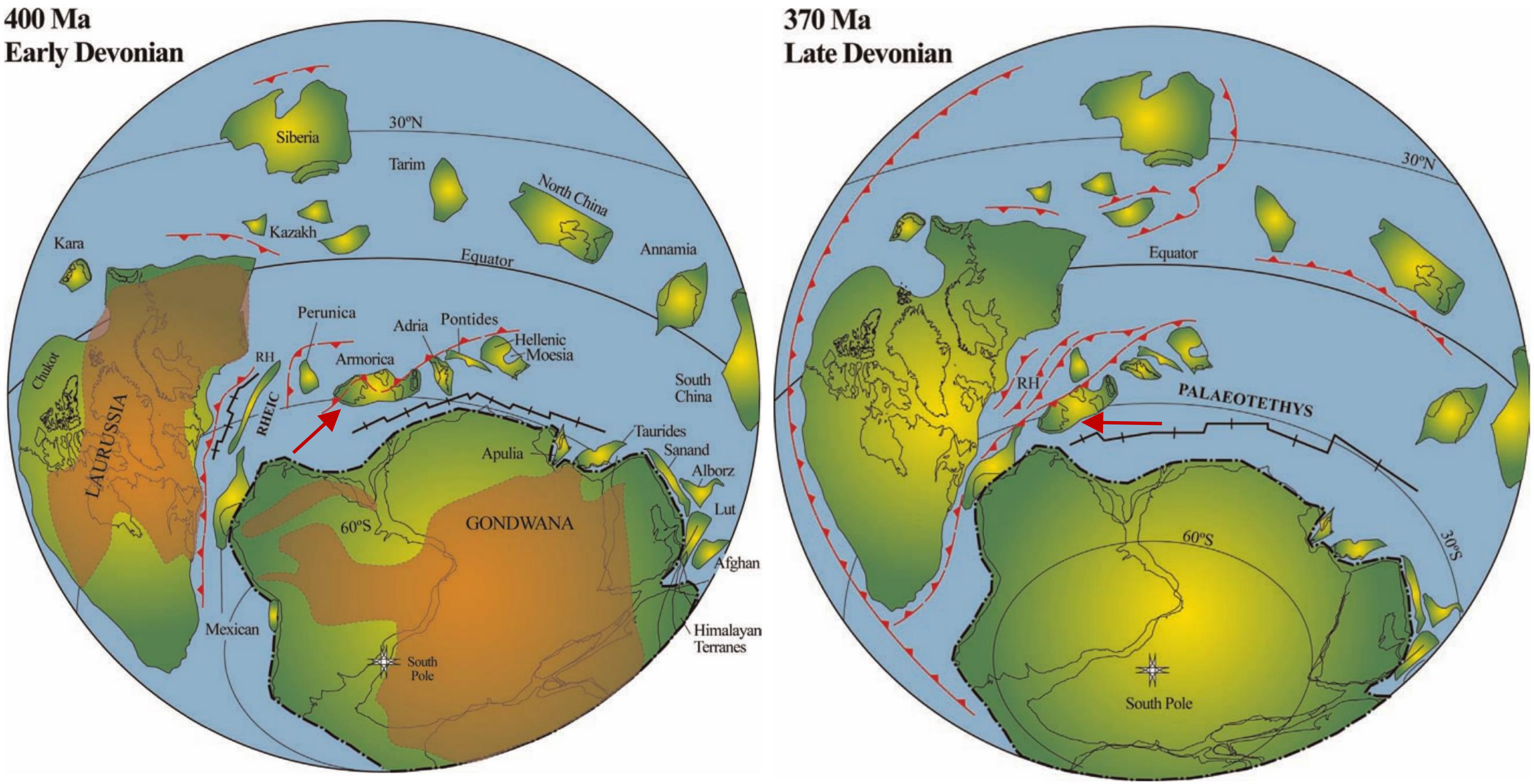


Figure 3. Palaeogeographic maps of the world during the Early and Late Devonian taken from Cocks & Torsvik (2006), themselves modified from Torsvik & Cocks (2004). The approximate position of Iberia is marked by the arrows.

charcoal deposits are unknown (Carpenter, 2014). An atmospheric O_2 concentration of 5% is far below the level required to sustain burning, therefore no natural charcoal forms. Despite this circumstantial support the present author questions the veracity of the finding. An O_2 concentration of 5% is an unfeasibly low amount for complex life to thrive on, as it did during the Middle Devonian with the evolution of trees and the rise of large fish (Willis & McElwain, 2002; Benton, 2005). In addition, there is now evidence refuting the charcoal gap; fossil charcoal may be rare during this period but it is not non-existent (Carpenter, 2014).

Despite the low atmospheric O_2 concentrations during

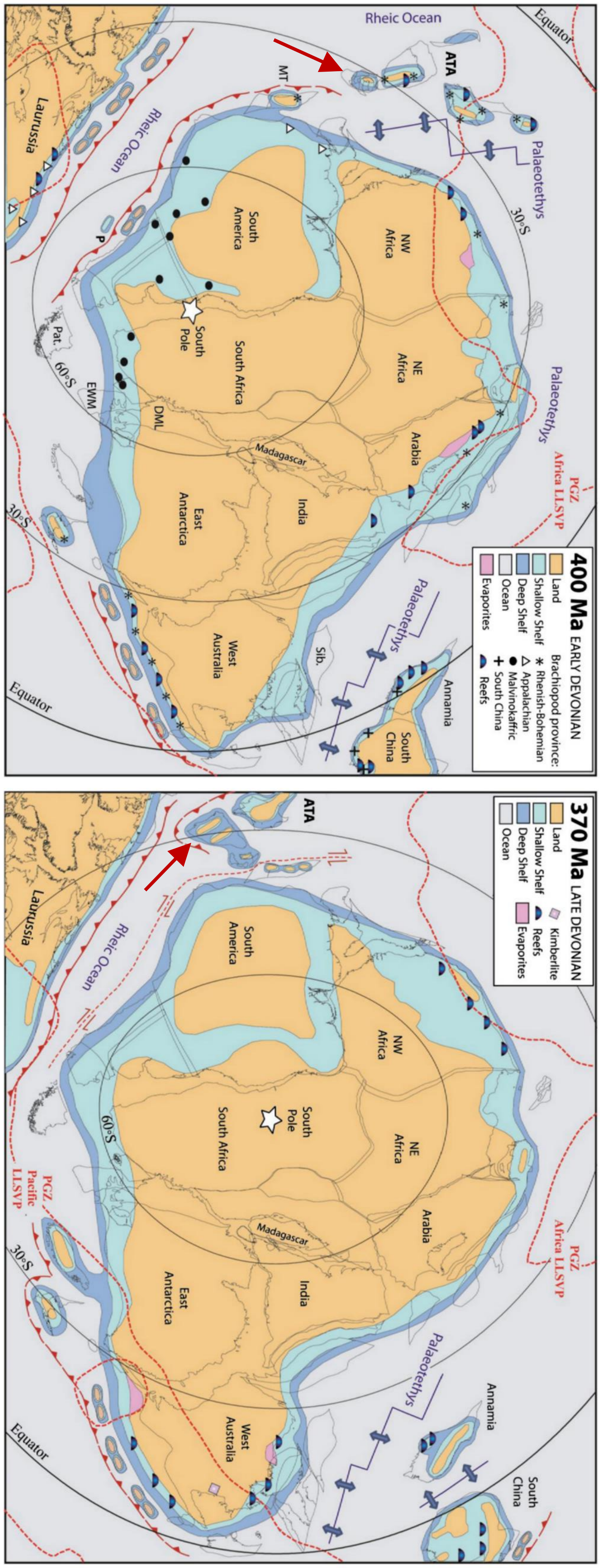


Figure 4. Palaeogeographic maps of Gondwana during the Early and Late Devonian taken from Torsvik & Cocks (2013a). The approximate position of Iberia is marked by the arrows.

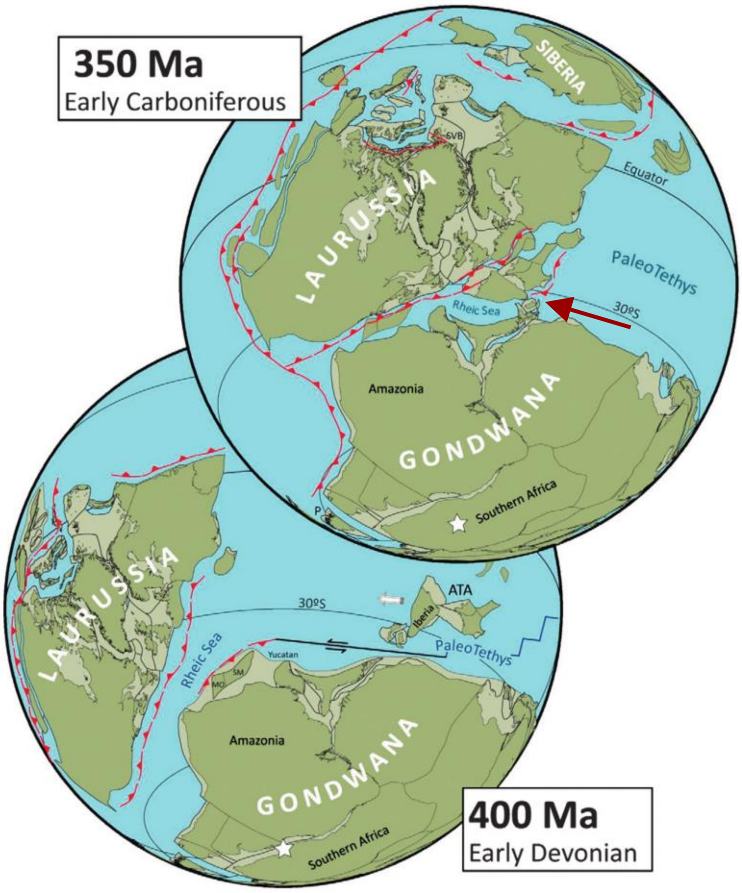


Figure 5. Palaeogeographic maps of the world during the Early Devonian and Early Carboniferous, covering the time period relevant to this study, taken from Torsvik et al. (2012). The approximate position of Iberia is marked by the arrow on the Early Carboniferous map; it is already marked on the Early Devonian map as part of the ATA. Note its more eastward position as related to the previous figures.

this period, evidence for a major oceanic oxygenation event around 400 Ma has been reported (Dahl et al., 2010) and linked to the aforementioned rise of vascular plants and large, predatory fish. This apparent paradox, of ocean oxygenation taking place at a major low point in atmospheric O_2 levels, can potentially be explained either by chemical processes or simple uncertainties about the timing of the events, as there was a major increase in atmospheric O_2 concentrations towards the Late Devonian.

Sea level and global temperatures show similar patterns to each other. Sea levels reached a minor low during the Early Devonian and were rising slowly to a high during the Early Frasnian, with levels during the Middle Devonian about 160 m above those of today (Haq & Schutter, 2008). Global temperatures exhibit a low point during the Early Givetian, determined to be about 23-25 ºC, incidentally promoting the rise of coral-stromatoporoid reefs as opposed to the microbial reefs which dominated in the Early and Late Devonian. Results from France also indicate lower temperatures and/or higher salinity in European-type shelf seas rather than the epicontinental seas which covered much of North America at this time (Joachimski et al., 2009).

The palaeoclimate reconstructions of Scotese (2001) place Iberia on the boundary between the arid and warm temperate zones during the Middle Devonian (see Fig. 9). This is evidenced by kaolinite deposits, usually indicative of warm temperate conditions, and more numerous evaporites indicating a prevailing arid environment. These become more dominant towards the Late Devonian. It should, however, be noted that these reconstructions place Iberia further

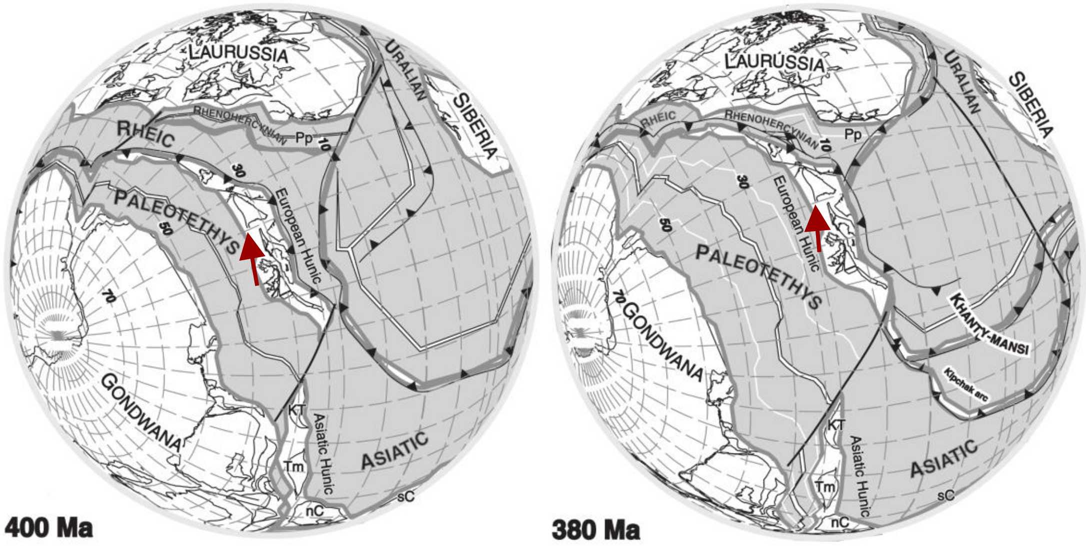


Figure 6. Palaeogeographic maps of the world during the Early and Late Devonian taken from Stampfli et al. (2002). The approximate position of Cantabria is marked by the arrows. Note its far more northward position by the Late Devonian as related to the previous figures.

south and closer to Gondwana than many other palaeogeographical reconstructions. Moving Iberia northwards in this reconstruction would place it more completely in an arid zone.

2.1.4 - Devonian Global Events

In addition to the above reconstructions of general environmental conditions during the Devonian, numerous transient events have been recognised throughout the period. The vast majority of these events are well characterised in marine environments where they were first recognised (García-Alcalde et al., 2002), but information concerning their impact on terrestrial ecosystems is often lacking.

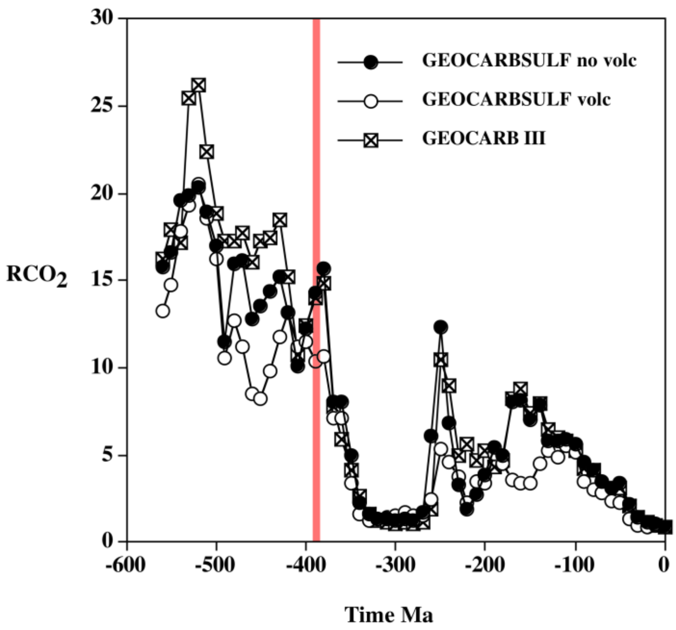


Figure 7. Plots of RCO_2 against time for the GEOCARBSULF and GEOCARB-III models. RCO_2 is the ratio of the mass of atmospheric CO_2 at a given time to its mass today. ‘volc’ and ‘no volc’ refer to the addition or non-addition to the model of variable volcanic weathering. The shaded area highlights the approximate time period addressed in this study (adapted from Berner (2006a)).

The Kačák Event is one such case. In common with many Devonian ‘Events’, the term ‘Kačák’ has been used differently by different authors (Truyóls-Massoni et al., 1990; Marshall et al., 2007), leading to differing accounts of its definition, timing and nomenclature. The present

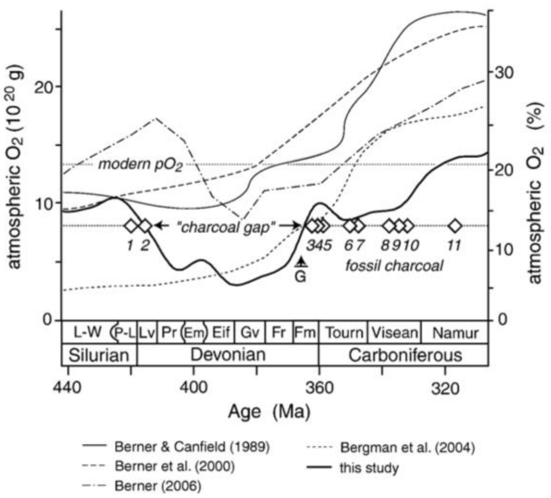


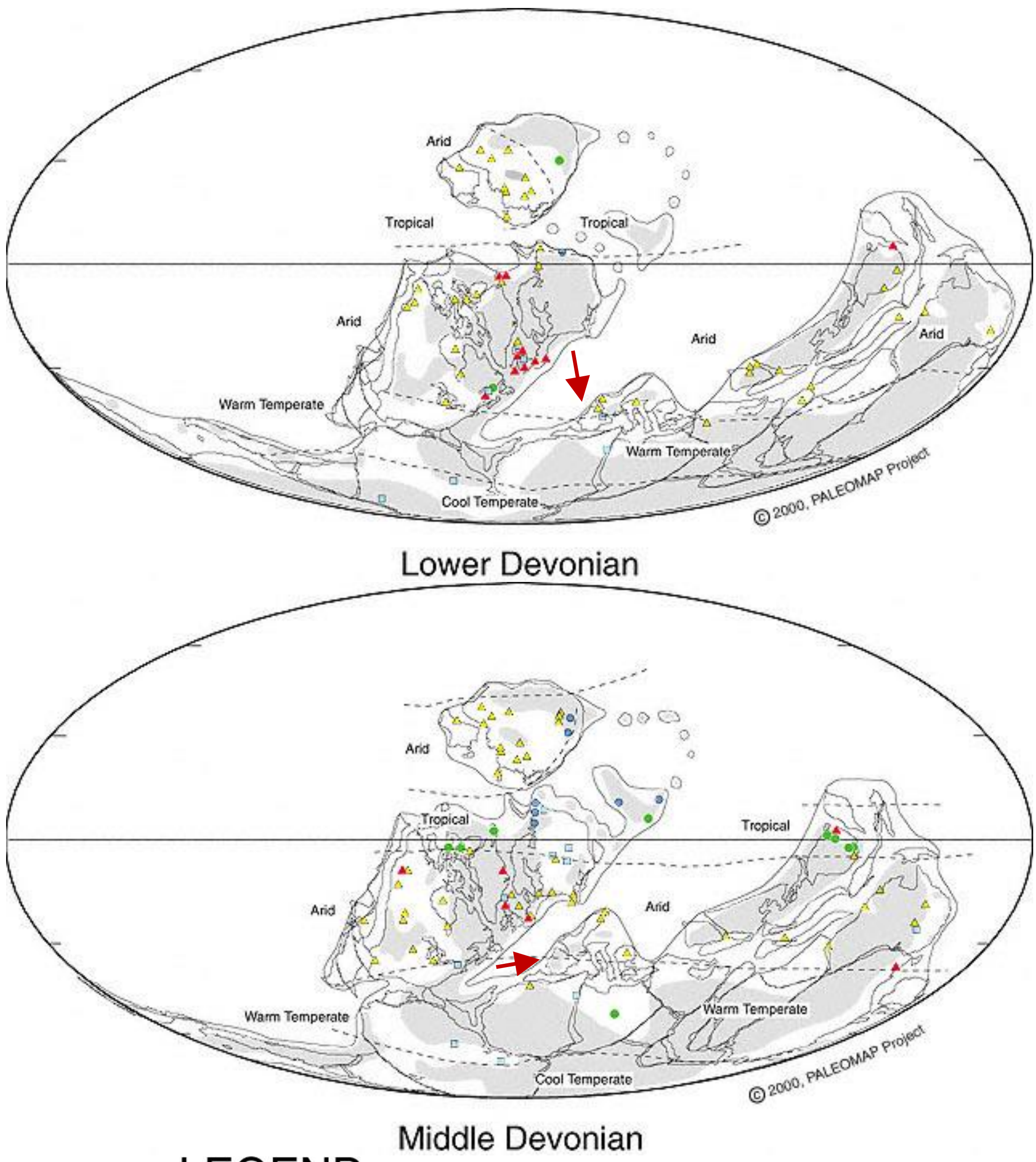
Figure 8. Models of atmospheric O_2 levels for the Silurian to Carboniferous (adapted from Algeo & Ingall (2007)). 'G' refers to minimum O_2 levels for the Famennian; diamonds refer to charcoal deposits. For the identities of these deposits and the precise references for the various models, see Algeo & Ingall (2007).

author sees no reason not to use its original name as derived from the lithological formation in which it was first recognised (Truyóls-Massoni et al., 1990; Marshall et al., 2007). It is sometimes referred to as the *otomari* event after the dacryoconarid *Nowakia otomari*, which frequently appears at the base of the event (Truyóls-Massoni et al., 1990; García-Alcalde, 1998; DeSantis et al., 2007; Marshall et al., 2007), however this and other supposedly associated taxa are of questionable validity and utility (Truyóls-Massoni et al., 1990).

The Kačák Event has seen various definitions and chronological placements during its study. Some treatments on the subject describe a series of closely-spaced anoxic events spread over the uppermost *kockelianus* and *ensensis* conodont zones (see Fig. 1) in the late Eifelian (DeSantis et al., 2007; House, 1996, 2002; Marshall et al., 2007; Truyols-Massoni et al., 1990). Others claim the event is longer, possibly polyphased and reaching into the earliest Givetian (Walliser & Bultynck, 2011; Becker et al., 2016; Grahn et al., 2016). This could potentially place the event as contemporary with the palynomorph assemblage analysed here.

Studies claim to have located this interval in northern Spain, in the Palentian domain, adjacent to the Asturo-Leónese domain. The event is said to occur around the Man Member of the Gustalapiedra formation (Truyóls-Massoni et al., 1990; García-Alcalde, 1998), which correlates well with the formations studied here. The normal index fossils are rare here (Truyóls-Massoni et al., 1990; García-Alcalde, 1998) leaving the event's location to be determined primarily using lithological evidence. The Kačák Event is almost always marked by black shales, intercalated within a pre-existing lithology which then resumes upon the termination of the event (Marshall et al., 2007). In the Palentian domain the lithology is predominantly limestones and marls (Truyóls-Massoni et al., 1990), while the Huergas and Naranco formations are siliciclastic (García-Alcalde, 1998), but both exhibit a sudden onset and similarly sudden cessation of shale deposition (García-Alcalde, 1998).

Various lines of speculation have been pursued as to the cause of the Kačák Event. It is associated with sea level rise and fall, usually a single cycle, with accompanying benthic



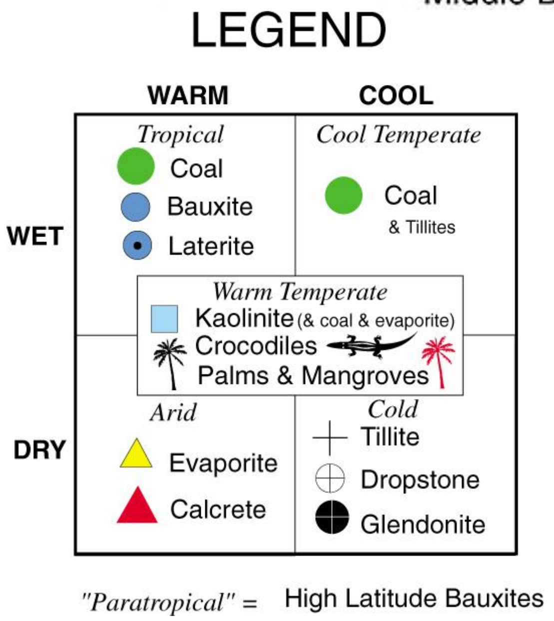


Figure 9. Palaeoclimate reconstructions for the Early (400 Ma) and Middle (380 Ma) Devonian. The approximate location of Iberia is marked by the arrows. Note other reconstructions place it further north (adapted from Scotese (2001)).

anoxia causing some degree of benthos turnover (House, 2002), though in some areas of Germany the original fauna was able to survive in shallow refugia before recolonizing the area as sea level fell (Marshall et al., 2007). It has also been associated with an increase in global temperature and increased clastic input to the oceans (Marshall et al., 2007), which could be due to increased runoff from the land or an increase in atmospheric dust. Marshall et al. (2007) have produced a convincing synthesis of these various phenomena based on study of the Orcadian Basin, Scotland. They describe how increased insolation could produce an increasingly monsoonal climate, increasing freshwater runoff from the land which carried with it clastic sediment and plant fossils, common in some European deposits. This increased runoff would have caused a reduction in surface salinity, enhancing stratification within the oceans, which were already deepening eustatically as a result of the increased insolation, and thus promoting benthic anoxia. Such conditions continued, probably cyclically, until insolation decreased again.

This model neatly explains the various changes seen in the Devonian world at this time and is supported by independent evidence of sea level changes (Bartholomew & Brett, 2007), increased continental weathering (House, 2002) and varying fortunes of faunal assemblages with or without access to shallow refugia (DeSantis et al., 2007). If true, it relies heavily on a terrestrial phenomenon, the monsoonal rains, which should produce a change in the land flora, possibly observable in a palynological assemblage.

2.2 - Devonian Geology of the Cantabrian Mountains

Spanish Devonian deposits have a long history of scientific study, well summarised by García-Alcalde et al. (2002). Cantabria was one of the first areas in Spain where the period was recognised, with one of the most complete Devonian sequences in the country. They, along with other Palaeozoic units, have been greatly deformed by tectonism and orogenic events, particularly the collision of Gondwana and Laurussia during the Carboniferous and Permian. Today the strata form a wide partial arc extending southwards from the coast of Asturias before taking on an east-west orientation in Castilla y León. Sediments become younger as one travels west or towards the centre of the arc, while towards the south of the Leónese domain Cenozoic deposits unconformably overlie some Devonian deposits (ITGE (Instituto Técnológico Geominero de España), 2004).

Devonian outcrops begin on the northern coast west of Gijón and extend south almost to León but do not extend particularly far eastwards (ITGE, 2004) (see Fig. 10). The Asturo-Leónese domain contains alternating calcareous and clastic facies, representing a former shelf environment. This domain represents a nearshore facies, as opposed to the further offshore facies of the Palentian domain, though both probably represent the same carbonate platform, periodically overtaken by a clastic influx (García-Alcalde et al., 2002). Interestingly sediment source is from the east or northeast (García-Alcalde et al., 2002), indicating an area of highland in this location which has since been disguised by the considerable tectonic distortion of the

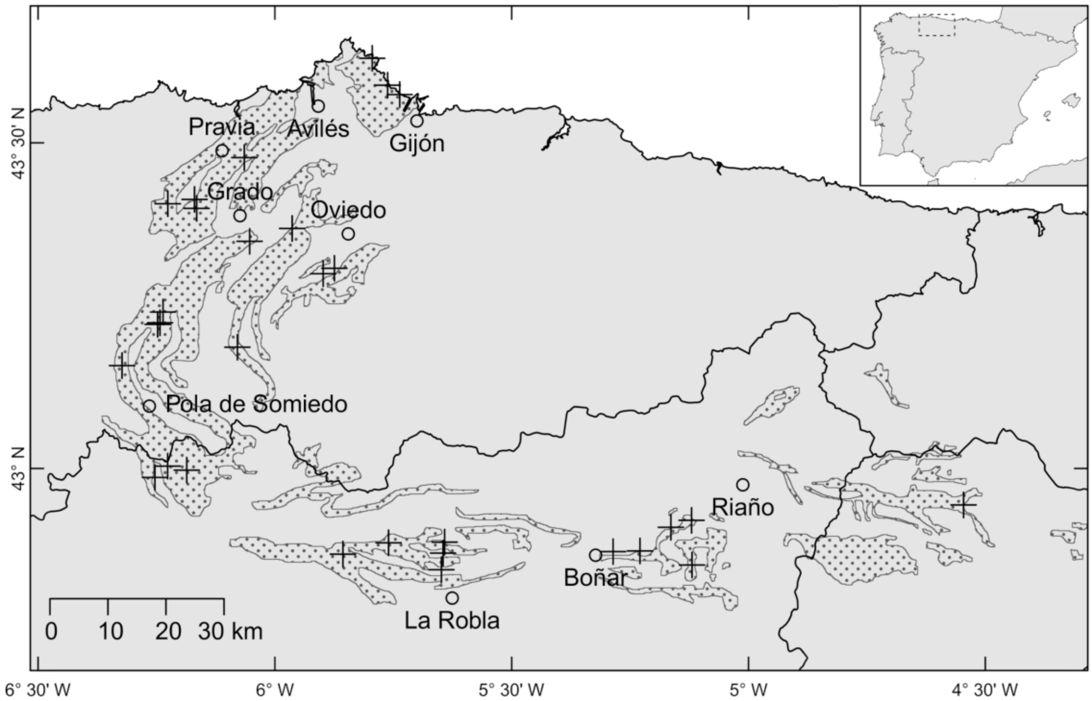


Figure 10. Outline map of northern Spain. Outlined areas marked with dots indicate the outcrop area of Devonian sediments (García-Alcalde et al., 2002). Sites surveyed in this study are marked with crosses.

area. Many of the deposits exhibit a regressive character due to local uplift, counteracting the global trend of rising sea levels (García-Alcalde et al., 2002; Haq & Schutter, 2008).

Over time, the various rock formations have been studied by different workers and often given different names in different outcrop areas. Many are now recognised as lateral equivalents and may be continuous (García-Alcalde et al., 2002). This study focuses on the correlative Middle Devonian Naranco, Huergas and Gustalapiedra formations of Asturias and León (see Fig. 11), though the Gustalapiedra has a comparatively impoverished assemblage.

Underlying the studied formations, the Moniello, Santa Lucía and equivalent formations comprise argillaceous limestones with occasional thin shales and reefal developments. There is a clear trend of shallowing towards the centre of the arc, apparent in the palaeontological remains and in the facies, with some supra-littoral deposits seen (García-Alcalde et al., 2002). The Naranco and Huergas formations represent a marked departure from this long-established sedimentary character (García-Ramos, 1978), detailed extensively below. The succeeding Candás and Portilla formations represent a return to reefal deposition (García-Alcalde et al., 2002).

2.2.1 - The Naranco, Huergas and Gustalapiedra formations

The Naranco and Huergas formations consist of sandstone beds alternating with siltstone, slate, shale or clay beds, with occasional limestone lenses. The sandstones are often described

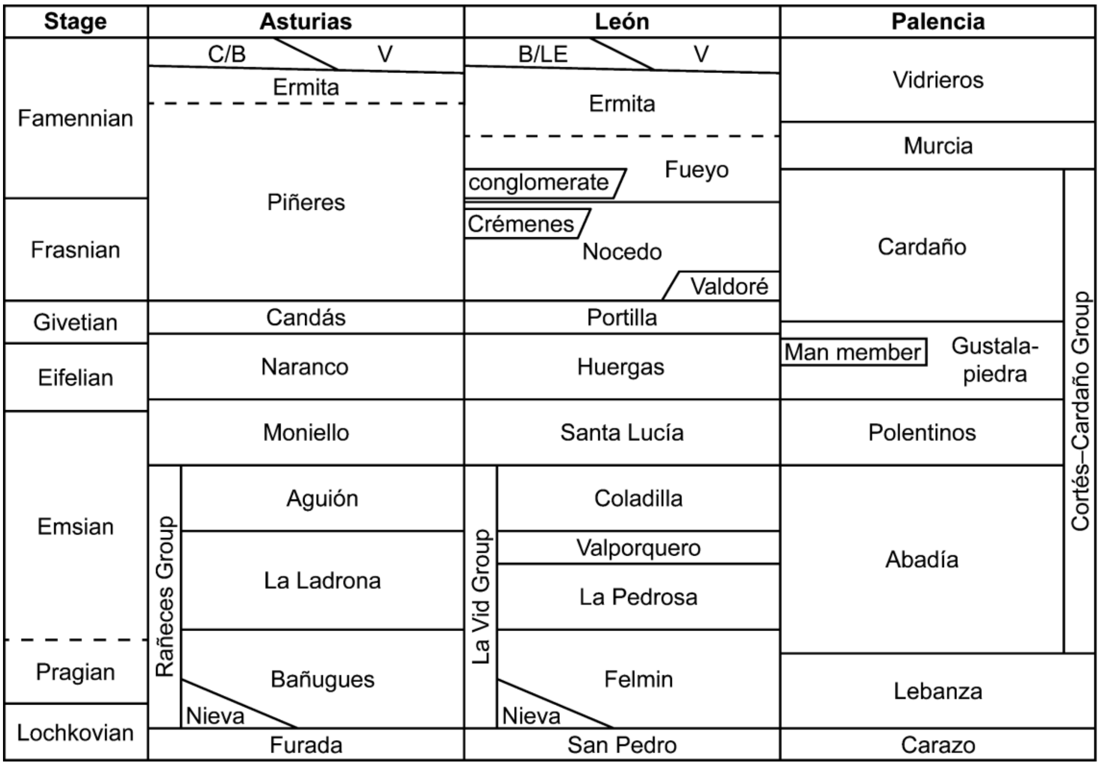


Figure 11. The age and correlation of Devonian deposits in the studied Iberian areas. Dashed lines indicate uncertainty in the boundary position. Diagram not to scale. Abbreviations for latest Famennian units: B, Baleas; C, Candamo; LE, Las Ermitas; V, Vegamián. Redrawn from García-Alcalde et al. (2002).

as ferruginous (Beroiz, Pignatelli, et al., 1972; Beroiz, Ramírez del Pozo, et al., 1972; Julivert et al., 1972, 1975a, 1975b; Pello, 1973; Martínez-Álvarez et al., 1973; Lobato et al., 1978; Crespo Zamorano, 1979; Navarro Vázquez, 1979; Heredia et al., 1989) and white (Martínez-Álvarez et al., 1973), grey (Pello, 1973; Marcos et al., 1979; Alonso et al., 1989), beige (Crespo Zamorano, 1979; Navarro Vázquez, 1979), brown (Martínez-Álvarez et al., 1973; Marcos et al., 1979; Alonso et al., 1989), green (Crespo Zamorano, 1979; Navarro Vázquez, 1979; Alonso et al., 1989), yellow (Marcos et al., 1979) or red (Beroiz, Pignatelli, et al., 1972; Caride et al., 1973; Marcos et al., 1979; Alonso et al., 1989) in colour. The sandstone is fine to medium grained and coarsening upwards (Pello, 1973; Alonso et al., 1989) with a siliceous (Caride et al., 1973; Pello, 1973; Leyva et al., 1980), quartzitic (Caride et al., 1973; Pello, 1973; Crespo Zamorano, 1979; Navarro Vázquez, 1979; Heredia et al., 1989), calcareous (Suárez Rodríguez et al., 1989), dolomitic (Alonso et al., 1989) or volcanic glass cement (Caride et al., 1973; Pello, 1973). Sandstone beds have been described as becoming both more (Beroiz, Pignatelli, et al., 1972; Caride et al., 1973) and less (García-Ramos et al., 1978; Manjón Rubio et al., 1978) frequent higher in the formation in different areas. Interspersed finer beds are described as brown (Beroiz, Ramírez del Pozo, et al., 1972; Julivert et al., 1972, 1975a, 1975b; García-Ramos et al., 1978; Manjón Rubio et al., 1978; Crespo Zamorano, 1979; Navarro Vázquez, 1979; Alonso et al., 1989), green (Beroiz, Pignatelli, et al., 1972; Beroiz, Ramírez del Pozo, et al., 1972; Julivert et al., 1972, 1975a, 1975b; Caride et al., 1973; Pello, 1973; Lobato et al., 1978; Marcos et al., 1979; Alonso et al., 1989), yellow (Beroiz, Pignatelli, et al., 1972; Caride et al., 1973; Pello, 1973), grey (Pello, 1973; Lobato et al., 1978; Alonso et al., 1989) or black (Lobato et al., 1978; Marcos et al., 1979; Leyva et al., 1980; Heredia et al., 1989) in colour.

The formation is described as detrital (Julivert et al., 1975a; Lobato et al., 1978; Crespo Zamorano, 1979; Marcos et al., 1979) and terrigenous (Lobato et al., 1978; Crespo Zamorano, 1979; Marcos et al., 1979; Heredia et al., 1989). The base of the formation is often described as gradational (Pello, 1973; Crespo Zamorano, 1979; Marcos et al., 1979; Leyva et al., 1980; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989) and the top is described as gradational in some areas (Lobato et al., 1978; Heredia et al., 1989). The formation has been described as containing both siliceous and phosphatic nodules (Lobato et al., 1978; Crespo Zamorano, 1979; Leyva et al., 1980; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989). The formation's thickness varies widely, from less than 60 m (Caride et al., 1973) to over 500 m (Beroiz, Pignatelli, et al., 1972).

The formation's depositional environment has been subject to some speculation. It has been described as a near shore (Lobato et al., 1978) reducing environment (García-Ramos et al., 1978; Manjón Rubio et al., 1978; Crespo Zamorano, 1979; Navarro Vázquez, 1979; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989), though more oxidative to the north-east (Navarro Vázquez, 1979; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989) in the direction of the depositional source (Crespo Zamorano, 1979; Navarro Vázquez, 1979; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989). It has been described as a calm setting (García-Ramos et al., 1978; Manjón Rubio et al., 1978; Leyva et al., 1980) with little oxygen (Lobato et al., 1978; Marcos et al., 1979), though one report claims an oxygenated environment with higher oxygen levels higher in the formation, as well as a higher energy environment (Leyva et al., 1980). The depositional setting has been interpreted as deepening towards León and in the Huergas formation, gaining a more pelagic fauna (Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989). Two models of sedimentation have been proposed for the Huergas formation; first a graded marine platform of medium to high energy with bars migrating towards land and with sheltered distal areas harbouring clay and a benthic fauna existed, before a significant transgression with decreased terrigenous input, a low, tidal coast and evidence of storm damage though still with areas sheltered by sand banks (Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989).

The age of the Naranco and Huergas formations has been subject to some debate, complicated by a lack of stratigraphically important fossils. An Eifelian to early Givetian date is most often cited (Beroiz, Ramírez del Pozo, et al., 1972; Julivert et al., 1975a, 1975b; García-Ramos et al., 1978; Lobato et al., 1978; Crespo Zamorano, 1979; Marcos et al., 1979; Navarro Vázquez, 1979; Alonso et al., 1989; Suárez Rodríguez et al., 1989; Heredia et al., 1989), though locally it may be Eifelian only (Caride et al., 1973), Eifelian to late Givetian (Martínez-Álvarez et al., 1973; Pello, 1973; Leyva et al., 1980) or late Eifelian to early Givetian (Julivert et al., 1972). Supporting this is the discovery of *Cabrieroceras*, the trilobite *Kayserops*? *cantarmoricus* and an unnamed Chonetacean brachiopod in the type locality of the Huergas formation (García-Alcalde et al., 1979) and early Eifelian brachiopods in the top of the Moniello formation (García-López et al., 2002). See section 2.3.1 for a more complete list of macrofauna.

Of more utility are conodonts, with their detailed biostratigraphic schemes. The upper part of the section at the Playa del Tranqueru (detailed below) has been determined as *Polygnathus costatus costatus* zone (mid Eifelian) or younger while the bottom of the Candás formation is *P. varcus* zone (early Givetian) (García-López et al., 2002). A more detailed picture is provided by García-López & Sanz-López (2002). They describe the top of the Santa Lucía formation as *P. c. partitus* zone (early Eifelian), while the lowermost beds of the Huergas formation are *P. c. costatus* zone based on the presence of *P. linguiformis pinguis*. This dates the lower boundary of the formation to ca. 391-392 Ma (Becker et al., 2012). Above the Huergas, the lowermost Portilla formation contains *P. l. klapperi*, *P. hemiansatus*, *P. eiflius*, *Icriodus eslaensis* and *I. obliquimarginatus*, an association linked to the lower *P. varcus* subzone (early Givetian) and giving an age of ca. 386-387 Ma (Becker et al., 2012). This evidence supports the established early Eifelian-early Givetian age of the Naranco and Huergas formations.

One site has been studied in the Gustalapiedra formation of Palencia, hence it is briefly described here. The formation consists of black or dark grey shales or slates (Ambrose et al., 1977; Lobato et al., 1983; Heredia et al., 1989) interspersed with sand, siltstone (Ambrose et al., 1977) or limestone (Lobato et al., 1983; Heredia et al., 1989) beds. The formation may contain nodules (Lobato et al., 1983; Heredia et al., 1989). The formation has been described as having a gradational base (Lobato et al., 1983) and to have been deposited in a euxinic basin (Ambrose et al., 1977; Heredia et al., 1989). Thickness varies between 50 m (Heredia et al., 1989) and 180 m (Ambrose et al., 1977) in different areas. Age estimates vary widely across the outcrop area, from Eifelian (Heredia et al., 1989), late Eifelian to early Frasnian (Ambrose et al., 1977), early Givetian to late Givetian, late Givetian only and late Givetian to early Frasnian (Lobato et al., 1983).

2.2.2 - Review of study sites

The sites chosen for study correspond to the outcrop area of Devonian strata detailed in García-Alcalde et al. (2002) and depicted in figure 10. The location and precise geological setting of each site is detailed below, also being indicated on figure 10. Geological maps of the sites are given as figures 12-19, taken from the ArcMap version of the GEODE 1:50,000 scale maps produced by IGME (2015). The name given to each site is provided, followed by its sample code, if applicable. An approximate location for each site within the thickness of the Naranco, Huergas or Gustalapiedra formation is given.

Moniello-Punta la Vaca - 1

Fig. 12

43°37'46.28" N, 5°47'39.96" W

Short coastal exposure consisting mostly of sea cliffs not accessible by land. A small cove allows access to a shallow beach from the direction of Moniello village. Despite the indications of the published geological maps, no exposures of the Naranco Fm. could be seen, only limestones presumably belonging to other deposits. Previously described by García-Ramos (1978).

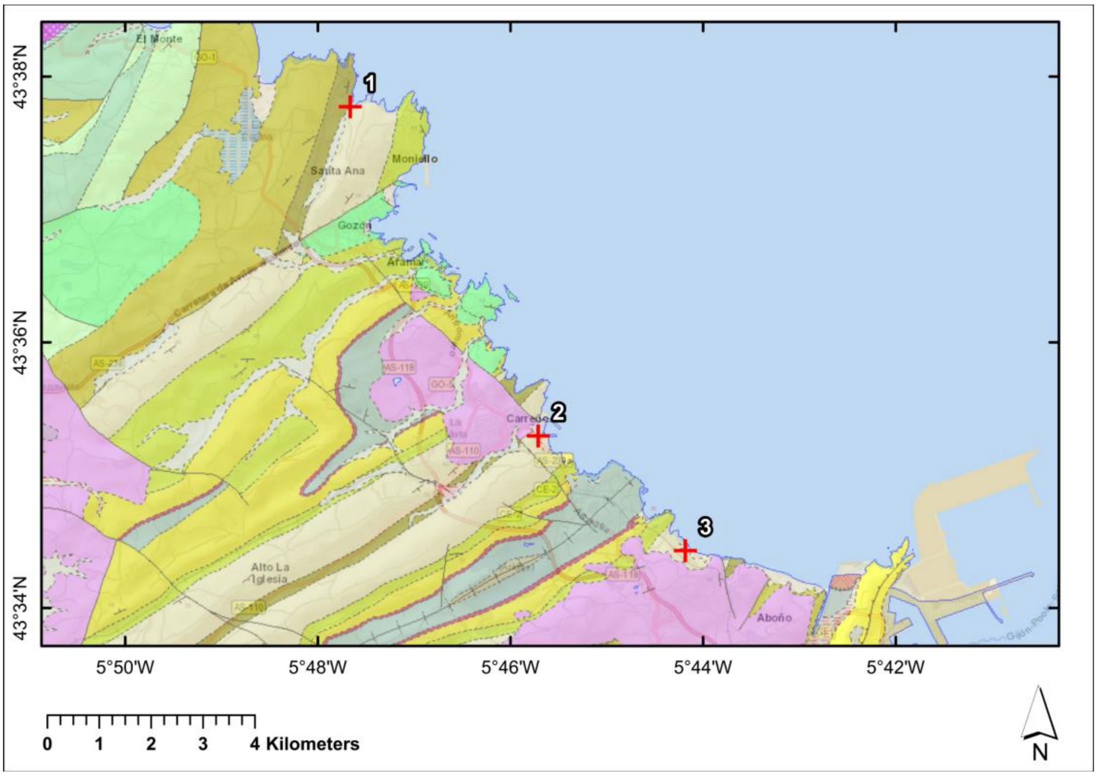


Figure 12. Geological map showing the Moniello-Punta la Vaca (1), Candás-Perán (2) and Playa del Tranqueru (3) sites. Basemap credit: Esri, HERE, DeLorme, USGS, Intermap, INCREMENT P, NRCan, Esri Japan, METI, Esri China (Hong Kong), Esri Korea, Esri (Thailand), MapmyIndia, NGCC, © OpenStreetMap contributors and the GIS User Community.

This exposure is in the south-eastern limb of an anticline oriented approximately NE-SW, however an intervening fault has orientated this exposure more E-W. The succession here should be completely exposed, with the Naranco Fm. bounded conformably by the older Moniello Fm. to the west and the younger Candás Fm. to the east. The shallow beach is around the base of the formation.

Candás-Perán - 2

Fig. 12

43°35’13.9” N, 5°45’40.40” W

Interrupted section present along the CE-8 road, exposed in cliff and as isolated blocks in the beach. Previously described by García-Ramos (1978).

These exposures are at the peak of an anticline, part of the same fold belt that includes site 1 (Moniello-Puna la Vaca) but without the fault-caused reorientation E-W. As such the Candás Fm. overlays the Naranco to the SE and NW, though with inconformable Quaternary deposits overlaying the Naranco in places. The exposure is located approximately in the middle of the formation.

Playa del Tranqueru - 3

Fig. 12

Approximately 43°34’33.37” N, 5°44’21.66” W to 43°34’22.10” N, 5°43’46.36” W

Long beach bounded by cliffs located between Perlora and Xivares, accessible completely at low tide. Excellent exposures forming the beach and sea cliffs, with further exposures on cliff tops. Accessed along the Tranqueru Greenway from Perlora Ciudad de Vacaciones. Previously described by García-Ramos (1978).

This exposure is in the south-eastern limb of a syncline, also part of the fold belt mentioned for the above two sites. The Naranco Fm. here is bounded by unconformable Triassic deposits to the SE and overlain conformably by the Candás Fm. to the NW. The published maps indicate most of the formation is exposed.

Veneros-Santoseso - 4

Fig. 13

43°28'37.55" N, 6°03'52.23" W

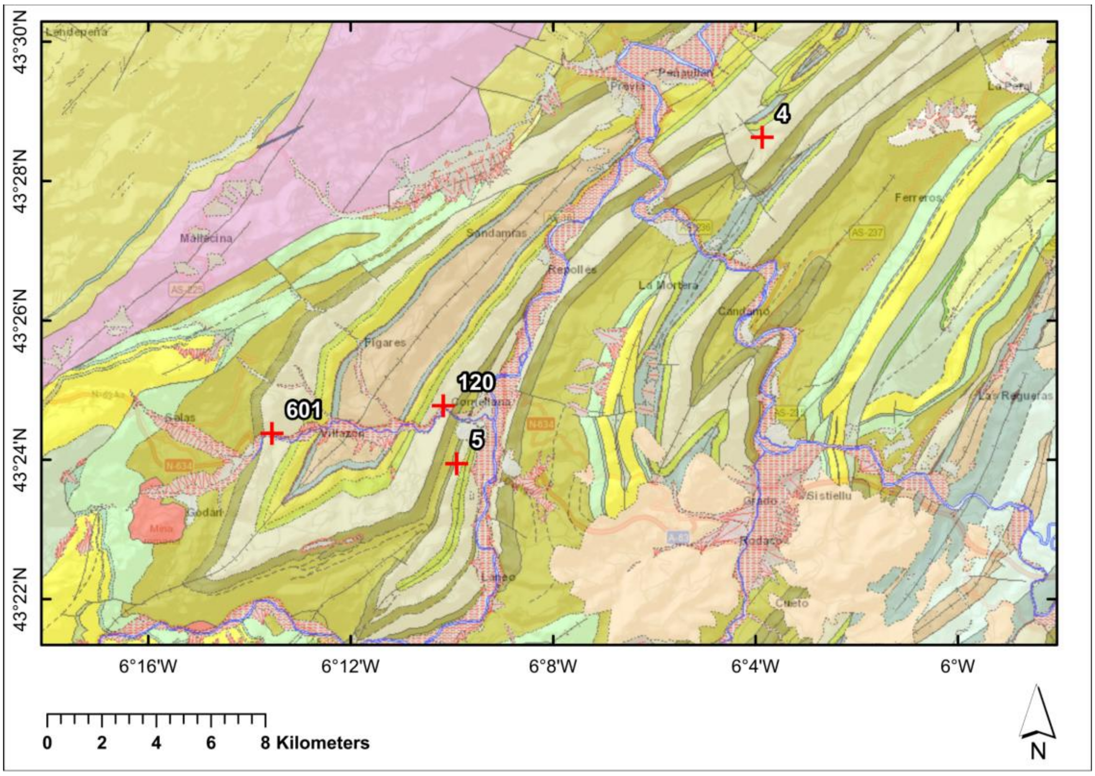


Figure 13. Geological map showing the Veneros-Santoseso (4), Sobrerriba-Santa Eufemia (5), 120 and 601 sites. Basemap credit as Fig. 12.

A large road cut on the AS-316 road from Veneros, at its junction with the AS-315 between Las Pandiellas and Santoseso. It is close to the Doña Palla-La Regata site of (García-Ramos, 1978) which could not be precisely located.

This exposure is formed from the south-eastern limb of another syncline, again oriented approximately NE-SW. The Naranco Fm. is bounded conformably by the Candás Fm. to the NW and the Moniello Fm. to the SE, which is then cut by a thrust fault which places it in contact with the Naranco Fm. again further to the SE. The exposure is in the upper third of the formation.

Sobrerriba-Santa Eufemia - 5

Fig. 13

43°23'56.70" N, 6°09'54.61" W

A series of road cuts around the summit of a hill a short distance south of Sobrerriba on the SL-7 road to Santa Eufemia. Previously described by García-Ramos (1978).

This exposure is formed from the eastern limb of a tight anticline oriented approximately north-north-east to south-south-west. The Naranco Fm. Is bounded conformably by the

Moniello Fm. lies to the west and the Candás Fm. to the east. The exposure is in the lower part of the formation.

La Gáraba-Coalla - 6

Fig. 14

43°20'54.93" N, 6°03'11.72" W

A road cut located on the GR-2 road between La Gáraba and Cuanxú, approximately 270 m south of the 2 km marker. Previously described by García-Ramos (1978).

This road cut is formed from the SE limb of a NE-SW oriented anticline. The Naranco Fm. is here bounded conformably by the Moniello Fm. to the NW and the Candás Fm. to the SE. The exposure is located near the top of the formation.

San Pedro de Nora - 7

Fig. 14

43°22'05.85" N, 5°57'48.59" W

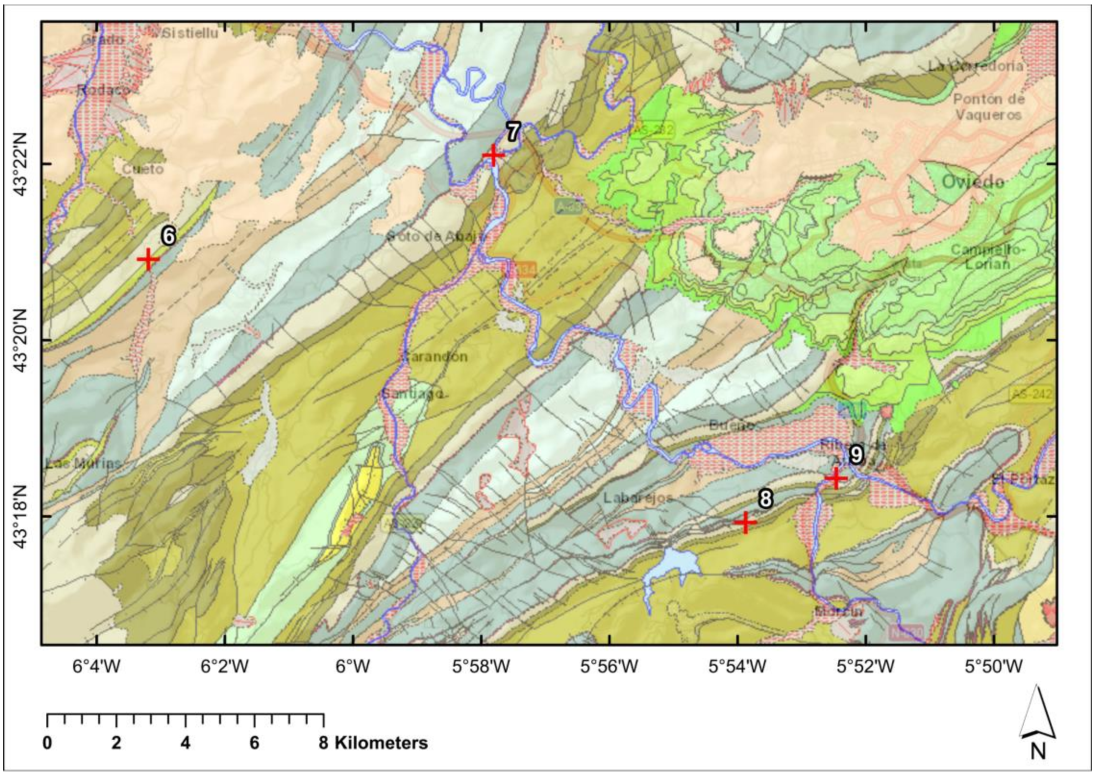


Figure 14. Geological map showing the La Gáraba-Coalla (6), San Pedro de Nora (7), Los Alfilorios (8) and Soto de Ribera-Tellego (9) sites. Basemap credit as Fig. 12.

A long road cut located near the AS-223 near the village of San Pedro. The Naranco Fm. is exposed in a very narrow area of land between the Río Nalon and Río Nora, across from San Pedro. Previously described by García-Ramos (1978).

This long exposure is formed from the NW arm of a NE-SW oriented anticline, with the Naranco Fm. bounded conformably by the Moniello Fm. to the SE and ostensibly conformably the Late Carboniferous Griotte-Sella-Alba Fm. to the NW. The section is located in the top half of the formation according to maps.

Los Alfilorios - 8

Fig. 14

43°17'55.69" N, 5°53'52.58" W

A small road cut located just outside La Carrera on the MO-5 road to Argame. This is a replacement for the 'Los Alfilorios' site of Garcia-Ramos (1978), which is now located beneath the Alfilorios reservoir.

This road cut is in the southern limb of a tight, roughly E-W oriented syncline, bounded conformably by the Moniello Fm. to the south and apparently conformably the usually Late Devonian Ermita Fm. to the north. The exposure is located near the middle of the formation.

Soto de Ribera-Tellego - 9

Fig. 14

43°18'25.74" N, 5°52'27.57" W

A very large road cut located just off the N-630 near Soto de Ribera on the road towards Tellego. Previously described by García-Ramos (1978).

This road cut is formed from the northern limb of an anticline connected to the syncline mentioned above for the Los Alfilorios site, though here it is thrust above the anticline's southern limb, producing the same outcrop pattern as Los Alfilorios. The exposure is located near the top of the formation.

Aguasmestas-Pigüeña - 10

Fig. 15

43°09'28.05" N, 6°19'21.60" W

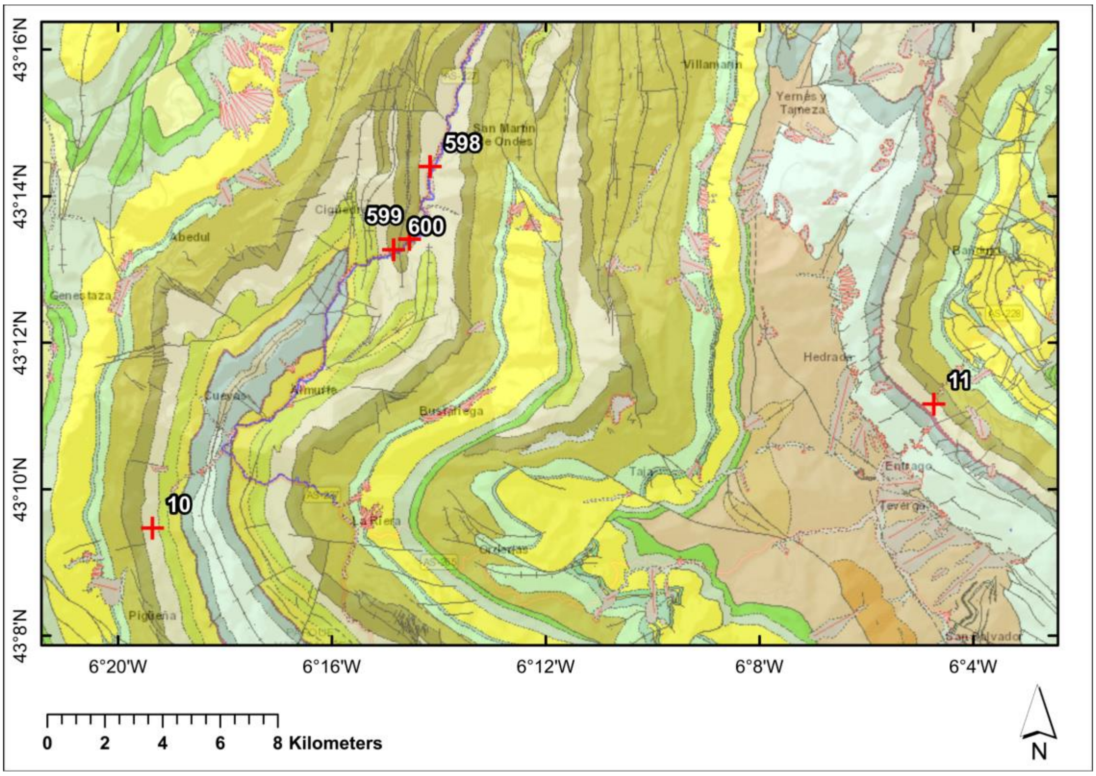


Figure 15. Geological map showing the Aguasmestas-Pigüeña (10), Las Ventas-Entrago (11), 598, 599 and 600 sites. Basemap credit as Fig. 12.

Exposure located on the road between Aguasmestas and Pigüeña, south of Santullano, close to the junction with the road to Pigüeces. Previously described by García-Ramos (1978).

Located in the western limb of a syncline oriented north-south with the Naranco Fm. bounded conformably by the Candás Fm. to the east and the Moniello Fm. to the west. The exposure is located in the middle of the formation.

Las Ventas-Entrago - 11

Fig. 15

43°11'09.65" N, 6°04'44.61" W

A road cut located on the AS-228 road between Las Ventas and Entrago. The Naranco Fm. is exposed between two tunnels as a cliff on the eastern side of the road and an isolated stack on the opposite side, approximately 350 m south of the 25 km marker. Previously described by García-Ramos (1978).

This exposure is in the western arm of a N-S oriented anticline, outcropping in a NW-SE orientation. The Naranco Fm. here is bounded conformably by the Moniello Fm. to the NE and by a narrow band of the Ermita Fm. to the SW. This exposure is located near the middle of the formation.

Lumajo - 12

Fig. 16

42°59'09.85" N, 6°15'11.62" W

Garcia-Ramos (1978) describes a locality north of Lumajo. The only possible location for this site is a series of outcrops on a hillside above the village of Lumajo, itself located 4.6 km north of Villaseca de Laciana. These exposures could not be located with certainty and the local geography was not conducive to good exposure.

This location is located in the SW limb of a roughly NW-SE oriented syncline, though this area has been thrusted closer to the synclinal core. The Huergas Fm. here is bounded conformably by the Santa Lucía Fm. to the SW and the Portilla Fm. to the NE. The possible site of exposure lies roughly in the middle of the formation.

Puerto de Somiedo - 13

Fig. 16

43°00'12.46" N, 6°13'35.04" W

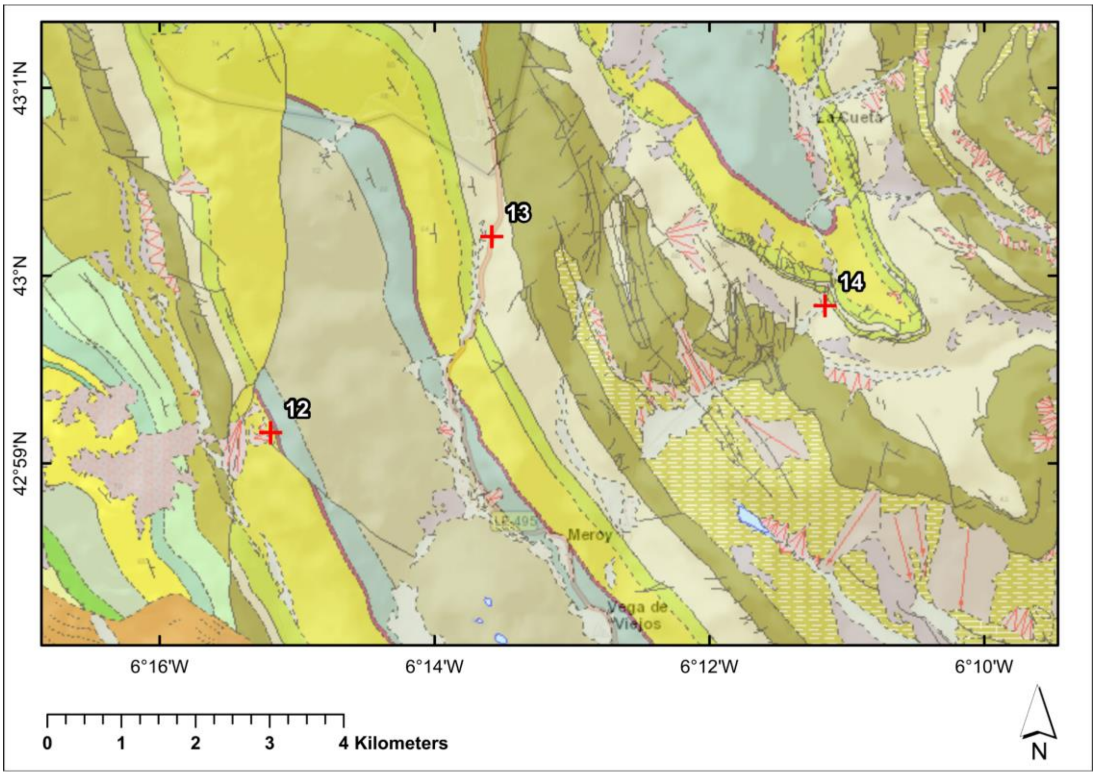


Figure 16. Geological map showing the Lumajo (12), Puerto de Somiedo (13) and Quejo (14) sites. Basemap credit as Fig. 12.

A large road cut located on the AS-227/C-633 road on the Leónese side of the Puerto de Somiedo, approximately 500 m south of the 8 km marker. Previously described by García-Ramos (1978).

This exposure is probably in the eastern limb of a N-S oriented syncline, though this area is very heavily tectonized. The Naranco Fm. is bounded conformably by the Moniello Fm. to the east and Candás Fm. to the west. The site is located approximately in the middle of the formation.

Quejo - 14

Fig. 16

42°59'50.37" N, 6°11'09.63" W

A road cut located 4.2 km from Vega de Viejos on the road towards La Cueta. Previously described by García-Ramos (1978).

This exposure is located in a circular synclinal structure, much like an inverted dome. Specifically, the site is located to the SW of the core of the structure. The Huergas Fm. is bounded conformably by the Santa Lucía Fm. to the SW and the Portilla Fm. to the NE. The exposure is located near the top of the formation.

Mirantes de Luna - 15

Fig. 17

42°52'05.98" N, 5°51'22.73" W

An extended series of road cuts and exposures through the majority of the Huergas Fm. on the CL-626 road on the eastern side of the Embalse de Los Barrios de Luna, between the village of Mirantes de Luna and a tunnel approximately 2.3 km to the south. Previously described by García-Ramos (1978).

This exposure is located in the nose of a syncline. This means the Huergas Fm. here is partially doubled and bounded conformably by the Santa Lucía Fm. both to the north and south. Various faults are evident within this exposure, notably a thrust fault just to the south of Mirantes village, which has shortened the exposure. The interrupted section here covers the whole of the syncline, though the top of the formation, in the centre of the structure, is not exposed.

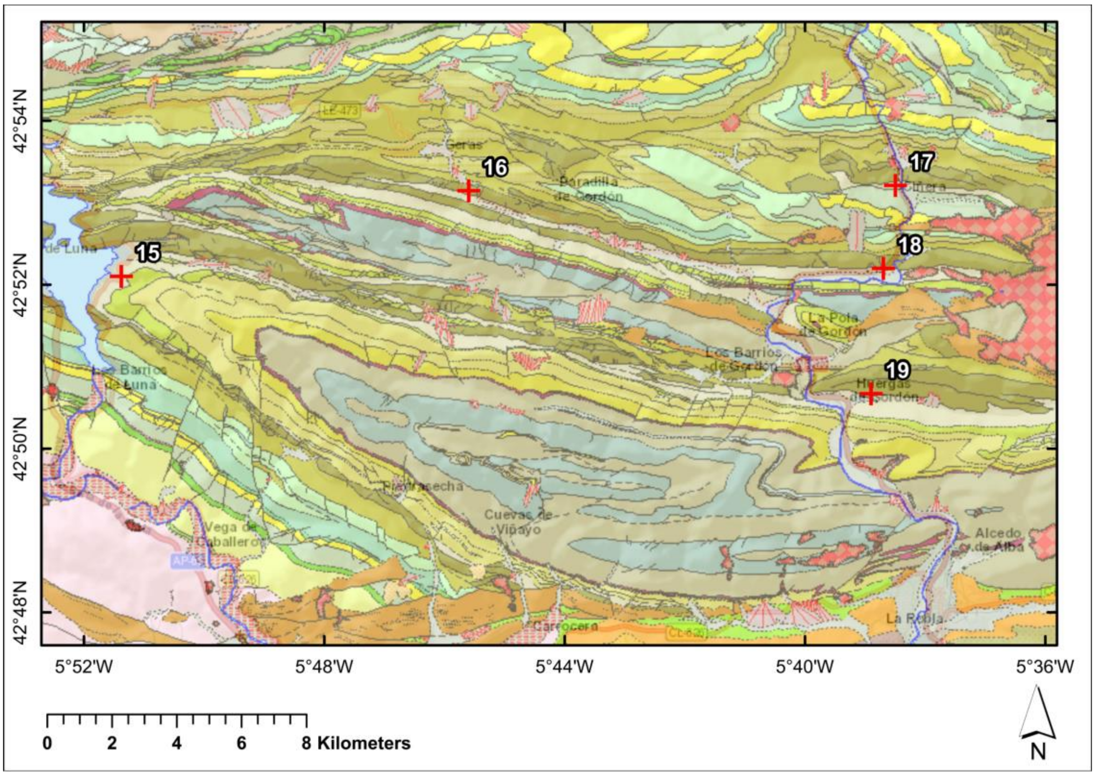


Figure 17. Geological map showing the Mirantes de Luna (15), Geras (16), Ciñera (17), Vega de Gordon (18) and Huergas de Gordon (19) sites. Basemap credit as Fig. 12.

Geras - 16

Fig. 17

42°53'08.70" N, 5°45'35.79" W

A small exposure close to a large limestone cliff on the LE-473 road to the SE of the village of Geras, a short distance west of the 8 km marker. Previously described by García-Ramos (1978).

This exposure is located in the northern arm of another syncline positioned to the north of the one described for site 15 (Mirantes de Luna). The overall structure is similar but the southern limb in particular is very heavily faulted, obscuring its original pattern. Here, the southern boundary of the Huergas Fm. is thrust faulted, placing it in unconformable contact with the Santa Lucía Fm. to the south, as well being in conformable contact to the north. This exposure is located near the top of the formation.

Ciñera - 17

Fig. 17

42°53'12.98" N, 5°38'28.92" W

Garcia-Ramos (1978) mentions a locality near Ciñera, though the only possible exposure found is in a hillside to the west of the town, in the valley of the Arroyo de Verciegos which proved inaccessible. Previously described by García-Ramos (1978).

This exposure is located in an E-W striking band of the Huergas Fm. probably connected with the faulted syncline described for site 16 (Geras), except here the formation itself is faulted and positioned more to the north. The formation here has an unconformable southern contact with the Middle Cambrian Oville Fm. and a conformable northern contact with the Santa Lucía Fm. The exposure is probably located near the base of the formation, though the southern boundary fault and the heavily faulted local area make the formation's thickness here hard to determine with any certainty.

Vega de Gordon - 18

Fig. 17

42°52'07.85" N, 5°38'37.89" W

A poorly accessible outcrop on the N-630 road, east of Vega de Gordon and SW of Santa Lucía, just to the east of the 108 km marker. Previously described by García-Ramos (1978).

This exposure is located in the same E-W striking band as site 16 (Geras), being situated further east. The Huergas Fm. here is bounded conformably by the Santa Lucía Fm. to the north and the Portilla Fm. to the south. This area is very heavily faulted with strata dipping at almost 90º thrusted above each other in various directions, obscuring any wider relationships with surrounding strata. This site is at the base of the formation.

Huergas de Gordon - 19

Fig. 17

42°50'39.84" N, 5°38'52.34" W

The type locality of the Huergas Fm., a series of now largely overgrown outcrops east of the village of Huergas de Gordon. Previously described by García-Ramos (1978).

This exposure is in the northern limb of the same large syncline that has site 15 (Mirantes de Luna) at its nose, with the Huergas Fm. bounded conformably by the Santa Lucía Fm. to the north and the Portilla Fm. to the south. The series of patchy exposures here are near the base of the formation.

Vozmediano - 20

Fig. 18

42°52'23.81" N, 5°13'44.91" W

An exposure located immediately to the south of Vozmediano on the road from Llama. Previously described by García-Ramos (1978).

This exposure is in an area of steeply dipping strata striking approximately E-W. No larger geological structures can be discerned owing to the large degree of tectonic distortion in the area and insufficient detail of mapping. The Huergas Fm. here is bounded conformably by the Santa Lucía Fm. to the north, however its southern boundary is marked by a thrust fault placing it in contact with the Middle Cambrian Láncara Fm. The exposure is near the base of the formation.

Corniero - 21

Fig. 18

42°54'34.38" N, 5°09'50.17" W

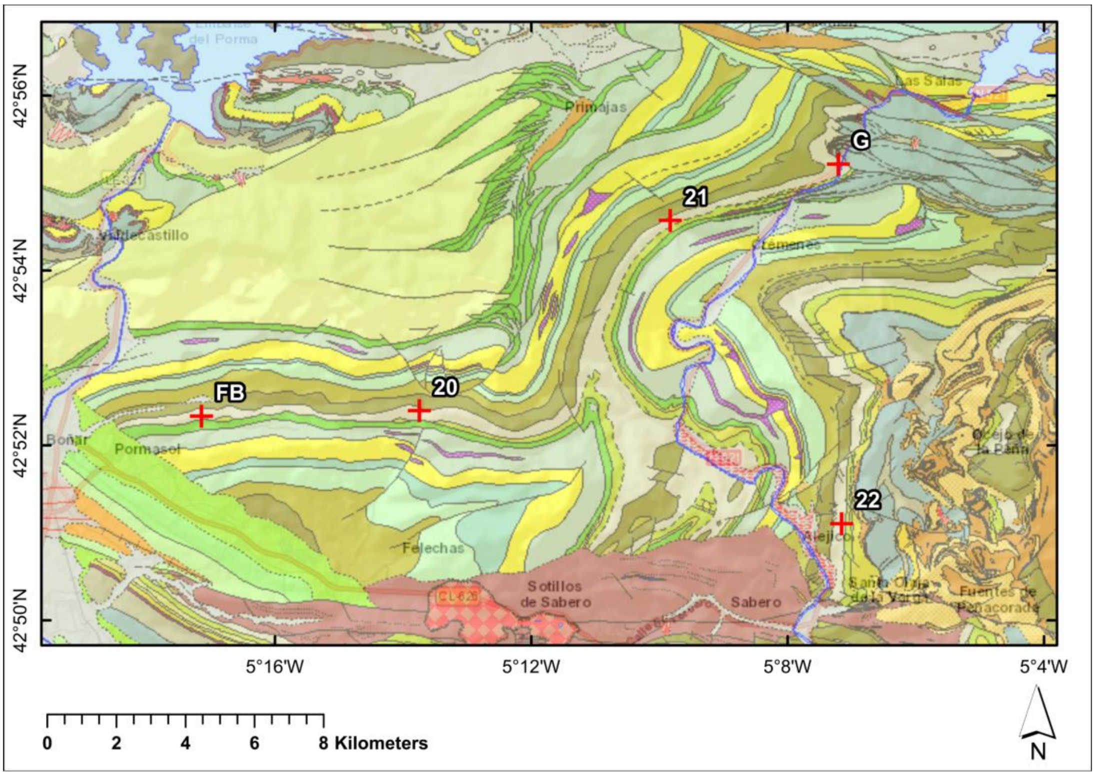


Figure 18. Geological map showing the Vozmediano (20), Corniero (21), Aleje (22), Fombella Blanco (FB) and Crémenes-Las Salas (G) sites. Basemap credit as Fig. 12.

A very poor exposure approximately 1 km SE of Corniero on the road towards Crémenes. Previously described by García-Ramos (1978).

This locality is positioned within part of a syncline oriented approximately NW-SE which has been thrusted upwards, placing the Huergas Fm. in contact with much younger deposits. This exposure is located near the nose of the syncline, with the Huergas formation bounded conformably by the Santa Lucía formation to the north-west and by the Portilla formation to the SE, with a contact that may be conformable or represent a thrust fault. The exposure is located near the middle of the formation.

Aleje - 22

Fig. 18

42°51'06.20" N, 5°07'09.60" W

Exposures in a hillside to the south and east of the village of Aleje, off the N-625 road. Previously described by García-Ramos (1978).

This site is part of a large syncline, heavily distorted by subsequent tectonism. An upthrust part of the structure contains sites 21 (Corniero) and G (Crémenes-Las Salas), creating two synclines nested within each other. The syncline is oriented approximately NW-SE, though in this location the SW limb is oriented almost exactly N-S. The Huergas Fm. here is bounded conformably by the Santa Lucía Fm. to the west and the Portilla Fm. to the east. The exposure is located very near the base of the formation.

120

Fig. 13

43°24'46.46" N, 6°10'10.39" W

A large road cut on the N-634 road a short distance west of Cornellana. This is the best candidate for the ‘120’ locality mentioned by Cramer (1969a), which could not be located with certainty.

This exposure is formed from the western limb of the same antcline in which site 5 (Sobrerriba-Santa Eufemia) is found, hence here the Candás Fm. lies to the west and the Moniello Fm. to the east, with the Naranco Fm. occurring again further to the east beneath the Río Narcea. The exposure is located approximately in the middle of the formation.

598; 599; 600

Fig. 15

43°14'24.06" N, 6°14'09.87" W; 43°13'24.61" N, 6°14'33.22" W; 43°13'15.97" N, 6°14'50.79" W

A number of large road cuts positioned near one another on the AS-227 road south of Belmonte. 598 is positioned approximate 165 m south of the 15 km marker on this road. 599 is located approximately 375 m south of the 17 km marker, while 600 is positioned approximately 520 m further south. All previously described by Cramer (1969a).

Positioned near the nose of a syncline oriented NE-SW on the south-eastern limb. 598 and 599 are positioned on an anticlinal fold with the Moniello Fm. on both sides of the Naranco Fm. 600 is positioned nearer the centre of the major syncline with the Moniello Fm. to the east and Candás Fm. to the west. These three sites are all located towards the bottom of the formation, with 599 and 600 located near the base.

601

Fig. 13

43°24'22.77" N, 6°13'33.64" W

A large road cut on the N-634 road between Rabadiello and Casazorrina. This exposure did not yield any shale. Previously described by Cramer (1969a).

Positioned on the same anticline as site 120, located further to the SW and with the same stratigraphic relationships. The site is the lower third of the formation.

Fombella Blanco - FB

Fig. 18

42°52'20.09" N, 5°17'09.03" W

A possible exposure on a hillside to the south of Adrados which proved inaccessible. Previously described by Fombella Blanco (1988).

This site is situated to the west of the site 20 (Vozmediano) in the same setting. However, here isolated outcrops of the Portilla Fm. are in conformable contact with the Huergas Fm. on its southern boundary before the thrust fault mentioned with site 20 (Vozmediano). The site is in the upper third of the formation.

Crémenes-Las Salas - G

Fig. 18

42°55'12.87" N, 5°07'12.76" W

A long exposure on the N-625 road between Crémenes and Las Salas, approximately 600 m NE of the 77 km marker. Previously described by Gill (2001).

This site is located in the same syncline as site 21 (Corniero), in the NE limb. The Huergas Fm. is, again, bounded conformably by the Santa Lucía Fm. to the NW and by the Portilla Fm. to the SE with a conformable or thrusted contact, however here an additional faulted contact with the Carboniferous Montaña Fm. is present to the NE. This section covers an unknown part of the formation, being bounded by a faulted contact with the Portilla Fm. above and another faulted contact with the Montaña Fm. below.

Man member - P

Fig. 19

42°56'38.02" N, 4°32'45.61" W

A small exposure by a path approximately 1.5 km NW of Polentinos. This is believed to be site α-166 of García-Alcalde (2010).

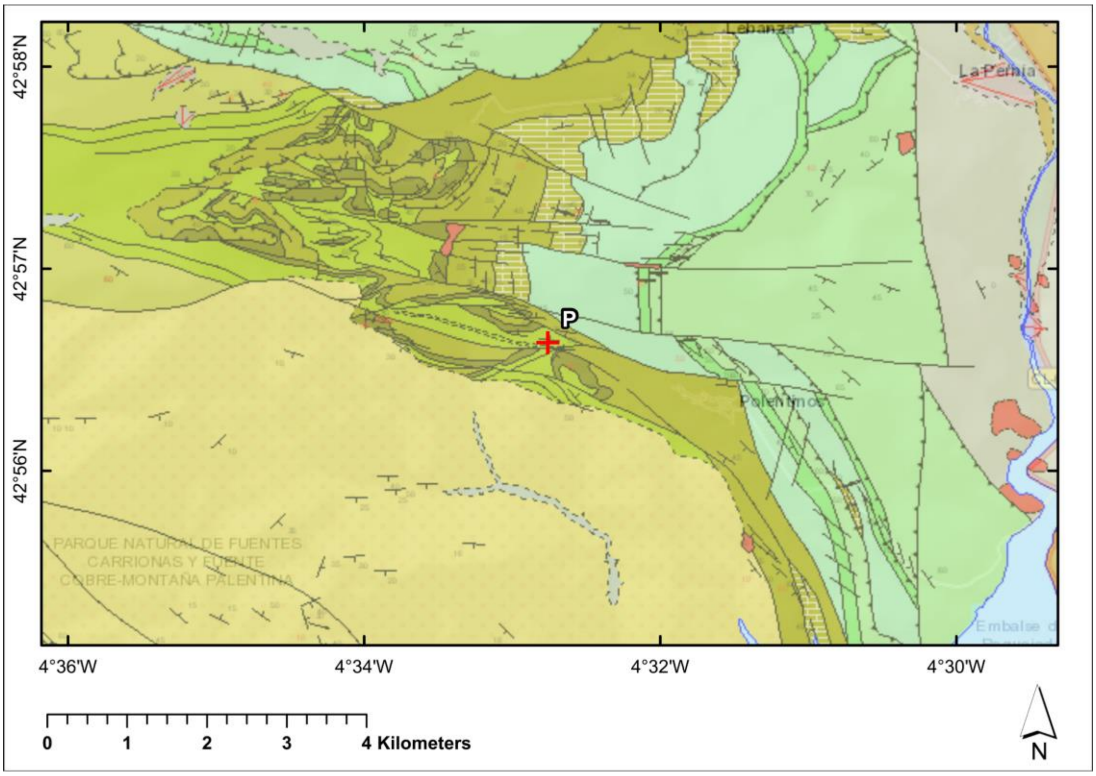


Figure 19. Geological map showing the Man member (P) site. Basemap credit as Fig. 12.

This site's precise geological setting is unclear. Official geological maps of the area from IGME depict this location as actually being in the older Abadía Fm. with no nearby exposures of the Gustalapiedra Fm. The Abadía Fm. is depicted as having an unconformable southern contact with the Curavacas Conglomerate of Westphalian B age, while the formation's northern contact is a faulted one with itself, the Famennian Cardaño Fm. and the latest Silurian-Early Devonian Carazo Fm. in a structure described elsewhere as the Polentinos Anticline (García-Alcalde, 2010). In contrast García-Alcalde (2010) depicts this site as being located in an elongate, tapering graben formed from the Gustalapiedra Fm., bounded by downthrown blocks of the Abadía Fm. on all sides. The strata in this area are depicted as very heavily folded and faulted with an overall north-south compression, producing a very complicated geological setting. The precise location of this site within the thickness of the Gustalapiedra formation is difficult to determine owing to the complicated and uncertain outcrop pattern. García-Alcalde (2010) depicts the formation as very thin here, so the exposure may cover much of its thickness.

2.3 - Previous palaeontological studies of the Middle Devonian deposits of the Cantabrian Mountains

Reports of the palaeontology of Middle Devonian deposits in Cantabria are somewhat lacking in the published literature. This may be due to a lack of systematic surveys owing to the paucity of stratigraphically important fossils in these rocks (García-Alcalde et al., 2002). A seemingly disproportionate number of studies of the Spanish Devonian focus on stratigraphy rather than palaeobiology. The following section will collate what is known about the palaeontology of the relevant sediments.

2.3.1 - Macrofossils

Plant macrofossils are exceedingly rare in the Spanish Devonian (Montero, 2008; Montero & Dieguez, 2010). Most that have been reported are of questionable identity, age or validity (Wagner, 2012). Various small lycopsid and sphenophyll fragments have been found in the Palentian domain but these are of at least Late Devonian age (Wagner, 2012). Macrofloral reconstructions of the Middle Devonian tend to be based on palynological analysis, with one study suggesting a two-tiered system of herbaceous and semi-arboreal floral assemblages (Montero & Dieguez, 2010), though this conclusion has been called into question (Wagner, 2012).

Animal fossils are somewhat more numerous, as expected in a marine environment. García-Alcalde (2002) report molluscs, bryozoans and brachiopods found in sandier facies of the Naranco and Huergas formations, with dacryoconarids, ostracods and ammonoids inhabiting shalier facies. Isolated nautiloid, trilobite and crinoid fragments are also found, with much of this fauna possibly being faecal debris from pelagic predators (García-Bellido & Castaño, 2007). In addition, a soft-bodied arthropod of uncertain affinity has been discovered in the Huergas formation, possibly providing evidence of a Konservat-Lagerstätte in the area (García-Bellido & Castaño, 2007).

Memoirs accompanying the maps of IGME contain a comprehensive survey of the fauna in this formation, with named taxa listed in table 1. More generally the fauna of the Naranco and Huergas formations is usually described as rare (Beroiz, Pignatelli, et al., 1972; Beroiz, Ramírez del Pozo, et al., 1972; Martínez-Álvarez et al., 1973; Julivert et al., 1975a, 1975b; García-Ramos et al., 1978; Lobato et al., 1978; Manjón Rubio et al., 1978; Marcos et al., 1979; Navarro Vázquez, 1979; Crespo Zamorano, 1979; Alonso et al., 1989; Suárez Rodríguez et al., 1989; Heredia et al., 1989). Groups represented in the formation include brachiopods (Beroiz, Pignatelli, et al., 1972; Pello, 1973; Julivert et al., 1975a; García-Ramos et al., 1978; Lobato et al., 1978; Manjón Rubio et al., 1978; Crespo Zamorano, 1979; Leyva et al., 1980; Alonso et al., 1989; Suárez Rodríguez et al., 1989; Heredia et al., 1989), crinoids (Beroiz, Pignatelli, et al., 1972; Pello, 1973; Julivert et al., 1975a; Navarro Vázquez, 1979; Leyva et al., 1980), rugose corals (Pello, 1973; García-Ramos et al., 1978; Lobato et al., 1978; Manjón Rubio et al., 1978; Heredia et al., 1989), other corals (Crespo Zamorano, 1979; Navarro Vázquez, 1979; Alonso et al., 1989; Suárez Rodríguez et al., 1989), bryozoans (Crespo Zamorano, 1979; Leyva et al., 1980), trilobites (García-Ramos et al., 1978; Lobato et al., 1978; Crespo Zamorano, 1979; Navarro Vázquez, 1979; Leyva et al., 1980; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989), lamellibranchs (García-Ramos et al., 1978; Lobato et al., 1978; Manjón Rubio et al., 1978; Crespo Zamorano, 1979; Navarro Vázquez, 1979; Leyva et al., 1980; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989), goniatites (García-Ramos et al., 1978; Lobato et al., 1978; Manjón Rubio et al., 1978; Crespo Zamorano, 1979; Navarro Vázquez, 1979; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989), tentaculites (García-Ramos et al., 1978; Lobato et al., 1978; Manjón Rubio et al., 1978; Crespo Zamorano, 1979; Navarro Vázquez, 1979; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989), bivalves (Lobato et al., 1978; Leyva et al., 1980; Heredia et al., 1989; Suárez Rodríguez et al., 1989) and ostracods (Lobato et al., 1978; Heredia et al., 1989; Suárez Rodríguez et al., 1989). Depositional features include bioturbation (Crespo Zamorano, 1979; Navarro Vázquez, 1979; Leyva et al., 1980; Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989), including burrows (Pello, 1973) and tracks (Lobato et al., 1978; Crespo Zamorano, 1979; Navarro Vázquez, 1979), ripples (Pello, 1973) and medium-scale planar cross-stratification (Alonso et al., 1989).

Table 1. List of macrofossil taxa reported in IGME memoirs from the Naranco and Huergas formations.

Taxon	References
Ammonoids	
Anarcestes noeggateri	García-Ramos et al., 1978; Lobato et al., 1978; Manjón Rubio et al., 1978; Heredia et al., 1989
Cabrieroceras rouvillei	García-Ramos et al., 1978; Lobato et al., 1978; Manjón Rubio et al., 1978; Heredia et al., 1989
Bivalve	
Gosseletia devonica	Beroiz, Ramírez del Pozo, et al., 1972
Brachiopods	
Cimicinella cf. *loxogonia*	Lobato et al., 1978
Cyrtina heteroclita	Caride et al., 1973
Devonochonetes cf. *kerfonei*	Marcos et al., 1979
Douvillina interstrialis	Beroiz, Ramírez del Pozo, et al., 1972
Eleutherokomma diluvianoides	Marcos et al., 1979
Euryspirifer intermedius	Caride et al., 1973; Pello, 1973
E. paradoxus	Beroiz, Ramírez del Pozo, et al., 1972; Caride et al., 1973
E. aff. *supraspeciosus*	Pello, 1973
E. sp.	Pello, 1973
Megastrophia praviana	Marcos et al., 1979
Mucrospirifer thedfordensis	Marcos et al., 1979
Oligoptycherhynchus hexatoma	Lobato et al., 1978; Marcos et al., 1979
Paraspirifer cultrijugatus	Marcos et al., 1979; Leyva et al., 1980
P. cf. *beclardi*	Lobato et al., 1978
P. sp.	Lobato et al., 1978
Plicochonetes minutus	Pello, 1973
Rhenothyris sp.	Leyva et al., 1980
Schizophoria cf. *schnuri*	Lobato et al., 1978
Spinocyrtia ostioloata	Pello, 1973
Xystostrophia sp.	Lobato et al., 1978
Corals	
Angustiphyllum cuneiformis	Marcos et al., 1979
A. sp.	Lobato et al., 1978
Crassicylus densiseptatus	Lobato et al., 1978; Marcos et al., 1979
Procteria granulifera	Marcos et al., 1979
Trilobite	
Alcaldops alcaldei	Marcos et al., 1979

Macrofossil remains in the Gustalapiedra formation have been described as very poor (Lobato et al., 1983) but include ammonoids (Heredia et al., 1989), goniatites (Ambrose et al., 1977; Lobato et al., 1983), trilobites (Lobato et al., 1983), gastropods (Lobato et al., 1983), lamellibranchs (Lobato et al., 1983) and tentaculites (Ambrose et al., 1977) with named taxa listed in table 2. Bioturbation is also seen (Heredia et al., 1989).

2.3.2 - Microfossils and Palynomorphs

Past palynological research specifically on the Naranco and Huergas formations is somewhat lacking, essentially comprising three papers (Cramer, 1966, 1969a; Fombella Blanco, 1988) and an MSc thesis (Gill, 2001). Tables 3 and 4 in Chapter 4 list the palynomorphs found in the Naranco and Huergas formations, with those also found in the present study marked.

Table 2. List of macrofossil taxa reported in IGME memoirs from the Gustalapiedra formation.

Taxon	Reference
Ammonoids	
Agoniatites cf. *costulatus*	Lobato et al., 1983
A. cf. *kayseri*	Ambrose et al., 1977
A. cf. *occultus*	Ambrose et al., 1977
A. cf. *vanuxemi*	Lobato et al., 1983
Anarcestes aff. *lateseptatus var. plebeja*	Ambrose et al., 1977
Cabreineceros sp.	Heredia et al., 1989
Maenioceras sp.	Lobato et al., 1983
Tornoceras sp.	Lobato et al., 1983
Bivalves	
Buchiola sp.	Ambrose et al., 1977
Guerichia sp.	Ambrose et al., 1977
Brachiopod	
Lingula sp.	Ambrose et al., 1977
Tentaculites	
Striatostyliolina aff. *striatula*	Ambrose et al., 1977
Styliolina fissurella	Ambrose et al., 1977

The Gustalapiedra formation has yielded conodonts, identified as *Ancyrodella rotundibiloba*, *Icriodus cf. obliquimarginatus*, *I. cymbiformis*, *I. nodosus*, *Polygnathus decorosa*, *P. linguiformis*, *P. pennata*, *P. timorensis* and *P. varca* (Lobato et al., 1983). Conodonts are rare in the Naranco and Huergas formations; those that have been reported are detailed above.

3 - Materials & methods

3.1 - Sampling

Two field trips were carried out, from the 19th to the 26th of January 2015 and from the 30th August to the 7th September 2015, yielding 130 samples for palynological analysis and 5 macrofossils in hand specimen, as well as those recorded in exposure. Samples were taken from road cuts and other exposures detailed elsewhere. Sampling consisted of using a hammer to obtain at least 50 g of material per sample and usually more, enough to allow multiple macerations if necessary. Sampling focussed on beds of dark (reduced) fine-grained sediments within the predominantly sandstone formation (as detailed in Appendix I), as these are the most likely to yield palynomorphs, though outcrops varied widely in quality owing to oxidation and weathering. Samples represent approximately 2-3 cm in vertical section through single horizons or spaced out at intervals through a thicker horizon. The locations of the sampled sites cover most of the extent of the outcrop area of the formations under consideration and are detailed elsewhere.

3.2 - Lithology

The majority of the rock samples studied here are siltstones with some mudstones. Some of these are calcareous as became apparent upon HCl acid maceration. Further details are given in Appendix I.

3.3 - Macrofossils

The macrofossils observed here comprise a selection of bryozoans, crinoid fragments, bivalves or brachiopods and a possible mollusc. Further details are given in Appendix II.

3.4 - Maceration

Each sample was washed and dried before 40 g was weighed out and crushed using a pestle and mortar to a fine gravel around 0.5 cm in diameter. 20 g of this was selected for acid maceration with the remainder stored with the remainder of the rock sample (2 samples did not include enough material for 20 g to be macerated, detailed in Appendix I). Maceration began with dissolution in 40% HCl for 1-3 days. Samples were then diluted by allowing the material to settle, then pouring off excess liquid and filling the reaction vessel with water. After 24 hours the water was poured off and 40% HF was added. The samples remained in HF for between 1 and 6 days, before additional HF and HCl were added. The samples were then left for between 12 and 45 days, depending on how readily they broke down. Some samples did still contain significantly sized particles even after an excessive time spent in acid, a not uncommon occurrence with this form of maceration and thought to represent a recrystallisation or precipitation of an unknown material. The samples were diluted back towards neutral by repeatedly decanting excess liquid and filling the reaction vessel with water, leaving the samples overnight between decants to minimise the loss of palynomorphs. The samples were sieved using a 15 µm sieve, small enough to catch the smallest phytoplankton found in prior studies. The samples were then subjected to heavy liquid centrifugation using zinc chloride ($ZnCl_2$) to separate heavy minerals and any remaining sand from organic material, which was then stored in water with 1-2 drops of 10% HCl added to ward off fungal growth.

3.5 - Oxidation

Following assessment of kerogen material all samples, except for three barren ones and one with very poor preservation, were oxidised using Schulze's solution (a solution of concentrated nitric acid saturated with potassium chlorate). Oxidation was for between 5 and 60 minutes, depending on thermal maturity and with regular checks on progress, with most samples taking less than 30 minutes. Four samples were oxidised overnight, ultimately for over 19 hours, as detailed in Appendix I. At this stage the samples were also spiked with *Lycopodium* tablets at a ratio of one tablet per 1ml of solid yield, in order to permit quantitative counting of fossil material. The resulting residue entered permanent storage with 1-2 drops of 10% HCl added.

3.6 - Mounting and imaging

Strew mounts of all slides following maceration (kerogen slides) and of oxidised samples were made using Petropoxy 154 and viewed using a light microscope. All light photomicrographs are multi-focus composites taken using a Meiji Techno Infinity 1-5C camera mounted on a Meiji Techno MT5300H transmitted light microscope, using a 40× or 100× magnification objective. Immersion oil was used with the 100× objective.

3.7 - Scanning Electron Microscopy

SEM materials were prepared in two ways. Individual picked chitinozoans and scolecodonts were attached to SEM stubs using carbon tabs. Strew mounting was also used. To facilitate this a glass cover slip was attached to an SEM stub using Araldite® brand epoxy resin, before a palynomorph sample was strewn over it. All stubs were gold-coated using an Edwards S150B sputter coater. All imaging was carried out using a Philips XL-20 SEM.

3.8 - Counts

Abundance counts were taken of most samples. This comprised traversing a slide sideways, beginning at the bottom and moving upwards after every pass. Every instance of palynomorphs recognisable to species level was recorded, as well as *Lycopodium*. Once the number of recognisable palynomorphs reached 200 the number of counted *Lycopodium* was recorded and counting ceased. The rest of the slide was traversed in the same fashion and any species which had not occurred in the 200 count were recorded as 'rare'. Scolecodonts were recorded but no effort was made at this stage at identification and they were recorded separately, not figuring in the final count. Some slides did not contain 200 recognisable palynomorphs; in these cases the result is still valid but has reduced statistical power (Traverse, 2008).

3.9 - Quantitative calculation

Calculation of the quantitative results, that is the number of a given species per unit of processed rock, used an equation derived from Stockmarr (1971):

$$\frac{\frac{\text{Number counted}}{\textit{Lycopodium}\text{ count}} \times (20{,}848 \times \text{Number of } \textit{Lycopodium} \text{ tablets used})^{1}}{\text{Amount of rock processed (g)}} = \text{Number per gram}$$

[1] This expression gives the total number of *Lycopodium* added to the sample, with their being 20,848 spores in each tablet.

3.10 - Figure production and data analysis

Stratigraphic logs of measured sections were produced using the Sedlog program (Zervas et al., 2009). Pollen diagrams were produced using the StrataBugs program. Quantitative charts were produced in this program using the 'split factor' functionality. This uses split factors to adjust counts of species taken from different size fractions of the same sample, to account for variations in size fraction volume. Here the 'split factor' supplied was derived from the above equation:

$$\frac{(20848 \times \text{Number of } \mathit{Lycopodium} \text{ tablets used})}{\mathit{Lycopodium} \text{ count}} = \text{split factor}$$

Sample weight was added in elsewhere in the program. This caused the program to calculate the correct quantitative number for each species, as checked against manual calculations.

3.10.1 - Cluster analysis

The cluster analysis presented here was calculated according to the UPGMA method using Euclidean distances between assemblages, calculated using the R program (R Core Team, 2018). Dendrogram figures were produced using the "dendextend" package for R (Galili, 2015). The other assemblages used in this analysis were selected based on their taxonomy and stratigraphic position. The studies used have confident taxonomic assignments, in line with or adapted to modern usage of taxa, and well-constrained upper Eifelian-lower Givetian ages, coeval with the present assemblage. Efforts were also made to achieve a widespread palaeogeographical coverage by using palynomorph assemblages reported from many palaeocontinents.

3.11 - Curation

All materials (rock, residue, slides, SEM stubs) are housed in the collections of the Centre for Palynology at the University of Sheffield, UK.

4 - Palynomorph communities and biostratigraphy

This section will profile the known palynomorph groups of the Spanish Devonian, together with their use in biostratigraphy and biozonation schemes, used to correlate disparate sediments.

4.1 - Phytoplankton

Phytoplankton (acritarchs and prasinophytes) represent the cysts of aquatic algae or similar organisms (Colbath & Grenfell, 1995; Traverse, 2008) and appear in sediments from the Proterozoic onwards. They are often distinctively sculptured and a well-established form taxonomy is in place for them, allowing them to be used as biostratigraphical markers. They invariably indicate marine conditions and the degree of variety in an assemblage, together with the relative proportions of phytoplankton and spores, can indicate proximity to a shoreline or reef (Strother, 1996; Wicander & Wood, 1997).

The Devonian period marked a high point in phytoplanktonic diversity. Numbers of genera and species rose steadily during the Palaeozoic and peaked during the Late Devonian before a sharp fall at the Devonian-Carboniferous boundary (Strother, 1996), the cause of which is unclear. This was followed by low diversity of encysting algae in general before the rise of the dinoflagellates in the Late Triassic, and a Cenozoic rise in phytoplankton diversity has been interpreted as being due to the sampling bias of more recent sediments (Strother, 1996).

The use of phytoplankton as index fossils is limited by the considerable number of exceedingly long-lived taxa such as *Veryhachium* and *Leiosphaeridia*. These genera often contain very large numbers of species which are difficult to distinguish, hence limiting their biostratigraphic utility (Strother, 1996). In addition, much of the work on Middle Devonian phytoplankton assemblages has been conducted in North America, where assemblages seem to have a degree of provinciality and differ from those elsewhere (Molyneux et al., 1996). Outside North America assemblages are often made up largely of cosmopolitan taxa (Zhu et al., 2008). Some taxa are characteristic of the Middle Devonian (see Fig. 20) such as *Polyedryxium pharaone*, *Duvernaysphaera angelae* and *Navifusa bacilla*, all of which are found in the studied formations (see Table 3). In contrast to the range chart in figure 20, Le Hérissé et al. (2000) present a chart with some important differences. They describe *D. angelae* and *Multiplicisphaeridium ramispinosum* as Givetian and later, indicating a somewhat later age for the studied formations.

Formal zonations are not particularly useful in resolving this problem. Limited study means it is difficult to assess the degree of provincialism of many taxa (Molyneux et al., 1996; Le Hérissé et al., 2000) and Middle Devonian zonation schemes are somewhat restricted, with two concerning Brazil (Brito, 1971; de Quadros, 1988) and two concerning the Algerian Sahara (Jardiné & Yapaudjan, 1968; Jardiné et al., 1974) (see Fig. 21). Of these the scheme of Jardiné et al. (1974) has the most utility in this time period, with the Middle Devonian corresponding to zones L1-L3. The L1 and L2 zones are characterised by the co-occurrence of (using updated taxonomic assignments) *Duvernaysphaera angelae, D. kraeuselii,*

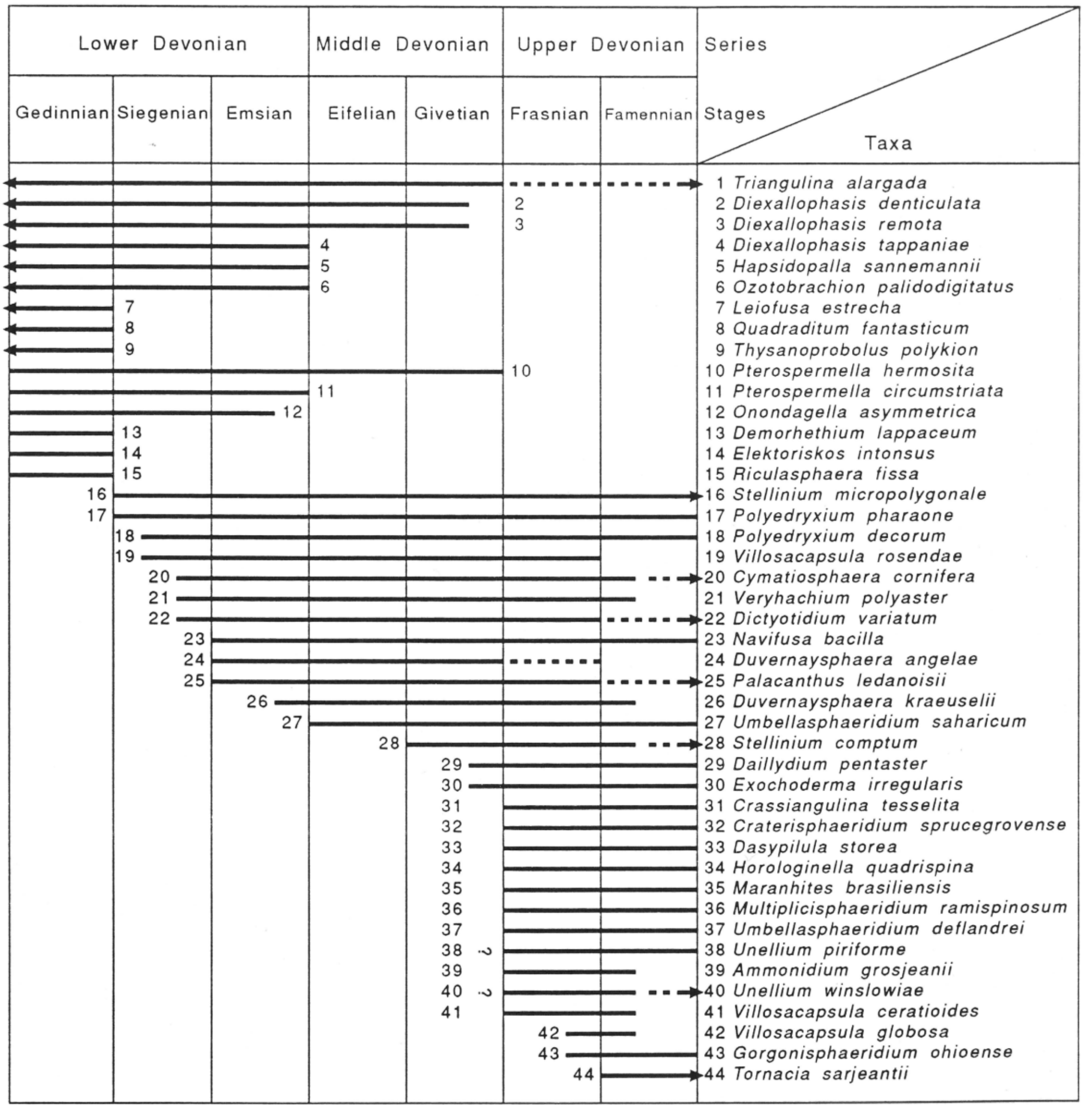


Figure 20. Range chart of selected Devonian phytoplankton taxa recorded on two continents or more. Taken from Molyneux et al. (1996).

Eisenackidium valentina, Multiplicisphaeridium exasperatum, Navifusa bacilla, Polyedryxium decorum, P. fragosulum, P. pharaone, Stellinium micropolygonale and Veryhachium libratum. This *Duvernaysphaera* assemblage carries over into the L3 zone where it is joined by *Daillydium pentaster*, '*Polyedryxium* cf. *decorum* Deunff, 1955', '*P.* cf. *talus* Deunff, 1966' and *Veryhachium stelligerum*. The previously described phytoplankton assemblage of the Huergas formation detailed in Table 3 contains *D. angelae*, *N. bacilla* and *Polyedryxium* (*Crameria*) *pharaone*. This indicates the Eifelian to Givetian L1-L2 zone, agreeing with the lithostratigraphic and conodont biostratigraphical dating mentioned above. Similarly, the range chart of Díez & Cramer (1977) indicates that *Micrhystridium stellatum*, *Veryhachium europeaum* and *V. trispinosum* occur together in the late Eifelian, although this study also depicts the extinction of *Polyedryxium asperum*, *P. embudum* and *Veryhachium valiente* (cited as *V. lairdii*) during the preceding Emsian stage.

Table 3. List of phytoplankton taxa previously reported from the Naranco, Huergas and Gustalapiedra formations, as originally cited. All taxa are taken from Gill (2001) other than those indicated † from Cramer (1969a) and the two indicated * from Fombella Blanco (1988). Taxa placed in synonymy with those described in this study are denoted with •.

Taxon	
Ammonidium sp. A	•
A. sp. B	
A.? sp. C	
Baltisphaeridium spp.†	
Chomotriletes spp.	
Cymatiosphaera carminae	•
*C. magnata**[1]	•
C. sp. A	•
C. sp. B	•
Dateriocradus spp.	•
Dictyotidium sp. A	
D. sp. B	•
Diexallophasis spp.	•
Duvernaysphaera angelae	•
Eisenackidium sp.†	
Exochoderma spp.	•
Gorgonisphaeridium sp. A	•
Hemiruptia spp.	
Micrhystridium stellatum (also †)	•
Multiplicisphaeridium ramispinosum	•
Navifusa bacilla	•
Polyedryxium asperum	•
P. embudum	•
P. pharaone	•
Pterospermella onondagaensis	
P. sp. A	•
Umbellasphaeridium huecospinosum	
*Veryhachium downiei**	•
V. europeaum	•
V. lairdii[2]	•
V. trispinosum (also †)	•
V. sp. A	•
Villosacapsula spp.	

[1]-since reassigned to *Orygmahapsis*
[2]-since synonymised with *V. valiente*

4.2 - Chitinozoans

Chitinozoans are an enigmatic group of uncertain affinity. They occur in marine sediments of Late Cambrian or Early Ordovician to Late Devonian age, and the current prevailing view is of their being the egg-cases of some unknown metazoan (Traverse, 2008), though in the past they have also been assigned to protozoans, protists and fungi (Miller, 1996); the debate is still ongoing. Some appear to have led a planktonic existence, others seem benthic (Miller, 1996). Chitinozoan diversity appears to be related to water depth and salinity, and their taxonomy is now sufficiently developed to identify biofacies and provincialism in chitinozoan distribution (Miller, 1996).

In contrast to the phytoplankton, chitinozoans were in decline during the Devonian period. Their diversity peaked during the Ordovician, a period in which 80% of morphological innovation took place (Grahn & Paris, 2011). Diversity reduced dramatically at the end-Ordovician extinction event before recovering to match or exceed its Ordovician high during the Silurian period (Paris & Nõlvak, 1999; Grahn & Paris, 2011). Diversity then fell fairly steadily during the Devonian period punctuated only by small rises during the Emsian and Givetian, before the group's eventual extinction in the latest Devonian (Paris & Nõlvak, 1999; Grahn & Paris, 2011). They do not seem to be greatly affected by the various anoxic crises that afflicted the Devonian world (Grahn & Paris, 2011), possibly indicating a pelagic mode of life unaffected by benthic anoxia. Through the Devonian the proportion of monospecific lineages increases (Grahn & Paris, 2011), possibly indicating a lack of genetic diversity or potential which may have contributed to the group's extinction.

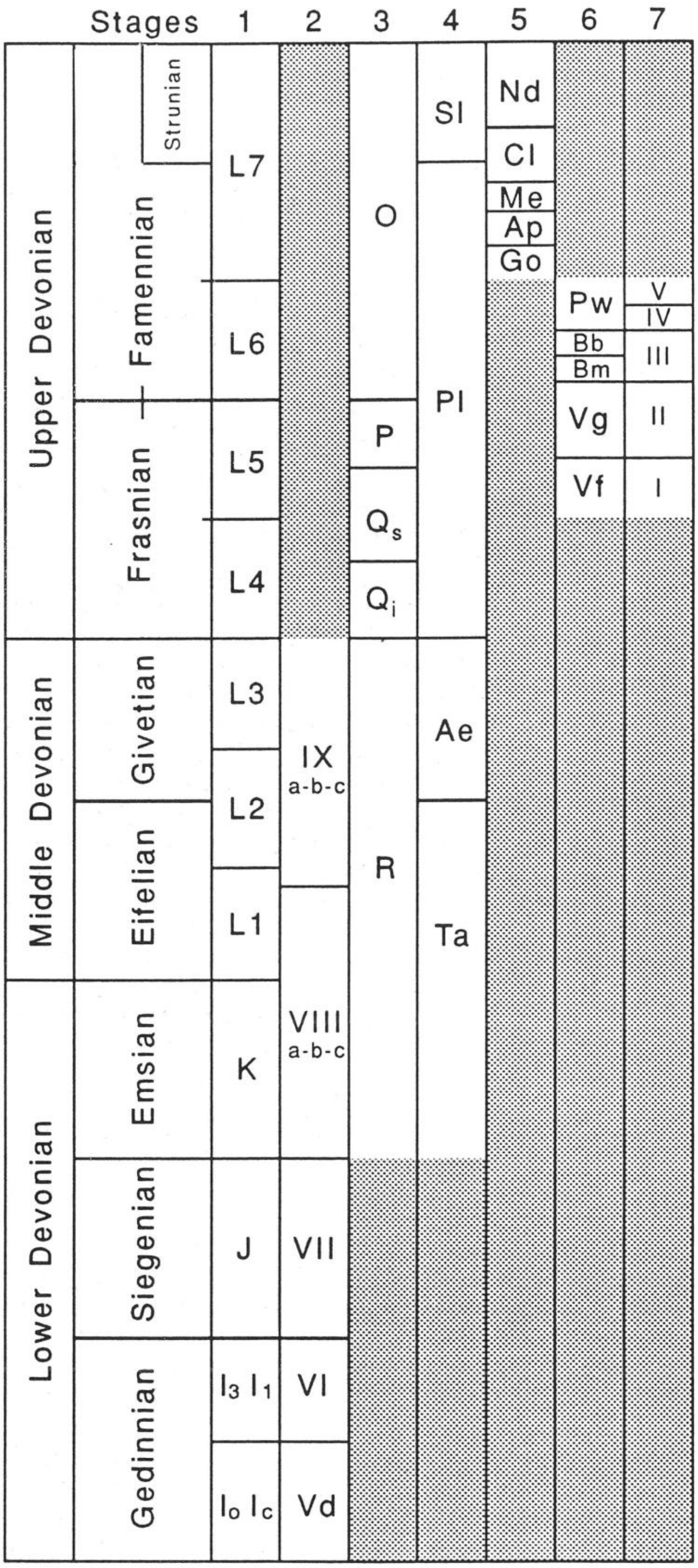


Figure 21. Correlation chart of phytoplankton zonation schemes of the Devonian period, applicable in various parts of the world. Schemes mentioned in the text are ① Jardiné et al. (1974) and ② Jardiné & Yapaudjan (1968) concerning the Algerian Sahara, together with ③ Brito (1971) and ④ de Quadros (1988) concerning Brazil. Taken from Molyneux et al. (1996).

Unfortunately, biozonation schemes for Devonian chitinozoans are not particularly well-developed. They are often partial or only applicable locally (Paris, 1996) (see Fig. 22). European schemes cease in the late Emsian (Díez & Cramer, 1978; Paris, 1981). The only complete schemes for the Middle Devonian, the focus of this study, concern South America (Lange, 1967; Grahn, 2005), however there is evidence to suggest that South American and West African assemblages differ greatly at the genus, and especially species, level from European assemblages (Miller, 1996), precluding their applicability to Cantabrian material. North African schemes from Algeria and Libya are more likely to be applicable to Spanish material but they are not as complete as the South American schemes (Jardiné & Yapaudjan, 1968; Boumendjel, 1987; Streel et al., 1988). More widely dispersed taxa such as *Alpenachitina eisenacki* can be used with some degree of

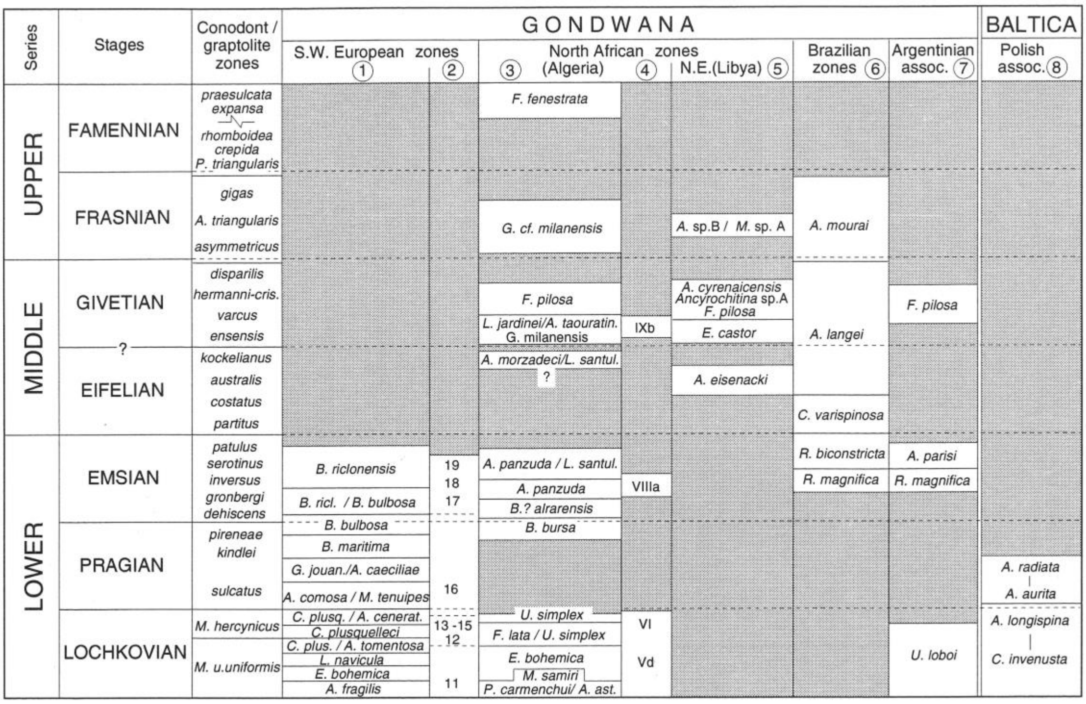


Figure 22. Correlation chart of chitinozoan zonation schemes of the Devonian period, applicable in various parts of the world. Schemes mentioned in the text are ① (Paris, 1981), ② (Díez & Cramer, 1978), ③ (Boumendjel, 1987), ④ (Jardiné & Yapaudjan, 1968), ⑤ (Streel et al., 1988) and ⑥ (Lange, 1967). Taken from Paris (1996).

precision. This species has a world-wide distribution and first occurs during the *costatus partitus* conodont zone (Paris et al., 2000) (see Fig 23). *Eisenackitina castor* has a similarly

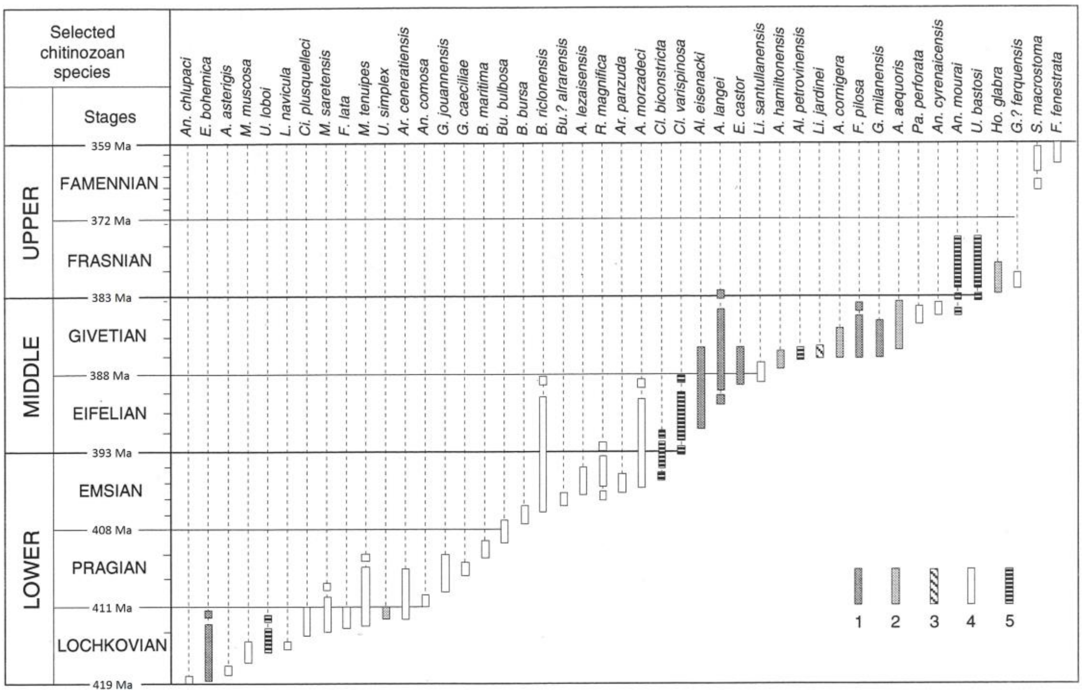


Figure 23. Range chart of selected Devonian chitinozoans. 1) world-wide distribution; 2) species found in northern Gondwana and Laurussia; 3) species found in northern Gondwana and South America; 4) species found in northern Gondwana only; 5) species found in South America only. Taken from Paris (1996) with updated absolute ages.

wide spatial distribution while *Linochitina jardinei* has a much more restricted temporal range (Paris, 1996) (see Fig. 23).

An attempt has been made at a global zonation scheme using cosmopolitan taxa (Paris et al., 2000) (see fig. 24). The Middle Devonian in this scheme is divided based on the first occurrences of *A. eisenacki* sometime in the early Eifelian, *E. aranea* in the late Eifelian and *Ancyrochitina cornigera* in the early Givetian. Unfortunately, none of these have been found in prior research on the Naranco, Huergas and Gustalapiedra formations.

Cramer (1969a) reports *Ancyrochitina* sp., while Gill (2001) found *Ancyrochitina*, *Angochitina* and *Sphaerochitina*, however no attempt was made at a specific identification and no biostratigraphical interpretation can be attempted.

4.3 - Scolecodonts

Scolecodonts are thought to be the mouth-parts of various unidentified, mostly marine polychaete worms, found from the Cambrian to the present (Traverse, 2008). In the Devonian only mouthparts of polychaetes of the Eunicida family are seen (Szaniawski, 1996). Their lack of a well-developed taxonomy somewhat hinders their use in stratigraphy, but they are sensitive to facies differences, possibly indicating preferences for different habitats, in line with their modern relatives (Szaniawski, 1996).

Stage	**Chitinozoan biozones**
Famennian	*ultima* total range
	fenestrata interval range
	avelinoi interval range
	hispida interval range
Frasnian	*glabra* interval range
	viridarium interval range
Givetian	*perforata* interval range
	jardinei interval range
	cornigera interval range
Eifelian	*aranea* interval range
	eisenacki interval range
Emsian	**not yet defined**
	panzuda interval range
	bursa interval range
Pragian	*bulbosa* interval range
	not yet defined
	caeciliae interval range
	comosa interval range
Lochkovian	*simplex* interval range
	lata interval range
	bohemica interval range

Figure 24. Provisional global zonation scheme for chitinozoans. Redrawn from Paris et al. (2000).

4.4 - Spores

Plant spores provide evidence of terrestrial vegetation. These are the reproductive propagules of embryophytic plants, technically including pollen, though this does not arise until the end of the Devonian. They exist in a high diversity of morphologically disparate forms, making them useful stratigraphically, while their land plant origin can indicate nearby land in aquatic sediment. They can also be used as indicators of the types of plant that existed in the area at the given time. This is far from being an exact science, as examples of a spore must be found in situ in a sporangium and that sporangium be assigned to a plant or group of plants in order for a spore's affinity to be determined. In addition, indistinguishable spores may be produced by different plants while a single plant may produce different spores (Traverse, 2008) or spores that differ in appearance at different developmental stages that we interpret as different taxa. Despite this, successive reviews of the field (Allen, 1980; Gensel, 1980; Balme, 1995) continue to improve our knowledge of the biological affinity of dispersed spore taxa.

The Devonian was a time of great botanical change. The period began with little more than diminutive early tracheophytes representing land plants and ended with a profusion of vascular plants including seed-producing progymnosperms (Traverse, 2008). Various new morphological features of spores developed during the Devonian, often exinal thickenings such as zonae and curvaturae, which are characteristic of Devonian spores. An increase in average size is also observed, together with various exinal features such as camarae, pseudosaccae and an increasing variety of sculptural elements, all presumed to be associated with new modes of dispersal, possibly using insects (Marshall, 1996a; Traverse, 2008). This is inferred as indicating increasing competition between plants as communities became more structured and covered a larger area.

Unfortunately, palynological studies concerning Devonian Gondwana are strongly biased towards purely stratigraphical works centred on North Africa, Arabia and South America. Palaeoecological studies of Middle Devonian Gondwana are somewhat lacking.

Probably owing to its largely complete record of Devonian strata, Cantabria has been subject to some past study, with the majority being of a stratigraphical or lithological nature, providing a good base for the current study to work from and largely detailed above. Palynological studies, however, are comparatively rare, comprising three papers (Cramer, 1966; 1969a; Fombella Blanco, 1988) and an MSc thesis (Gill, 2001). Table 4 lists the spores recorded in these sources.

The forms known from these studies are not particularly remarkable; most are known from Gondwanan and/or Eurasian deposits (Breuer & Steemans, 2013). The spores for which a botanical affinity is known mostly identify with rhyniopsids, zosterophyllopsids, lycopsids or trimerophytes. *Rhabdosporites*, however, is characteristic of progymnosperms (Allen, 1980; Gensel, 1980), indicating some of these more advanced plants may have colonised the area by this time.

Their recently increased diversity makes spores more useful in biostratigraphy. Some degree of provincialism is seen as communities become more complex, with miospore zones in Iberia correlating well with those of Western Gondwana, that is North Africa, Arabia and

Table 4. List of spore taxa found in the Naranco, Huergas and Gustalapiedra formations, as originally cited. Taxa placed in synonymy with those described in this study are denoted with •. Original sources are denoted thus: 1=Cramer, 1966b; 2=Cramer, 1969a; 3=Fombella Blanco, 1988; 4=Gill, 2001.

Taxon	Source(s)		Taxon	Source(s)	
Acanthotriletes espinositus	2		*Emphanisporites obscurus*	2	•
A. heterodontus	3		*E. robustus*	2	•
A. tenuispinosus tenuispinosus	2		*E. rotatus*	1, 2, 3, 4	•
A. sp.	3	•	*E. spinaeformis*	4	•
Acinosporites sp. A	4	•	*Geminospora cf. tuberculata*	3	•
Anapiculatisporites carminae	1, 2	•	*Grandispora cf. gabesensis*	4	•
A. rosendae	1	•	*G. macrotuberculata*	4	•
Aneurospora gregsii	3	•	*G. permulta*	4	•
Apiculatasporites perpusillus	4	•	*G. sp. A* Paris et al., 1985	3	•
Apiculiretusispora arenorugosa	3	•	*G. sp. B* Paris et al., 1985	3	
A. brandtii	4	•	*G. sp. C* Paris et al., 1985	3	•
A. cf. brandtii	3	•	*G. sp. A*	4	•
A. densiconata	4	•	*G. sp. B*	3	
A. plicata	4	•	*Hymenozonotriletes argutus* "I"	1	•
Calamospora atava	4	•	*H. argutus* "II"	1	•
C.? sp. A	4	•	*cf. H. discors*	3	
Calyptosporites argutus	2	•	*H. cf. deliquescens*	1	•
C. cf. deliquescens	2	•	*H. cf. domanicus*	1	•
C. cf. domanicus	2	•	*H. cf. eximius ?*	1	•
C. microspinosus	2	•	*H. narancae*	1	•
C. (?) narancae	2	•	*Hystricosporites delectabilis*	2	
C. optivus	2	•	*Leiotriletes bonitus*	2	•
C. velatus	2	•	*Punctatisporites spp.*	4	
Camerozonotriletes? concavus	4	•	*Raistrickia aratra*	3	•
Camptotriletes araneosus	1		*Retusotriletes actinomorphus*	4	•
Contagisporites cf. optivus	4		*R. barbutus*	2	•
Convolutispora disparalis	4		*R. microgranulatus*	4	•
Cyclogranisporites plicatus	2	•	*R. pychovii major*	2	•
C. rosendae	1	•	*R. rotundus*	2, 4	•
Dibolisporites echinaceus	3, 4	•	*R. rugulatus*	4	
D. cf. eifeliensis	4	•	*R. triangulatus*	3	•
D. cf. wettledorfensis	4		*R. sp.* Paris et al., 1985	3	
D.? sp. A	4		*Rhabdosporites butifarrus*	2	
Dictyotriletes cf. emsiensis	4	•	*R. prosperus*	2	•
Emphanisporites annulatus	1, 2, 4	•	*R. langii*	4	•
E. cf. annulatus	3	•	*Samarisporites sp. B* Paris et al., 1985	3	
E. augusta	3	•	*Verrucosisporites premnus*	4	•
E. erraticus	1	•	*V. scurrus*	4	•
E. mcgregorii	1, 2	•	*V. cf. tuberosus*	3	
E. cf. micrornatus	4	•			

South America, as opposed to Europe (Streel & Loboziak, 1996; Loboziak & Melo, 2002). This is hypothesized to be a result of increased competition among the more structured plant communities forcing the evolution of heterospory, with a large megaspore able to retain more sustenance for the seedling, giving a greater chance of survival but also limiting dispersal

(Marshall, 1996a). Interestingly the degree of provincialism seems to positively correlate with plant size, suggesting large size was also a response to increased competition (Marshall, 1996a). Not all plants evolved heterospory at this time, while some widely distributed megaspore taxa may be homeomorphs, developed independently by already widely distributed plants (Marshall, 1996a). Attempts at quantitative analysis of Middle Devonian floral provinces are hampered by taxonomic confusion and the different taxonomic prejudices of different workers (Marshall, 1996a). The Middle Devonian seems to have been a period of comparatively low provinciality across many different fossil groups (Boucot, 1974, 1988), sometimes taken as evidence that no seas separated Gondwana and Laurussia during the Middle Devonian (Streel & Loboziak, 1996; Robardet, 2003; Steemans et al., 2011), in stark contrast to the palaeogeographic models detailed above which largely rely on palaeomagnetism. This view is not universally supported, however, with various independent studies finding differences between Gondwanan and Laurussian floras (Paris et al., 1985; Marshall, 1996a; Wnuk, 1996; Xingxue & Xiuyuan, 1996; di Pasquo et al., 2009).

Various different biostratigraphical schemes have been developed for use with Devonian spores with two widely cited examples, one based on characteristic assemblages (Richardson & McGregor, 1986), the other using interval zones based on first and last occurrences of single indicator species, usually nested within assemblage zones (Streel et al., 1987). These approaches have their differing advantages; assemblage zones should be applicable more widely, being based on an assemblage rather than a single species, while interval zones are more easily recognised and more objective, simply being based on the presence or absence of one or two taxa. These two schemes have advantages and disadvantages concerning their use, with Richardson & McGregor (1986) citing many more index species than Streel et al. (1987). These schemes largely focus on Euramerican areas and utilise largely cosmopolitan taxa, making them useful in this study, however a more modern scheme focusing on northwestern Gondwana (Breuer & Steemans, 2013) is also useful as it uses an assemblage containing more taxa in common with Iberia. These schemes are also well correlated with each other (see Fig. 25), aiding chronological dating of the Naranco, Huergas and Gustalapiedra assemblage. Abbreviated descriptions of relevant Middle Devonian zones in each scheme with taxonomic updates are given below and related to the known Naranco, Huergas and Gustalapiedra miospore assemblage (Table 4). It should be noted that this assemblage shows important differences from that found in the present study. This section represents a review of previous knowledge; the reader is referred to Chapter 7 for a biostratigraphical synthesis using the present assemblage.

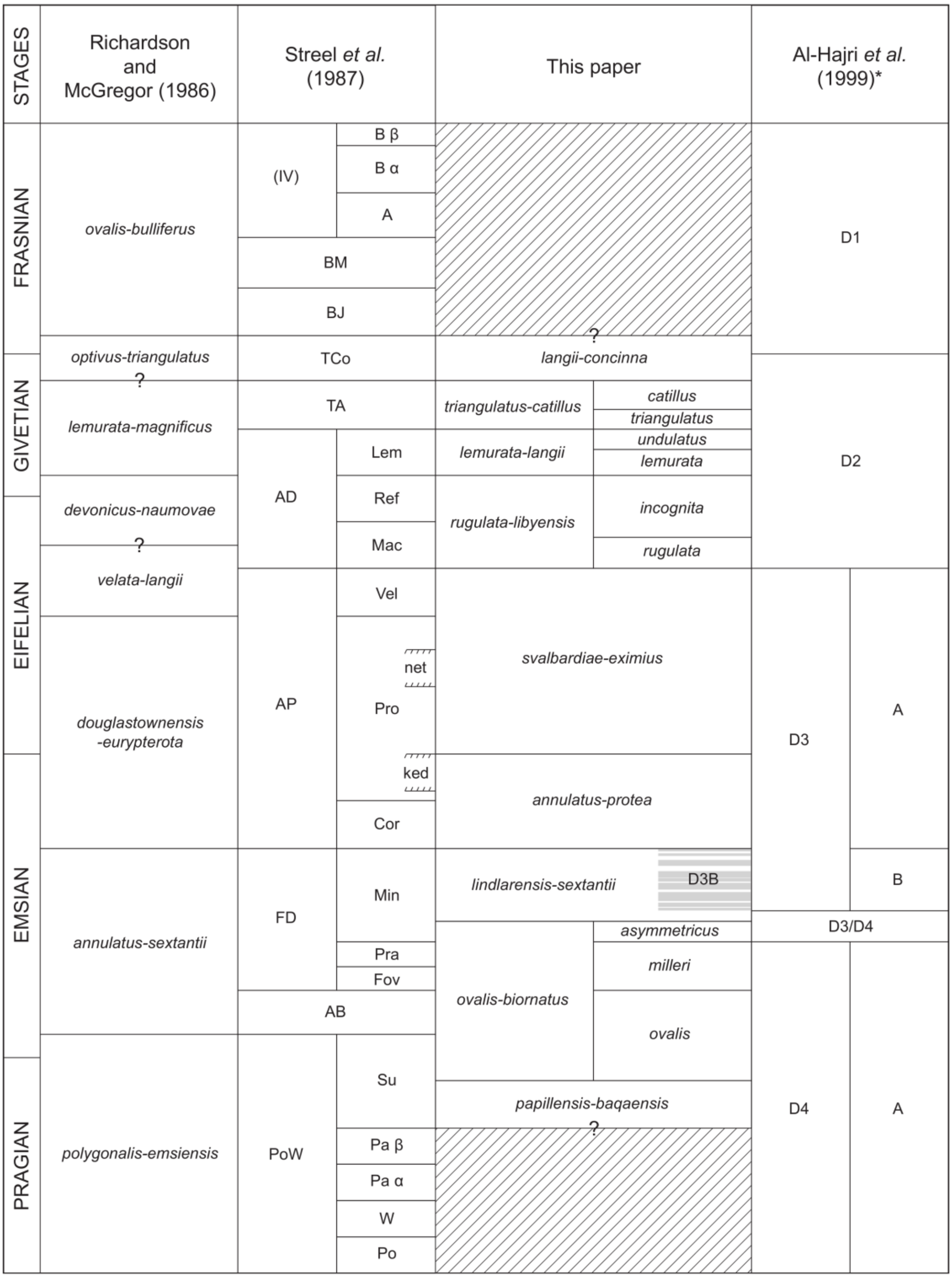


Figure 25. Correlation chart of spore zonation schemes of the Devonian period for Euramerica (Richardson & McGregor, 1986; Streel et al., 1987) and Gondwana (Al-Hajri et al., 1999; Breuer & Steemans, 2013). The scheme of Al-Hajri et al. is figured here with revisions by P. Breuer. Taken from Breuer & Steemans (2013).

4.4.1 - Richardson & McGregor (1986)

The zones of Richardson & McGregor (1986) are defined by one or two nominal species, usually first appearing at the zone's base, a characteristic assemblage, and sometimes by a morphological event or innovation at the zone's base.

****Grandispora douglastownensis-Ancyrospora eurypterota* Assemblage Zone**

Characteristic species:

Grandispora douglastownensis McGregor, 1973

Ancyrospora eurypterota Riegel, 1973

Acinosporites apiculatus (Streel) Streel, 1967

Ancyrospora kedoae (Riegel) Turnau, 1974

A. nettersheimensis Riegel, 1973

A. loganii McGregor, 1973

Apiculiretusispora gaspiensis McGregor, 1973

**Calyptosporites* sp. nov. Riegel, 1975

* *Calyptosporites proteus* (Naumova) Allen, 1965

Dibolisporites echinaceus (Eisenack) Richardson, 1964

Grandispora eximia (Allen) McGregor and Camfield, 1982

Hystricosporites cf. *corystus* Richardson, 1964

H. microancyreus Riegel, 1973

**Spinozonotriletes arduinnae* Riegel, 1973

This zone is marked by the appearance of bifurcate appendages and the proliferation of large, apiculate, spinose, zonate-pseudosaccate spores. There is also a marked increase in spore size, while *Dibolisporites echinaceus, Apiculatasporites microconus* and *Verruciretusispora dubia* persist from the previous zone.

***Grandispora velata-Rhabdosporites langii* Assemblage Zone**

Characteristic species:

Grandispora velata (Richardson) McGregor, 1973

Rhabdosporites langii (Eisenack) Richardson, 1960

Acinosporites acanthomammillatus Richardson, 1964

A. macrospinosus Richardson, 1964

Anapiculatisporites petilus Richardson, 1964

Ancyrospora ancyrea (Eisenack) Richardson var. *ancyrea* Richardson, 1962

Corystisporites multispinosus Richardson, 1964

Densosporites concinnus (Owens) McGregor and Camfield, 1982

Grandispora longa Chi and Hills, 1976

Kraeuselisporites acerosus (Arkhangelskaya) McGregor and Camfield, 1982

Kraeuselisporites ollii? (Chibrikova) McGregor and Camfield, 1982

Periplecotriletes tortus Egorova, 1974

Perotrilites bifurcatus Richardson, 1962

Retusotriletes distinctus Richardson, 1964

R. rugulatus Riegel, 1973

This zone is marked by a proliferation of zonate-pseudosaccate spores with fine sculpture, intermediate in size between megaspores and miospores. Spores appear that are both zonate and camerate and with a flimsy exoexine. Murornate-spinose spores become more diverse, while most spores from the previous zone persist here.

***Densosporites devonicus*-*Grandispora naumovae* Assemblage Zone**

Characteristic species:

Densosporites devonicus Richardson, 1960

Grandispora naumovae (Kedo) McGregor, 1973

Acinosporites acanthomammillatus Richardson, 1964

A. macrospinosus Richardson, 1964

Ancyrospora grandispinosa Richardson, 1960

Cristatisporites orcadensis Richardson, 1960 (sometimes referred to *Samarisporites*)

Densosporites inaequus (McGregor) McGregor and Camfield, 1982

Grandispora inculta Allen, 1965

G. mammillata Owens, 1971

Hystricosporites gravis Owens, 1971

H. reflexus Owens, 1971

Kraeuselisporites rugosus (Owens) McGregor and Camfield, 1982

Lophotriletes devonicus (Naumova ex Chibrikova) McGregor and Camfield, 1982

Perotrilites conatus Richardson, 1964

Retispora archaelepidophyta (Kedo) McGregor and Camfield, 1982

Retusotriletes distinctus Richardson, 1964

R. rugulatus Riegel, 1973

Rhabdosporites langii (Eisenack) Richardson, 1960

Verrucosisporites premnus Richardson, 1964

V. scurrus (Naumova) McGregor and Camfield, 1982

This zone is marked by the first appearance of cingulizonate spores with bifurcate spines, as well as the appearance of large, irregular verrucate sculpture. Foveoreticulate sculpture on pseudosaccate spores begins, while all characteristic species of the previous zone persist here.

***Geminospora lemurata-Cymbosporites magnificus* Assemblage Zone**

Characteristic species:

Geminospora lemurata Balme, 1962, emend. Playford, 1983

Cymbosporites magnificus (McGregor) McGregor and Camfield, 1982

Ancyrospora langii (Taugourdeau-Lantz) Allen, 1965

Aneurospora goensis Street, 1964

A. greggsii (McGregor) Streel, in Becker et al., 1974

Archaeozonotriletes variabilis Naumova, 1953

A. timanicus Naumova, 1953

Biharisporites parviornatus Richardson, 1964

Corystisporites serratus (Naumova) McGregor and Camfield, 1982

Geminospora? *bislimbata* (Chibrikova) McGregor and Camfield, 1982

Grandispora tomentosa Taugourdeau-Lantz, 1967

Hymenozonotriletes celeber Chibrikova, 1959

Perotrilites conatus Richardson, 1964

P. heclaensis McGregor and Camfield, 1982

This zone is marked by the appearance of camerate spores with a thick exoexine and small sculpture. Irregular verrucate to baculate sculpture proliferates, while patinate spores diversify.

Frustratingly few of these characteristic species have been seen in the Naranco, Huergas and Gustalapiedra deposits. The best attribution to a particular zone is from Gill (2001); the assemblage therein is best assigned to the *velata-langii* to *devonicus-naumovae* zones.

4.4.2 - Streel et al. (1987)

The scheme of Streel et al. (1987) contains a mixture of types of zone nested within one another, each with their own definitions and usually defined by the first appearance of one or two nominal species, with a small characteristic assemblage.

The **AP (*Acinosporites apiculatus-Calyptosporites proteus*) Assemblage Zone** is defined by the first appearance of *Acinosporites apiculatus* together with 'several species' of *Ancyrospora*, *Hystricosporites*, *Perotrilites*, *Samarisporites*, *Calyptosporites* and *Spinozonotriletes*, though the latter two are now considered synonyms of *Grandispora*. Within this are interval zones defined by the successive appearances of *Hystricosporites* cf. *corystus* (***Cor* Zone**), *Grandispora* (*Calyptosporites*) *protea* (***Pro* Zone**) and *Grandispora velata* (***Vel* Zone**), with two acme zones (of *Ancyrospora kedoae* and *A. nettersheimensis*) recognised within the *Pro* Zone.

The **AD (*Acinosporites acanthomammillatus-Densosporites devonicus*) Assemblage Zone** is characterised by the first appearance of *Acinosporites acanthomammillatus*, *A. macrospinosus*, *Rhabdosporites langii* and *Densosporites devonicus*. Interval zones within this are marked by the appearances of *Acinosporites macrospinosus* (***Mac* Zone**), *Hystricosporites reflexus* (***Ref* Zone**) and *Geminospora lemurata* (***Lem* Zone**).

The succeeding **TA Assemblage Zone** is defined by its nominal species, *Samarisporites triangulatus* and *Ancyrospora ancyrea* var. *ancyrea*, as well as by its lack of *Rhabdosporites langii*. This zone contains no subsidiary interval zones.

Again, very few Naranco, Huergas and Gustalapiedra species are mentioned in this scheme. Gill (2001) found *Rhabdosporites langii* which is only seen in the AD Assemblage Zone, correlating well with the *devonicus*-*naumovae* zone of Richardson & McGregor (1986) mentioned above. Cramer (1969a) found *Grandispora velata*, characteristic of the *Vel* zone onwards including the AD zone. It should, however, be noted that Cramer's samples are from multiple sites and no mention is made of which spores were seen at which sites, precluding geographic placement of differently dated assemblages.

4.4.3 - Breuer & Steemans (2013)

The northwestern Gondwanan scheme of Breuer & Steemans (2013) is structured similarly to that of Streel et al. (1987), with large assemblage zones subdivided into interval zones. The zones are defined on the basis of a single index species with the assemblage zones also defined with a characteristic assemblage to be used in the absence of the index species, while the disappearances of taxa and some morphological innovations are also noted.

The ***Emphanisporites annulatus*-*Grandispora protea* Assemblage Zone** has its base at the first appearance of *E. annulatus*. The assemblage is primarily characterised by the first occurrence of large, apiculate zonate-pseudosaccates, such as the *Grandispora/Samarisporites* complex. Characteristic species are *Craspedispora ghadamensis*, *Geminospora convoluta*, *Grandispora douglastownensis*, *G. protea* and *Granulatisporites concavus*. This zone has no subsidiaries.

The ***Geminospora svalbardiae-Samarisporites eximius* Assemblage Zone** is based on the appearance of *G. svalbardiae*. The most characteristic species to appear are *Acinosporites acanthomammillatus*, *Ancyrospora nettersheimensis*, *Auroraspora minuta*, *Camarozonotriletes rugulosus*, *Grandispora cassidea*, *G. gabesensis*, *G. velata*, *Samarisporites eximius*, *S. praetervisus*, *Zonotriletes armillatus* and *Z. simplicissimus*. The pseudosaccates continue to diversify in this zone while grapnel-tipped spines appear.

The base of the ***Scylaspora rugulata-Grandispora libyensis* Assemblage Zone** is marked by the more or less synchronous appearance of *Camarazonotriletes*? *concavus*, *Chelinospora timanica*, *Craspedispora paranaensis*, *Dictyotriletes hemeri*, *Grandispora libyensis*, *G. naumovae*, *G. stolidota*, *Scylaspora rugulata* and *Verrucosisporites premnus*. In addition to these *Archaeozonotriletes variabilis*, *Camarozonotriletes asperulus*, *Cristatisporites streeli*, *Elenisporites gondwanensis*, *Grandispora incognita*, *G. permulta* and *Verrucosisporites scurrus* all appear in this zone. Ancient species such as *Ancyrospora nettersheimensis* and *Grandispora protea* disappear in this zone. In addition the appearances of ***Scylaspora***

rugulata and ***Grandispora incognita*** define their own interval zones within the *rugulata-libyensis* Zone.

The ***Geminospora lemurata-Rhabdosporites langii*** **Assemblage Zone** is defined by the appearance of *G. lemurata*. *G. punctata* and *R. langii* appear at about the same time. *Cymbosporites variegatus*, *Camarozonotriletes parvus*, *Contagisporites optivus*, *Corystisporites undulatus*, *Dibolisporites turriculatus* and *Lophozonotriletes media* also appear in this zone. *Apiculiretusispora brandtii*, *Geminospora svalbardiae*, *Grandispora velata* and *Rhabdosporites minutus* are notable disappearances in this zone while monolete spores and megaspores increase in abundance. ***Geminospora lemurata*** and ***Corystisporites undulatus*** define subsidiary interval zones.

The ***Samarisporites triangulatus-Cymbosporites catillus*** **Assemblage Zone** is based on the appearance of *S. triangulatus*. The appearances of *C. catillus*, *C. cyathus*, *Grandispora fibrilabrata* and *Verrucosisporites ellesmerensis* are somewhat younger. *Contagisporites optivus*, *Craspedispora ghadamensis*, *Dictyotriletes hemeri*, *Elenisporites gondwanensis*, *Grandispora douglastownensis*, *Scylaspora rugulata* and *Zonotriletes rotundus* all disappear in this zone, as part of a general decrease in diversity and spore size. The appearances of ***Samarisporites triangulatus*** and ***Cymbosporites catillus*** define interval zones.

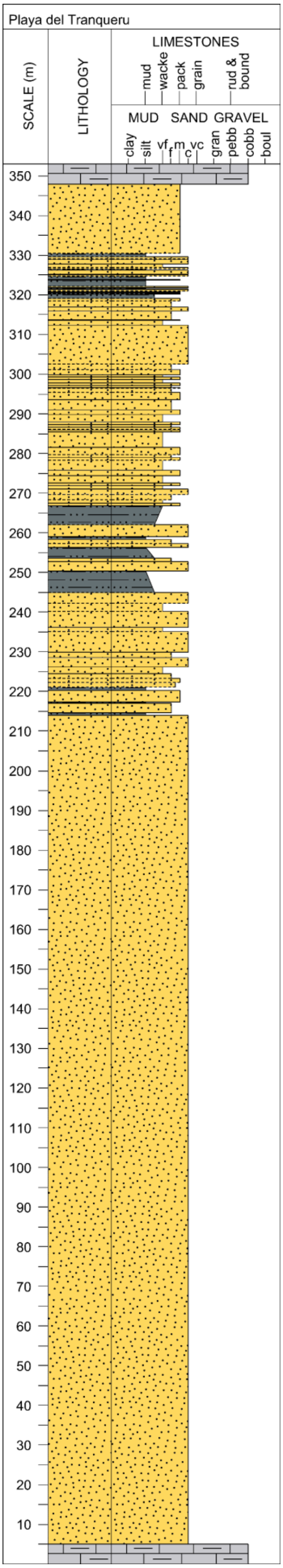
This scheme mentions more species seen in the Naranco, Huergas and Gustalapiedra assemblage than the Euramerican schemes. The assemblages of Cramer (1969a) and Fombella Blanco (1988) contain only long-ranging taxa, while the assemblage of Gill (2001) presents a number of problems. It contains a variety of index species such as *E. annulatus*, *V. premnus*, *V. scurrus*, *G. gabesensis*, *G. permulta* and *R. langii* but they appear in the wrong order for this scheme to be properly applied.

5 - Results

A full taxonomic treatment of the assemblage recovered from the Naranco, Huergas and Gustalapiedra formations is given in Chapter 6.

5.1 - Stratigraphic logs

Stratigraphic logs for the four logged sections at the Playa del Tranqueru, San Pedro de Nora, Mirantes de Luna and Crémenes-Las Salas sites are presented in figures 26-29.



5.2 - Palynomorph counts

The quantitative data pertaining to the three counted sections are found in Charts 1-3. Across all 113 samples 5,458 phytoplankton in 82 taxa, 448 chitinozoans in 32 taxa and 13,847 spores in 99 taxa were counted. Count data is available on the ORDA database (Askew, 2018). Stacked quantitative abundance charts of the three major palynomorph categories are presented as figures 30-32.

5.3 - Assemblage descriptions

5.3.1 - Phytoplankton

The phytoplankton assemblage consists of 82 taxa (61 identified species or subspecies placed in 27 genera) with 10 of these placed in open nomenclature.

Gorgonisphaeridium cumulatum is extraordinarily abundant here. Assessed quantitatively, this species alone represents ca. 70% of the assemblage. Of the remaining groups, Multiplicisphaerids are the most common, constituting 9% of the assemblage (30% excluding *G. cumulatum*), followed by *Cymatiosphaera* (6%; 20%), *Palacanthus* (5%; 15%), *Polyedryxium* (3%; 9%), *Micrhystridium* & *Solisphaeridium* (2%; 7%) and *Veryhachium* & *Villosacapsula* (2%; 6%). Other species of *Gorgonisphaeridium* constitute 2% (6%) of the assemblage.

5.3.2 - Chitinozoans

The chitinozoan assemblage consists of 32 taxa (21 identified species or subspecies placed in 10 genera) with 8 in open nomenclature.

The most abundant single genus here is *Sphaerochitina*, representing 28% of the assemblage when assessed quantitatively, followed by *Hoegisphaera* (25%) and

Figure 26. Stratigraphic log of the Playa del Tranqueru site. Log produced using the Sedlog program (Zervas et al., 2009) and subsequently hand coloured.

Fungochitina (25%). At the sub-family level, the Angochitininae are dominant (33%), followed by the Lagenochitininae (28%), the Desmochitininae (25%), the Ancyrochitininae (13%) and the rare Conochitininae (0.27%).

5.3.3 - Spores

The spore assemblage consists of 99 taxa (57 identified species placed in 28 genera) with 23 in open nomenclature.

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

6 - Taxonomic section

6.1 - Phytoplankton taxonomy

The phytoplankton described below are treated as form genera and species in accordance with the ICN (Melbourne Code) (McNeill et al., 2012) and arranged alphabetically by genera under the unranked group Acritarcha and as prasinophyte phycomata, in line with identifications given by Le Hérissé et al. (2009). Those genera not mentioned by Le Hérissé et al. (2009) (*Chomotriletes*, *Crameria*, *Exochoderma*, *Stellechinatum*) are considered acritarchs here. Full citations are taken predominantly from Fensome et al.

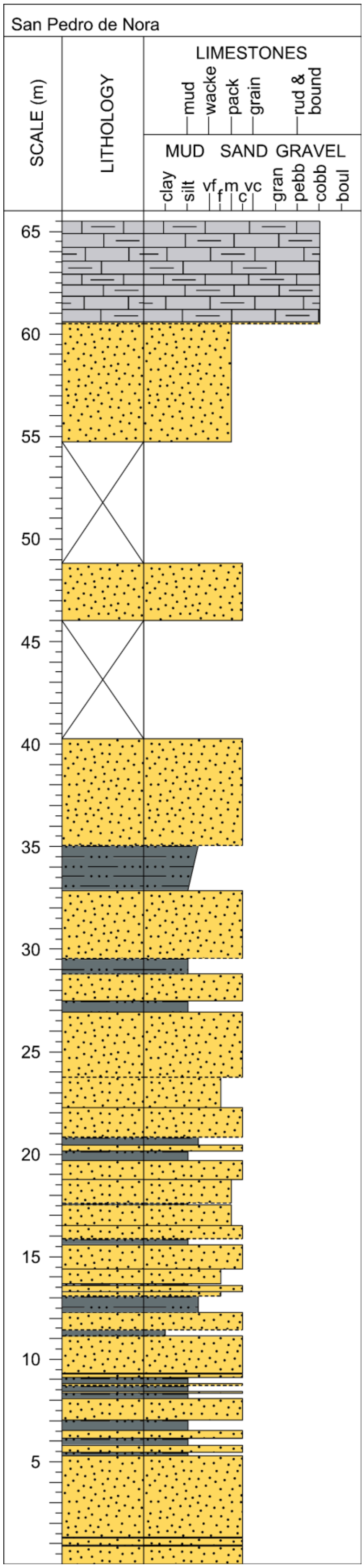


Figure 27. Stratigraphic log of the San Pedro de Nora site. Log produced using the Sedlog program (Zervas et al., 2009) and subsequently hand coloured.

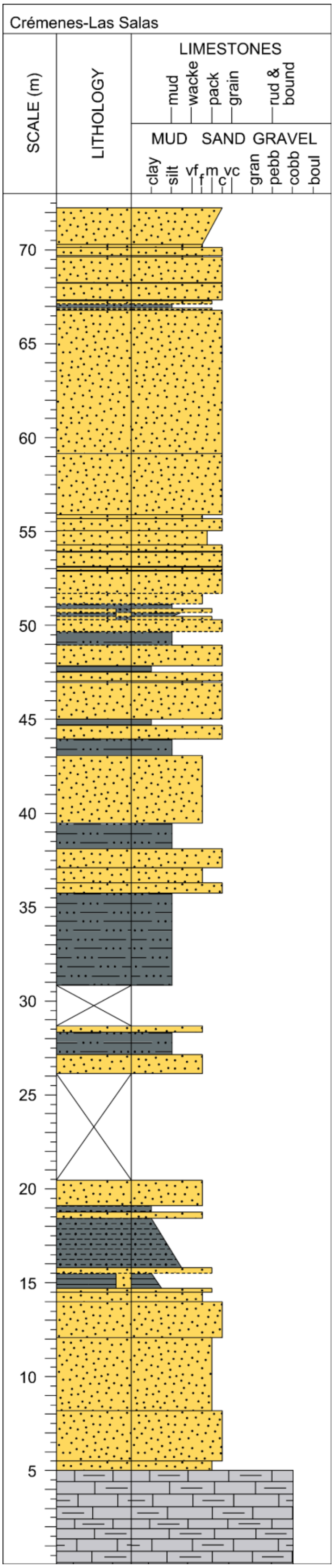


Figure 28. Stratigraphic log of the Crémenes-Las Salas site. Log produced using the Sedlog program (Zervas et al., 2009) and subsequently hand coloured.

(1990) with newer sources where relevant. A limited synonymy is provided for species previously recorded from the Naranco and Huergas formations, reproduced as cited in their original sources. Dimensions are given for each species and where three numbers are given these correspond to the minimum value (arithmetic mean) and maximum values. The number of specimens measured is given. The sites in which each species occurs in this study are given. Previous records are noted following consultation of the John Williams Index of Palaeopalynology (for details see Riding et al. (2012)).

Group **ACRITARCHA** Evitt, 1963

Genus ***Ammonidium*** Lister, 1970

Type species: *Ammonidium microcladum* (Downie) Lister, 1970

Ammonidium microfurcatum ? (Deunff) Fensome et al., 1990

Plate I, fig. 1

cf. 2001 *Ammonidium* sp. A; Gill, p. 54, pl. 3, fig. 1

Description: Vesicle originally globular. Wall psilate. Numerous (~17) thin, apparently solid processes arise from vesicle wall with a sharp proximal contact. Processes taper slightly to acuminate tips, simple or with a short dichotomous branch at the distal extremity. No excystment structure observed.

Dimensions: Vesicle diameter: 22 (26) 30 µm. (2 specimens measured) Process length: 9-13 µm. Process width: ~1 µm.

Remarks: Poor preservation and a low number of specimens preclude a more confident identification, though the specific description is met.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Geras, Aleje, '120', Crémenes-Las Salas and Man member localities.

Previous records: *A. microfurcatum* is reported from the Llandovery to late Wenlock (Martin, 1966, 1967, 1969) and Frasnian to early Famennian (Stockmans & Willière, 1962a, 1969) of Belgium, the Wenlock to Early Devonian of Romania (Beju, 1967; Iliescu, 1976; Iordan et al., 1984), the Silurian to Pragian of France (Doubinger, 1963; Moreau-Benoit, 1969), the early Lochkovian of Spain (Cramer, 1964a, 1964b) and the Emsian to middle Givetian of Canada (Deunff, 1957, 1966; Playford, 1977).

Genus ***Chomotriletes*** Naumova, 1939

Type species: *Chomotriletes vedugensis* Naumova, 1953

Chomotriletes ?*bistchoensis* ? Staplin, 1961

Plate I, fig. 2

Description: Vesicle originally ovoid. Wall sculptured with at least 10 concentric rings ~1 µm wide, otherwise psilate. No excystment structure observed.

Dimensions: Vesicle diameter: 27 (40) 57 µm. (4 specimens measured)

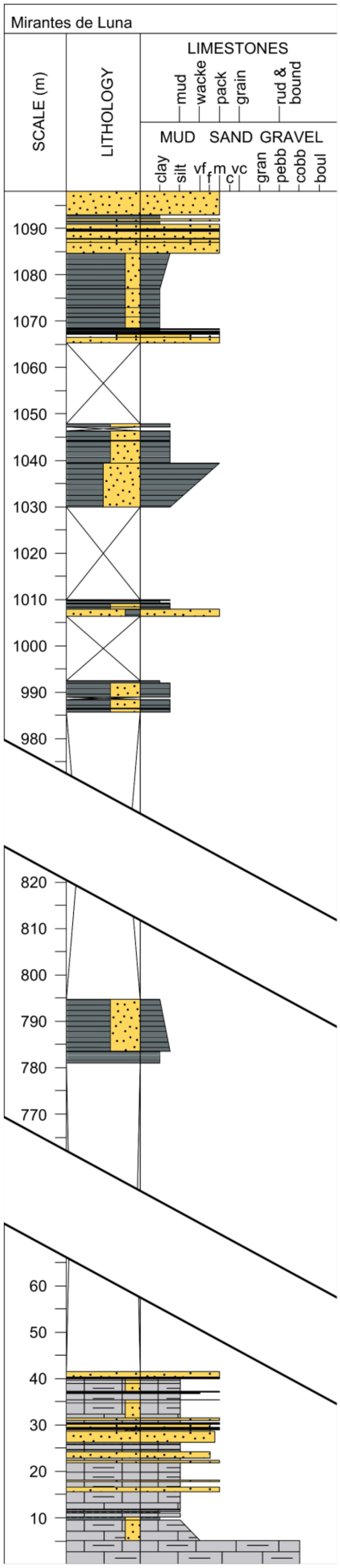
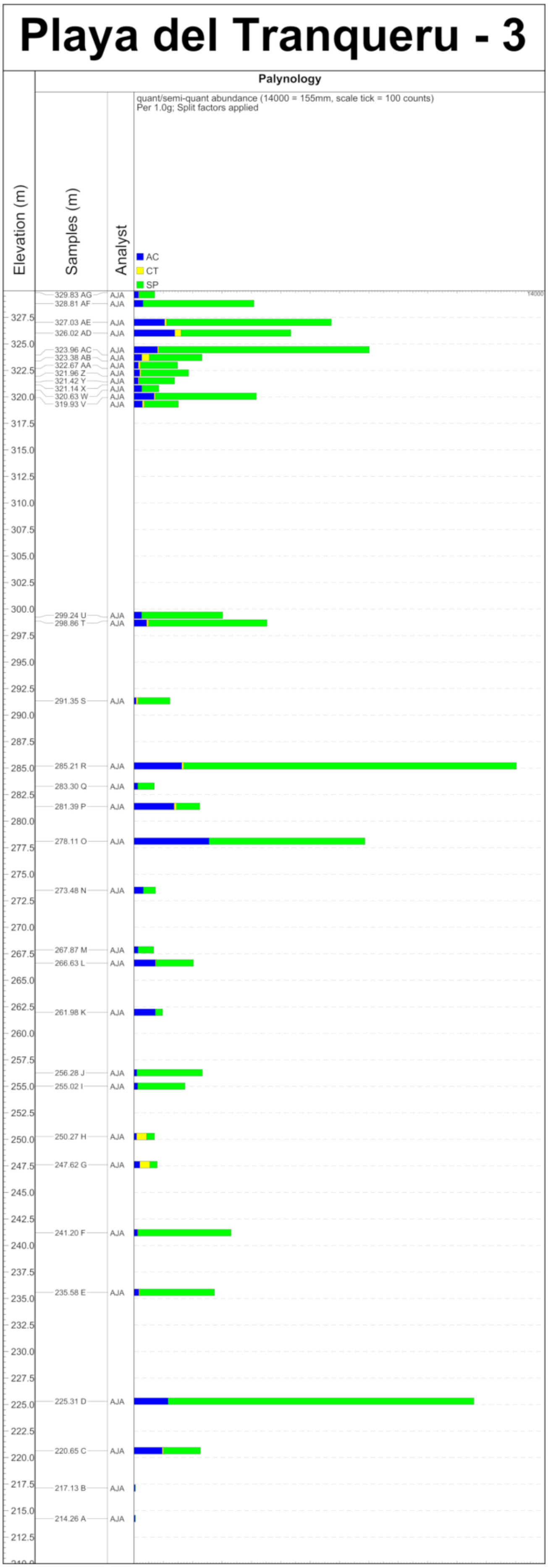


Figure 29. Stratigraphic log of the Mirantes de Luna site. Slanted lines indicate large areas without deposition which have been omitted for clarity. Log produced using the Sedlog program (Zervas et al., 2009) and subsequently hand coloured.



Remarks: *C. vedugensis* Naumova, 1953 has wider ridges than the specimens seen here (Balme, 1962; Playford & Dring, 1981). *C. ?bistchoensis* as originally described is slightly larger and has slightly more ridges, though the specimens described here otherwise resemble it, including the thicker region around the margin. Poor preservation and a low number of specimens preclude a more confident identification. Staplin questionably assigned this species to *Chomotriletes* though others have used it with confident assignment, e.g. Wicander & Playford (1985).

Occurrence: Found at the Playa del Tranqueru locality.

Previous records: *C. ?bistchoensis* is reported from the Eifelian to Frasnian of Iran (Ghavidel-Syooki, 1994, 1995, 2003; Hashemi & Tabea, 2009; Hashemi, 2011), the Late Devonian of Canada (Staplin, 1961), the early Frasnian of Morocco (Rahmani-Antari & Lachkar, 2001) and the late Frasnian of the USA (Wicander & Playford, 1985).

Figure 30. Stacked quantitative palynomorph abundance chart of the Playa del Tranqueru site. Horizontal scale represents number of palynomorphs per gram of rock. Colours represent phytoplankton ●, chitinozoans ● and spores ●.

Genus ***Comasphaeridium*** Staplin et al. emend. Sarjeant & Stancliffe, 1994

Type species: *Comasphaeridium cometes* (Valensi) Staplin et al., 1965

Comasphaeridium hirsutum ? Johnson, 1985

Plate I, fig. 3

Description: Vesicle originally globular. Wall bears dense ornament of thin, tapering processes that obscure the wall between them. No excystment structure observed.

Dimensions: Vesicle diameter: 22 (26) 30 µm. (2 specimens measured) Process length: up to 4 µm.

Remarks: A low number of specimens and poorly figured type material preclude a more confident identification. The specific description is met, despite the species being originally described in the Silurian. Distinguished from *C. silesiense* ? in this study by its shorter, more densely distributed processes.

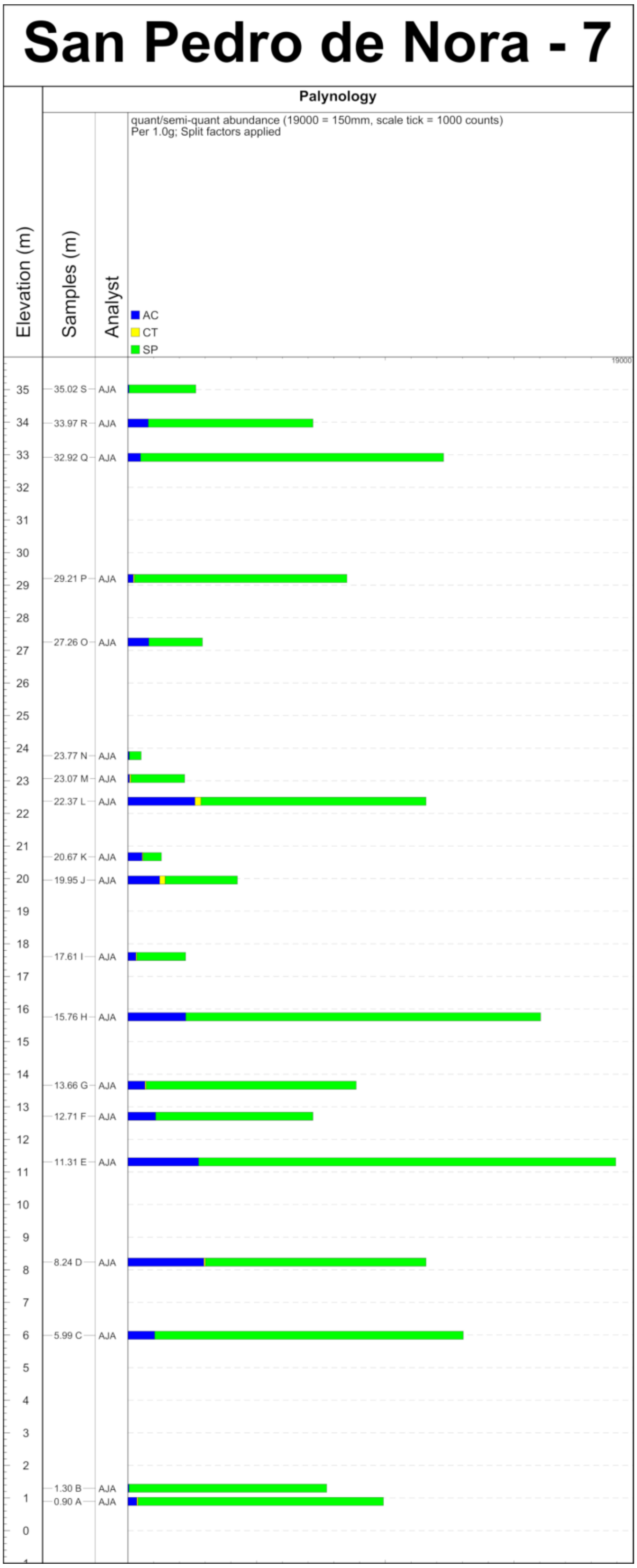


Figure 31. Stacked quantitative palynomorph abundance chart of the San Pedro de Nora site. Horizontal scale represents number of palynomorphs per gram of rock. Colours represent phytoplankton ●, chitinozoans ● and spores ●.

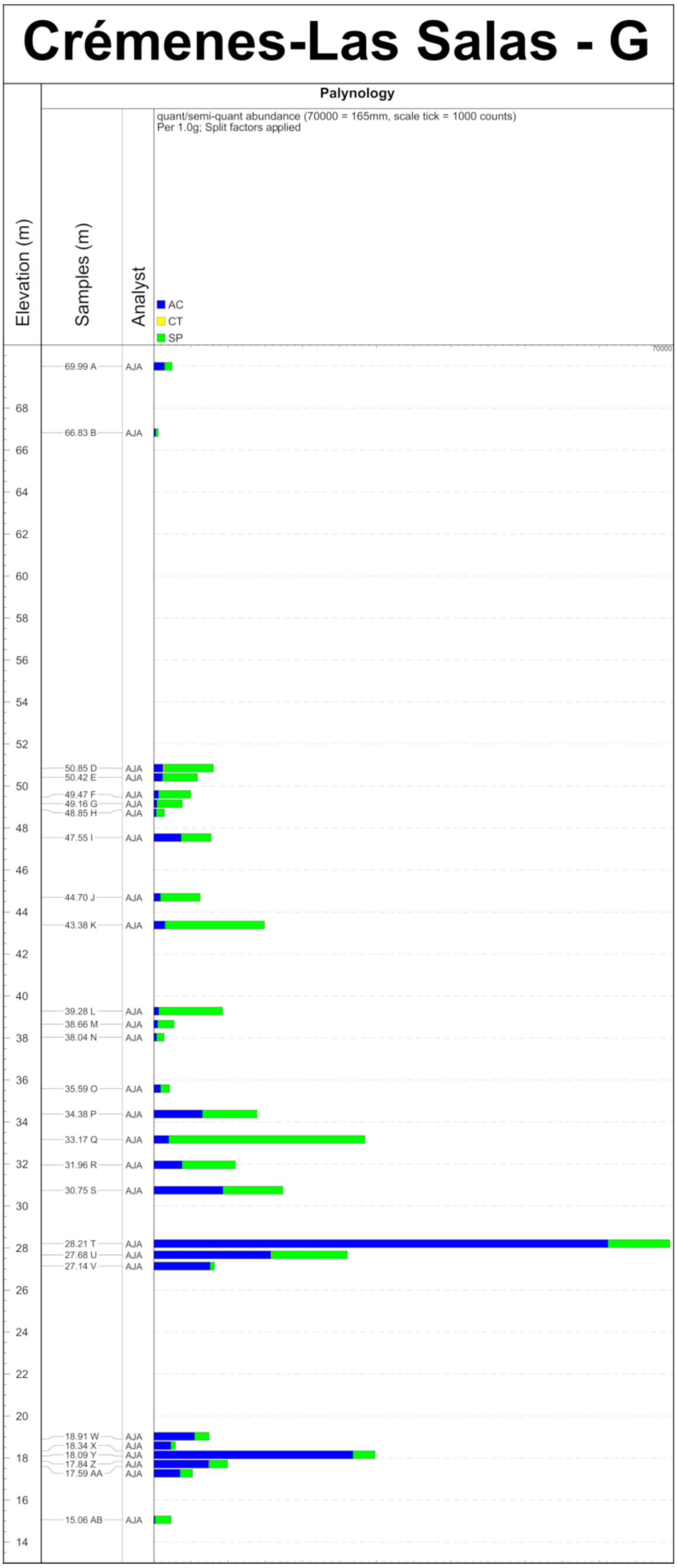


Figure 32. Stacked quantitative palynomorph abundance chart of the Crémenes-Las Salas site. Horizontal scale represents number of palynomorphs per gram of rock. Colours represent phytoplankton ●, chitinozoans ● and spores ●.

Occurrence: Found at the Veneros-Santoseso and Sobrerriba-Santa Eufemia localities.

Previous record: *C. hirsutum* is reported from the Llandovery of the USA (Johnson, 1985).

Comasphaeridium silesiense ? Moczydłowska, 1998

Plate I, fig. 4

Description: Vesicle originally globular. Wall bears dense ornament of thin, tapering processes, otherwise psilate. No excystment structure observed.

Dimensions: Vesicle diameter: 24-25 µm. (1 specimen measured) Process length: up to 12 µm.

Remarks: The single specimen described here resembles *C. silesiense* Moczydłowska, 1998, a much older species. The specimen also resembles *Elektoriskos williereae* (Deflandre & Deflandre ex Lister) Vanguestaine emend. Martin, 1989 but the length of the processes is not “at least one and a half times the vesicle diameter” as indicated for that species. That said the specimens of *E. williereae* figured by Martin (1989) rarely meet that criterion either, attributed by that author to damage.

Occurrence: Found at the Vozmediano locality.

Previous records: *C. silesiense* is reported from the Early to Late Cambrian of Ireland (Moczydłowska & Crimes, 1995; Brück & Vanguestaine, 2004; Vanguestaine & Brück, 2008), the Middle Cambrian of Sweden (Hagenfeldt, 1989), the Middle to Late Cambrian of Spain (Fombella Blanco, 1979, 1986, 1987, Palacios et al., 2004, 2006; Palacios, 2010) and Poland (Moczydłowska, 1998, 1999, Jachowicz-Zdanowska, 2010, 2013), the Late Cambrian of Libya (Albani et al., 1991) and the Middle Cambrian to Tremadocian of Canada (Martin, 1992; Palacios et al., 2009).

Genus ***Crameria*** Lister, 1970

Type species: *Crameria duplex* (Cramer) Lister, 1970

Remarks: Considerable confusion between *Crameria* and *Eisenackidium* Cramer & Díez ex Eisenack et al., 1973 is evident in the literature. The genera have been repeatedly synonymised with each other and other genera in the past, well summarised by Fensome et al. (1990). *Crameria* is the senior name to *Eisenackidium*, if they are synonymous, but they are currently separate. The present author differentiates them based on presence or absence of ornament on the inner body; *Eisenackidium* has an inner body which “may be microsculptured” (Eisenack et al., 1973), whereas the diagnosis of *Crameria* by Lister (1970) does not mention ornament and it is considered psilate here. The only valid species in the genus *Crameria* according to Fensome et al. (1990), *C. duplex*, is psilate. The type species of *Eisenackidium*, *E. triplodermum*, has an ornamented inner body and it is proposed that unornamented species of *Eisenackidium* should be transferred to *Crameria*.

Crameria duplex (Cramer) Lister, 1970

Plate I, fig. 5

Description: Vesicle wall two-layered. Inner body originally globular. Inner body bears four very thin processes positioned equidistant around margin. Outer wall layer produced outward by these processes, giving the appearance of a thin flange around the processes. Outer wall strongly convex between the processes so as to contact the inner wall. Both layers psilate. No excystment structure observed.

Dimensions: Vesicle diameter: 13 (17) 22 µm. (4 specimens measured) Process length: 10-18 µm.

Remarks: The specimens seen here bear some resemblance to species of *Cymatiosphaera* Wetzel ex Deflandre, 1954 but have distinct processes, rather than surface flanges. The species as originally described (as *Baltisphaeridium*) is markedly larger than the species described here, though Lister (1970) described a much smaller species with fewer processes, with as few as four cited. The original description of *B. duplex* by Cramer (1964c) specifies 6-10 processes, yet the supposedly restated "Original diagnosis" in Eisenack et al. (1973) describes 4-10 processes for *Eisenackidium duplex*. The correct genus for this species is open to debate. If only the original descriptions are used for *C. duplex* and *Eisenackidium* cf. *carminae* (Cramer) Eisenack et al., 1973, neither of which have been emended, then the two species are distinguished solely on overall size and proportionate length of processes. Lister (1970) described a *C. duplex* assemblage with a vesicle size much closer to that of *E. carminae*, therefore leaving process length as the only distinguishing feature between the species. The present author considers this insufficient for distinguishing them. If the two species were to be synonymised then *carminae* would be the senior name and should be placed in *Crameria* on account of its psilate inner body, in accordance with the remarks under *Crameria* in the present study. Attempts have been made to move *E. carminae* into *Crameria* before (Lister, 1970; Jardiné et al., 1972), though neither of them referenced the basionym correctly and the reassignments were therefore invalid.

Occurrence: Found at the Aleje and Crémenes-Las Salas localities.

Previous records: Reported from the early Llandovery to late Ludlovian (Pöthe de Baldis, 1996, 1997, 2000) and Givetian to Frasnian (Barreda, 1986) of Argentina, the Llandovery of Romania (Iordan et al., 1984), the Ludlovian of England (Lister, 1970; Lister & Downie, 1974), the Emsian of Uruguay (Pöthe de Baldis, 1977), the Emsian to early Eifelian of Spain (Cramer, 1964c; Cramer & Díez, 1976) and the Middle Devonian of Paraguay (Pöthe de Baldis, 1974).

Genus ***Dateriocradus*** Tappan & Loeblich Jr., 1971

Type species: *Dateriocradus polydactylus* Tappan & Loeblich Jr., 1971

Dateriocradus sp. A

Plate I, fig. 6

Description: Vesicle originally pentagonal. Wall psilate. Seven hollow, tapering processes arise from the vesicle, with a smooth proximal contact, freely communicating with vesicle interior. Processes positioned at corners of vesicle and on each face. Distally processes may branch dichotomously. No excystment structure observed.

Dimensions: Vesicle width: 21-23 µm. (1 specimen measured) Process length: up to 17 µm.

Remarks: This species is distinguished from described species of *Dateriocradus* by its distinctly pentagonal shape; it meets the generic diagnosis in all other respects. This species is distinguished from the often similarly shaped *Diexallophasis remota* by its psilate wall. Only a single specimen was found.

Occurrence: Found at the Crémenes-Las Salas locality.

Genus ***Diexallophasis*** Loeblich Jr., 1970

Type species: *Diexallophasis denticulata* (Stockmans & Willière) Loeblich Jr., 1970

Remarks: There is considerable confusion between the genera *Diexallophasis*, *Evittia* and *Exochoderma*. Distinguishing them in this study was not problematic but is difficult to quantify. *Evittia* tends to have quite short processes (*E. longispinosa* being an exception) and was not recovered in this study. *Diexallophasis* and *Exochoderma* were distinguished by their processes, with *Diexallophasis* having narrower, more strongly tapering processes which branched nearer their tips than *Exochoderma*. That genus tends to have much wider, more tubular processes which do not taper very strongly and branch early, resulting in large, finger-like projections with rounded tips. The present author is aware that this distinction is not rigorous enough for the published literature and the *Diexallophasis*-*Evittia*-*Exochoderma* complex remains in need of revision.

Diexallophasis remota (Deunff) emend. Playford, 1977

Plate I, figs. 7-8

p.2001 *Dateriocradus* spp.; Gill, p. 60, pl. 3, fig. 8

cf. 2001 *Diexallophasis* spp.; Gill, p. 63, pl. 3, fig. 12

Description: Vesicle originally tetrahedral or octahedral. Wall microgranulate. Four or six tapering processes arise from the corners of the vesicle, freely communicating with vesicle interior. Process surface also microgranulate. Proximal contacts smooth. Distal tips acuminate, simple or with a single dichotomous branch. No excystment structure observed.

Dimensions: Vesicle width: 18 (28) 41 µm. (7 specimens measured) Process length: 18-34 µm. Process width: 3-8 µm at base.

Remarks: Though the emended description of Playford (1977) specifies a vesicle that is "originally spherical or nearly so" it allows for polygonal outlines, as seen here. Specimens which resemble those seen here are figured in Pl. 7, fig. 8 of Playford (1977) and Pl. 5, fig. 1 of Lister (1970) (as *Evittia remota*, since synonymised by Playford (1977)).

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Crémenes-Las Salas and Man member localities.

Previous records: Reported from Late Ordovician to late Tournaisian strata and with an almost worldwide distribution, being absent from Australia.

Diexallophasis cf. *remota* (Deunff) emend. Playford, 1977

Plate I, fig. 9

Description: Vesicle originally globular. Wall microgranulate. 8 hollow, tapering processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate, sometimes with a dichotomous branch. Process surface also microgranulate. No excystment structure observed.

Dimensions: Vesicle diameter: 16 (23) 32 µm. (5 specimens measured) Process length: 9-19 µm.

Remarks: The specimens seen here have processes that are too short to meet the "0.8 to 2.0 times vesicle diameter" specified in Playford's emended description, though the same can be said of the specimen figured in Pl. 6, fig. 13 of Playford (1977).

Occurrence: Found at the Playa del Tranqueru, Crémenes-Las Salas and Man member localities.

Genus ***Estiastra*** Eisenack, 1959

Type species: *Estiastra magna* Eisenack, 1959

Estiastra cf. *culcita* Wicander, 1974

Plate I, fig. 11

Description: Vesicle originally polyhedral, octagonal or triangular. Wall bears microgranulate ornament. 6 hollow, broad-based processes arising from vesicle corners and faces, freely communicating with vesicle. Process bases obscure true vesicle shape to some degree and show no ornamental differentiation from the vesicle wall. Processes distally acuminate. No excystment structure observed.

Dimensions: Vesicle width: 15 (21) 24 µm where distinguishable. (2 specimens measured) Process length: 15-23 µm.

Remarks: The species as originally described is somewhat larger than the specimens described here and with even less distinct processes, though the description is compatible with the present specimens. These specimens approach the morphology of *Veryhachium polyaster* Staplin, 1961, however that species has five processes and a psilate wall.

Occurrence: Found at the Playa del Tranqueru, Vozmediano and Crémenes-Las Salas localities.

Previous records: *E. culcita* is reported from the Famennian of the USA (Wicander, 1974, 1975; Wicander & Playford, 2013).

cf. *Estiastra* sp. A

Plate I, fig. 10

Description: Vesicle globular. Wall psilate. Four hollow, broad-based processes arise from vesicle, freely communicating with its interior. Processes in a tetrahedral arrangement. Proximal contacts sharp. Processes distally acuminate. No excystment structure observed.

Dimensions: Vesicle diameter: 13 (17) 24 µm. (2 specimens measured) Process length: 11-15 µm. Process width: 4-6 µm at base.

Remarks: This species is tentatively assigned to *Estiastra* due to its broad-based processes, but the existence of a visible vesicle may refute this assignment.

Occurrence: Found at the Playa del Tranqueru and San Pedro de Nora localities.

Genus ***Exochoderma*** Wicander, 1974

Type species: *Exochoderma irregularis* Wicander, 1974

Remarks: The genus *Exochoderma* has been subject to some confusion in the literature. Distinguishing features used here are detailed under the above remarks for the genus *Diexallophasis*.

Exochoderma arca Wicander & Wood, 1981

Plate I, fig. 18

2001 *Exochoderma* spp.; Gill, p.65, pl. 3, fig. 14

Description: Vesicle polyhedral, originally a square pyramid or octahedral shape. Vesicle wall may be faintly granulate. 5-6 hollow processes arising at vesicle corners, freely communicating with vesicle interior. Processes may taper slightly but are broadly cylindrical. Proximal contacts smooth. Processes may dichotomously branch distally up to the 2^{nd} order, with rounded tips. Process wall granulate. No excystment structure observed.

Dimensions: Vesicle width: 16 (32) 50 µm. (10 specimens measured) Process length: 24-37 µm. Process width: 4-10 µm.

Remarks: No specimens with 4 or 7 processes, as mentioned in the original diagnosis, were found in the present study.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Vozmediano, Aleje and Crémenes-Las Salas localities.

Previous records: Reported from middle Ludlovian to Famennian strata and with an almost worldwide distribution, being absent from Australia.

Exochoderma triangulata Wicander & Wood, 1981

Plate II, fig. 1

Description: Vesicle originally triangular. Vesicle wall may be faintly granulate. 3 hollow processes arising at vesicle corners, freely communicating with vesicle interior. Processes may taper slightly but are broadly cylindrical. Proximal contacts smooth. Processes may dichotomously branch distally up to the 3rd order, with rounded tips. Process wall microgranulate. No excystment structure observed.

Dimensions: Vesicle width: 30 (38) 50 µm. (8 specimens measured) Process length: 22-37 µm. Process width: 4-7 µm.

Remarks: No specimens with 4 processes, as mentioned in the original diagnosis, were found in the present study.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Previous records: Reported from Ludlovian to late Famennian strata and with an almost worldwide distribution, being absent from Asia and Australia.

Genus ***Gorgonisphaeridium*** Staplin et al. emend. Kiryanov, 1978

Type species: *Gorgonisphaeridium winslowiae* Staplin et al., 1965

Gorgonisphaeridium cf. *absitum* Wicander, 1974

Plate I, fig. 12

? 1969a *Acanthotriletes tenuispinosus* Naumova *tenuispinosus* Naumova; Cramer, p. 434

p.2001 *Gorgonisphaeridium sp. A*; Gill, p. 66, pl. 3, fig. 10

Description: Vesicle originally globular. Wall psilate except for numerous short processes, tapering to acuminate tips. Processes appear solid and are distributed quite widely over vesicle surface. No excystment method observed.

Dimensions: Vesicle diameter: 23 (33) 48 µm. (14 specimens measured) Process length: up to 5 µm.

Remarks: The species as originally described has a markedly larger vesicle and proportionately shorter processes than the specimens seen here, though the widely spaced processes are certainly present and serve to distinguish these specimens from other species of *Gorgonisphaeridium* in this study.

Occurrence: Found at the Playa del Tranqueru, Vozmediano, Aleje, ‘120’, ‘599’, Crémenes-Las Salas and Man member localities.

Previous records: *G. absitum* is reported from Early Ordovician to Early Triassic strata and with a worldwide distribution.

Gorgonisphaeridium cumulatum Playford, 1977

Plate I, figs. 13-14

? 1969a *Acanthotriletes espinositus* Cramer; Cramer, p. 434, pl. II, fig. 18

p.2001 *Gorgonisphaeridium sp. A*; Gill, p. 66, pl. 3, fig. 10

Description: Vesicle originally globular. Wall relatively thick, densely ornamented with short processes, ranging from microgranulate to small spinose grade. Excystment by splitting of vesicle wall (see Pl. I fig. 14).

Dimensions: Vesicle diameter: 20 (28) 42 µm. (52 specimens measured) Process length: up to 2 µm.

Remarks: This species is distinguished from other species of *Gorgonisphaeridium* in this study by its short, dense ornament and thick wall. The specimens seen here resemble specimens of *G. inflatum* Wicander & Wood (1981) figured by Wicander & Wood (1981), Wicander & Playford (2017a) and Wicander & Playford (2017b), however that species is larger and has longer processes. Where this form occurs in this study, it is often extremely numerous.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Mirantes de Luna, Geras, Huergas de Gordon, Vozmediano, Aleje, ‘120’, ‘598’, ‘599’, ‘600’, Crémenes-Las Salas and Man member localities.

Previous records: Reported from the late Ludlovian to Emsian of Germany (Walter & Berger, 1998), the Early Devonian (Ghavidel-syooki, 1998) and Early Triassic (Châteauneuf

& Stampfli, 1978) of Iran, the Lochkovian to early Frasnian of Egypt (El Shamma et al., 2012), the Pragian to Givetian of Canada (Playford, 1977; Wicander, 1984), the Middle Devonian of Poland (Turnau, 2011) and the late Eifelian of China (Zhu et al., 2008).

Gorgonisphaeridium disparatum ? Playford, 1977

Plate I, fig. 19

Description: Vesicle originally globular. Wall ornament not observed. 23 processes visible around vesicle margin, tapering to acuminate tips. Process tips usually simple with one incidence of dichotomous branching. No excystment structure observed.

Dimensions: Vesicle diameter: 24 (35) 42 µm. (2 specimens measured) Process length: 3-8 µm.

Remarks: This species is distinguished from other species of *Gorgonisphaeridium* in this study primarily by its long processes with one that branches strongly, a feature not seen on other species of the genus. The species as originally described has a majority of branching processes and is larger than the specimens seen here, despite these being among the largest specimens of *Gorgonisphaeridium* seen here. Poor preservation and a low number of specimens preclude a more confident identification.

Occurrence: Found at the Crémenes-Las Salas locality.

Previous records: *G. disparatum* is reported from the Pragian of China (Gao, 1996), the Pragian to Emsian of Canada (Playford, 1977), the Eifelian of Egypt (El Shamma et al., 2012), the early Givetian of the Czech Republic (Vavrdová & Dašková, 2011), the early Frasnian of Spain (González et al., 2004) and the Frasnian of Germany (Amirie, 1984).

Gorgonisphaeridium evexispinosum Wicander, 1974

Plate I, fig. 15

p.2001 *Gorgonisphaeridium sp. A*; Gill, p. 66, pl. 3, fig. 10

Description: Vesicle originally globular. Wall psilate except for numerous rod-shaped processes with rounded tips that are often slightly bulbous. Small bifurcations may be present occasionally. No excystment structure observed.

Dimensions: Vesicle diameter: 23 (32) 47 µm. (9 specimens measured) Process length: up to 5 µm.

Remarks: This species is distinguished from other species of *Gorgonisphaeridium* in this study by its distinctly rod-shaped processes.

Occurrence: Found at the Playa del Tranqueru, Geras, Huergas de Gordon, '120' and Crémenes-Las Salas localities.

Previous records: Reported from Early Ordovician to early Mississippian strata and with an almost worldwide distribution, being absent from Australia.

Genus ***Micrhystridium*** Deflandre emend. Staplin emend. Lister emend. Sarjeant & Stancliffe, 1994

Type species: *Micrhystridium inconspicuum* (Deflandre) Deflandre, 1937

Micrhystridium cf. *adductum* Wicander, 1974

Plate I, fig. 20

Description: Vesicle originally globular. Wall psilate. 12 long, thin processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle diameter: 8 (13) 15 µm. (3 specimens measured) Process length: 8-17 µm.

Remarks: This species is distinguished from *M. stellatum* in this study by its greater process to vesicle ratio. This is the basis of its uncertain assignment to *M. adductum* though it is smaller than that species as originally described and has more processes.

Occurrence: Found at the Playa del Tranqueru locality.

Previous records: *M. adductum* is reported from the Middle Devonian of northwest Europe (Lefort et al., 1984), the Frasnian of Germany (Amirie, 1984), the middle to late Frasnian of England (Le Gall et al., 1985), the late Frasnian to Famennian of the USA (Wicander, 1974, 1975; Wicander & Loeblich Jr., 1977; Di Pasquo et al., 2012; Wicander & Playford, 2013), the Famennian of Libya (Moreau-Benoit, 1984) and the Tournaisian of Wales (McNestry, 1988).

Micrhystridium cortracumense Stockmans & Willière, 1963

Plate I, fig. 16

Description: Vesicle originally globular. Wall psilate. 12 short, strongly tapering processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate, occasionally with a dichotomous branch. Processes may be solid at their tips. No excystment structure observed.

Dimensions: Vesicle diameter: 16 (24) 35 µm. (2 specimens measured) Process length: 6-10 µm.

Remarks: The specimens seen here strongly resemble Pl. III, fig. 13 of Stockmans & Willière (1963), possibly due to a similar state of preservation. This species is distinguished from other species of *Micrhystridium* in this study by its short, sharp processes and rare branching. It is retained in its original genus by Sarjeant & Vavrdová (1997), which does permit "very brief branches" (Lister, 1970). The species' very wide based processes and the rarity of process branches are arguments against its previous placement in *Multiplicisphaeridium*.

Occurrence: Found at the Playa del Tranqueru and Vozmediano localities.

Previous records: Reported from the Middle Ordovician of Finland (Tynni, 1975), the Llandovery of Belgium (Stockmans & Willière, 1963) and the Ludlovian of Argentina (Rubinstein, 1989a, 1989b).

Micrhystridium stellatum Deflandre, 1945

Plate I, fig. 17

2001 *Micrhystridium stellatum* Deflandre, 1945; Gill, p. 68, pl. 3, fig. 16

Description: Vesicle originally globular. Wall psilate. 8-20 thin, tapering processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth to quite sharp, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle diameter: 7 (13) 22 µm. (26 specimens measured) Process length: 5-14 µm.

Remarks: This species has a lower process to vesicle ratio than *M.* cf. *adductum* (this study), though this distinction is not definite and the latter species may be accommodated in

M. stellatum. The specimens seen here can seem pseudopolygonal due to distortion by the process bases. These processes can be quite broad and conical, as seen in the original figured specimens (Deflandre, 1945).

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Huergas de Gordon, Vozmediano, Aleje, '120', Crémenes-Las Salas and Man member localities.

Previous records: An extremely abundant taxon reported from Cambrian to early Pleistocene strata and with a worldwide distribution.

Micrhystridium cf. *stellatum* Deflandre, 1945

Plate II, fig. 2

Description: Vesicle originally globular. Wall psilate. 7 thin, tapering processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle diameter: 10 (14) 19 µm. (3 specimens measured) Process length: 5-14 µm.

Remarks: This species has fewer processes than specified for *M. stellatum* but meets the specific diagnosis in all other respects.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Micrhystridium sp. A

Plate II, fig. 5

Description: Vesicle originally globular. Wall microgranulate. Around 11 tapering processes arise from the vesicle, freely communicating with vesicle interior. Process surface also microgranulate. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 19 (27) 35 µm. (3 specimens measured) Process length: up to 17 µm.

Remarks: Distinguished from other *Micrhystridium* species in this study by its microgranulate ornament and by its rather large size for the genus. Described species exist with ornament but it does not cover the entire vesicle and processes, as here.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Genus ***Multiplicisphaeridium*** Staplin emend. Staplin et al. emend. Eisenack emend. Lister emend. Turner emend. Sarjeant & Vavrdová, 1997

Type species: *Multiplicisphaeridium ramispinosum* Staplin emend. Sarjeant & Vavrdová, 1997

Multiplicisphaeridium ramispinosum Staplin emend. Sarjeant & Vavrdová, 1997

Plate II, fig. 7

cf. 2001 *Multiplicisphaeridium ramispinosum* Staplin, 1961; Gill, p. 69, pl. 3, fig. 17

Description: Vesicle originally globular. Wall psilate. 6-10 hollow, slightly tapering processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate, usually dichotomously branched up to 5th order. No excystment structure observed.

Dimensions: Vesicle diameter: 12 (17) 23 µm. (13 specimens measured) Process length: 9-20 µm. Process width: 2-4 µm.

Remarks: *M. ramispinosum* as originally described has processes “usually twelve in number” and 9-14 in the emended diagnosis, in contrast to the 6-10 observed here. This species has regularly been confused with “*M. ramusculosum*” (Deflandre) emend. Lister (1970). This species is older, but Lister (1970) retained *M. ramispinosum* as the type species of the genus despite re-assigning “*M. ramusculosum*” in the same publication. The latter species was referred to *Oppilatala* Loeblich Jr. & Wicander, 1976 by Dorning (1981), with no mention of *M. ramispinosum*.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Vozmediano, Aleje, ‘120’, Crémenes-Las Salas and Man member localities.

Previous records: Reported from Late Ordovician to early Tournaisian strata and with a worldwide distribution.

Multiplicisphaeridium cf. *rochesterense* (Cramer & Díez de Cramer) Eisenack et al., 1973

Plate II, fig. 6

Description: Vesicle originally globular. Wall psilate. Very numerous hollow processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate, dichotomously branched up to 5th order. No excystment structure observed.

Dimensions: Vesicle diameter: 16 (20) 31 µm. (5 specimens measured) Process length: 4-10 µm.

Remarks: This species is distinguished from other species of *Multiplicisphaeridium* in this study by its short, extremely numerous multifurcate processes. *M. rochesterense* as originally described does not seem to possess enough processes, but a better assignment could not be found in the literature.

Occurrence: Found at the Crémenes-Las Salas locality.

Previous records: *M. rochesterense* is reported from the Late Ordovician to middle Llandovery of Argentina (Pöthe de Baldis, 1996, 1997; Rubinstein & Vaccari, 2004), the Early Silurian of Wales (Hill & Dorning, 1984; Davies et al., 1997), the Llandovery of the USA (Cramer, 1968, 1969b; Cramer & Díez de Cramer, 1972), the middle Llandovery to middle Přídolí of Libya (Le Hérissé, 2002; Loydell et al., 2013), the Llandovery to Wenlockian of England (Dorning, 1981; Downie, 1984), the late Llandovery of Belgium (Vanguestaine & Wauthoz, 2003), the USSR (Sheshegova, 1984) and Norway (Smelror, 1987), the late Llandovery to Ludlovian of Turkey (Erkmen & Bozdoğan, 1979), the late Llandovery to early Lochkovian of Spain (Cramer, 1969c) and the Wenlockian of Sweden (Le Hérissé, 1989).

Genus ***Navifusa*** Combaz et al. ex Eisenack, 1976

Type species: *Navifusa navis* (Eisenack) Eisenack, 1976

Navifusa bacilla (Deunff) Playford, 1977

Plate II, fig. 9

2001 *Navifusa bacilla* (Deunff) Playford, 1977; Gill, p. 70, pl. 3, fig. 21

Description: Vesicle originally an elongate cylindrical shape with rounded ends. Wall bears a fine microgranulate ornament, occasionally with very fine longitudinal ridges positioned at the vesicle midline. No excystment structure observed.

Dimensions: Vesicle length: 82 (139) 182 µm. (3 specimens measured) Vesicle width: 30-31 µm. (2 specimens measured)

Remarks: Species of *Navifusa* are frequently distinguished based on length:width ratios; no such distinction was considered plausible with this assemblage.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, '598' and Crémenes-Las Salas localities.

Previous records: Reported from Middle Proterozoic to early Viséan strata and with a worldwide distribution.

Genus ***Ozotobrachion*** Loeblich Jr. & Drugg, 1968
Type species: *Ozotobrachion dactylos* Loeblich Jr. & Drugg, 1968

Ozotobrachion cf. *furcillatus* (Deunff) Playford, 1977

Plate II, figs. 3-4

Description: Vesicle originally square or tetrahedral. Wall seemingly thick, psilate. Four thin, tapering processes arise from vesicle at corners. Processes do not communicate with vesicle interior and have a thinner wall, lending the vesicle the appearance of a separate, central body. Proximal contacts smooth, distal tips acuminate, branching dichotomously up to 2nd order. No excystment structure observed.

Dimensions: Vesicle width: 14 (16) 18 µm. (2 specimens measured) Process length: 6-11 µm.

Remarks: *O. furcillatus* as originally described does not seem to have such a marked difference in vesicle and process wall thicknesses as the specimens seen here and tends to have proportionately longer processes. That said, Loeblich Jr. & Wicander (1976) figure some specimens with shorter processes approaching the morphology of those seen here. The processes of these specimens, which branch at a variety of different levels, serve to distinguish them from the digitate processes of *O. palidodigitatus* (Cramer) Playford, 1977 (which may also have somewhat shorter processes), though these species may not be realistically distinguishable (Playford, 1977).

Occurrence: Found at the Vozmediano locality.

Previous records: *O. furcillatus* is reported from Late Ordovician to late Famennian strata and with an almost worldwide distribution, being absent from Asia and Australia.

Genus ***Solisphaeridium*** Staplin et al. emend. Sarjeant, 1968

Type species: *Solisphaeridium stimuliferum* (Deflandre) Pocock, 1972

Solisphaeridium cf. *inaffectum* Playford *in* Playford & Dring, 1981

Plate II, fig. 10

Description: Vesicle originally globular. Wall psilate. 20-29 short, possibly hollow processes arise from vesicle wall. Proximal contacts sharp, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle diameter: 15 (27) 36 µm. (5 specimens measured) Process length: 4-9 µm.

Remarks: The assignment of these specimens is doubtful owing to their sometimes-greater size than the species as originally described. Sarjeant & Stancliffe (1994) reassigned this species to *Micrhystridium*, however the form of the processes and especially their sharp proximal contacts is not characteristic of this genus.

Occurrence: Found at the Playa del Tranqueru, Puerto de Somiedo and Crémenes-Las Salas localities.

Previous records: *S. inaffectum* is reported from the Ordovician of Estonia (Uutela & Tynni, 1991), the Middle Ordovician of China (Yin & Playford, 2003), the Givetian to Frasnian of Australia (Playford & Dring, 1981; Colbath, 1990), the Frasnian to Famennian of England (Selwood et al., 1998) and Iran (Hashemi & Playford, 1998; Ghavidel-syooki &

Owens, 2007; Hashemi & Farhadiani, 2011) and the Middle Carboniferous of China (Gao, 1987).

Genus ***Stellechinatum*** Turner, 1984

Type species: *Stellechinatum celestum* (Martin) Turner, 1984

Stellechinatum spiciferum (Deunff) Sarjeant & Vavrdová, 1997

Plate III, fig. 1

Description: Vesicle originally globular. Wall psilate. 7-9 long, hollow, tapering processes arise from vesicle wall, freely communicating with its interior. Process wall bears microgranulate ornament. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle diameter: 20 (28) 38 µm. (4 specimens measured) Process length: 33-44 µm. Process width: 3-4 µm.

Remarks: *S. spiciferum* as originally described has a minimum of 8 processes. The specimens seen here bear a strong resemblance to *Diexallophasis simplex* Wicander & Wood, 1981 and *D. remota*, however they differ in having a psilate vesicle. The species was previously placed in the genus *Multiplicisphaeridium* by Eisenack et al. (1973), despite its lack of branching processes. The reassignment of the species to *Stellechinatum* by Sarjeant & Vavrdová (1997) is followed here. While the three species originally referred to *Stellechinatum* by Turner (1984) when the genus was erected have a somewhat stellate outline, this is not specified in the genus description, only wide-based processes, therefore this species does not specifically contravene the genus diagnosis. The present specimens and the three forms assigned to the species doubtfully, below, do not show classic wide-based processes like those of *Palacanthus*, but they do resemble the processes of *S. helosum* Turner (1984).

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso and Crémenes-Las Salas localities.

Previous records: Reported from the Middle Devonian of the USA, France, Tunisia and Canada (Deunff, 1955, 1966).

Stellechinatum cf. *spiciferum* (Deunff) Sarjeant & Vavrdová, 1997 (var. A)

Plate III, fig. 2

Description: Vesicle originally octahedral. Wall psilate. Six long, hollow, tapering processes arise from vesicle corners, freely communicating with its interior. Process wall bears microgranulate ornament. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 19 (28) 31 µm. (5 specimens measured) Process length: 31-40 µm. Process width: 3-5 µm.

Remarks: This taxon is distinguished from *S. spiciferum* by its octahedral vesicle and correspondingly low number of processes.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, '120' and Crémenes-Las Salas localities.

Stellechinatum cf. *spiciferum* (Deunff) Sarjeant & Vavrdová, 1997 (var. B)

Plate III, fig. 3

Description: Vesicle a triangular bipyramid shape. Wall psilate. Five hollow, tapering processes arise from vesicle corners, freely communicating with its interior. Process wall bears microgranulate ornament. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 12 (26) 40 µm. (12 specimens measured) Process length: 24-35 µm. Process width: 4-5 µm.

Remarks: This taxon is distinguished from *S. spiciferum* by its triangular bipyramid shaped vesicle and correspondingly low number of processes. Some specimens may have a square pyramid shape but they were too damaged to be certain.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Las Ventas-Entrago, Vozmediano, Aleje and Crémenes-Las Salas localities.

Stellechinatum cf. *spiciferum* (Deunff) Sarjeant & Vavrdová, 1997 (var. C)

Plate II, fig. 11

Description: Vesicle originally globular. Wall psilate. Five hollow, tapering processes arise from vesicle wall, freely communicating with its interior. Process wall bears microgranulate ornament. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle diameter: 16 (17) 20 µm. (2 specimens measured) Process length: 9-15 µm. Process width: up to 2 µm.

Remarks: This taxon is distinguished from *S. spiciferum* in this study by its lower number of processes and overall much smaller size, though it is only slightly below the minimum size described by Deunff (1955).

Occurrence: Found at the Crémenes-Las Salas locality.

Genus ***Tunisphaeridium*** Deunff & Evitt, 1968

Type species: *Tunisphaeridium concentricum* Deunff & Evitt, 1968

Tunisphaeridium caudatum Deunff & Evitt, 1968

Plate II, fig. 8

Description: Vesicle originally globular. Wall psilate. Around 17 long, thin, solid processes arise from vesicle wall. Proximal contact sharp, distal tips usually exhibit multifurcate branching, forming a widened rosette at the very end of the process. Two neighbouring processes are seen which are somewhat longer than those around them. A thin membrane, enclosing the inner vesicle, interconnects the process tips. No excystment structure observed.

Dimensions: Vesicle diameter: 23 (35) 43 µm. Overall width: 52 (64) 79 µm. (2 specimens measured) Process length: 13-27 µm.

Remarks: This species differs from *T. tentaculaferum* in having "a single process or a small group of neighbouring processes being conspicuously longer than most of the rest of the processes" (Deunff & Evitt, 1968). The specimens seen here do not show this idiosyncrasy as prominently as the type material, but it is still discernible.

Occurrence: Found at the Aleje and Crémenes-Las Salas localities.

Previous records: Reported from Early Ordovician to early Frasnian strata and with an almost worldwide distribution, being absent from Australia.

Genus ***Tylotopalla*** Loeblich Jr., 1970

Type species: *Tylotopalla digitifera* Loeblich Jr., 1970

Tylotopalla sp. A

Plate II, figs. 12-13

Description: Vesicle originally globular. Wall bears microgranulate ornament. 3-5 quite thick, tapering processes arise from vesicle wall, freely communicating with its interior. Process wall psilate. Proximal contacts smooth, distal tips exhibit multifurcate branching, forming a rosette of small projections at the tip of each process. No excystment structure observed.

Dimensions: Vesicle diameter: 16 (26) 45 µm. (3 specimens measured) Process length: 10-17 µm. Process width: 2-3 µm.

Remarks: This species meets the generic criteria for *Tylotopalla* but cannot be accommodated within any previously described species. It differs from *Villosacapsula* Loeblich Jr. & Tappan, 1976 in having a globular vesicle and from *Visbysphaera* (Lister) emend. Kiryanov, 1978 in having a single-layered vesicle wall with free communication between the process and vesicle interior. The species resembles *Florisphaeridium toyetae* (Cramer) Cramer & Díez, 1976 except for this species' microgranulate ornament; *F. toyetae* is described only as having wrinkled walls.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Genus ***Veryhachium*** Deunff emend. Downie & Sarjeant emend. Turner, 1984

Type species: *Veryhachium trisulcum* Deunff ex Deunff, 1959

Veryhachium arcarium Wicander & Loeblich Jr., 1977

Plate III, fig. 4

p.2001 *Veryhachium sp. A*; Gill, p. 78, pl. 3, fig. 28

Description: Vesicle originally octahedral. Wall psilate. Six processes arise from the corners of the vesicle in an octahedral layout, freely communicating with vesicle interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 11 (22) 40 μm. (14 specimens measured) Process length: 12-31 μm. Process width: up to 4-12 μm where distinguishable.

Remarks: The original description for this species includes specimens with 7 processes, with "1 to 3" arising from the faces. No such forms were found here. Sarjeant & Stancliffe (1994) proposed reassignment of this species to *Dorsennidium* Wicander emend. Sarjeant & Stancliffe, 1994 based on its possession of processes in multiple planes, however this has not reached wide acceptance.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Aleje, '120', Crémenes-Las Salas and Man member localities.

Previous records: Reported from the late Emsian to middle Frasnian of Poland (Turnau & Racki, 1999; Marynowski et al., 2008; Filipiak, 2011; Turnau, 2011), the Eifelian of Egypt (El Shamma et al., 2012), the Eifelian to late Famennian of the USA (Wicander & Loeblich Jr., 1977; Wicander & Playford, 1985, 2013; Huysken et al., 1992; Wicander & Wood, 1997), the Famennian of China (Lu & Wicander, 1988), the late Famennian of England (Dean, 1992) and the early Tournaisian of Wales (McNestry, 1988).

Veryhachium cf. *arcarium* Wicander & Loeblich Jr., 1977

Plate II, fig. 14

Description: Vesicle originally a square pyramid shape. Wall psilate. Five processes arise from the corners of the vesicle, freely communicating with vesicle interior. Proximal contacts very smooth, almost obscuring the true vesicle shape, tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 17 (20) 26 μm. (2 specimens measured) Process length: up to 17 μm. Process width: up to 10 μm where distinguishable.

Remarks: The taxon is questionably assigned to *V. arcarium* owing to its very wide-based processes which obscure the vesicle, not specifically allowed for in the original diagnosis. The damaged state of both specimens precludes a more confident identification.

Occurrence: Found at the Playa del Tranqueru locality.

Veryhachium downiei Stockmans & Willière, 1962b

Plate II, fig. 15

1988 *Veryhachium downiei* Stockmans & Willière, 1962b; Fombella Blanco, pl. 1, fig. 3

2001 *Veryhachium trispinosum*; Gill, p. 76, pl. 3, fig. 25

Description: Vesicle triangular. Wall psilate. Three hollow, tapering processes arise from vesicle corners, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 11 (19) 28 µm. (8 specimens measured) Process length: 8-29 µm.

Remarks: Previous records of this species show a great deal of morphological variation, detailed elsewhere. Some specimens in this material appear to display a small dichotomous branch at the tip of one process, though whether this is simply damage is uncertain. This species is distinguished from *V. trispinosum* (Eisenack) Stockmans & Willière, 1962b by its more well-defined vesicle, as seen in the figured material of Stockmans & Willière (1962b).

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Aleje, '120', Crémenes-Las Salas and Man member localities.

Previous records: Reported from Early Ordovician to Middle Triassic strata and with a worldwide distribution.

Veryhachium europaeum Stockmans & Willière, 1960

Plate III, fig. 5

2001 *Veryhachium europeaum*; Gill, p. 77, pl. 3, fig. 27

Description: Vesicle originally a tetrahedral shape. Wall psilate. Four processes arise from vesicle corners, freely communicating with vesicle interior. Proximal contacts smooth, tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 14 (20) 28 µm. (6 specimens measured) Process length: 11-40 µm.

Remarks: Sarjeant & Stancliffe (1994) proposed reassignment of this species to *Dorsennidium* Wicander emend. Sarjeant & Stancliffe, 1994 based on its possession of processes in multiple planes, however this has not reached wide acceptance.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Vozmediano, '120', Crémenes-Las Salas and Man member localities.

Previous records: Reported from Early Ordovician to late Eocene strata and with a worldwide distribution.

Veryhachium polyaster Staplin, 1961

Plate III, fig. 6

p.2001 *Veryhachium sp. A*; Gill, p. 78, pl. 3, fig. 28

Description: Vesicle a triangular bipyramid shape. Wall psilate. Five hollow, tapering processes arise from vesicle corners, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 17 (35) 58 µm. (2 specimens measured) Process length: 19-38 µm.

Remarks: Sarjeant & Stancliffe (1994), in their review of the *Veryhachium* complex, transferred *V. polyaster* to *Polygonium* Vavrdová emend. Sarjeant & Stancliffe, 1994 due to it possessing more than 11 processes. This is not the case in the original diagnosis and therefore this reassignment is invalid. By their own definition, Sarjeant & Stancliffe should have transferred the species to *Dorsennidium* due to it possessing processes in more than one plane.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Previous records: Reported from Llandovery to Early Triassic strata and with a worldwide distribution.

Veryhachium polyaster var. *hexaster* Staplin, 1961

Plate IV, fig. 1

Description: Vesicle octahedral. Wall psilate. Six hollow, tapering processes arise from vesicle corners, freely communicating with its interior. Processes merge strongly with vesicle wall proximally, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 12 (21) 35 µm. (2 specimens measured) Process length: 32-40 µm.

Remarks: Wicander (1983) considered this variety synonymous with *V. polyaster*, however Fensome et al. (1990) later considered it valid. Identification here somewhat dubious owing to poor preservation and a low number of specimens.

Occurrence: Found at the Crémenes-Las Salas locality.

Veryhachium polyaster cf. var. *hexaster* Staplin, 1961

Plate IV, fig. 2

Description: Vesicle outline square. Wall psilate. 7 hollow, tapering processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 11 (24) 40 µm. (5 specimens measured) Process length: 10-25 µm.

Remarks: Potentially an aberrant form of *V. p. hexaster* possessing 7 processes.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Veryhachium stelligerum Deunff, 1957

Plate IV, fig. 4

Description: Vesicle pentagonal. Wall psilate. Five hollow, tapering processes arise from vesicle corners, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 26 (30) 37 µm. (2 specimens measured) Process length: 17-23 µm.

Remarks: Sarjeant & Stancliffe (1994) transferred *V. stelligerum* to *Dorsennidium* due to it possessing processes in more than one plane. This is not the case in the original diagnosis and therefore this reassignment is invalid.

Occurrence: Found at the Crémenes-Las Salas locality.

Previous records: Reported from Early Ordovician to late Famennian strata and with an almost worldwide distribution, being absent from Australia.

Veryhachium cf. *trispininflatum* Cramer, 1964c

Plate IV, fig. 5

Description: Vesicle shape unclear, presumed to be triangular. Wall psilate. Three hollow, tapering processes arise from vesicle corners, freely communicating with its interior. The confluence of the process bases form the vesicle outline, obscuring its true shape. Distal tips bluntly rounded. No excystment structure observed.

Dimensions: Vesicle width: 15 (23) 30 µm where distinguishable. (4 specimens measured) Process length: 26-35 µm.

Remarks: *V. trispininflatum* has a similar overall shape to the specimens seen here but its process tips are not as blunt. No other species with sufficiently blunt-tipped processes could be found in the literature.

Occurrence: Found at the Playa del Tranqueru, '599' and Crémenes-Las Salas localities.

Previous records: *V. trispininflatum* is reported from Late Ordovician to late Famennian strata and with an almost worldwide distribution, being absent from North America and Australia.

Veryhachium valiente Cramer, 1964c

Plate IV, fig. 6

2001 *Veryhachium lairdii*; Gill, p. 77, pl. 3, fig. 27

Description: Vesicle square. Wall psilate. Four hollow, tapering processes arise from vesicle corners, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 11 (15) 21 µm. (5 specimens measured) Process length: over 19 µm.

Remarks: *V. valiente* as originally described may have proportionately shorter processes than the specimens seen here, though no measurements are given in the original description. This species is often incorrectly cited as *V. lairdii* Deflandre ex Loeblich Jr., 1970. The two species are considered synonymous (Martin, 1969; Turner, 1984), but *V. valiente* is the senior name as *V. lairdii* was not validly published until 1970 by Loeblich Jr., being a nomen nudum in Deflandre (1946) and Deunff (1954a) and having no holotype designated by Deunff (1959).

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Crémenes-Las Salas and Man member localities.

Previous records: Reported from Early Cambrian to late Coniacian strata and with a worldwide distribution.

Veryhachium valiente ? Cramer, 1964c

Plate IV, fig. 7

Description: Vesicle a square pyramid shape. Wall psilate. Five hollow, tapering processes arise from vesicle corners, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 17 (24) 32 µm. (7 specimens measured) Process length: 17-33 µm.

Remarks: The original description of the species allows for the occasional appearance of a fifth process. Poor preservation and a low number of specimens preclude a more confident identification.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Las Ventas-Entrago, '120', Crémenes-Las Salas and Man member localities.

Genus ***Villosacapsula*** Loeblich Jr. & Tappan, 1976

Type species: *Villosacapsula setosapellicula* (Loeblich Jr.) Loeblich Jr. & Tappan, 1976

Villosacapsula cazurra ? (Cramer) Sarjeant & Vavrdová, 1997

Plate IV, fig. 8

Description: Vesicle originally triangular. Wall bears microgranulate ornament. Three large, tapering processes arise from vesicle corners, freely communicating with its interior. Process wall also microgranulate. Proximal contacts smooth, distal tips finely branched, forming rosette-like structures. No excystment structure observed.

Dimensions: Vesicle width: 34-36 µm. (1 specimen measured) Process length: 16-18 µm. Process width: 6 µm.

Remarks: Cramer (1964c) described a tetrahedral vesicle with four processes, but no other taxa to which this species could be attributed could be found in the literature. The fact that only a single, damaged specimen was found hampered this. This species was previously doubtfully placed in the genus *Multiplicisphaeridium* by Eisenack et al. (1973), despite its polyhedral vesicle. The reassignment of the species to *Villosacapsula* by Sarjeant & Vavrdová (1997), in accordance with the generic diagnosis, is followed here.

Occurrence: Found at the Man member locality.

Previous records: *V. cazurra* is reported from the early Emsian of Germany (Hammann et al., 1989) and the Emsian (Cramer, 1964c, 1966) of Spain.

Villosacapsula globosa Vanguestaine et al., 1983

Plate IV, figs. 9-10

Description: Vesicle originally globular. Wall bears microgranulate ornament. 4-6 thin, hollow processes arise from vesicle wall, freely communicating with its interior. Proximal contacts smooth, distal tips acuminate. Processes arranged in geometric layout e.g. tetrahedral or octahedral. No excystment structure observed.

Dimensions: Vesicle width: 10 (16) 21 µm. (2 specimens measured) Process length: 18-33 µm.

Remarks: Specimens described here meet the specific diagnosis in all particulars. This species is cited as being figured in Pl. 2 fig. 4-5, 7-8 of Vanguestaine et al. (1983), as the authors also state. This is incorrect; the plate descriptions for plates 1 and 2 are reversed in the published volume.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: Reported from the Frasnian to Famennian of Egypt (El Shamma et al., 2012), the late Frasnian to early Famennian of Belgium (Vanguestaine et al., 1983; Martin, 1993) and France (Loboziak et al., 1983) and the late Frasnian to middle Famennian of Libya (Paris et al., 1985; Streel et al., 1988).

Genus ***Visbysphaera*** (Lister) emend. Kiryanov, 1978

Type species: *Visbysphaera dilatispinosa* (Downie) emend. Lister, 1970

Visbysphaera cf. *pirifera* (Eisenack) Kiryanov, 1978

Plate IV, fig. 3

Description: Vesicle originally globular. Wall bears numerous processes with a more or less spatulate shape. These processes widen along their length and end in a rounded tip. They have the appearance of being thin and flat, being of lighter colour than the vesicle. No excystment structure observed.

Dimensions: Vesicle diameter: 26-30 µm. (1 specimen measured) Process length: up to 8 µm.

Remarks: This species as originally described is markedly larger than the specimen seen here, though the ratio of process length to vesicle width is similar. *Visbysphaera* is described as having a two-layered wall; this is not properly observed in this specimen, though the layers are described as being closely adpressed (Lister, 1970), while the much paler processes compared to the vesicle may indicate the presence of an extra wall layer in the vesicle. The processes are not as smoothly rounded in this specimen as in the original figured specimens, but this could be due to damage. Only a single specimen was found.

Occurrence: Found at the Crémenes-Las Salas locality.

Previous records: *V. pirifera* is reported from Early Ordovician to late Ludlovian strata and with an almost worldwide distribution, being absent from Australia.

Division **CHLOROPHYTA** Pascher, 1914

Class **PRASINOPHYCEAE** Christensen, 1962

Genus ***Cymatiosphaera*** Wetzel ex Deflandre, 1954

Type species: *Cymatiosphaera radiata* Wetzel, 1933

Cymatiosphaera cuba Deunff ex Deunff, 1961

Plate IV, figs. 11-12

2001 *Cymatiosphaera carminae* Cramer, 1964c; Gill, p. 58, pl. 3, fig. 4

2001 *Polyedrixium embudum* Cramer, 1964c; Gill, p. 72, pl. 3, fig. 18

Description: Vesicle originally globular. Wall psilate except for narrow flanges crossing the face and projecting at the vesicle boundary. Flanges may appear as concentric squares with diagonal flanges joining their corners. Flange projecting at boundary has a square or rectangular outline and is supported by diagonal flanges at its corners. No excystment structure observed.

Dimensions: Vesicle diameter: 14 (22) 34 µm. (3 specimens measured) Overall width: 21 (30) 45 µm. (3 specimens measured)

Remarks: *C. cuba* is distinguished from other species of *Cymatiosphaera* in this study by its rectangular flange arrangement. The specimen figured in Pl. IV fig. 12 recalls the micro-ornament of *C. winderi* Deunff emend. Playford, 1977 but this specimen is interpreted as damaged, possibly by pyrite.

Occurrence: Found at the Playa del Tranqueru, '120', '598', Crémenes-Las Salas and Man member localities.

Previous records: An often-reported taxon reported from Early Silurian to early Turonian strata from North America, Europe and China.

Cymatiosphaera octoplana ? Downie, 1959

Plate V, fig. 1

2001 *Cymatiosphaera* sp. *B*; Gill, p. 59, pl. 3, fig. 7

Description: Vesicle originally globular. Wall microgranulate and bears narrow flanges crossing the face and projecting at the vesicle boundary. No excystment structure observed.

Dimensions: Vesicle width: 22 (39) 53 µm. (6 specimens measured) Flange height: 7-21 µm.

Remarks: This species is distinguished from other species of *Cymatiosphaera* in this study by its relatively high flanges and microgranulate surface. The species as originally figured seems to have a proportionately lower flange, though no measurement is given. Poor preservation and a low number of specimens preclude a more confident identification.

Occurrence: Found at the Candás-Perán and Vozmediano localities.

Previous records: *C. octoplana* is an often-reported taxon reported from Late Ordovician to Early Devonian strata from North and South America, Europe (including Scandinavia), Turkey, India and China.

Cymatiosphaera pavimenta (Deflandre) Deflandre, 1954

Plate IV, fig. 13

2001 *Cymatiosphaera* sp. A; Gill, p. 58, pl. 3, fig. 6

Description: Vesicle originally globular. Wall psilate except for narrow flanges crossing the face and projecting at the vesicle boundary. Projecting flange circular and supported by 10-12 perpendicular flanges. No excystment structure observed.

Dimensions: Vesicle diameter: 17 (25) 34 µm. (20 specimens measured) Flange height: 3-4 µm.

Remarks: This species is distinguished from other species of *Cymatiosphaera* in this study by its low flanges and distinctly circular projecting flange. The specimens seen here have a larger size range than the species as originally described but are distinguished from *C. nebulosa* (Deunff) Deflandre, 1954 by the more regular appearance of the flange.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Las Ventas-Entrago, Mirantes de Luna, Geras, Huergas de Gordon, Vozmediano, Aleje, Crémenes-Las Salas and Man member localities.

Previous records: Reported from Late Cambrian to Late Devonian strata and with an almost worldwide distribution, being absent from Australia.

Cymatiosphaera cf. *pavimenta* (Deflandre) Deflandre, 1954

Plate IV, fig. 14

Description: Vesicle originally globular. Wall psilate except for narrow flanges crossing the face and extending onto the opposite face. Flanges on face arranged in concentric hexagons with flanges joining their corners and extending past the vesicle margin, presumably onto the opposite face. No excystment structure observed.

Dimensions: Vesicle diameter: 23-32 µm. (1 specimen measured) Flange height: 3 µm.

Remarks: This species lacks a projecting flange at the vesicle boundary, however the height of the existing flanges and the overall size are similar to *C. pavimenta* described above. This species probably simply represents a damaged *C. pavimenta*.

Occurrence: Found at the San Pedro de Nora locality.

Cymatiosphaera cf. *perimembrana* Staplin, 1961

Plate V, fig. 2

Description: Vesicle originally globular. Wall psilate except for narrow flanges crossing the face and projecting at the vesicle boundary. Projecting flange large, roughly circular and supported by around 10 perpendicular flanges. No excystment structure observed.

Dimensions: Vesicle diameter: 18-22 µm. Overall width: 32-36 µm. (1 specimen measured) Flange height: 5-8 µm.

Remarks: The species as originally described has slightly different flange to vesicle proportions but the same irregular appearance. This species is distinguished from other species of *Cymatiosphaera* in this study by its proportionately tall flanges in relation to vesicle size. Only a single specimen was found in this study.

Occurrence: Found at the Playa del Tranqueru locality.

Previous records: *C. perimembrana* is reported from Llandovery to late Mississippian strata and with a worldwide distribution.

Cymatiosphaera cf. *vespertilio* Deunff, 1976 (var. A)

Plate V, fig. 3

Description: Vesicle originally globular. Wall psilate except for narrow flanges crossing the face and projecting prominently at the vesicle boundary. The projecting flange curves inward, towards the vesicle, very prominently between the 5-7 points where flanges meet. No excystment structure observed.

Dimensions: Vesicle diameter: 9 (18) 24 µm. (11 specimens measured) Flange height: up to 9-18 µm.

Remarks: This species is distinguished from other species of *Cymatiosphaera* in this study by its convex projecting flange and proportionately high flange where flanges meet. The psilate vesicle wall serves to distinguish these specimens from *C. canadensis* Deunff, 1961 and *C. cornifera* Deunff, 1955. Comparison with *Crameria* is possible but the specimens seen here show flanges across the vesicle face, rather than distinct processes. The species as originally described is markedly smaller than the specimens described here, hence the doubtful identification, though the proportions are similar.

Occurrence: Found at the Playa del Tranqueru, Vozmediano, Aleje and Crémenes-Las Salas localities.

Previous records: *C. vespertilio* is reported from the late Ludlovian to early Lochkovian of Peru (Vavrdová et al., 2011), the Lochkovian of Bulgaria (Lakova, 1999) and the Lochkovian to early Frasnian of France (Deunff, 1976, 1980, 1981).

Cymatiosphaera cf. *vespertilio* Deunff, 1976 (var. B)

Plate V, fig. 4

Description: Vesicle originally globular. Wall psilate except for narrow flanges crossing the face and projecting prominently at the vesicle boundary. The projecting flange has a distinct polygonal shape approaching a distorted pentagon. The supporting perpendicular flanges appear to meet in the middle of the vesicle, reminiscent of the spokes of a wheel. No excystment structure observed.

Dimensions: Vesicle diameter: 12 (13) 14 µm. Overall width: 31 (34) 37 µm. (2 specimens measured) Flange height: up to 18 µm.

Remarks: This species is distinguished from other species of *Cymatiosphaera* in this study by its distinctly polygonal projecting flange, which also serves to distinguish it from *C.* cf. *vespertilio* (var. A). These specimens also have a psilate vesicle surface, the ramifications of which are discussed under the remarks for *C.* cf. *vespertilio* (var. A). *C. vespertilio* has somewhat lower flanges relative to vesicle size and is not specifically pentagonal, but it was the only *Cymatiosphaera* species that could be found that possessed the correct combination of overall size, roughly correct proportions and polygonal shape.

Occurrence: Found at the Playa del Tranqueru locality.

Genus ***Dictyotidium*** Eisenack emend. Staplin, 1961

Type species: *Dictyotidium dictyotum* (Eisenack) Eisenack, 1955a

Dictyotidium variatum Playford, 1977

Plate V, fig. 5

Description: Vesicle originally globular. Surface psilate except for a dense reticulate ornament around 1 µm high and wide enclosing small, rounded to polygonal lacunae 1-2 µm across. No excystment structure observed.

Dimensions: Vesicle diameter: 42-44 µm. (1 specimen measured)

Remarks: This species' dense ornament and small lacunae are believed to be responsible for a diaphanous flange-like structure visible around the vesicle boundary. Only a single specimen was found in this study.

Occurrence: Found at the Candás-Perán locality.

Previous records: Reported from Llandovery to early Pennsylvanian strata and with an almost worldwide distribution, being absent from Australia.

Genus ***Duvernaysphaera*** Staplin emend. Deunff, 1964a

Type species: *Duvernaysphaera tenuicingulata* Staplin, 1961

Duvernaysphaera angelae Deunff, 1964a

Plate V, figs. 7-8

2001 *Duvernaysphaera angelae* Deunff, 1964a; Gill, p. 64, pl. 3, fig. 13

Description: Vesicle originally a square shape with straight to somewhat concave sides. Wall psilate. Each corner supports 1-2 small, thin processes. Processes support a very thin, rounded flange. Faint diagonal structures sometimes seen joining the corners of the vesicle. No excystment structure observed.

Dimensions: Vesicle width: 18 (23) 30 µm. (3 specimens measured) Flange width: 4-9 µm.

Remarks: Vesicle shape sometimes appears pen-, hex- or heptagonal (see Pl. V, fig. 8), though this is attributed to taphonomic distortion.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Previous records: Reported from Emsian to early Pennsylvanian strata and with an almost worldwide distribution, being absent from Asia and Australia.

Duvernaysphaera cf. *angelae* Deunff, 1964a

Plate V, fig. 9

Description: Vesicle originally polygonal, subrectangular with straight sides. Wall psilate. Each corner supports 1-2 small, thin processes. Processes support a very thin, rounded flange which may extend past the tips of the processes. No excystment structure observed.

Dimensions: Vesicle width: 23 (34) 50 µm. (2 specimens measured) Process length: 3-5 µm. Flange width: 8-13 µm.

Remarks: This taxon is tentatively assigned to *D. angelae* on the basis of its polygonal vesicle, which precludes assignment to *Pterospermella* Eisenack, 1972. The lack of a definitely square vesicle and its flange extending past the processes make this assignment doubtful. The 'granules' visible on the figured specimen are believed to be a degradation product.

Occurrence: Found at the Playa del Tranqueru locality.

Duvernaysphaera tenuicingulata ? Staplin, 1961

Plate V, fig. 6

Description: Vesicle originally globular. Wall psilate. Around 8 narrow, very short processes spaced evenly around vesicle margin. Possible signs of a thin flange around some processes. No excystment structure observed.

Dimensions: Vesicle diameter: 22 (26) 30 µm. (4 specimens measured)

Remarks: Poor preservation precludes a more confident identification in this study. The species is very similar to, and may be a senior synonym of, *D. kräuseli* (Stockmans & Willière) Stockmans & Willière, 1962b, distinguished only by a slightly larger flange, though this isn't seen in the holotype of *D. tenuicingulata*.

Occurrence: Found at the Aleje and Crémenes-Las Salas localities.

Previous records: *D. tenuicingulata* is reported from Emsian to late Famennian strata and with an almost worldwide distribution, being absent from Asia.

Genus ***Palacanthus*** Wicander emend. Sarjeant & Stancliffe, 1994
Type species: *Palacanthus acutus* Wicander, 1974

Palacanthus cf. *ledanoisii* (Deunff) emend. Playford, 1977

Plate V, figs. 10; 13-14

Description: Vesicle originally stellate. Wall psilate or bears fine microgranulate ornament. 4-5 very wide-based, tapering processes arise from vesicle wall in one plane, freely communicating with its interior. The confluence of the process bases form the vesicle outline, obscuring its true shape. Process wall psilate or bears very fine microgranulate ornament. Distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 11 (16) 22 µm where distinguishable. (4 specimens measured) Process length: 10-12 µm where distinguishable. Process width: 6-7 µm.

Remarks: The range of morphologies seen in these specimens is within the specific description, though the specimens seen here are often smaller than the species as originally described. None of the specimens found here exhibit the elongate processes figured by Playford (1977), rendering their identification doubtful. This could be due to damage but none of the specimens studied show signs of such damage. The species was distinguished from *P. signum* (Deunff) Wicander, 1974 by Playford (1977) on the basis of size and process shape, see remarks under that species for further comment.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Vozmediano, Aleje, Crémenes-Las Salas and Man member localities.

Previous records: *P. ledanoisii* is reported from Early Ordovician to Tournaisian strata and with a worldwide distribution.

Palacanthus signum (Deunff) Wicander, 1974

Plate V, fig. 12

Description: Vesicle originally stellate. Wall psilate. 7 very wide-based, tapering processes arise from vesicle wall in one plane, freely communicating with its interior. The confluence of the process bases form the vesicle outline, obscuring its true shape, with fine ridges seen between process bases meeting in the vesicle centre. Distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width: 13-14 µm where distinguishable. (1 specimen measured) Process length: 8-11 µm. Process width: 5-7 µm.

Remarks: The reassignment by Wicander (1974) of this species from the genus *Veryhachium* Deunff emend. Downie & Sarjeant emend. Turner, 1984 is followed here, despite Fensome et al. (1990) not recognising the reassignment. Playford (1977) distinguished *P. ledanoisii* from *P. signum* by the latter's shorter processes and smaller overall size, but as the *P.* cf. *ledanoisii* specimens seen here lack the elongate process tips and are markedly smaller than originally described, the two species are rendered very similar. The diagnosis of *P. signum* is limited to seven processes; that of *P. ledanoisii* includes 3-8 processes. There is probably considerable crossover between these two species, requiring them to be re-assessed, in which case *P. signum* has priority. Only a single specimen of this species was found.

Occurrence: Found at the Playa del Tranqueru locality.

Previous records: Reported from the Middle Devonian (Deunff, 1964b) and early Frasnian (Deunff, 1981) of France.

Palacanthus tripus Martin, 1984

Plate V, fig. 17

Description: Vesicle originally triangular. Wall psilate. Three wide-based, tapering processes arise from vesicle corners in one plane, freely communicating with its interior. The confluence of the process bases form the vesicle outline, obscuring its true shape. Process wall bears very fine microgranulate ornament. Distal tips acuminate. No excystment structure observed.

Dimensions: Vesicle width 11 (21) 39 µm. (8 specimens measured) Process length: up to 37 µm.

Remarks: *P. tripus* as originally described exhibits spinose ornament across its whole surface; here it could only be clearly observed on the processes.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, Vozmediano, Aleje and Crémenes-Las Salas localities.

Previous records: Reported from the early Famennian of Belgium (Martin, 1984) and the Famennian of Portugal (Cunha & Oliveira, 1989; Pereira et al., 2008; Pereira & Matos, 2012).

Genus ***Polyedryxium*** Deunff emend. Deunff, 1971

Type species: *Polyedryxium deflandrei* Deunff ex Deunff, 1961

Polyedryxium cf. *accuratum* Deunff, 1971

Plate V, fig. 16

cf. 2001 *Polyedrixium asperum* Cramer, 1964c; Gill, p. 71, pl. 3, fig. 22

Description: Vesicle polygonal, with a straight-sided square outline formed of multiple polygonal facets bordered by low ridges. Wall psilate. Around 11 prominent processes at ridge junctions and at points along the ridges, processes have branched tips. No excystment structure observed.

Dimensions: Vesicle width: 29 (32) 34 µm. (2 specimens measured)

Remarks: The pyramidal or prism shape of this taxon could not be determined in these specimens.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Previous records: *P. accuratum* is reported from the Middle Devonian of Canada (Deunff, 1966, 1971; Wicander, 1983), the USA, France and Tunisia (Deunff, 1966).

Polyedryxium cf. *decorum* Deunff, 1955

Plate V, fig. 18

Description: Vesicle polygonal, with a roughly hexagonal outline formed of multiple polygonal facets bordered by low ridges. Vesicle sides straight to slightly concave. Wall psilate. Ridge junctions bear a small extended process, processes have branched tips. Ridges sometimes topped by a thin crenelated flange. No excystment structure observed.

Dimensions: Vesicle width: 25 (31) 39 µm where clearly distinguishable. (2 specimens measured) Overall width: 34 (45) 61 µm. (4 specimens measured)

Remarks: The pentagonal shape of this taxon could not be determined in these specimens.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: *P. decorum* is reported from Late Silurian to late Famennian strata and with an almost worldwide distribution, being absent from Australia.

Polyedryxium deflandrei Deunff ex Deunff, 1961

Plate V, fig. 15

Description: Vesicle polygonal, with a rectangular outline formed of multiple polygonal facets bordered by low ridges. Vesicle sides slightly concave. Wall bears microgranulate ornament. Around 7 prominent processes at ridge junctions and at points along the ridges, processes have dichotomously branched or multi-branched digitate tips. Ridges topped by a thin flange. No excystment structure observed.

Dimensions: Vesicle width: 27 (50) 63 µm. (5 specimens measured)

Remarks: These specimens appear rather more rectangular than the original diagnosis but the wall ornament and branch process structures are diagnostic.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Previous records: Reported from the early Ludlovian to Přídolí of Argentina (Rubinstein, 1990, 1993a, 1995), the late Eifelian to Givetian of Canada (Deunff, 1954a, 1966; Schopf, 1969; Nautiyal, 1975; Playford, 1977) and the late Givetian of the USA (Wicander, 1984).

Polyedryxium cf. *fragosulum* Playford, 1977

Plate V, fig. 19

Description: Vesicle originally a rounded tetrahedral shape. Wall psilate. Six wide, thin flanges cross vesicle wall. Flanges are extended at their junctions into long, process-like structures, positioned at the corners of the tetrahedral vesicle. No excystment structure observed.

Dimensions: Vesicle width: 20 (27) 34 µm. (5 specimens measured) “Process” length: 17-24 µm.

Remarks: These specimens lack the granulate to finely verrucate wall sculpture originally described for the species. This species’ rounded vesicle risks confusion with *Cymatiosphaera*, indeed Wicander & Wood (1981) listed *C. triangularis* Pöthe de Baldis, 1974 as a possible junior synonym of *P. fragulosum* (though in this case *C. triangularis* would be the senior name).

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Vozmediano, Crémenes-Las Salas and Man member localities.

Previous records: *P. fragulosum* is reported from Late Silurian to late Famennian strata and with an almost worldwide distribution, being absent from Asia and Australia.

Polyedryxium mirum Deunff, 1957

Plate V, fig. 11

Description: Vesicle polygonal, formed of multiple polygonal facets bordered by low ridges. Vesicle sides mostly straight. Wall psilate. Around 9 prominent processes at ridge junctions, processes are short and end in bluntly rounded tips. Ridges topped by a thin flange. No excystment structure observed.

Dimensions: Vesicle width: 31 (42) 54 µm. (4 specimens measured) Flange width: 3 µm.

Remarks: This species strongly resembles the figured drawing of *P. mirum*, though the written description describes at least some concave faces.

Occurrence: Found at the Playa del Tranqueru, Geras and Crémenes-Las Salas localities.

Previous records: Reported from the Early Devonian of China (Gao, 1978), the Middle Devonian of France, Tunisia (Deunff, 1966) and Canada (Deunff, 1957, 1966, 1971), the Eifelian to Givetian of the USA (Deunff, 1966), the Frasnian of Germany (Amirie, 1984) and the Famennian of Paraguay (Pöthe de Baldis, 1979).

Polyedryxium pharaone Deunff ex Deunff, 1961

Plate VI, fig. 1

2001 *Polyedrixium pharaone* (Deunff, 1954b) Deunff, 1971; Gill, p. 72, pl. 3, fig. 23

Description: Vesicle originally a rounded cubic shape. Wall psilate. 12 wide, thin flanges arise from vesicle edges. Flanges are extended at their junctions into long, process-like structures, positioned at the corners of the cubic vesicle. No excystment structure observed.

Dimensions: Vesicle width: 13 (16) 20 µm. (2 specimens measured) “Process” length: 18-27 µm.

Remarks: The specimens found here strongly resemble cubic versions of *P. fragulosum*, raising similar questions over confusion with *Cymatiosphaera*. The original description is of a sharp-edged cubic vesicle, though a rounded vesicle has been depicted elsewhere (Wicander & Wood, 1981).

Occurrence: Found at the Playa del Tranqueru, ‘120’, Crémenes-Las Salas and Man member localities.

Previous records: Reported from early Llandovery to early Tournaisian strata and with a worldwide distribution.

Polyedryxium primarium ? Deunff, 1980

Plate V, fig. 20

Description: Vesicle polygonal, with a rounded outline formed of multiple polygonal facets bordered by low ridges. Vesicle sides mostly straight. Wall psilate. Ridge junctions bear a small, extended process, processes have branched tips. Ridges topped by a thin flange. No excystment structure observed.

Dimensions: Vesicle width: 30 (46) 65 µm. (5 specimens measured) Flange width: 3-8 µm.

Remarks: This assignment is based in part on the rounded shape of the figured type specimen of *P. primarium*, though the image does not show the complete vesicle. The membrane is described as crenelated, though this is not evident in the figure.

Occurrence: Found at the Crémenes-Las Salas locality.

Previous records: *P. primarium* is reported from the early to middle Lochkovian of France (Deunff, 1980; Steemans, 1989).

Polyedryxium robustum Deunff, 1971

Plate VI, fig. 2

Description: Vesicle polygonal, with a roughly hexagonal outline formed of multiple polygonal facets bordered by low ridges. Vesicle sides straight to slightly concave. Wall bears microgranulate ornament. Around 9 prominent processes at ridge junctions, processes are short and end in bluntly rounded tips. No excystment structure observed.

Dimensions: Vesicle width: 33 (42) 56 µm. (6 specimens measured)

Remarks: *P. robustum* as originally described is markedly larger than the specimens described here.

Occurrence: Found at the Playa del Tranqueru, '120' and Crémenes-Las Salas localities.

Previous records: Reported from the Ludlovian to Pragian of India (Prasad & Asher, 2001), the Middle Devonian of Tunisia (Deunff, 1966), the Early to Middle Devonian of Canada (Deunff, 1966, 1971), the Eifelian to Givetian of the USA (Deunff, 1966) and the late Givetian to early Frasnian of France (Deunff, 1966, 1981).

Polyedryxium "*talum*" Deunff, 1971

Plate VI, fig. 3

Description: Vesicle polygonal, with a roughly square outline formed of multiple polygonal facets bordered by low ridges. Vesicle sides straight to slightly concave. Wall psilate. Around 10 prominent processes at ridge junctions and at points along ridges, processes are short and end in bluntly rounded tips. No excystment structure observed.

Dimensions: Vesicle width: 28 (41) 69 µm. (5 specimens measured)

Remarks: *P.* "*talum*" as originally described has a crenelated edge, interpreted as corresponding to the numerous unbranched projections of the specimens described here. *P.* "*talum*" is an invalid name as a holotype has never been validly published, being originally described in a thesis and never re-figured. See Fensome et al. (1990) for a full discussion.

Occurrence: Found at the Playa del Tranqueru, '120' and Crémenes-Las Salas localities.

Previous records: Reported from Pragian to Famennian strata and with an almost worldwide distribution, being absent from Asian and Australia.

Polyedryxium sp. A

Plate VI, fig. 5

Description: Vesicle polygonal, with a roughly hex- or heptagonal outline formed of multiple polygonal facets bordered by low ridges. Vesicle sides concave. Wall psilate. Around 9 prominent processes at ridge junctions, processes have branched tips. Ridges topped by a thin flange. No excystment structure observed.

Dimensions: Vesicle width: 28 (38) 57 µm. (5 specimens measured) Flange width: 2-5 µm.

Remarks: This species is most similar to *P. decorum* but lacks the latter's crenelated flanges.

Occurrence: Found at the Crémenes-Las Salas locality.

Polyedryxium sp. B

Plate VI, fig. 6

Description: Vesicle polygonal, with a roughly hexagonal outline formed of multiple polygonal facets bordered by low ridges. Vesicle sides straight to slightly concave. Wall bears microgranulate ornament. Around 7 prominent processes at ridge junctions, processes are short and end in bluntly rounded tips. Ridges topped by a thin flange. No excystment structure observed.

Dimensions: Vesicle width: 36 (45) 62 µm. (5 specimens measured)

Remarks: This species resembles *P. mirum* but possesses a microgranulate ornament. This species differs from *P. robustum* in possessing a flange on the ridges.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Vozmediano, '120' and Crémenes-Las Salas localities.

Polyedryxium sp. C

Plate VI, fig. 4

Description: Vesicle polygonal, with an irregular outline formed of multiple polygonal facets bordered by low ridges. Vesicle sides slightly concave. Wall bears microgranulate ornament. Around 8 prominent processes at ridge junctions and at points along ridges, processes have branched tips. No excystment structure observed.

Dimensions: Vesicle width: 25 (36) 51 µm. (3 specimens measured)

Remarks: This species resembles *P.* cf. *accuratum* in this study but possesses a microgranulate ornament. Specimens of this species are poorly preserved; the figured specimen is incomplete, representing isolated facets of a once full specimen, the nature of which is determined by this and other specimens.

Occurrence: Found at the Playa del Tranqueru, '120' and Crémenes-Las Salas localities.

Polyedryxium sp. D

Plate VI, fig. 9

Description: Vesicle originally globular to somewhat polygonal. Wall microgranulate. Surface divided into large polygonal lacunae by low ridges around 1 µm high and wide. Lacunae often pentagonal or hexagonal. Some ridge junctions possess a small granule or tubercle. No excystment structure observed.

Dimensions: Vesicle diameter: 38-46 µm. (1 specimen measured)

Remarks: This single specimen is poorly preserved, with a vaguely polygonal shape the best feature to assign it to *Polyedryxium*. Small processes are visible at ridge junctions, but their more precise nature cannot be determined. The specimen resembles *Dictyotidium granulatum* Playford *in* Playford & Dring, 1981 but has a somewhat polygonal shape.

Occurrence: Found at the Crémenes-Las Salas locality.

Genus ***Pterospermella*** Eisenack, 1972

Type species: *Pterospermella aureolata* (Cookson & Eisenack) Eisenack, 1972

Pterospermella bernardinae (Cramer) Eisenack et al., 1973

Plate VI, fig. 10

Description: Vesicle originally globular. Wall psilate. Thin rounded flange seen around vesicle margin bearing very thin ridges or folds, extending up to the vesicle radius. No excystment structure observed.

Dimensions: Vesicle diameter: 20 (25) 30 µm. Overall width: 34 (47) 60 µm. (2 specimens measured)

Remarks: The size of the specimens seen here ranges somewhat higher than the size as originally described.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: Reported from the Middle Ordovician of Czechoslovakia (Vavrdová, 1986), the late Llandovery to early Wenlockian of Lithuania (Jankauskas & Gritytė, 2004), the Ludlovian to middle Přídolí (Rubinstein, 1989b, 1990, 1993a, 1993b, 1995) of Argentina, the Ludlovian of France (Deunff et al., 1971) and England (Dorning, 1981), the Wenlockian (Iordan et al., 1984) and Early Devonian (Beju, 1967) of Romania and the Emsian of Spain (Cramer, 1964c).

Pterospermella cf. *hermosita* (Cramer) Fensome et al., 1990

Plate VI, figs. 7-8

Description: Vesicle originally globular. Wall bears microgranulate ornament. Thin, rounded, unsupported flange seen around the vesicle margin. No excystment structure observed.

Dimensions: Vesicle diameter: 18 (23) 27 µm. Overall diameter: 34 (37) 39 µm. (2 specimens measured) Flange width: 2-10 µm.

Remarks: The specimens here seem to subdivide into two variants based on flange size; some have a flange extending up to ½ of the vesicle radius (see Pl. VI, fig. 7), others are well over ½ the vesicle radius (see Pl. VI, fig. 8). The original description of *P. hermosita* does not specify a flange:vesicle ratio or supply measurements for the flange width, while also depicting the flange with a smoother margin than the specimens seen here. The large-flanged variant resembles *P. verrucaboia* Loeblich Jr. & Wicander, 1976 but differs in having a microgranulate vesicle.

Occurrence: Found at the Playa del Tranqueru, Vozmediano, Aleje and Man member localities.

Previous records: *P. hermosita* is reported from Early Ordovician to Late Devonian strata and with a worldwide distribution.

Pterospermella rajada (Cramer) Eisenack et al., 1973

Plate VI, fig. 11

cf. 2001 *Pterospermella sp. A*; Gill, p. 74, pl. 3, fig. 20

Description: Vesicle originally globular. Wall bears a very fine microgranulate ornament. Thin, unsupported flange seen around vesicle margin. Flange has an irregularly scalloped edge, with numerous points connected by concave areas. No excystment structure observed.

Dimensions: Vesicle diameter: 13 µm. Overall diameter: 30-31 µm. (1 specimen measured)

Remarks: The low verrucae "with a small central depression" mentioned in the original description for *P. rajada* could not be observed in these specimens. Only a single specimen was found.

Occurrence: Found at the Crémenes-Las Salas locality.

Previous records: Reported from the Emsian of Spain (Cramer, 1964c) and the Frasnian of Belgium (Dricot, 1968).

Genus ***Stellinium*** Jardiné et al., 1972

Type species: *Stellinium micropolygonale* (Stockmans & Willière) Playford, 1977

Remarks: This genus has been subject to some confusion with *Veryhachium* and other genera. Here structures often described as central nerves in the processes are taken as diagnostic. These are interpreted here as extremely wide bases of other processes, positioned parallel to one another.

Stellinium comptum Wicander & Loeblich Jr., 1977

Plate VI, fig. 13

Description: Vesicle originally a square pyramid or octahedral shape, appears quadrate, rarely rendered pentagonal by processes. Wall bears fine microgranulate ornament. Usually six, rarely five, very wide based processes arising from vesicle corners, freely communicating with its interior. Distal tips acuminate. The confluence of the process bases mostly form the vesicle outline, partially obscuring its true shape. The bases of the one or two processes in a different plane from the other four become narrow away from the process axis, forming parallel ridges or 'nerves' extending over the other processes. No excystment structure observed.

Dimensions: Vesicle width: 15 (20) 25 µm where distinguishable. (13 specimens measured) Process length: 18-30 µm.

Remarks: *S. comptum* as originally described is markedly larger than the specimens described here.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Las Ventas-Entrago, Vozmediano, '120', Crémenes-Las Salas and Man member localities.

Previous records: Reported from early Givetian to early Tournaisian strata and with an almost worldwide distribution, being absent from Africa and Australia.

Stellinium cf. *comptum* Wicander & Loeblich Jr., 1977

Plate VI, fig. 14

Description: Vesicle originally a triangular bipyramid shape. Wall bears fine microgranulate ornament. Five very wide based processes arising from vesicle corners, freely communicating with its interior. Distal tips acuminate. The confluence of the process bases form the vesicle outline, obscuring its true shape. The bases of the two processes in a different plane from the other three become narrow away from the process axis, forming parallel ridges or 'nerves' extending over the other processes. No excystment structure observed.

Dimensions: Overall width: 26 (42) 55 µm. (2 specimens measured)

Remarks: *S. comptum* as originally described has a quadrate outline and usually six processes.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Stellinium micropolygonale (Stockmans & Willière) Playford, 1977

Plate VI, fig. 16

Description: Vesicle polygonal, usually quadrate or pentagonal. Wall psilate or with a very fine microgranulate ornament. 7 (possibly 8) very wide based processes arising from vesicle wall, freely communicating with its interior. Distal tips acuminate. The confluence of the process bases mostly form the vesicle outline, partially obscuring its true shape. The bases of the processes in a different plane from the others become narrow away from the process axis, forming parallel ridges or 'nerves' extending over the other processes. No excystment structure observed.

Dimensions: Vesicle width: 15 (19) 23 µm. (2 specimens measured) Process length: 13-20 µm.

Remarks: This species is distinguished from *S. comptum* in this study by its greater number of processes and correspondingly more irregular shape. Specimens with 7 processes are interpreted as being damaged; a low number of specimens precludes a more detailed analysis. Wicander & Playford (2013) considered this species senior to *S. octoaster*, the original type species of the genus. Eisenack et al. (1979) considered this species to belong to *Veryhachium*.

Occurrence: Found at the Playa del Tranqueru, Las Ventas-Entrago and Crémenes-Las Salas localities.

Previous records: Reported from early Tremadocian to early Pennsylvanian strata and with a worldwide distribution.

Stellinium ?*tetrahedroide* (Cramer) Eisenack et al., 1976

Plate VI, fig. 12

Description: Vesicle square. Wall psilate. Four processes arising from vesicle corners, proximal contact smooth, distal tips acuminate. Processes joined by low flanges crossing face in an X-shape; processes may be extensions of these flanges. No excystment structure observed.

Dimensions: Vesicle width: 13 (16) 22 µm. (5 specimens measured) Process length: 7-12 µm.

Remarks: This species was questionably assigned to *Stellinium* by Eisenack et al. (1976). Specimens found here most closely resemble the specimen figured in Pl. XV: 7 of Cramer (1964c).

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: Reported from Early Ordovician to Late Devonian strata and with an almost worldwide distribution, being absent from North America and Australia.

Stellinium sp. A

Plate VI, fig. 15

Description: Vesicle originally a square pyramid shape. Wall psilate. Five very wide based processes arising from vesicle corners, freely communicating with its interior. Distal tips acuminate, simple or exhibiting dichotomous or trichotomous branching up to 2nd order. The confluence of the process bases mostly form the vesicle outline, partially obscuring its true shape. The bases of the process in a different plane from the other four becomes narrow away from the process axis, forming parallel ridges or 'nerves' extending over the other processes. No excystment structure observed.

Dimensions: Vesicle width: 15-17 µm. (1 specimen measured) Process length: 7 µm. Process width: 2-3 µm.

Remarks: This species is distinguished from other species of *Stellinium* in the literature by its branched processes. Only a single specimen was found.

Occurrence: Found at the Crémenes-Las Salas locality.

Stellinium sp. B

Plate VI, fig. 17

Description: Vesicle appears globular. Wall psilate. 8 very wide based processes arising from vesicle corners, freely communicating with its interior. Distal tips acuminate, simple or exhibiting dichotomous or digitate branching up to 3rd order. The confluence of the process bases form the vesicle outline, obscuring its presumably polygonal shape. The bases of the processes become narrow away from the process axis, forming parallel ridges or 'nerves' extending over the other processes. No excystment structure observed.

Dimensions: Vesicle width: 18 (25) 35 µm. (2 specimens measured) Process length: 14-16 µm. Process width: 4-6 µm.

Remarks: This species is distinguished from other species of *Stellinium* in the literature by its branched processes and from *S.* sp. A in this study by its greater number of processes and more pronounced branching.

Occurrence: Found at the Crémenes-Las Salas locality.

6.2 - Chitinozoan taxonomy

The chitinozoans described below are arranged alphabetically by genera and treated as genera and species in accordance with the ICZN (ICZN, 1999), though the true origin of chitinozoans is not certain. The reader is referred to Paris et al. (1999) for supra-generic classification. Full citations have proven difficult to obtain; many species have since been reassigned to new genera, however the author responsible for the reassignment is not always cited in the existing literature on the species. Where this is the case only the original citation is given, placed in parentheses, in accordance with the previous literature. Previous records of chitinozoans from the Naranco and Huergas formations are limited to Cramer (1969) who figured 3 specimens of *Ancyrochitina* sp., and Gill (2001) who named genera but made no attempt to identify species and whose figured specimens are mere single representatives of the genus. These figured specimens are here placed with species found in the present study. Dimensions are given for each species and follow the scheme of Paris (1981) where L=total length; Dp=chamber diameter; Lp=chamber length; Dc=neck diameter; Ln=neck length. Dimensions are given in micrometres (µm), no correction factors allowing for compression are used and where three numbers are given for a dimension these correspond to the minimum value (arithmetic mean) and maximum values. The number of specimens measured is given, though occasionally not all measurements could be obtained from all specimens owing to damage. In this case, the number measured corresponds to the highest number of measurements for any one dimension (e.g. up to 2 specimens, where some dimensions will have two measurements, others one owing to loss of features in those specimens). The sites in which each species occurs in this study are given. Previous records are noted following consultation of the John Williams Index of Palaeopalynology.

Genus ***Alpenachitina*** Dunn & Miller, 1964

Type species: *Alpenachitina eisenacki* Dunn & Miller, 1964

Alpenachitina eisenacki Dunn & Miller, 1964

Plate VII, fig. 1

Description: Chamber ovoid to cylindrical with a flat to slightly convex base. The neck occupies ~20% of the total length. The flexure is conspicuous and the aperture flares, gaining ~40% extra width at the aperture versus its narrowest point. Granulate ornament seen near aperture. Flanks bear large processes with up to 4th order dichotomous branching arranged in rings on the margin and shoulder, up to 4 µm wide and up to 20 µm high.

Dimensions: L=118-132; Dp=79-80; Lp=91-99; Dc=30 – 41; Ln=27-32 (up to 2 specimens measured)

Remarks: *A. eisenacki* as originally described has a proportionately longer, non-flaring neck bearing a ring of processes, though if the synonymy with *A. ontariensis* Legault, 1973, as proposed by Almeida-Burjack & Paris (1989), is accepted then the flaring neck without true oral processes of the specimens seen here comes within the diagnosis of *A. eisenacki*, despite the poor preservation of the present material.

Occurrence: Found at the Playa del Tranqueru and Geras localities.

Previous records: *A. eisenacki* is considered characteristic of the Middle Devonian, though it has a much larger reported range. It is known from late Pragian to Frasnian strata and with an almost worldwide distribution, being absent from Europe, Asia and Australia.

Genus ***Ancyrochitina*** Eisenack, 1955a

Type species: *Ancyrochitina ancyrea* (Eisenack) Eisenack, 1955a

Ancyrochitina ancyrea ? (Eisenack) Eisenack, 1955a

Plate VII, fig. 2

Description: Chamber conical with a flat to slightly convex base. The neck may occupy ~50% of the total length, though damage makes this unclear. The flexure is conspicuous and the aperture flares, though damage precludes measurement of its magnitude. Possible microgranulate ornament observed on surface. Processes seen on margin with up to 5th order dichotomous branching, up to 24 µm high.

Dimensions: L=106; Dp=90-92; Lp=67; Dc=32 – [unknown]; Ln=51 (up to 2 specimens measured)

Remarks: The specimens recovered here are damaged, precluding a more confident identification. Those characteristics which are preserved, namely the small surface ornament and ramified processes, match previously described specimens of *A. ancyrea*, a well-known species.

Occurrence: Found at the Quejo and Crémenes-Las Salas localities.

Previous records: *A. ancyrea* is reported from Middle Ordovician to middle Frasnian strata and with an almost worldwide distribution, being absent from Australia.

Ancyrochitina cf. *flexuosa* Burjack, 1996 (var. A)

Plate VII, fig. 6

Description: Chamber conical with a flat to slightly convex base. The neck occupies ~40% of the total length. The flexure is conspicuous and the aperture does not flare. Processes seen with up to 3rd order dichotomous branching arranged in a ring on the margin and irregularly arranged on the neck towards the aperture, up to 8 µm wide and up to 39 µm high, smaller on the neck.

Dimensions: L=132 (135) 139; Dp=74 (84) 95; Lp=69 (74) 78; Dc=31 (38) 45; Ln=52 (58) 61 (up to 4 specimens measured)

Remarks: *A. flexuosa* as originally described has a flaring neck and a discrete ring of oral processes. The neck processes on the specimens seen here are rather more disorganised. This is common across the three varieties of *A.* cf. *flexuosa* here described, while neck shape is also variable. This was also seen by Burjack (1996) and allowed for in the original description. Many of the specimens seen here resemble *A. postdesmea* Grahn, 2002, since synonymised with *A. flexuosa* (Grahn, 2011).

Occurrence: Found at the Playa del Tranqueru, Puerto de Somiedo, Quejo and Crémenes-Las Salas localities.

Previous records: Reported from the Lochkovian to Givetian of Brazil (Lange, 1967; Burjack, 1996; Grahn, 2002; Grahn & de Melo, 2004, 2005; Grahn et al., 2006, 2008) the early Givetian of Paraguay (Grahn et al., 2002) and Canada (Legault, 1973) and the early to middle Givetian of Bolivia (Grahn, 2002).

Ancyrochitina cf. *flexuosa* Burjack, 1996 (var. B)

Plate VII, fig. 5

Description: Chamber lenticular. The neck occupies ~40% of the total length. The flexure is conspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Processes seen with up to 2nd order dichotomous branching arranged on the flanks and irregularly arranged on the neck, up to 5 µm wide and up to 31 µm high, smaller on the neck.

Dimensions: L=120 (132) 155; Dp=83 (92) 105; Lp=77 (83) 92; Dc=35 (38) 45 – 40 (45) 50; Ln=41 (52) 63 (3 specimens measured)

Remarks: These specimens are distinguished from *A.* cf. *flexuosa* (var. A) by their more lenticular chamber and slightly flaring neck.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

Ancyrochitina cf. *flexuosa* Burjack, 1996 (var. C)

Plate VII, fig. 4

Description: Chamber conical with a flat to slightly convex base. The neck occupies ~50% of the total length. The flexure is conspicuous and the aperture flares, gaining ~18% extra width at the aperture versus its narrowest point. Processes seen with up to 4th order dichotomous branching arranged in a ring on the margin and irregularly arranged on the neck towards the aperture, up to 6 µm wide and up to 56 µm high, smaller on the neck.

Dimensions: L=117 (142) 167; Dp=93 (101) 115; Lp=55 (76) 97; Dc=33 (37) 45 – 36 (44) 48; Ln=52 (71) 98 (up to 10 specimens measured)

Remarks: These specimens are distinguished from *A.* cf. *flexuosa* (var. A) by their longer neck, giving a more slender outline. The aperture also flares slightly.

Occurrence: Found at the Playa del Tranqueru locality.

Ancyrochitina taouratinensis Boumendjel, 1985

Plate VII, fig. 3

Description: Chamber conical to slightly lenticular with a flat to slightly convex base. The neck occupies ~37% of the total length. The flexure is conspicuous and the aperture flares, gaining ~27% extra width at the aperture versus its narrowest point. Granulate ornament observed on surface. Processes seen on margin with up to 4th order dichotomous branching, 3-8 µm wide and 7-23 µm high.

Dimensions: L=106 (116) 128; Dp=55 (76) 83; Lp=66 (76) 89; Dc= 28 (34) 40 – 37 (43) 58; Ln=28 (43) 58 (up to 7 specimens measured)

Remarks: Specimens included in this taxon exhibit various degrees of damage resulting in loss of processes, though some remnant remains in all cases. The species is distinguished from *A. ancyrea* by its granulate surface ornament.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Las Ventas-Entrago, Quejo and Crémenes-Las Salas localities.

Previous records: Reported from the early Givetian of Algeria (Boumendjel, 1985; Boumendjel et al., 1988), the early to middle Givetian of Morocco (Rahmani-Antari & Lachkar, 2001), Bolivia (Grahn, 2002) and Brazil (Burjack, 1996; Grahn & de Melo, 2004, 2005; Grahn et al., 2006) and the middle to late Givetian of Paraguay (Grahn et al., 2002).

Ancyrochitina cf. *tomentosa* Taugourdeau & de Jekhovsky, 1960

Plate VII, fig. 7

Description: Chamber conical with a flat to slightly convex base. The neck occupies ~40% of the total length. The flexure is conspicuous and the aperture does not flare. Microgranulate and spinose or elongated filamentous ornament seen on neck up to 6 µm high. Processes seen on margin with dichotomous branching, up to 11 µm high.

Dimensions: L=130; Dp=78-83; Lp=53-78; Dc=34-43; Ln=52 (up to 2 specimens measured)

Remarks: The thin, filamentous neck ornament of this species serves to distinguish it from other members of the genus. The specimens seen here are damaged, rendering their identification uncertain. Their squat shape resembles *A. t. compactus* Taugourdeau, 1965.

Occurrence: Found at the Playa del Tranqueru and San Pedro de Nora localities.

Previous records: *A. tomentosa* is reported from middle Llandovery to Frasnian strata and with an almost worldwide distribution, being absent from Australia.

Genus ***Angochitina*** Eisenack, 1931

Type species: *Angochitina echinata* Eisenack, 1931

Angochitina cf. *capillata* Eisenack, 1937

Plate VII, fig. 8

Description: Chamber spherical to ovoid in shape. The neck occupies ~39% of the total length. The flexure is conspicuous and the aperture may flare, gaining ~15% extra width at the aperture versus its narrowest point when it does so. Microgranulate, granulate and spinose ornament up to 5 µm high evenly distributed across surface.

Dimensions: L=106 (127) 153; Dp=57 (74) 101; Lp=71 (80) 86; Dc=29 (35) 45 – 39 (41) 42; Ln=37 (50) 67 (up to 6 specimens measured)

Remarks: The species as originally described has an ovoid chamber, though Jenkins (1969) describes and figures specimens with a much more spherical chamber similar to that seen here. Some previously recorded specimens appear to have thicker spines than those seen here, thought his measurement is never specified in the original description.

Occurrence: Found at the Playa del Tranqueru, Aguasmestas-Pigüeña and Crémenes-Las Salas localities.

Previous records: *A. capillata* is reported from Middle Ordovician to Famennian strata and with a worldwide distribution.

Angochitina devonica Eisenack, 1955b

Plate VII, fig. 9; Plate VIII, fig. 15

? 1969a *Ancyrochitina* sp.; Cramer, pl. IV, fig. 46

? 1969a *Ancyrochitina* sp.; Cramer, pl. IV, fig. 47

Description: Chamber spherical to ovoid in shape. The neck occupies ~40% of the total length. The flexure is conspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Spinose ornament seen on surface with rare branching spines and larger branching processes, up to 6 µm wide and up to 14 µm high. Simple ornament more common on the neck, branching spines and processes are largely limited to the chamber.

Dimensions: L=131-147; Dp=65-87; Lp=84-92; Dc=36-38 – 44-48; Ln=47-55 (2 specimens measured)

Remarks: These specimens seem to have a proportionately shorter neck than the species as originally described, however they are well distinguished from *A. milanensis* by possessing fewer wide-based spines and granulae. This is seen in both the transmitted light and SEM images given in the plates; no more than three wide-based structures are seen in *A. devonica* specimens here, while they are common in *A. milanensis*.

Occurrence: Found at the Playa del Tranqueru locality.

Previous records: Reported from Middle Ordovician to Famennian strata and with an almost worldwide distribution, being absent from Australia.

Angochitina devonica ? Eisenack, 1955b

Plate VII, fig. 10

Description: Chamber ovoid. The neck occupies ~34% of the total length. The flexure is conspicuous and the aperture flares, gaining ~25% extra width at the aperture versus its narrowest point. Ornament of microgranulae, granulae and unbranched processes on chamber, up to 6 µm wide and up to 22 µm high.

Dimensions: L=195; Dp=81-83; Lp=118; Dc=30-33 – 36-43; Ln=56-77 (up to 2 specimens measured)

Remarks: The damaged nature of the specimens found here prevents their confident assignment to *A. devonica*.

Occurrence: Found at the Playa del Tranqueru, Geras and Crémenes-Las Salas localities.

Angochitina milanensis Collinson & Scott, 1958

Plate VII, fig. 11; Plate VIII, fig. 16

2001 *Ancyrochitina*; Gill, pl. 4, fig. 1

Description: Chamber ovoid. The neck occupies ~33% of the total length. The flexure is conspicuous and the aperture often flares, gaining ~28% extra width at the aperture versus its narrowest point when it does so. Ornament of spines, simple or with up to 3rd order dichotomous branching and up to 27 µm high, with wide-based, branching granulae mostly limited to the chamber, up to 23 µm wide and up to 15 µm high.

Dimensions: L=95 (117) 156; Dp=58 (71) 91; Lp=65 (80) 104; Dc=15 (32) 44 – 35 (41) 53; Ln=27 (39) 57 (up to 27 specimens measured)

Remarks: This species is distinguished in this assemblage by its wide-based elements. *A. devonica* can exhibit the same ornament type but it is usually smaller and the overall shape is more elongate.

Occurrence: Found at the Playa del Tranqueru, Aguasmestas-Pigüeña and Crémenes-Las Salas localities.

Previous records: Reported from the Late Silurian to Pragian of Egypt (El Shamma et al., 2012) the Pragian to Famennian of North Africa (Taugourdeau et al., 1967), the Pragian to Middle Devonian of Algeria (Taugourdeau & de Jekhovsky, 1960; Taugourdeau, 1962; Jardiné & Yapaudjan, 1968; Boumendjel et al., 1988), the Eifelian of North America (Taugourdeau et al., 1967), the Middle Devonian of Canada (Boneham, 1967; Legault, 1973) and Australia (Jansonius, 1969), the Givetian of the USA (Collinson & Scott, 1958; Dunn, 1959; Wicander & Wood, 1997) and Libya (Paris et al., 1985) and the Late Devonian of Morocco (Grignani & Mantovani, 1964).

Angochitina mourai Lange, 1952

Plate VII, fig. 12

Description: Chamber spherical or nearly so. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~10% extra width at the aperture versus its narrowest point. Granulate and spinose ornament up to 3 µm high seen across whole surface.

Dimensions: L=42 (86) 115; Dp=29 (57) 76; Lp=29 (61) 78; Dc=17 (29) 37 – 20 (32) 40; Ln=13 (27) 42 (3 specimens measured)

Remarks: Distinguished from *A.* cf. *capillata* by its more often spherical chamber. The specimens seen here strongly resemble the specimen figured as Plate II, 1 of Grahn & de Melo (2002).

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Puerto de Somiedo and Crémenes-Las Salas localities.

Previous records: Reported from Early Silurian to early Famennian strata and with an almost worldwide distribution, being absent from Asia.

Angochitina sp. A

Plate VII, fig. 13

Description: Chamber ovoid. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~30% extra width at the aperture versus its narrowest point. Microgranulate ornament seen on the chamber and neck, with a spinose ornament clustered on the shoulder up to 5 µm high.

Dimensions: L=140-155; Dp=71-103; Lp=97-118; Dc=32-39 – 44-48; Ln=37-46 (2 specimens measured)

Remarks: These specimens most closely resemble *A.* cf. *capillata* in this assemblage, except for their more ovoid chamber and particularly the restricted distribution of these specimens' spinose ornament. No existing species could be found to which these specimens could be confidently assigned.

Occurrence: Found at the Playa del Tranqueru and San Pedro de Nora localities.

Angochitina sp. B

Plate VII, fig. 14

Description: Chamber ovoid. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~40% extra width at the aperture versus its narrowest point. Microgranulate ornament seen along with large, pointed cones up to 7 µm high distributed sparsely across the surface.

Dimensions: L=119; Dp=47-76; Lp=80-105; Dc=25 – 34; Ln=36 (up to 2 specimens measured)

Remarks: The distinctive ornament of large cone-like elements distinguishes these specimens, for which no analogue could be found in the literature. The ornamental elements could represent the bases of eroded spines but their rounded tips and lack of obvious signs of breakage do not support this interpretation.

Occurrence: Found at the Puerto de Somiedo and Crémenes-Las Salas localities.

Angochitina sp. C

Plate VII, fig. 15

Description: Chamber very slightly ovoid. The neck is unknown. Sparse granulate and spinose ornament up to 4 µm high, distributed across surface. A single multi-rooted spine is seen on the shoulder.

Dimensions: Dp=80; Lp=87; Dc=39 (1 specimen measured)

Remarks: This single specimen is unique in this assemblage in possessing multi-rooted spine ornamentation. The specimen strongly resembles *A. communis* Jenkins, 1967, though it is too damaged to permit a confident identification.

Occurrence: Found at the Aguasmestas-Pigüeña locality.

Angochitina sp. D

Plate VII, fig. 16; Plate VIII, fig. 17

Description: Chamber ovoid. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~10% extra width at the aperture versus its narrowest point. Granulate and spinose ornament seen, dense on neck and occasionally seen on chamber, up to 4 µm high. Those seen on the chamber may be broken spine bases

Dimensions: L=120 (134) 160; Dp=63 (76) 88; Lp=88 (94) 107; Dc=30 (40) 52 – 34 (45) 57; Ln=32 (42) 54 (up to 3 specimens measured)

Remarks: The specimens found here resemble *A. toyetae* Cramer, 1964c figured by Legault (1973) as Plate VI, figure 10, though that specimen is acknowledged to be damaged. The same is probably true of the specimens seen here.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Aguasmestas-Pigüeña localities.

Angochitina sp. E

Plate VII, fig. 17

Description: Chamber spherical. Neck absent or very short. Surface glabrous except for a very fine microgranulate ornament seen around the aperture.

Dimensions: L=69 (77) 82; Dp=67 (72) 80; Lp=63 (71) 82; Dc=20 (24) 28 (up to 5 specimens measured)

Remarks: These specimens present few diagnostic features, other than their unusual proportions. The overall shape of these specimens is very similar to the genus *Desmochitina* Eisenack, 1931, but they do not possess the correct surface texture.

Occurrence: Found at the Playa del Tranqueru, Aguasmestas-Pigüeña and Crémenes-Las Salas localities.

Genus ***Clavachitina*** Taugourdeau, 1966

Type species: *Rhabdochitina claviformis* (Taugourdeau, 1961)

Clavachitina ? sp. A

Plate VII, fig. 18

Description: Chamber claviform. The flexure is inconspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Microgranulate and fine spinose ornament up to 6 μm high seen on surface.

Dimensions: L=125-135; Dp=52-69; Dc=31-32 – 36-38 (2 specimens measured)

Remarks: *Clavachitina* is described by Paris et al. (1999) as being glabrous, precluding the spinose ornament of this species. However, they do not give an example of a spinose genus with a claviform chamber. The few specimens found here are very poorly preserved, rendering the generic assignment uncertain and a specific assignment impossible.

Occurrence: Found at the Playa del Tranqueru locality.

Genus ***Fungochitina*** Taugourdeau, 1966

Type species: *Fungochitina fungiformis* (Eisenack, 1931)

Fungochitina cf. *lata* (Taugourdeau & de Jekhovsky, 1960)

Plate VII, fig. 19

Description: Chamber conical with a more or less rounded margin and a flat to convex base. The neck occupies ~35% of the total length. The flexure is conspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Fine microgranulate ornament seen across surface with occasional larger elements up to 2 µm high.

Dimensions: L=90 (117) 140; Dp=70 (81) 92; Lp=53 (77) 93; Dc=16 (31) 43 – 29 (37) 43; Ln=20 (40) 52 (up to 11 specimens measured)

Remarks: The specimens seen here have shorter necks than the species as originally described, though they are damaged. This is the source of these specimens' tentative identification, despite their overall shape and ornamentation characteristic of *F. lata*.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Puerto de Somiedo, Quejo, Geras, '598', '600' and Crémenes-Las Salas localities.

Previous records: *F. lata* is reported from the Late Silurian to the Late Devonian of Algeria (Taugourdeau & de Jekhovsky, 1960; Magloire, 1967; Paris, 1996; Boumendjel, Brice, et al., 1997; Boumendjel, Morzadec, et al., 1997; Paris et al., 1997; Alem, 1998; Khodjaoui, 2008), the Early to Middle Devonian of the English Channel (Lefort & Deunff, 1970), the Lochkovian of Bulgaria (Lakova, 1985, 1993, 1995a, 1995b, 1999, 2001a, 2001b; Haydoutov & Yanev, 1997), France (Paris, 1976) and Romania (Vaida & Verniers, 2005a, 2005b, 2006a, 2006b) and the late Lochkovian of the USA (Bevington et al., 2010)

Fungochitina pilosa (Collinson & Scott, 1958)

Plate VII, fig. 20

Description: Chamber lenticular to conical with a convex base. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~20% extra width at the aperture versus its narrowest point. Microgranulate and spinose ornament up to 2 µm high seen on surface.

Dimensions: L=102 (123) 148; Dp=76 (87) 103; Lp=61 (85) 105; Dc=26 (37) 42 – 39 (45) 51; Ln=27 (41) 49 (up to 4 specimens measured)

Remarks: This species is distinguished from *F.* cf. *lata* in this assemblage principally by its shorter neck and more rounded, sometimes lenticular chamber.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, '598' and Crémenes-Las Salas localities.

Previous records: Reported from Late Silurian to late Frasnian strata and with an almost worldwide distribution, being absent from Asia and Australia.

Fungochitina cf. *pistilliformis* (Eisenack, 1931)

Plate VIII, fig. 1

Description: Chamber conical with a flat to slightly convex base. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture does not flare. Microgranulate, granulate and spinose or elongated filamentous ornament seen on neck up to 5 µm high.

Dimensions: L=77 (98) 110; Dp=58 (79) 101; Lp=63 (68) 78; Dc=20 (32) 38; Ln=12 (32) 46 (up to 4 specimens measured)

Remarks: *Conochitina pistilliformis* as described by Eisenack (1931) has a proportionately much longer neck than the specimens seen here, though many of these specimens are damaged and missing part of the neck. They are distinguished from *F.* cf. *lata* primarily by their restricted covering of ornamental elements, seen only on the neck.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña and Crémenes-Las Salas localities.

Previous records: *F. pistilliformis* is reported from the Middle Ordovician to Přídolí of the Baltic (Eisenack, 1931; Nestor, 1992), the Middle Ordovician to Middle Devonian of France (Doubinger & Ruhland, 1963; Doubinger et al., 1966; Poncet & Doubinger, 1966; Lefort & Deunff, 1971), the Late Silurian of Germany (Eisenack, 1955a; Behr et al., 1965), the Wenlock of Ireland (Holland & Smith, 1979), the Wenlock to Early Devonian of China (Hou, 1978; Wang et al., 2006), the Ludlovian of England (Lister & Downie, 1967; Sutherland, 1994), the late Ludlovian to Early Devonian of Romania (Beju, 1967; Popescu, 1987; Olaru & Tabără, 2011) and Tunisia (Grignani, 1967), the Přídolí of Estonia (Nestor, 2011), the Devonian of the Sahara (Taugourdeau, 1979), the Lochkovian of Algeria (Magloire, 1967) and the Late Devonian of Morocco (Grignani & Mantovani, 1964).

Genus ***Hoegisphaera*** Staplin emend. Paris et al., 1999

Type species: *Hoegisphaera glabra* Staplin, 1961

Hoegisphaera cf. *glabra* Staplin, 1961

Plate VIII, figs. 2-3

Description: Chamber spherical. Neck absent. Operculum obvious. This structure is frequently found detached from the chamber (see Pl. VIII, fig. 3). Surface otherwise glabrous.

Dimensions: Overall diameter: 65 (92) 114 (14 specimens measured); annular ring diameter: 22 (37) 49 (33 specimens measured)

Remarks: This species is often extremely numerous in this material, possibly because of the ease with which damaged specimens can be identified by the prominent operculum. This may also be the reason for its seemingly large stratigraphic range elsewhere (see below).

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, '120', '599' and Man member localities.

Previous records: *H. glabra* is reported from Late Ordovician to Late Permian strata and with an almost worldwide distribution, being absent from Asia, though it is often considered characteristic of the Late Devonian (Paris et al., 2000). Reports of the species occurring more widely may be instances of homeomorphs.

Genus ***Lagenochitina*** Eisenack emend. Paris et al., 1999

Type species: *Lagenochitina baltica* Eisenack, 1931

Lagenochitina sp. A

Plate VIII, fig. 5

Description: Chamber ovoid. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture flares, gaining ~30% extra width at the aperture versus its narrowest point. Surface glabrous.

Dimensions: L=148; Dp=79; Lp=99; Dc= 34 – 44; Ln=49 (1 specimen measured)

Remarks: This single specimen is placed in the genus *Lagenochitina* by its glabrous surface. The lack of SEM imagery of the specimen might render this identification doubtful, but no trace of ornament could be seen even under 100× magnification. No specific identification has been attempted owing to the specimen's damaged state.

Occurrence: Found at the Aguasmestas-Pigüeña locality.

Genus ***Ramochitina*** Sommer & van Boekel emend. Paris et al., 1999

Type species: *Ramochitina ramosi* Sommer & van Boekel, 1964

Ramochitina corniculata ? (Laufeld, 1974)

Plate VIII, figs. 8-9

Description: Chamber lenticular with a more or less convex base. The neck occupies ~35% of the total length. The flexure is conspicuous and the aperture may flare, gaining ~10% extra width at the aperture versus its narrowest point when it does so. Broken process bases seen on chamber, roughly arranged in longitudinal rows, up to 5 µm wide and up to 11 µm high. These bases may appear as isolated granules (Pl. VIII, fig. 9) and may be disproportionately wide-based (Pl. VIII, fig. 8).

Dimensions: L=85 (91) 102; Dp=66 (70) 75; Lp=55 (59) 67; Dc=24 (29) 31 – 29 (31) 33; Ln=30 (32) 35 (3 specimens measured)

Remarks: These specimens are doubtfully assigned to the species on account of their relatively short necks and few spines, both attributed to damage. They do, however, bear a great similarity to the holotype of *R. corniculata* depicted in Figure 47B of Laufeld (1974) and the specimen figured here in Pl. II, 8 shows one orally curved process, characteristic of the species.

Occurrence: Found at the Playa del Tranqueru and San Pedro de Nora localities.

Previous records: *R. corniculata* is reported from the late Llandovery to middle Wenlock of Belgium (Verniers & Rickards, 1979; Verniers, 1981, 1999; Verniers et al., 2002) and the Wenlock of Sweden (Laufeld, 1974; Jenkins & Legault, 1979) and Wales (Verniers, 1999).

Ramochitina derbyi ? Grahn & de Melo, 2002

Plate VIII, fig. 7

Description: Chamber a strongly rounded conical shape with a flat base. The neck occupies ~50% of the total length. The flexure is conspicuous and the aperture flares, gaining ~35% extra width at the aperture versus its narrowest point, though the neck is damaged. Spinose ornament observed arranged in rough longitudinal rows, up to 8 µm high and limited to the aboral end of the chamber around the margin.

Dimensions: L=103; Dp=62; Lp=53; Dc=26 – 35; Ln=50 (1 specimen measured)

Remarks: This single specimen differs from the species as originally described by its lack of spines on the neck and fewer spines generally, though the latter may be due to damage. The general form and proportions of this specimen are comparable with *R. derbyi*.

Occurrence: Found at the Crémenes-Las Salas locality.

Previous records: *R. derbyi* is reported from the early Frasnian of Brazil (Grahn & de Melo, 2002; Grahn et al., 2002).

Ramochitina cf. *magnifica* Lange, 1967

Plate VIII, figs. 4; 19

? 1969a *Ancyrochitina* sp.; Cramer, pl. IV, fig. 45

Description: Chamber ovoid. The neck occupies ~35% of the total length. The flexure is conspicuous and the aperture does not flare. Ornament of processes with up to 3rd order dichotomous and trichotomous branching, occasionally with wide bases. Processes 1-9 µm wide and 13-36 µm high. Processes arranged in longitudinal crests.

Dimensions: L=155 (166) 185; Dp=79 (89) 102; Lp=97 (106) 123; Dc=34 (45) 58; Ln=36 (58) 81 (up to 4 specimens measured)

Remarks: The specimens found here are considerably smaller than the species as originally described but conform with it physically.

Occurrence: Found at the Playa del Tranqueru, '120' and Man member localities.

Previous records: *R. magnifica* is reported from the Early to Late Devonian of Argentina (Volkheimer et al., 1986; Noetinger & Di Pasquo, 2009), the late Lochkovian to Pragian of the Falkland Islands (Marshall, 2008), the late Lochkovian to Emsian of Canada (Achab et al., 1997), the Pragian of Paraguay (Grahn et al., 2000) and the Pragian to Emsian of Brazil (Lange, 1967; da Costa, 1971; Grahn, 1992, 1995, Grahn et al., 2000, 2010, 2013) and Bolivia (Vavrdová et al., 1996; Grahn, 2002; Troth et al., 2011).

Ramochitina sp. A

Plate VIII, fig. 6

Description: Chamber conical with a slightly convex base. The neck occupies ~20% of the total length. The flexure is conspicuous and the aperture does not flare. Microgranulate and longitudinal crest-like ornament seen on chamber, possibly made up of coalesced smaller elements. One small branching process also seen on margin.

Dimensions: L=104; Dp=61; Lp=85; Dc=25; Ln=20 (1 specimen measured)

Remarks: This single specimen is reminiscent of *R. spinosa* (Eisenack, 1932), though it has a shorter neck and smaller ornament, possibly due to damage.

Occurrence: Found at the Crémenes-Las Salas locality.

Genus ***Saharochitina*** Paris & Grahn *in* Paris et al., 1999

Type species: *Saharochitina jaglini* (Oulebsir & Paris) Paris et al., 1999

Saharochitina sp. A Oulebsir & Paris, 1993

Plate VIII, fig. 10

Description: Chamber conical with a very slightly convex base. The neck occupies ~30% of the total length. The flexure is conspicuous and the aperture does not flare. Surface glabrous.

Dimensions: L=93; Dp=69; Lp=62; Dc=28; Ln=30 (1 specimen measured)

Remarks: This single specimen strongly resembles *Fungochitina* ? sp. A of Oulebsir & Paris (1993), though with a slightly shorter neck. It is this short neck that distinguishes the form from *F*. ? *jaglini* Oulebsir & Paris, 1993, since reassigned as the type species of *Saharochitina*.

Occurrence: Found at the Man member locality.

Previous records: Oulebsir & Paris (1993) report their specimens from the Early and Middle Ordovician of Algeria.

Genus ***Sphaerochitina*** (Eisenack) emend. Paris et al., 1999

Type species: *Sphaerochitina sphaerocephala* (Eisenack) Eisenack, 1955a

Sphaerochitina cf. *compactilis* Jenkins, 1969

Plate VIII, fig. 11

Description: Chamber ovoid to almost spherical. The neck occupies ~20% of the total length. The flexure is conspicuous and the aperture may flare slightly. Surface glabrous.

Dimensions: L=97 (103) 109; Dp=56 (68) 82; Lp=73 (79) 85; Dc=15 (28) 39 – 17 (18) 18; Ln=12 (24) 30 (up to 5 specimens measured)

Remarks: *S. compactilis* as originally described has a conical to spherical chamber, however the figured specimens are better described as ovoid in the opinion of the present author. The species is also described as having a neck occupying up to ⅓ of the total length, something that is not obvious in the figured specimens. Indeed, the specimens seen here bear a marked resemblance to the specimen figured in Plate 9, fig. 16 of Jenkins (1969).

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Geras, Crémenes-Las Salas and Man member localities.

Previous records: *S. compactilis* is reported from the Middle Ordovician of Saudi Arabia (Al-Hajri, 1995) and Spain (Cramer-Díez et al., 1972) and the Late Ordovician of Canada (Martin, 1975, 1980, 1983; Jenkins, 1984) and the USA (Jenkins, 1969, 1970).

Sphaerochitina cuvillieri Taugourdeau, 1962

Plate VIII, figs. 13; 18

cf. 2001 *Sphaerochitina*; Gill, pl. 4, fig. 2

Description: Chamber spherical to ovoid. The neck occupies ~ 37% of the total length. The flexure is conspicuous and the aperture flares, gaining ~17% extra width at the aperture versus its narrowest point. Microgranulate or, occasionally, granulate ornament seen on surface.

Dimensions: L=92 (116) 130; Dp=50 (68) 89; Lp=62 (76) 97; Dc=25 (31) 39 – 31 (37) 49; Ln=29 (43) 64 (up to 14 specimens measured)

Remarks: The specimens seen here do not show the tendency for their ornament to cluster that Taugourdeau (1962) described.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Aguasmestas-Pigüeña, '598' and Crémenes-Las Salas localities.

Previous records: Reported from the Early Silurian of Saudi Arabia (McClure, 1988), the Late Silurian of Tunisia (Grignani, 1967), the Frasnian (Taugourdeau, 1962) of Algeria, the Early to Middle Devonian of Brazil (van Boekel, 1966, 1968a, 1968b; da Costa, 1971), the early Emsian to early Eifelian of Spain (Díez & Cramer, 1978), the Frasnian of France (Moreau-Benoit, 1965) and the Late Devonian of Morocco (Grignani & Mantovani, 1964).

Sphaerochitina cf. *ricardi* Díez & Cramer, 1978

Plate VIII, figs. 12; 20

Description: Chamber spherical to lenticular in shape. The neck occupies ~60% of the total length. The flexure is conspicuous and the aperture does not flare. A sparse microgranulate ornament is seen on the surface, with elements well separated from each other.

Dimensions: L=153; Dp=79; Lp=68; Dc=29; Ln=85 (1 specimen measured)

Remarks: This single specimen strongly resembles *S. ricardi* in proportions and ornament, except it does not have the conical shape specified for the species. It does resemble some of the specimens figured by Díez & Cramer (1978). The SEM image seen in Pl. VIII, fig. 20 shows a specimen with an apparent ornament, however this is believed to be mineral growth.

Occurrence: Found at the Aguasmestas-Pigüeña locality.

Previous records: *S. ricardi* is reported from the Pragian of Australia (Winchester-Seeto & Carey, 2000) and the early Emsian to early Eifelian of Spain (Díez & Cramer, 1978).

Sphaerochitina sphaerocephala (Eisenack) Eisenack, 1955a *sensu* Díez & Cramer, 1978

Plate VIII, fig. 14; 21

Description: Chamber ovoid. The neck occupies ~35% of the total length. The flexure is conspicuous and the aperture may flare, gaining ~15% extra width at the aperture versus its narrowest point when it does so. A faint microgranulate ornament is seen on the surface, with elements quite well separated from each other.

Dimensions: L=103 (120) 133; Dp=56 (80) 100; Lp=73 (82) 98; Dc=28 (36) 47 – 36 (40) 48; Ln=23 (42) 65 (up to 7 specimens measured)

Remarks: One specimen (see Pl. VIII, fig. 14) appears to have a single spine on the shoulder, though this may not be original; no other spines or spine bases are seen on this specimen. This species is distinguished from *S. cuvillieri* in this study by its much fainter, more widely spaced microgranulate ornament. *S. sphaerocephala* as originally described has a much longer neck than the specimens seen here. Díez & Cramer (1978) figure shorter, more squat specimens, referencing a 1968 publication by Eisenack which included specimens of a similar shape. These show a marked similarity to those seen in the present study, though they may simply represent part of the considerable variation seen in *S. sphaerocephala*, rather than a distinct form. The SEM image seen in Pl. VIII, fig. 21 shows a misshapen specimen, probably due to mineral growth.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, '120' and Crémenes-Las Salas localities.

Previous records: *S. sphaerocephala* is reported from Early Ordovician to Famennian strata and with an almost worldwide distribution, being absent from Australia. Díez & Cramer (1978) describe specimens similar to those found here from the early Emsian to early Eifelian of Spain and reference specimens found from the Ordovician to Silurian of the Baltic (Eisenack, 1968).

6.3 - Spore taxonomy

The spores described below are treated as form genera and species in accordance with the ICN (Melbourne Code) (McNeill et al., 2012). The suprageneric Turma system of Potonié (1956, 1970) has not been used as no definite cryptospores and only a small number of monolete taxa have been found, rendering turmal division largely superfluous. Genera have been listed alphabetically for ease of use. Full citations are taken from recent sources in an effort to provide up to date names, except where stated. A limited synonymy is provided for species previously recorded from the Naranco and Huergas formations, reproduced as cited in their original sources. Dimensions are given for each species as diameters and where three numbers are given these correspond to the minimum value (arithmetic mean) and maximum values. The number of specimens measured is given. The sites in which each species occurs in this study are given. Previous records are noted following consultation of the John Williams Index of Palaeopalynology.

Morphologial terminology follows Punt et al. (2007). In this scheme, granulae are defined as rounded elements, while coni and spinae are pointed elements with spinae being proportionately longer than coni, arbitrarily defined as more than twice as tall as they are wide. The prefix micro- denotes ornamental elements 1 µm in size or below. 'Fine' denotes particularly small ornamentation. Clavae are club-shaped units with a bulbous tip supported on a narrower 'stalk'. Muri are ridges, and separate luminae in a reticulate ornament. Laevigate taxa have a smooth surface without ornament.

Genus ***Acinosporites*** Richardson, 1964

Type species: *Acinosporites acanthomammillatus* Richardson, 1964

Acinosporites acanthomammillatus ? Richardson, 1964

Plate IX, fig. 1

? 2001 *Dibolisporites echinaceus* (Eisenack, 1954) Richardson, 1964; Gill, p. 35, pl. 1, fig. 10

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

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

Remarks: The identification of these specimens should be regarded as dubious in the highest order, being based entirely on the characteristic ornament of rounded ridges topped by spines. Poor preservation and a low number of specimens preclude a more confident identification.

Occurrence: Found at the Playa del Tranqueru, Las Ventas-Entrago and Crémenes-Las Salas localities.

Previous records: *A. acanthomammillatus* is reported from Eifelian to Frasnian strata and with a worldwide distribution (Breuer & Steemans, 2013).

Acinosporites lindlarensis Riegel, 1968

Plate IX, fig. 2

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. 2-4 µm equatorial thickening observed, with some minor separation of the exoexine from a possible inner body. Proximal surface laevigate. Distal surface bears an ornament of microgranulae, large conate elements up to 3 µm high and wide as well as more irregular, parallel sided, potentially biform elements of a similar height.

Dimensions: 50 (85) 153 µm. (6 specimens measured)

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

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

Genus ***Ambitisporites*** Hoffmeister, 1959

Type species: *Ambitisporites avitus* Hoffmeister, 1959

Ambitisporites avitus Hoffmeister, 1959

Plate IX, fig. 3

Description: Amb circular to subcircular. Laesurae straight, extending from ¾ to the whole amb radius. 2-3 µm equatorial thickening observed. Surface laevigate.

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

Remarks: The widening of the equatorial thickening opposite the trilete rays originally described for this species could not be clearly discerned here.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Las Ventas-Entrago, Huergas de Gordon, '120', '598' and Crémenes-Las Salas localities.

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

Ambitisporites dilutus (Hoffmeister) Richardson & Lister, 1969

Plate IX, fig. 4

cf. 2001 *Calamospora atava* (Naumova, 1953) McGregor, 1964; Gill, p. 23, pl. 1, fig. 1

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. Wall ~1 µm thick. Surface laevigate.

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

Remarks: This species differs from *A. avitus* in lacking an obvious equatorial thickening.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Mirantes de Luna, Huergas de Gordon, Aleje, '120', '598', '599', Crémenes-Las Salas and Man member localities.

Previous records: Reported from Late Ordovician to Eifelian strata and with an almost worldwide distribution, being absent from Australia.

Ambitisporites sp. A

Plate IX, fig. 5

Description: Amb circular to subcircular. Laesurae straight, extending from ½ to ⅚ of the amb radius. Wall 1-2 µm thick. Surface laevigate.

Dimensions: 18 (36) 65 µm. (138 specimens measured)

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Mirantes de Luna, Huergas de Gordon, '120', '598', '599', Crémenes-Las Salas and Man member localities.

Ambitisporites cf. sp. A

Plate IX, fig. 6

Description: Amb circular to subcircular. Laesurae straight, usually open, extending from ⅓ to ¾ of the amb radius. Tips of the laesurae may be slightly spatulate. Wall ~1 µm thick. Surface may be ornamented but details of sculptural elements cannot be distinguished.

Dimensions: 31 (37) 43 µm. (4 specimens measured)

Remarks: This taxon is distinguished from *A.* sp. A by the different shape of the laesurae and the possibility of an ornamented exine. Neither of these are considered as sufficient justification to erect a separate taxon.

Occurrence: Found at the San Pedro de Nora locality.

Ambitisporites sp. B

Plate IX, fig. 7

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from ½ to ⅔ of the amb radius. Wall ~1 µm thick. Surface laevigate.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Aleje, '120', '598', '599', Crémenes-Las Salas and Man member localities.

Ambitisporites sp. C

Plate IX, fig. 8

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from ¾ to the whole amb radius. Wall ~1 µm thick. Surface laevigate to occasionally scabrate.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Huergas de Gordon, Vozmediano, Aleje, '120', '598', '599', Crémenes-Las Salas and Man member localities.

Genus ***Anapiculatisporites*** Potonié & Kremp, 1954

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

Anapiculatisporites abrepunius Cramer, 1966

Plate IX, fig. 12

Description: Amb circular to subcircular. Laesurae straight, extending from ½ to the whole amb radius. 1-4 µm equatorial thickening observed. Proximal surface laevigate. Distal surface bears a sparse ornament of microgranulae and small spines separated by at least 2 µm.

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

Remarks: Specimens seen here occasionally have shorter trilete rays than specified in the original description, though this was not seen as sufficient to justify an alternative identification.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Mirantes de Luna, '120' and '598' localities.

Previous records: Reported from the Pragian to Emsian of Spain (Cramer, 1966).

Anapiculatisporites carminae Cramer, 1966

Plate IX, fig. 9

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

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

Description: Amb circular to subcircular. Laesurae straight, extending from ¾ to the whole amb radius. 1-4 µm equatorial thickening observed. Proximal surface laevigate. Distal surface bears an ornament of microgranulae and granulae above 1 µm in size.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Huergas de Gordon, Vozmediano, Aleje and Crémenes-Las Salas localities.

Previous records: Reported from the late Eifelian to early Frasnian of Spain (Cramer, 1966, 1969a).

Anapiculatisporites picantus Cramer, 1966

Plate IX, fig. 10

Description: Amb circular to subcircular. Laesurae straight, extending from ⅖ to the whole amb radius. 1-3 µm equatorial thickening observed. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Geras, Huergas de Gordon, Vozmediano, Aleje, '120', '598' and Crémenes-Las Salas localities.

Previous records: Reported from the Pragian of Belgium (Steemans, 1989) and the Pragian to Emsian of Spain (Cramer, 1966).

Genus ***Apiculatasporites*** Potonié & Kremp, 1956

Type species: *Apiculatasporites spinulistratus* (Loose) Ibrahim 1933

Apiculatasporites perpusillus (Naumova ex Chibrikova) McGregor, 1973

Plate IX, fig. 11

2001 *Apiculatasporites perpusillus* (Naumova 1953) McGregor 1973; Gill, p. 34, pl. 1, fig. 12

Description: Amb circular to subcircular. Laesurae straight, extending from ½ to ¾ of the amb radius. Proximal surface laevigate. Distal surface bears a sparse ornament of microgranulae separated by at least 2 µm.

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

Remarks: This taxon meets the specific description for *A. perpusillus* in all respects.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Puerto de Somiedo, Huergas de Gordon, Aleje and Crémenes-Las Salas localities.

Previous records: Reported from Late Silurian to Famennian strata and with an almost worldwide distribution, being absent from Australia.

Genus ***Apiculatisporis*** Potonié & Kremp, 1956

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

Apiculatisporis cf. *elegans* McGregor, 1960

Plate IX, fig. 13

Description: Amb circular to subcircular. Laesurae straight, usually open, extending from ½ to ¾ of the amb radius. Proximal surface laevigate. Distal surface bears a dense ornament of large micrograndulae up to 1 µm in size.

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

Remarks: The species as originally described has a less variable trilete size and slightly larger ornament than the specimens found here. Owens (1971) considered *A. elegans* to be one end member of a morphological series, with *Planisporites minimus* McGregor, 1960 as the other extreme. This series shows an increase in ornament size with amb dimensions. This study recovered both end members of the series but no intermediate forms. The decision was taken to preserve them as separate, tentatively assigned species, as *P. minimus* is not formally included under synonymy with *A. elegans* by Owens (1971) or McGregor (1964) and *A. elegans* has only ever been synonymized with a tentatively identified assemblage of *Apiculatasporites dilucidus* (McGregor) McGregor, 1964 (Owens, 1971), which does not resemble the specimens found here.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: *A. elegans* is reported from the late Eifelian to early Givetian of the USA (Urban, 1968), the middle to late Givetian of Greenland (Friend et al., 1983), the

Frasnian of Canada (McGregor, 1960) and the Late Devonian of Romania (Venkatachala et al., 1968)

Genus ***Apiculiretusispora*** (Streel) Streel, 1967

Type species: *Apiculiretusispora brandtii* Streel, 1964

Apiculiretusispora cf. *brandtii* Streel, 1964

Plate IX, fig. 14

cf. 1988 *Apiculiretusispora cf. brandtii* Streel 1964; Fombella Blanco, pl. 4, figs. 3, 5

2001 *Apiculiretusispora brandtii* Streel, 1964; Gill, p. 31, pl. 1, fig. 8

Description: Amb circular to subcircular. Laesurae straight, extending from ⅓ to ¾ of the amb radius. Laesurae connected by curvaturae perfectae delimiting obvious proximal contact areas. Proximal surface bears thickened kyrtomes in the interradial areas, often reaching the tips of the laesurae and often leaving a thinner, triangular polar area immediately around the laesurae. Distal surface bears an ornament of microgranulae and granulae.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Vozmediano, Aleje, '598' and Crémenes-Las Salas localities.

Previous records: *A. brandtii* is reported from Pragian to Givetian strata and with a worldwide distribution (Breuer & Steemans, 2013).

Apiculiretusispora plicata (Allen) Streel, 1967

Plate IX, fig. 15

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

? 1988 *Apiculiretusispora arenorugosa* McGregor 1973; Fombella Blanco, pl. 2, fig. 6

? 1988 *Aneurospora gregsii* Clayton et al. 1977; Fombella Blanco, pl. 4, figs. 2, 6

2001 *Calamospora? sp. A*; Gill, p. 23, pl. 1, fig. 2

2001 *Apiculiretusispora densiconata* Tiwari & Schaarschmidt 1975; Gill, p. 32, pl. 1, fig. 9

2001 *Apiculiretusispora plicata* (Allen, 1965) Streel, 1967; Gill, p. 32, pl. 1, fig. 11

Description: Amb circular to subcircular. Laesurae straight, extending from ~½ to ¾ of the amb radius. Laesurae connected by curvaturae perfectae delimiting obvious proximal contact areas. Distal surface bears an ornament of microgranulae and granulae.

Dimensions: 20 (51) 100 µm. (42 specimens measured)

Remarks: Distinguished from *A. brandtii* by its lack of proximal kyrtomes.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Mirantes de Luna, Huergas de Gordon, Vozmediano, Aleje, '120', '598', Crémenes-Las Salas and Man member localities.

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

Apiculiretusispora cf. *plicata* (Allen) Streel, 1967

Plate IX, fig. 16

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending ½ of the amb radius. Laesurae connected by curvaturae perfectae delimiting obvious proximal contact areas. Distal surface bears an ornament of microgranulae.

Dimensions: 48 (68) 82 µm. (3 specimens measured)

Remarks: This taxon includes poorly preserved specimens similar to *A. plicata* aside from their possession of labra, which may be a preservational artefact.

Occurrence: Found at the Playa del Tranqueru locality.

Apiculiretusispora ? sp. A

Plate X, figs. 1-2

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. Possible 2-3 µm wide equatorial thickening observed. Proximal face bears subcircular thickened region extending from ⅔ to ¾ of the distance to the equator. Distal surface bears an ornament of microgranulae.

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

Remarks: These specimens are doubtfully assigned to this genus owing to their lack of obvious curvaturae, though these could be the origin of their possible thickened wall. Some specimens of *Apiculiretusispora* may not show obvious curvaturae either, such as Fig. 10F of Breuer & Steemans (2013). This species' interradial thickenings are reminiscent of the structures seen in *A. arabensis* Al-Ghazi, 2009 (mis-cited in Breuer & Steemans (2013) as "*A. arabiensis*"), though they are not of such a clear rounded shape.

Occurrence: Found at the Crémenes-Las Salas locality.

cf. *Apiculiretusispora* sp. B

Plate X, fig. 3

Description: Amb circular to subcircular. Laesurae straight, extending almost to the equator. Laesurae connected by curvaturae perfectae delimiting obvious proximal contact areas, up to 15 µm away from the equator. Distal surface bears an ornament of microgranulae and granulae together with a prominent, 10 µm wide annulus, positioned ½ of the distance of the equator.

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

Remarks: This species closely resembles species of *Apiculiretusispora*, however its size exceeds the normal size range for the genus. Indeed, it approaches megaspores in size.

Occurrence: Found at the Crémenes-Las Salas locality.

Genus ***Brochotriletes*** Naumova ex Ishchenko, 1952

Type species: *Brochotriletes magnus* Ishchenko, 1952

Brochotriletes foveolatus ? Naumova, 1953

Plate IX, fig. 17

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. 1-2 µm equatorial thickening observed. Proximal surface laevigate. Distal surface bears an ornament of anastomosing muri, 1-3 µm wide and enclosing ~6 µm wide circular luminae.

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

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: *B. foveolatus* is reported from Late Silurian to late Famennian strata and with a worldwide distribution.

Genus ***Camarozonotriletes*** Naumova ex Naumova, 1953

Type species: *Camarozonotriletes devonicus* Naumova, 1953

Camarozonotriletes? *concavus* Loboziak & Streel, 1989

Plate IX, fig. 18

2001 *Camerozonotriletes? concavus* Loboziak & Streel, 1989; Gill, p. 47, pl. 1, fig. 23

Description: Amb subtriangular with slightly concave to slightly convex interradial margins. Laesurae straight, may be accompanied by narrow labra along their length, extending from ⅔ to the whole amb radius. 1-4 µm equatorial thickening observed, wider in the interradial areas though this is not always obvious. Proximal surface laevigate. Distal surface bears an ornament of micrograrulae.

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

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

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

Camarozonotriletes parvus Owens, 1971

Plate X, fig. 4

Description: Amb subtriangular with straight to convex interradial margins. Laesurae straight, extending from ½ to ⅔ of the amb radius. Equatorial thickening observed only in the interradial areas. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

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

Remarks: The specimens described here meet the specific diagnosis in all particulars.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

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

Genus ***Concavisporites*** Pflug *in* Thomson & Pflug, 1953

Type species: *Concavisporites rugulatus* Pflug *in* Thomson and Pflug, 1953

Concavisporites ? sp. A

Plate X, fig. 5

Description: Amb subtriangular with straight to slightly convex interradial margins. Laesurae straight, simple or accompanied by narrow labra along their length, extending from ½ to ⅔ of the amb radius. Proximal surface bears thickened kyrtomes in the interradial areas, reaching the tips of the laesurae. Surface otherwise laevigate.

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

Remarks: This species meets the generic criteria for *Concavisporites* but no record of the genus could be found from Palaeozoic material, hence this species' tentative identification.

Occurrence: Found at the San Pedro de Nora locality.

Genus ***Corystisporites*** Richardson, 1964
Type species: *Corystisporites multispinosus* Richardson, 1964

Corystisporites cf. sp. Turnau, 1996

Plate X, fig. 9

Description: Amb subcircular to vaguely subtriangular. Laesurae not easily discerned, believed to extend to the equator. Proximal surface presumed to be laevigate. Distal surface bears an ornament of densely packed, tapering spines up to 19 µm high. Spines often have wide bases with marked shoulders at around ⅓ to ½ of their height, before a thinner tapering portion begins. Large, rounded granulae are also seen, though these are probably broken spine bases.

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

Remarks: The specimens seen here are sometimes smaller than those of Turnau (1996) and with less variation in the length of the spines. Aside from this the present author draws similar conclusions: the species resembles *Acinosporites macrospinosus* Richardson, 1964 except for having more densely distributed spines not clearly superimposed on convolute ridges.

Occurrence: Found at the Crémenes-Las Salas locality.

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

Genus ***Deltoidospora*** Miner, 1935

Type species: *Deltoidospora hallii* Miner, 1935

Deltoidospora priddyi (Berry) McGregor, 1973

Plate X, fig. 6

Description: Amb subtriangular with straight interradial margins. Laesurae straight, accompanied by narrow labra along their length, extending ¾ of the amb radius. Surface laevigate.

Dimensions: 23 (30) 41 µm. (6 specimens measured)

Remarks: This species was originally placed with the genus *Zonales-sporites* by Berry (1937).

Occurrence: Found at the Playa del Tranqueru and San Pedro de Nora localities.

Previous records: Reported from the late Pragian to early Emsian of France (Le Hérissé, 1983), the Emsian to early Eifelian of Bolivia (McGregor, 1984), the Emsian to middle Eifelian of Canada (McGregor, 1973), the Eifelian of Russia (Chibrikova & Olli, 1992) and the Emsian to Eifelian (Andrews et al., 1977) and Pennsylvanian of the USA (Ravn, 1986; Willard, 1992; Gennett & Ravn, 1993; Peppers, 1993; Eble, 1996).

Deltoidospora sp. A

Plate X, fig. 8

Description: Amb subtriangular with concave interradial margins. Laesurae straight, accompanied by narrow labra along their length, extending from ⅔ to ¾ of the amb radius. Surface laevigate.

Dimensions: 31 (39) 48 µm. (2 specimens measured)

Remarks: This species identifies with the genus *Cyathidites*, synonymised with *Deltoidospora* by McGregor (1973), though no exactly comparable species could be obtained from the literature.

Occurrence: Found at the Playa del Tranqueru, Las Ventas-Entrago and ‘599’ localities.

Genus ***Devonomonoletes*** Arkhangelskaya, 1985

Type species: *Devonomonoletes microtuberculatus* (Chibrikova) Arkhangelskaya, 1985

Devonomonoletes cf. sp. 1 Breuer & Steemans, 2013

Plate X, fig. 10

Description: Amb circular to subcircular. Monolete mark observed, extending from ½ to the whole amb radius. Curvaturae perfectae may be observed at the laesurae tips. 1-2 µm equatorial thickening observed. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Puerto de Somiedo, Quejo and Crémenes-Las Salas localities.

Previous records: *D.* sp. 1 is reported from the Pragian to middle Emsian of Saudi Arabia (Breuer & Steemans, 2013).

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

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

Diatomozonotriletes cf. *franklinii* McGregor & Camfield, 1982

Plate X, fig. 7

Description: Amb subtriangular with straight to slightly convex interradial margins. Laesurae straight, extending from ⅔ to the whole amb radius. Proximal surface laevigate. Distal surface bears an ornament of micrograngulae, with a prominent row of spines around 1 μm high in the interradial regions. The areas opposite the laesurae are laevigate to very finely scabrate.

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

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

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

Genus ***Dibolisporites*** Richardson, 1964

Type species: *Dibolisporites echinaceus* (Eisenack) Richardson, 1964

Dibolisporites tuberculatus Breuer & Steemans, 2013

Plate X, figs. 13-14

? 1988 *Dibolisporites echinaceous* (Eisenack) Richardson, 1964; Fombella Blanco, p. 35, pl. 3, fig. 3

2001 *Dibolisporites* cf. *eifeliensis* (Lanninger, 1968) McGregor, 1973; Gill, p. 35, pl. 1, fig. 13

Description: Amb circular to subcircular. Laesurae straight, extending from ¾ to the whole amb radius. An up to 4 μm equatorial thickening is sometimes observed. Curvaturae perfectae joining the tips of the laesurae are sometimes observed, often coincident with equator. Proximal surface laevigate. Distal surface bears an ornament of rounded granules and pointed spines. Well-preserved specimens may show slightly bulbous tips on the spines. These ornamental units are 2-3 µm high and separated by at least 1-2 µm.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Las Ventas-Entrago, Vozmediano, '120' and '598' localities.

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

Dibolisporites sp. A

Plate X, fig. 12

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

Dimensions: 60-70 µm. (1 specimen measured)

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

Occurrence: Found at the Aguasmestas-Pigüeña locality.

Genus ***Dictyotriletes*** Naumova ex Ishchenko, 1952

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

Dictyotriletes gorgoneus Cramer, 1966

Plate X, fig. 11

Description: Amb circular to subcircular. Trilete unclear, possibly extending to the equator. Proximal surface laevigate. Distal surface bears a reticulate ornament with muri up to 1 µm high and wide, enclosing irregularly shaped luminae 4-7 µm wide.

Dimensions: 38-40 µm. (1 specimen measured)

Remarks: Distinguished from *D.* cf. *hemeri* in this study by its rather more substantial looking muri and more irregularly shaped luminae. The figured specimen in Plate V, fig. 6 could be interpreted as having an interradially thickened wall, in the fashion of *Camarozonotriletes*, but the present author interprets this specimen as having a widely opened trilete mark, leaving the proximal exine gathered around the margins. Only a single specimen was found.

Occurrence: Found at the Playa del Tranqueru locality.

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

Dictyotriletes cf. *hemeri* Breuer & Steemans, 2013

Plate X, figs. 15-16

? 1988 *Cymatiosphaera magnata* Pilchler, 1971; Fombella Blanco, pl. 3, fig. 1

2001 *Dictyotriletes* cf. *emsiensis* (Allen 1965) McGregor 1973; Gill, p. 42, pl. 1, fig. 22

2001 *Dictyotidium* sp. B; Gill, p. 62, pl. 3, fig. 11

Description: Amb circular to subcircular or ovoid. Laesurae straight, sometimes accompanied by narrow labra along their length, extending from ½ to the whole amb radius.

Proximal surface laevigate. Distal surface bears a reticulate ornament with muri, ~1-2 µm high and wide, enclosing mostly polygonal luminae 2-6 µm wide. Small projections may occur at muri junctions.

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

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Las Ventas-Entrago, '598', Crémenes-Las Salas and Man member localities.

Previous records: *D. hemeri* is reported from the Eifelian to Givetian of Spain (Cramer, 1969a) and the late Eifelian to middle Givetian of Saudi Arabia (Breuer & Steemans, 2013).

Genus ***Emphanisporites*** McGregor, 1961

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

Emphanisporites annulatus McGregor, 1961

Plate XI, fig. 1

1966 *Emphanisporites annulatus* McGregor 1961; Cramer, p. 263, pl. III, fig. 63

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

2001 *Emphanisporites annulatus* McGregor, 1961; Gill, p. 43, pl. 2, fig. 1

Description: Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending from ¾ to the whole amb radius. 2 µm equatorial thickening observed. Proximal face bears interradial muri, 3-6 per sector. Distal surface bears a 2 µm annulus, positioned ⅗ of the distance to the equator, otherwise laevigate.

Dimensions: 28 (34) 45 µm. (5 specimens measured)

Remarks: This assignment is based on the more detailed description of the species from McGregor (1973). That description placed the distal annulus closer to the pole than observed here.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Vozmediano and Crémenes-Las Salas localities.

Previous records: Reported from Emsian to Tournaisian strata and with a worldwide distribution (Taylor et al., 2011).

Emphanisporites cf. *annulatus* McGregor, 1961 (var. A)

Plate XI, fig. 2

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. Laesurae accompanied by structures reminiscent of labra but positioned quite distant from the laesurae. 4-5 µm equatorial thickening observed. Proximal face bears interradial muri, 3-4 per sector. Distal surface bears a large annulus, otherwise laevigate.

Dimensions: 29 (41) 62 µm. (5 specimens measured)

Remarks: These specimens are questionably assigned to *E. annulatus* due to their very wide equatorial thickening and a structure accompanying the laesurae of uncertain origin.

Occurrence: Found at the San Pedro de Nora, Aleje and Crémenes-Las Salas localities.

Emphanisporites cf. *annulatus* McGregor, 1961 (var. B)

Plate XI, fig. 3

Description: Amb circular to subcircular. Monolete mark observed, extending to the equator. 3 µm equatorial thickening observed. Proximal face bears interradial muri, 6 in each half. Distal surface bears an annulus, otherwise laevigate.

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

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

Occurrence: Found at the San Pedro de Nora locality.

Emphanisporites annulatus ? McGregor, 1961

Plate XI, fig. 4

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending to the equator. 2 µm equatorial thickening observed. Proximal face bears interradial muri, 4-6 per sector. Distal surface may bear an annulus, otherwise laevigate.

Dimensions: 25 (33) 44 µm. (5 specimens measured)

Remarks: These specimens are questionably assigned to *E. annulatus* owing to their poor state of preservation.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora and Crémenes-Las Salas localities.

Emphanisporites augusta Fombella Blanco, 1988

Plate XI, fig. 5

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from ½ to ¾ of the amb radius. 1-2 µm equatorial thickening observed. Proximal face bears interradial muri, 2-3 per sector. Distal surface bears an ornament of microgranulae.

Dimensions: 33 (34) 35 µm. (2 specimens measured)

Remarks: The species as originally described is much larger than the specimens seen here, with a wider cingulum, but no other species to which these specimens could be attributed could be found.

Occurrence: Found at the Candás-Perán, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Puerto de Somiedo, Quejo, Huergas de Gordon, Vozmediano, Aleje and Crémenes-Las Salas localities.

Previous record: Reported from the Middle Devonian of Spain (Fombella Blanco, 1988).

Emphanisporites cf. *augusta* Fombella Blanco, 1988

Plate XI, fig. 8

Description: Amb circular to subcircular. Laesurae straight, extending from ½ to ⅔ of the amb radius. Proximal face bears interradial muri, 2 per sector. Distal surface bears an ornament of micrograpulae.

Dimensions: 28 (35) 45 µm. (6 specimens measured)

Remarks: These specimens lack the labra seen on the figured holotype of *E. augusta*.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Emphanisporites cf. *hoboksarensis* Lu, 1997

Plate XI, fig. 6

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. 2 µm equatorial thickening. Proximal face bears interradial muri, 2-3 per sector. Distal surface laevigate.

Dimensions: 26 (33) 38 µm. (4 specimens measured)

Remarks: The specimens seen here may have fewer interradial muri than the species as originally described, but no better identification could be found in the literature.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Huergas de Gordon localities.

Previous record: *E. hoboksarensis* is reported from the Givetian of China (Lu, 1997).

Emphanisporites cf. *laticostatus* Breuer & Steemans, 2013

Plate XI, fig. 9

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra, extending from ⅔ to ¾ of the amb radius. 1-3 µm equatorial thickening observed. Proximal face bears interradial muri, 2-4 per sector. Distal surface laevigate.

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

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

Occurrence: Found at the Playa del Tranqueru and San Pedro de Nora localities.

Previous records: *E. laticostatus* reported from the middle Givetian of Brazil (Breuer & Grahn, 2011) and the late Givetian to Frasnian of Tunisia and Saudi Arabia (Breuer & Steemans, 2013).

Emphanisporites mcgregorii Cramer, 1966

Plate XI, fig. 7

1969a *Emphanisporites McGregorii* Cramer; Cramer, p. 432, pl. I, fig. 13

2001 *Emphanisporites spinaeformis* Schultz, 1968; Gill, p. 45, pl. 2, fig. 4

Description: Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra, extending from ⅓ to the whole amb radius. 1-2 µm equatorial thickening observed. Proximal face bears interradial muri, 4-12 per sector and arranged parallel to one another, producing a distinct herringbone pattern. Distal surface laevigate.

Dimensions: 23 (35) 48 µm. (15 specimens measured)

Remarks: The description of McGregor (1961), restated by Cramer (1966), does not specify the number of interradial ridges this species should possess. The present author has included specimens with laesurae shorter than the radius in this species as this measurement varies in other members of the genus. The description of this species and that of *E. spinaeformis* Schultz, 1968 do not differ in their important characteristics and the synonymisation of the two by Breuer & Steemans (2013) is followed here.

Occurrence: Found at the Playa del Tranqueru, Sobrerriba-Santa-Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, '598' and Crémenes-Las Salas localities.

Previous records: Reported from the Lochkovian to Eifelian of Germany (Lanninger, 1968; Riegel, 1968; Schultz, 1968; Edalat, 1974; Steemans, 1989; Pflug & Prössl, 1991), the late Lochkovian to Emsian of France (Steemans, 1989; Moreau-Benoit, 1994) and Belgium (Steemans, 1989), the Pragian to late Givetian of Libya (Massa & Moreau-Benoit, 1976; Moreau-Benoit, 1979, 1989; Paris et al., 1985; Moreau-Benoit & Massa, 1988; Streel et al., 1988; Breuer & Steemans, 2013), the Pragian to middle Emsian of Poland (Turnau, 1986;

Turnau & Jakubowska, 1989), the Pragian to Givetian of Spain (Cramer, 1966, 1969a), the late Pragian to early Emsian of Brazil (Mendlowicz Mauller et al., 2007), the late Pragian to late Givetian of Saudi Arabia (Breuer & Steemans, 2013), the Emsian to early Eifelian of Bolivia (McGregor, 1984), the Emsian to Famennian of Algeria (Abdesselam-Rouighi, 1986; Moreau-Benoit et al., 1993), the late Emsian to early Frasnian of Tunisia (Breuer & Steemans, 2013), the early Givetian of Egypt (Schrank, 1987) and the Late Devonian to Tournaisian of Ireland (Naylor et al., 1977; Sleeman et al., 1978).

Emphanisporites cf. *micrornatus* Richardson & Lister, 1969 (var. A)

Plate XI, fig. 10

Description: Amb circular to subcircular. Laesurae straight, extending from ⅔ to the whole amb radius. Proximal face bears interradial muri, 7-8 per sector. Distal surface bears an ornament of microgranulae.

Dimensions: 30 (37) 45 µm. (11 specimens measured)

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

Occurrence: Found at the Candás-Perán, Veneros-Santoseso, San Pedro de Nora, Aguasmestas-Pigüeña, Puerto de Somiedo, Quejo, Huergas de Gordon, Aleje and Crémenes-Las Salas localities.

Previous records: *E. micrornatus* is reported from Lochkovian to Emsian strata and with a worldwide distribution (Taylor et al., 2011).

Emphanisporites cf. *micrornatus* Richardson & Lister, 1969 (var. B)

Plate XI, fig. 11

Description: Amb circular to subcircular. Monolete mark observed, extending to the equator. Proximal face bears interradial muri, 3-12 in each half. Distal surface bears an ornament of microgranulae.

Dimensions: 30 (35) 40 µm. (2 specimens measured)

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

Occurrence: Found at the San Pedro de Nora, Puerto de Somiedo and Crémenes-Las Salas localities.

Emphanisporites orbicularis Turnau, 1986

Plate XI, fig. 12

Description: Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending ⅔ of the amb radius. 1-2 µm equatorial thickening observed. Proximal face bears interradial muri, 3-8 per sector. Distal surface laevigate.

Dimensions: 22 (32) 50 µm. (16 specimens measured)

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora. Las Ventas-Entrago and Crémenes-Las Salas localities.

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

Emphanisporites cf. *orbicularis* Turnau, 1986 (var. A)

Plate XI, fig. 15

? 1966 *Emphanisporites erraticus* (Eisenack) 1944; Cramer, p. 263, pl. III, figs. 60, 61

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from ⅓ to ¾ of the amb radius. 2-5 µm equatorial thickening observed. Proximal face bears interradial muri, 3-5 per sector. Distal surface laevigate.

Dimensions: 22 (32) 50 µm. (48 specimens measured)

Remarks: These specimens are questionably assigned to *E. orbicularis* as they may have shorter trilete rays than specified in the original description.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Huergas de Gordon, Aleje, ‘120’, ‘598’, Crémenes-Las Salas and Man member localities.

Emphanisporites cf. *orbicularis* Turnau, 1986 (var. B)

Plate XI, fig. 14

Description: Amb circular to subcircular. Laesurae straight, extending from ⅓ to ⅔ of the amb radius. 2 µm equatorial thickening observed. Proximal face bears interradial muri, 6-10 per sector. Distal surface laevigate.

Dimensions: 29 (39) 58 µm. (6 specimens measured)

Remarks: These specimens are questionably assigned to *E. orbicularis* as they have shorter trilete rays and more interradial muri than specified in the original description.

Occurrence: Found at the Playa del Tranqueru and San Pedro de Nora localities.

Emphanisporites cf. *orbicularis* Turnau, 1986 (var. C)

Plate XI, fig. 13

Description: Amb circular to subcircular. Monolete mark observed, extending from ½ to ¾ of the amb radius. Proximal face bears interradial muri, 8-15 in each half. Distal surface laevigate.

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

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

Occurrence: Found at the Playa del Tranqueru and Man member localities.

Emphanisporites protoannulatus Rodríguez, 1978a

Plate XI, fig. 16

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending ⅔ of the amb radius. Proximal face bears interradial muri, 3-4 per sector. Distal surface bears a 3-4 µm annulus, otherwise laevigate.

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

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

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

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

Emphanisporites rotatus McGregor emend. McGregor, 1973

Plate XI, fig. 17

1966 *Emphanisporites rotatus* McGregor 1961; Cramer, p. 262, pl. III, figs. 57, 58, 62

1969a *Emphanisporites rotatus* McGregor; Cramer, p. 431

1969a *Emphanisporites obscurus* McGregor; Cramer, p. 432

1969a *Emphanisporites robustus* McGregor; Cramer, p. 434, pl. I, fig. 11

1988 *Emphanisporites rotatus* McGregor; Fombella Blanco, pl. 2, fig. 3

2001 *Retusotriletes actinomorphus* Chibrikova, 1962; Gill, p. 26, pl. 1, fig. 4

2001 *Emphanisporites rotatus* (McGregor, 1961) McGregor, 1973; Gill, p. 44, pl. 2, figs. 2, 3

2001 cf. *Emphanisporites cf. micrornatus* Richardson & Lister 1969; Gill, p. 46, pl. 2, fig. 5

Description: Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending from ¾ to the whole amb radius. 1-4 µm equatorial thickening observed. Proximal face bears interradial muri, 3-10 per sector. Polar confluence of these muri may produce a darkened area. Distal surface laevigate.

Dimensions: 21 (34) 52 µm. (144 specimens measured)

Remarks: This species has a rather broad original description, leading to this assemblage being very varied in relation to other members of the genus.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Huergas de Gordon, Vozmediano, Aleje, '120', '598', '599', Crémenes-Las Salas and Man member localities.

Previous records: Reported from Lochkovian to Tournaisian strata and with a worldwide distribution (Taylor et al., 2011).

Emphanisporites cf. *rotatus* McGregor emend. McGregor, 1973 (var. A)

Plate XI, fig. 18

Description: Amb circular to subcircular. Laesurae straight, extending from ⅔ to the whole amb radius. Proximal face bears interradial muri, 8-11 per sector. Distal surface laevigate.

Dimensions: 28 (37) 48 µm. (17 specimens measured)

Remarks: These specimens are distinguished from *E. rotatus* in this study by possessing more interradial muri.

Occurrence: Found at the San Pedro de Nora, Crémenes-Las Salas and Man member localities.

Emphanisporites cf. *rotatus* McGregor emend. McGregor, 1973 (var. B)

Plate XI, fig. 19

Description: Amb circular to subcircular. Monolete mark observed, extending to the equator. 1-3 µm equatorial thickening observed. Proximal face bears interradial muri, 6-9 in each half. Distal surface laevigate.

Dimensions: 23 (37) 48 µm. (4 specimens measured)

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Las Ventas-Entrago localities.

Emphanisporites sp. A

Plate XI, fig. 20

Description: Amb circular to subcircular. Laesurae straight, extending ½ of the amb radius. Proximal face bears interradial muri, 2-4 per sector. Distal surface bears a large annulus and an ornament of microgranulae.

Dimensions: 33 (39) 51 µm. (3 specimens measured)

Remarks: This species is similar to *E. augusta* except for its possession of an annulus and to *E. annulatus* except for its distal ornament.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Emphanisporites sp. B

Plate XI, fig. 21

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

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

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

Occurrence: Found at the San Pedro de Nora, Aguasmestas-Pigüeña, Puerto de Somiedo, Quejo and Crémenes-Las Salas localities.

Emphanisporites sp. C

Plate XI, fig. 22

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. Proximal face bears interradial muri, 2-4 per sector. Distal surface bears an ornament of microgranulae.

Dimensions: 28 (39) 52 µm. (16 specimens measured)

Remarks: This species is similar to *E. augusta* except for its lack of labra. This species possesses more interradial muri than *E.* cf. *augusta* in this study.

Occurrence: Found at the Candás-Perán, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Huergas de Gordon, Aleje and Crémenes-Las Salas localities.

Emphanisporites sp. D

Plate XI, fig. 26

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending ⅔ of the amb radius. Proximal face bears interradial muri, 8 per sector. Distal surface bears an ornament of microgranulae.

Dimensions: 34 (37) 40 µm. (4 specimens measured)

Remarks: This species possesses more interradial muri than *E. micrornatus*.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Emphanisporites sp. E

Plate XI, fig. 24

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from ½ to ⅔ of the amb radius. Proximal face bears interradial muri, 4-6 per sector. Distal surface bears an ornament of microgranulae.

Dimensions: 26 (36) 43 µm. (8 specimens measured)

Remarks: This species has shorter trilete rays than *E. micrornatus*.

Occurrence: Found at the Candás-Perán, Veneros-Santoseso, Aguasmestas-Pigüeña, Quejo, Huergas de Gordon, Vozmediano, Aleje and Crémenes-Las Salas localities.

Emphanisporites sp. F

Plate XI, fig. 27

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending ¾ of the amb radius. Proximal face bears interradial muri, 6-7 per sector and arranged parallel to one another, producing a distinct herringbone pattern. Distal surface bears an ornament of microgranulae.

Dimensions: 25 (39) 53 µm. (7 specimens measured)

Remarks: This species has the herringbone muri pattern of *E. mcgregorii* but possesses a distal ornament. This species possesses labra and shorter trilete rays than *E.* sp. B.

Occurrence: Found at the Aguasmestas-Pigüeña, Geras, Huergas de Gordon, Aleje and Crémenes-Las Salas localities.

Emphanisporites sp. G

Plate XI, fig. 23

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending to the equator. Proximal face bears interradial muri, 3 per sector. Distal surface bears an ornament of microgranulae.

Dimensions: 25 (37) 45 µm. (8 specimens measured)

Remarks: This species is similar to *E. augusta* except for its longer trilete rays.

Occurrence: Found at the Candás-Perán, Veneros-Santoseso, Aguasmestas-Pigüeña, Puerto de Somiedo, Quejo, Huergas de Gordon, Aleje and Crémenes-Las Salas localities.

Emphanisporites sp. H

Plate XI, fig. 25

1988 *Emphanisporites cf. anulatus* McGregor 1961; Fombella Blanco, pl. 2, fig. 4

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending ⅔ to the whole amb radius. Proximal face bears interradial muri, 4-5 per sector. Distal surface bears an annulus, positioned from ½ to ⅔ of the distance to the equator, with an ornament of micrograngulae.

Dimensions: 35 (38) 40 µm. (2 specimens measured)

Remarks: This species is similar to *E. annulatus* except for its distal ornament and to *E. augusta* except for its possession of an annulus and longer trilete rays.

Occurrence: Found at the Huergas de Gordon and Crémenes-Las Salas localities.

Genus ***Geminospora*** Balme, 1962

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

Geminospora lemurata Balme emend. Playford, 1983

Plate XII, figs. 1-6

Description: Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to perimeter of intexine. Exoexine extends past intexine perimeter by ¼ to ⅓ the radius of the intexine. Exoexine markedly thick, always over 1 µm. Proximal surface laevigate. Exoexine distally sculptured with densely distributed microgranulae up to 1 µm high.

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

Remarks: The specimens described here correspond to the specific designation in all respects. They are distinguished from species of *Grandispora* by the thickness of their exoexine and by their laesurae always extending to the perimeter of the intexine.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: Reported from Givetian to Frasnian strata and with a worldwide distribution (Breuer & Steemans, 2013).

Geminospora cf. *svalbardiae* (Vigran) Allen, 1965

Plate XII, figs. 7-9

? 1988 *Geminospora cf. tuberculata* (Kedo) Allen 1965; Fombella Blanco, pl. 2, fig. 7

2001 *Grandispora cf. gabesensis* Loboziak & Streel, 1989; Gill, p. 49, pl. 2, fig. 6

Description: Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to perimeter of intexine. Exoexine extends past intexine perimeter by ¼ to ⅓ the radius of the intexine. Exoexine markedly thick, always over 1 µm. Proximal surface laevigate. Exoexine distally sculptured with densely distributed granulae and occasional spines 1-4 µm high.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora and Aguasmestas-Pigüeña localities.

Previous records: *G. svalbardiae* is reported from Pragian to late Famennian strata and with an almost worldwide distribution, being absent from Australia.

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

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

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

Plate XIII, fig. 6

1953 *Hymenozonotriletes argutus* Naum. Sp. n.; Naumova, pl IX, fig. 9

1966 *Hymenozonotriletes argutus* "II" Naumova, 1953; Cramer, p. 46, pl III: 73

non. 1969 *Calyptosporites argutus* (Naumova) New Combination; Cramer, p. 436, pl III, fig. 33

p.1969 *Calyptosporites* cf. *deliquescens* (Naumova) New Combination; Cramer, p. 438, pl III, fig. 32

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

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

Remarks: This taxon has a complicated taxonomic history. Naumova (1953) described and illustrated two new species, very different in structure and morphology, but called them both *Hymenozonotriletes argutus* sp. n. These were described as spore number 73 (p. 41) and spore number 169 (p. 67), illustrated as line figures in her Plate IV, fig. 10 and Plate IX, fig. 9, respectively. Cramer (1966) identified both species in the Spanish Middle Devonian, referring to them as *Hymenozonotriletes argutus* "I" Naumova, 1953 and *Hymenozonotriletes argutus* "II" Naumova, 1953 with I referring to spore number 73 and II referring to spore number 169. Subsequently Cramer (1969) placed *Hymenozonotriletes argutus* "II" Naumova, 1953 in the genus *Calyptosporites* as a new combination: *Calyptosporites* (*Hymenozonotriletes*) *argutus* (Naumova) Cramer, 1969 (although it should be noted that Cramer appears to have inadvertently mislabelled his plates and Plate III, fig. 32 almost certainly represents this taxon rather than Plate III, fig. 33). In this work, Cramer (1966)'s *Hymenozonotriletes argutus* "I" Naumova, 1953 has been included in synonymy with *Grandispora* cf. *inculta* Allen, 1965 (see below). Cramer (1966)'s *Hymenozonotriletes argutus* "II" Naumova, 1953 (*Calyptosporites* (*Hymenozonotriletes*) *argutus* (Naumova) Cramer, 1969) has also been positively identified but placed with the genus *Grandispora*. This follows recent taxonomic practise for Devonian spores that considers the genus *Calyptosporites* to be a junior synonym of *Grandispora* (e.g. Playford 1971; Breuer & Steemans 2013). The species is here named *'Grandispora' (Hymenozonotriletes) argutus* Naumova, 1953 *sensu* Cramer (1969) because the author is not able to propose a formal new combination. This is because comparison with Naumova's material is tentative as she provided only line drawings of spores (as also noted by Cramer (1969)) and because Naumova (1953)'s first described species has priority over the second described species of the same name, the one used here.

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

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

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

Grandispora douglastownensis ? McGregor, 1973

Plate XII, fig. 10

? 1966 *Hymenozonotriletes* cf. *eximius* ? Naumova 1953; Cramer, p. 268, fig. 6: 1

1966 *Hymenozonotriletes* cf. *deliquescens* ? Naumova 1953; Cramer, p. 269, pl. IV, fig. 77

? 1969a *Calyptosporites argutus* (Naumova) *New Combination*; Cramer, p. 436, pl. III, fig. 33

p.1969a *Calyptosporites* cf. *deliquescens* (Naumova) New Combination; Cramer, p. 438, pl. II, fig. 26

Description: Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending from ⅔ to the whole radius of intexine. Exoexine extends past intexine perimeter by ⅓ to ⅔ the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with faint microgranulae and occasional, isolated, large granulate and spinose elements with some distortion of the exoexine around them.

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

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

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Previous records: *G. douglastownensis* is reported from the Emsian to Givetian of Canada (McGregor, 1973; McGregor & Camfield, 1976, 1982), the Emsian to middle Givetian of Libya (Moreau-Benoit, 1989; Ghavidel-Syooki, 2003), the late Emsian to early Eifelian of Algeria (Moreau-Benoit et al., 1993), the late Emsian to Eifelian of Libya (Breuer & Steemans, 2013), the late Emsian to early Givetian of Brazil (Loboziak et al., 1992; Melo & Loboziak, 2003), the Eifelian of Germany (Loboziak et al., 1990) and Tunisia (Breuer & Steemans, 2013), the Givetian of France (Loboziak & Streel, 1980), the Eifelian to late

Givetian of Saudi Arabia (Breuer & Steemans, 2013) and the Frasnian of Bolivia (Perez-Leyton, 1990).

Grandispora cf. *inculta* Allen, 1965

Plate XII, fig. 11

? 1966 *Hymenozonotriletes argutus* "I" Naumova 1953; Cramer, p. 268, pl. IV, fig. 74

1966 *Hymenozonotriletes narancae* Cramer; p. 269, pl. III, fig. 70

cf. 1969a *Calyptosporites optivus* (Chibrikova) Allen; Cramer, p. 440, pl. IV, fig. 38

p.1969a *Calyptosporites microspinosus* (Richardson) Richardson; Cramer, p. 439, pl. III, figs. 35, 36

p.1969a *Calyptosporites* (?) *narancae* (Cramer) New Combination; Cramer, p. 439

? 1988 *Grandispora sp.C* Paris et al. 1985; Fombella Blanco, pl. 1, fig. 5, pl. 2, fig. 1

Description: Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, may be accompanied by labra or triradiate folds, extending from ⅔ the radius of the intexine to the spore equator. Exoexine extends past intexine perimeter by ⅕ to ¾ the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with micrograņulae, larger granulae and small spines.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Vozmediano, Aleje, '120', '598' and Crémenes-Las Salas localities.

Previous records: *G. inculta* is reported from the Emsian to middle Givetian of Libya (Paris et al., 1985; Streel et al., 1988; Moreau-Benoit, 1989), the Emsian to Frasnian of Algeria

(Boumendjel et al., 1988; Moreau-Benoit et al., 1993), the Eifelian to Givetian of Morocco (Rahmani-Antari & Lachkar, 2001), the late Eifelian of Shetland (Marshall, 1988), the late Eifelian of Russia (Avkhimovitch et al., 1993), the late Eifelian to early Givetian of Canada (McGregor & Camfield, 1982), the late Eifelian to Givetian of Poland (Turnau, 1996; Turnau & Racki, 1999), the Givetian of Spitsbergen (Allen, 1965), the Givetian to early Frasnian of Brazil (Loboziak et al., 1988), the early Givetian of Libya, the late Givetian of Saudi Arabia (Breuer & Steemans, 2013), the late Givetian to late Frasnian of France (Brice et al., 1979; Loboziak & Streel, 1980, 1988; Loboziak et al., 1983) and the Frasnian of Bolivia (Perez-Leyton, 1990).

Grandispora permulta (Daemon) Loboziak et al., 1999

Plate XIII, fig. 1

1988 *Grandispora sp. A*, Paris et al. 1985; Fombella Blanco, pl. 1, fig. 1

cf. 2001 *Grandispora permulta* (Daemon, 1974) Loboziak, Streel & Melo, 1999; Gill, p. 51, pl. 2, fig. 7

Description: Amb subcircular to slightly subtriangular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to the spore equator. Exoexine extends past intexine perimeter by ⅓ the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with microgranulae.

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

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

Occurrence: Found at the Candás-Perán and Crémenes-Las Salas localities.

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

Grandispora protea (Naumova) Moreau-Benoit, 1980

Plate XIII, fig. 2

non 1966 *Hymenozonotrilates* cf. *domanicus* Naumova 1953; Cramer, p. 268, pl. III, fig. 71

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

2001 *Grandispora macrotuberculata* McGregor, 1973; Gill, p. 50, pl. 2, fig. 8

Description: Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to the spore equator. Exoexine extends past intexine perimeter by ⅔ to the whole of the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with very widely separated granulae and spines up to 3 µm high.

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

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

Occurrence: Found at the San Pedro de Nora, Las Ventas-Entrago and Vozmediano localities.

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

Grandispora cf. *stolidota* (Balme) Breuer & Steemans, 2013

Plate XIII, fig. 3

2001 *Grandispora sp.A*; Gill, p. 52, pl. 2, fig. 9

Description: Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to the spore equator. Exoexine extends past intexine perimeter by a distance equal 1 to 1.5 times the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with microgranulae.

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

Remarks: This species is distinguished from other *Grandispora* species in this study by its much larger exoexine:intexine ratio. The present author uses this to refer the specimens provisionally to *G. stolidota*, though no intexine measurement is given in the original description and none of the complex, biform sculptural elements could be seen in these specimens.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: *G. stolidota* is reported from the late Eifelian to early Frasnian of Tunisia, Libya and Saudi Arabia (Breuer & Steemans, 2013) and the middle Givetian to early Frasnian of Australia (Balme, 1988; Grey, 1991).

Grandispora velata (Richardson) McGregor, 1973

Plate XII, fig. 12

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

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

Description: Amb subtriangular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending to the spore equator. Exoexine extends past intexine perimeter by ¾ the radius of the intexine. Proximal surface laevigate. Exoexine distally sculptured with microgranulae and small spinose ornament.

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

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Vozmediano and Crémenes-Las Salas localities.

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

Genus ***Granulatisporites*** Ibrahim emend. Potonié & Kremp, 1954

Type species: *Granulatisporites granulatus* Ibrahim, 1933

Granulatisporites concavus Breuer & Steemans, 2013

Plate XII, fig. 13

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

Description: Amb subtriangular with slightly concave interradial margins. Laesurae straight, extending to the equator. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

Dimensions: 28 (32) 36 µm. (3 specimens measured)

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

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Previous records: Reported from the middle Emsian to early Givetian of Libya the late Emsian to late Eifelian of Saudi Arabia (Breuer & Steemans, 2013).

Granulatisporites cf. *concavus* Breuer & Steemans, 2013 (var. A)

Plate XII, fig. 14

Description: Amb subtriangular with straight or slightly concave interradial margins. Laesurae straight, accompanied by narrow labra along their length, extending from ½ to ⅔ of the amb radius. Proximal surface laevigate. Distal surface bears an ornament of fine microgranulae.

Dimensions: 20 (24) 31 µm. (3 specimens measured)

Remarks: These specimens have shorter trilete rays than *G. concavus* as originally described.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Huergas de Gordon and Crémenes-Las Salas localities.

Granulatisporites cf. *concavus* Breuer & Steemans, 2013 (var. B)

Plate XII, fig. 15

Description: Amb subtriangular with straight interradial margins. Laesurae straight, extending from ¾ to the whole amb radius. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

Dimensions: 23 (33) 47 µm. (2 specimens measured)

Remarks: These specimens are doubtfully assigned to *G. concavus* as they lack the obvious concave interradial margins in most figured specimens of *G. concavus*, though the margins can be straight in the original description.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Las Ventas-Entrago, Huergas de Gordon and Crémenes-Las Salas localities.

Granulatisporites cf. *muninensis* Allen, 1965

Plate XII, fig. 16

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

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

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

Occurrence: Found at the Playa del Tranqueru, Aleje and Man member localities.

Previous records: *G. muninensis* is reported from Late Silurian to middle Tournaisian strata and with a worldwide distribution.

Genus ***Latosporites*** Potonié & Kremp, 1954

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

Latosporites sp. 1 Breuer & Steemans, 2013

Plate XII, fig. 17

Description: Amb subcircular to ovoid. Monolete mark observed, extending from ½ to the whole amb radius. Curvaturae perfectae often observed at the laesurae tips. Surface laevigate.

Dimensions: 24 (36) 62 µm. (18 specimens measured)

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

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, '120', Crémenes-Las Salas and Man member localities.

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

Latosporites cf. sp. 1 Breuer & Steemans, 2013

Plate XII, fig. 21

Description: Amb circular to subcircular. Monolete mark observed, extending from ½ to ⅔ of the amb radius. Surface laevigate.

Dimensions: 35 (38) 41 µm. (2 specimens measured)

Remarks: These specimens have a shorter monolete mark than originally described for the species and lack curvaturae.

Occurrence: Found at the San Pedro de Nora locality.

Genus ***Planisporites*** (Knox) Potonié & Kremp, 1954

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

Planisporites cf. *minimus* McGregor, 1960

Plate XII, fig. 18

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

1969a *Rhabdosporites prosperus* (Cramer) New Combination; Cramer, p. 443, pl. II, figs. 21, 23, 24, 25

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

Description: Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending from ⅓ to the whole amb radius. 1-3 µm equatorial thickening observed. Proximal surface laevigate. Distal surface bears an ornament of micrograanulae.

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

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Veneros-Santoseso, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Quejo, Huergas de Gordon, Vozmediano, Aleje, '120', '598', '599', '600', Crémenes-Las Salas and Man member localities.

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

Genus ***Raistrickia*** Schopf et al. emend. Potonié & Kremp, 1954

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

Raistrickia ? sp. A

Plate XIII, fig. 4

Description: Amb circular to subcircular. Laesurae straight, extending ½ of the amb radius. Possible 4 µm wide equatorial thickening observed. Proximal surface laevigate. Distal surface bears an ornament of granulae and spines up to 5 µm high, often narrower than they are tall and terminating in a pointed, rounded or flat-topped tip. Some of these flattened tips develop into a bifurcation.

Dimensions: 49 (59) 66 µm. (2 specimens measured)

Remarks: This species is tentatively assigned to the genus *Raistrickia* based on its varied ornament including flat-topped elements. No directly comparable species could be obtained from the literature.

Occurrence: Found at the San Pedro de Nora locality.

Genus ***Retusotriletes*** Naumova emend. Streel, 1964

Type species: *Retusotriletes simplex* Naumova, 1953

Retusotriletes atratus Breuer & Steemans, 2013

Plate XII, fig. 19

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. Proximal face bears subtriangular, thickened regions in each interradial area, not touching the laesurae and extending up to ⅔ of the distance to the equator. Distal surface laevigate.

Dimensions: 33 (40) 54 µm. (3 specimens measured)

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

Occurrence: Found at the Playa del Tranqueru, '120' and '598' localities.

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

Retusotriletes cf. *atratus* Breuer & Steemans, 2013

Plate XII, fig. 20

Description: Amb circular to subcircular. Laesurae straight, extending ½ of the amb radius. Possible 2-3 µm wide equatorial thickening observed. Proximal face bears a very faint, subcircular thickened region extending up to ⅔ of the distance to the equator. Distal surface laevigate.

Dimensions: 34 (41) 48 µm. (2 specimens measured)

Remarks: This specimen is doubtfully assigned to this species as its proximal thickened area is very indistinct and its trilete rays are rather shorter than originally described.

Occurrence: Found at the San Pedro de Nora locality.

Retusotriletes goensis Lele & Streel, 1969

Plate XIII, fig. 5

Description: Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending from ½ to the whole amb radius. Curvaturae perfectae sometimes observed joining the laesurae tips. Proximal surface bears an apical, subcircular to subtriangular thickened area extending from ~⅓ to ½ of the distance to the equator. Distal surface laevigate.

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

Remarks: Labra accompanying the laesurae are not always mentioned in descriptions of this species, though they have been figured (Breuer, 2008; Breuer & Steemans, 2013). These specimens bear a resemblance to *Concentricosporites sagittarius* (Rodríguez) Rodríguez González, 1983, though they have no obvious crassitude and a diffuse outer margin to their thickened area, as opposed to the hard edge seen in *C. sagittarius*.

Occurrence: Found at the Playa del Tranqueru, Veneros-Santoseso, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, '598', Crémenes-Las Salas and Man member localities.

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

Retusotriletes cf. *microgranulatus* ? (Vigran) Streel, 1967

Plate XIII, fig. 7

2001 *Retusotriletes microgranulatus* (Vigran, 1964) Streel 1967; Gill, p. 27, pl. 1, fig. 5

Description: Amb circular to subcircular. Laesurae straight, extending slightly over ½ of the amb radius. Proximal surface bears an apical, subcircular thickened area extending ⅖ of the distance to the equator. Distal surface bears an ornament of fine microgranulae.

Dimensions: 50 (61) 80 µm. (2 specimens measured)

Remarks: The species as originally described is distally infragranulate; this could not be determined with certainty in the specimens recovered here.

Occurrence: Found at the Candás-Perán and Veneros-Santoseso localities.

Previous records: *R* cf. *microgranulatus* is reported from the Pragian to early Emsian of France (Le Hérissé, 1983), the late Pragian to early Givetian of Libya (Massa & Moreau-Benoit, 1976; Lejal-Nicol & Moreau-Benoit, 1978, 1979, Moreau-Benoit, 1979, 1989), the early Emsian of Germany (Moreau-Benoit & Kremer, 1985), the Emsian to Late Devonian of Belgium (Streel, 1967) and the Frasnian of Spitsbergen (Vigran, 1964).

Retusotriletes pychovii Naumova, 1953

Plate XIV, fig. 1

1969a *Retusotriletes pychovii* Naumova *major* Naumova; Cramer, p. 430, pl. I, figs. 3, 7

Description: Amb circular to subcircular. Laesurae straight, extending from ½ to ¾ of the amb radius. Laesurae sometimes accompanied by thickened areas either side, possibly related to the opening of the laesurae. Very prominent, thickened curvaturae perfectae observed, joining the tips of the laesurae and producing an obvious trefoil shape. 1-2 µm equatorial thickening observed. Surface laevigate.

Dimensions: 30 (43) 50 µm. (4 specimens measured)

Remarks: These specimens have been assigned to this species based on their strongly pronounced curvaturae. Thickened areas around the laesurae have not previously been described but this is thought to be an artefact of germination in this assemblage. The specimens show a marked outward resemblance to *Scylaspora rugulata* (Riegel) Breuer et al., 2007 but they lack that species' proximal ornament.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Las Ventas-Entrago and Crémenes-Las Salas localities.

Previous records: Reported from Přídolí to Anisian strata and with a worldwide distribution.

Retusotriletes cf. *pychovii* Naumova, 1953

Plate XIV, fig. 2

Description: Amb circular to subcircular. Laesurae straight, extending from ½ to ⅔ of the amb radius. Laesurae sometimes accompanied by thickened areas either side, possibly related to the opening of the laesurae. Prominent, thickened curvaturae perfectae observed, joining the tips of the laesurae and producing an obvious trefoil shape. Proximal surface laevigate. Distal surface bears an ornament of fine micrograndulae.

Dimensions: 31 (48) 61 µm. (7 specimens measured)

Remarks: These specimens have been doubtfully assigned to *R. pychovii* owing to their distal ornament.

Occurrence: Found at the Candás-Perán, San Pedro de Nora, Vozmediano and Crémenes-Las Salas localities.

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

Plate XIV, fig. 4

1969a *Retusotriletes barbutus* Cramer; Cramer, p. 430

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

2001 *Retusotriletes rotundus* (Streel, 1964) Lele & Streel 1969; Gill, p. 28, pl. 1, fig. 6

Description: Amb circular to subcircular. Laesurae straight, extending from ½ to the whole amb radius. Curvaturae perfectae observed joining the tips of the laesurae. 1-4 µm equatorial thickening observed. Proximal surface bears an apical, subcircular to subtriangular thickened area with a thinner, lighter area at the proximal pole, sometimes giving the appearance of an annulus. Distal surface laevigate or with an ornament of fine microgranulae.

Dimensions: 23 (45) 63 µm. (12 specimens measured)

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, Sobrerriba-Santa Eufemia, San Pedro de Nora, Aguasmestas-Pigüeña, Huergas de Gordon and Crémenes-Las Salas localities.

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

Retusotriletes cf. *rotundus* (Streel) Streel emend. Lele & Streel, 1969

Plate XIV, fig. 5

Description: Amb circular to subcircular. Laesurae straight, extending ⅓ of the amb radius. Proximal surface bears an apical, subtriangular thickened area with a thinner, lighter area at the proximal pole. Distal surface bears an ornament of fine microgranulae.

Dimensions: Dimensions: 29 (39) 51 µm. (2 specimens measured)

Remarks: These specimens have shorter trilete rays than the species as originally described.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Puerto de Somiedo, Huergas de Gordon, Vozmediano, Aleje and Crémenes-Las Salas localities.

Retusotriletes semizonalis McGregor, 1964

Plate XIV, fig. 3

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from ⅔ to ¾ of the amb radius. Prominent curvaturae perfectae observed joining the tips of the laesurae. Proximal surface laevigate. Distal surface bears an ornament of fine microgranulae.

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

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

Occurrence: Found at the Candás-Perán, San Pedro de Nora, Las Ventas-Entrago, Puerto de Somiedo, Huergas de Gordon and Crémenes-Las Salas localities.

Previous records: An often-reported taxon reported from late Pragian to early Famennian strata from North America, China and Europe.

Retusotriletes tenerimedium Chibrikova, 1959

Plate XIII, fig. 8

Description: Amb circular to subcircular. Laesurae straight, possibly accompanied by narrow labra, extending ⅔ of the amb radius. Proximal surface bears a poorly delimited, apical, subtriangular thickened area 4-5 µm wide with a thinner, lighter area at the proximal pole. Distal surface bears an ornament of fine microgranulae.

Dimensions: 28 (41) 52 µm. (4 specimens measured)

Remarks: This species is distinguished from *R. rotundus* in this assemblage by the more diffuse margins of its thickened area, which is positioned nearer the equator.

Occurrence: Found at the Playa del Tranqueru and Crémenes-Las Salas localities.

Previous records: Reported from the late Pragian to late Emsian of Saudi Arabia (Breuer & Steemans, 2013), the Emsian of Germany (Schultz, 1968), the late Emsian of Tunisia (Breuer & Steemans, 2013), the late Emsian to early Eifelian of Russia (Avkhimovitch et al., 1993) and the middle Givetian of Libya (Breuer & Steemans, 2013).

Retusotriletes triangulatus (Streel) Streel, 1967

Plate XIV, fig. 6

? 1988 *Retusotriletes triangulatus* (Streel) Streel 1967; Fombella Blanco, pl. 2, fig. 2

Description: Amb circular to subcircular. Laesurae straight, extending from ⅓ to ½ of the amb radius. Curvaturae perfectae observed joining the tips of the laesurae. 2-3 µm equatorial thickening observed. Proximal surface bears an apical, subtriangular thickened area with concave sides, extending ½ of the distance to the equator. Distal surface laevigate.

Dimensions: 25 (43) 70 µm. (63 specimens measured)

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

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Huergas de Gordon, '120', '598', '599', Crémenes-Las Salas and Man member localities.

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

Retusotriletes cf. *triangulatus* (Streel) Streel, 1967

Plate XIV, fig. 10

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra, extending to the equator. Proximal surface bears an apical, subtriangular thickened area with straight sides, extending ~ ½ of the distance to the equator. Distal surface bears an ornament of microgranulae.

Dimensions: 36 (49) 69 µm. (5 specimens measured)

Remarks: These specimens are doubtfully assigned to *R. triangulatus* due to their distal ornament and possession of labra.

Occurrence: Found at the San Pedro de Nora and Crémenes-Las Salas localities.

Retusotriletes sp. A

Plate XIII, fig. 9

Description: Amb circular to subcircular. Laesurae straight, accompanied by narrow labra along their length, extending from ½ to ¾ of the amb radius. Curvaturae sometimes observed at the tips of the laesurae. Equatorial thickening observed, usually 2-3 µm wide but occasionally up to 6 µm. Surface laevigate.

Dimensions: 26 (41) 57 µm. (9 specimens measured)

Remarks: This species is referable to *Retusotriletes* due to its curvaturae, though it lacks other diagnostic characters that might give a specific identification.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

Retusotriletes sp. B

Plate XIV, fig. 7

Description: Amb circular to subcircular. Laesurae straight, extending from ½ to ⅗ of the amb radius. Curvaturae sometimes observed at the tips of the laesurae. 1-6 µm equatorial thickening observed. Surface laevigate.

Dimensions: 44 (49) 52 µm. (2 specimens measured)

Remarks: This species is referable to *Retusotriletes* due to its curvaturae. Distinguished from *R.* sp. A by its lack of labra.

Occurrence: Found at the Playa del Tranqueru locality.

Retusotriletes sp. C

Plate XIV, fig. 8

Description: Amb circular to subcircular. Laesurae straight, extending to the equator. Curvaturae observed at the tips of the laesurae. An area of thinner exine surrounds the laesurae with concave sides and rounded ends, extending ¾ of the distance to the equator. Proximal surface laevigate. Distal surface bears an ornament of microgranulae.

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

Remarks: This species is referable to *Retusotriletes* due to its curvaturae. No established species could be found in the literature with a similar thinned exinal structure.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru and '598' localities.

Genus ***Rhabdosporites*** Richardson emend. Marshall & Allen, 1982

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

Rhabdosporites minutus Tiwari & Schaarschmidt, 1975

Plate XIV, fig. 9

Description: Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, extending from ⅔ to the whole radius of the intexine. Exoexine just extends past intexine perimeter by 2-4 µm. Proximal surface laevigate. Exoexine distally sculptured with micrograngulae.

Dimensions: Exoexine: 25 (42) 58 µm. (10 specimens measured)

Remarks: Some specimens found here may have a rather coarser ornament than previously described for the species but no meaningful distinction or alternative identification was forthcoming. The species can bear a resemblance to *Apiculiretusispora brandtii*, though it has a completely detached exoexine.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Las Ventas-Entrago, Puerto de Somiedo, Huergas de Gordon, Vozmediano, Aleje, ‘120’, ’598’, Crémenes-Las Salas and Man member localities.

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

Rhabdosporites cf. *minutus* Tiwari & Schaarschmidt, 1975

Plate XIV, fig. 11

p.2001 *Rhabdosporites langii* (Eisenack, 1954); Gill, p. 48, pl. 1, fig. 19, 20

Description: Amb circular to subcircular. Cavate. Exoexine attached proximally, detached equatorially and distally. Intexine forms distinct inner body. Laesurae straight, may be accompanied by narrow labra along their length, extending from ½ to ⅔ of the radius of the intexine. Exoexine just extends past intexine perimeter by 2-8 µm. Proximal surface laevigate. Exoexine distally sculptured with microgranulae.

Dimensions: Exoexine: 37 (60) 91 µm. (5 specimens measured)

Remarks: These specimens are distinguished from *R. minutus* by their shorter trilete rays, which may fall outside the specific assignment.

Occurrence: Found at the Candás-Perán, Playa del Tranqueru, San Pedro de Nora, Aguasmestas-Pigüeña, Vozmediano, '120' and Crémenes-Las Salas localities.

Genus ***Samarisporites*** Richardson, 1964

Type species: *Samarisporites orcadensis* (Richardson) Richardson, 1964

Samarisporites cf. *praetervisus* (Naumova) Allen, 1965

Plate XIV, fig. 12

2001 *Acinosporites sp. A*; Gill, p. 40, pl. 1, fig. 18

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

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

Remarks: The assignation of the specimens seen here to *S. praetervisus* is dubious owing to their poor preservation and rare preservation of exine remnants. The distal ornament and size range of these specimens is the basis of their identification.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Quejo and Crémenes-Las Salas localities.

Previous record: *S. praetervisus* is reported from the Eifelian to middle Givetian of Libya (Paris et al., 1985; Streel et al., 1988; Moreau-Benoit, 1989; Breuer & Steemans, 2013) and Tunisia (Breuer & Steemans, 2013), the late Eifelian to early Givetian of Brazil (Melo &

Loboziak, 2003), the early Givetian of Algeria (Boumendjel et al., 1988) and the Givetian of Saudi Arabia (Breuer & Steemans, 2013) and Spitsbergen (Allen, 1965).

Genus ***Verrucosisporites*** Ibrahim emend. Smith, 1971

Type species: *Verrucosisporites verrucosus* (Ibrahim) Ibrahim, 1933

Verrucosisporites scurrus (Naumova) McGregor & Camfield, 1982

Plate XIV, fig. 13

1988 *Raistrickia aratra* Allen 1965; Fombella Blanco, pl. 2, fig. 5, pl. 4, fig. 4

2001 *Verrucosisporites premnus* Richardson, 1964; Gill, p. 38, pl. 1, fig. 17

2001 *Verrucosisporites scurrus* (Naumova, 1953) McGregor & Camfield 1982; Gill, p. 39, pl. 1, fig. 16

Description: Amb circular to subcircular. Laesurae straight, may be accompanied by narrow labra along their length, extending from ⅔ to the whole amb radius. 1-2 µm equatorial thickening observed. Proximal surface laevigate. Distal surface bears an ornament of micrograpulae and larger granulae up to 7 µm high, usually narrower than they are high, with rounded or flat tops. Some of these flattened tips develop into a short bifurcation.

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

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

Occurrence: Found at the Playa del Tranqueru, Aguasmestas-Pigüeña, Quejo and Crémenes-Las Salas localities.

Previous records: Reported from early Eifelian to early Famennian strata and with an almost worldwide distribution, being absent only from Asia (Breuer & Steemans, 2013).

Verrucosisporites tumulentis Clayton & Graham, 1974 *in* McGregor & Camfield, 1982

Plate XV, figs. 1-2

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

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

Remarks: The exoexine of the specimens seen here is sometimes detached, though this is interpreted as due to damage. A comparison can be drawn between these specimens and *Acinosporites tristratus* Breuer & Steemans 2013, but the specimens seen here have a primarily granule-based ornament rather than consisting primarily of ridges. This also precludes their confident assignment to *A. lindlarensis*. The specimens described here are very similar to specimens described by McGregor & Camfield (1982) which also exhibit biform ornament, not mentioned in Clayton & Graham's original description of *V. tumulentus*. Neither the specimens of McGregor & Camfield (1982), nor the ones described here are assignable to *V. tumulentus sensu stricto*, hence the precise assignation used here.

Occurrence: Found at the Playa del Tranqueru locality.

Previous records: *Verrucosisporites tumulentus* is reported from the Eifelian to middle Givetian (McGregor & Camfield, 1982) and late Famennian to early Tournaisian (Braman & Hills, 1992) of Canada, the Givetian to Frasnian of Ireland (Clayton & Graham, 1974) and the late Givetian to early Frasnian of the USA (Traverse & Schuyler, 1994) and Argentina (Ottone, 1996).

Genus ***Zonotriletes*** Luber & Waltz, 1938

Type species: None designated (Breuer & Steemans, 2013)

Zonotriletes armillatus Breuer et al., 2007

Plate XV, figs. 4-5

Description: Amb subcircular to subtriangular. Laesurae straight, extending from ¼ to the whole amb radius. 3-9 µm equatorial thickening observed. Proximal surface laevigate. Distal surface bears a 4-7 µm wide subcircular to subtriangular annulus, positioned around ½ to ⅗ of the distance to the equator, otherwise laevigate. A thin flange is present at the equatorial margin, extending by ¼ to ½ the radius of the main body of the spore interradially but narrowing opposite the trilete rays so as to disappear entirely.

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

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

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora, Puerto de Somiedo, '120', '598' and Crémenes-Las Salas localities.

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

Zonotriletes simplicissimus Breuer et al., 2007

Plate XV, fig. 6

Description: Amb subtriangular. Laesurae straight, extending to the equator. 5-10 µm equatorial thickening observed. Surface laevigate. A thin flange is present at the equatorial margin, extending by ¼ to ⅓ the radius of the main body of the spore interradially but narrowing opposite the trilete rays.

Dimensions: Main body: 41-43 µm; Flange: 51-54 µm. (1 specimen measured)

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

Occurrence: Found at the '120' locality.

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

Other forms

Tetrad

Plate XV, fig. 3

Description: A tetrad. Components ovoid and bearing an ornament of microgranulae and occasional small spines. Curvaturae very prominent, probably thickened.

Dimensions: Components: 25-45 µm. (4 specimens measured)

Remarks: One specimen recorded. This form was classified separately owing to its unusually shaped, prominent curvaturae.

Occurrence: Found at the San Pedro de Nora locality.

Unidentified spore A

Plate XV, figs. 7-10

Description: Amb ovoid. Laesurae observed, in an arrangement reminiscent of a monolete mark with ends that bifurcate around ⅓ of the distance to the equator. These secondary branches terminate a little over halfway between their point of branching and the equator. The entire laesural structure is surrounded by narrow labra. A structure at the perimeter of the spore may be an equatorial thickening of 2-6 µm thickness or a separated exoexine. Surface laevigate.

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

Remarks: This spore seems partially trilete, yet otherwise a mutant form. All specimens assigned to this form are consistent in their morphology, unusually for a mutant. The regularity of the laesural structure dissuades the present author from assigning the specimens to a cryptospore genus. The perimeter structure of this species is reminiscent of the surrounding bladder of the Carboniferous genus *Schulzospora* Kosanke, 1950.

Occurrence: Found at the Playa del Tranqueru, San Pedro de Nora and Crémenes-Las Salas localities.

7 - Interpretation & discussion

7.1 - Descriptions of logged sections

The below sections will interpret the sections logged in this study, referring to their lithological logs (figs. 26-29) and their quantitative palynomorph logs (figs. 30-32).

7.1.1 - Playa del Tranqueru

The Playa del Tranqueru section (fig. 26) was found to contain at least the majority of the thickness of the formation, represented by coarse to very fine grained sandstones with secondary deposits of siltstone, sometimes of a grain size intermediate between clay and silt grade. The strata dips to the NW at an angle between 39° and 63°. The upper boundary of the formation is with a large limestone, through which a tunnel has been bored for the light railway that formally existed on the site, interpreted as the Candás Fm. According to the published geological map (IGME, 2015) the SE boundary is an unconformable one with a Triassic formation, though the base of the logged section is with a large limestone dipping at the same angle as the sandstone and forming a small promontory, much like the overlying formation. This may be the older Moniello Fm. underlying the Naranco, in which case the Triassic formation presumably exists at the top of the promontory in an area not visited by the present author. All evidence suggests this is the case, therefore the entirety of the Naranco is represented here.

The formation here was clearly deposited with two distinct modes of deposition. The lower part, making up more than half the thickness observed here, is composed entirely of sandstone, while the upper part is heavily interbedded with finer siltstone beds. These fine beds make up around 15% of the thickness of this upper part of the formation. This dichotomy between the upper and lower parts of the formation has been previously described in a number of IGME memoria (Alonso et al., 1989; Heredia et al., 1989; Suárez Rodríguez et al., 1989) (see Chapter 2).

The palynomorph log for this site (fig. 30) displays obvious changes in the abundance and character of the palynomorph assemblage. The lowermost two samples are very poor, with few palynomorphs per gram. There follows a marked increase in the richness of the assemblage, dominated mostly by spores. Samples G and H show a less abundant assemblage, but with a large proportion of chitinozoans, almost entirely *Hoegisphaera* cf. *glabra*. The succeeding samples are dominated by spores before a phytoplankton resurgence in samples K and L. Samples N to S show large variations in overall abundance, including the richest sample in the log, broadly dominated by spores but with a strong phytoplankton component and a noticeable chitinozoan community. Samples T to AG show a generally spore-dominated assemblage persisted for the remainder of the sampled interval, with a significant increase in overall abundance around samples AC to AF, accompanied by a return of abundant *H.* cf. *glabra*.

7.1.2 - San Pedro de Nora

The section at San Pedro de Nora (fig. 27) is interpreted as representing the upper part of the formation, with the lower part and lower contact not exposed. The strata are composed of fine to coarse grained sandstone, making up the majority of the exposure's thickness, almost perfectly alternating with siltstone beds with one bed of even finer mudstone, dipping at an angle between 39° and 80° to the NW. The Naranco formation is here described as having a conformable contact with a Carboniferous limestone and shale formation (Martínez-Álvarez et al., 1973; IGME, 2015). This is better described as a disconformity, with the Late Devonian not represented in this area. In light of this, it is interesting that the uppermost sandstone bed seen here gradually transitions into a limestone. This sandstone bed bears similar ball and pillow structures to those seen slightly lower and is considered to belong to the Naranco by the present author. Either the transition is towards the overlying Candás Fm., not represented on published maps, or a small amount of Carboniferous sandstone appears just below the limestone and the precise point of disconformity was not seen when the section was logged.

This site's palynomorph log (fig. 31) is similar in many respects to that of the Playa del Tranqueru. It is clearly dominated by spores with, at times, a significant phytoplankton component. There is a sustained period of low abundance between samples I and O, punctuated by the rich sample L, during which chitinozoans are at their commonest in the section. The section as a whole is broadly similar in richness to the Playa del Tranqueru, also showing large differences in richness along the log. These two logs represent a relatively near-shore habitat, dominated by spores derived from the nearby land.

7.1.3 - Crémenes-Las Salas

The Crémenes-Las Salas section (fig. 28) represents an isolated portion of the Huergas Fm. The log cannot be said to definitely include an upper contact with the Portilla Fm. owing to a lack of exposure, while the exposure's basal contact is with the Carboniferous limestones of the Montaña Fm. This contact is marked as a faulted one on maps (IGME, 2015) and the contact is certainly sharp at outcrop. Again, the exposure consists mostly of sandstone with beds of siltstone, mudstone and shale interspersed within it. This exposure shows a greater number of mixed-lithology beds, with sand- and siltstone occurring together, as well as thick siltstone beds of a size not seen elsewhere. The strata dip at an angle of 55° to 82°

predominantly to the NE, though in one area a dip of 52° to the SW is observed. Considerable distortion is seen in a number of areas of the outcrop, reflecting the greater tectonism observed in the southern and eastern parts of the Devonian outcrop area. This exposure also exhibited onion-skin weathering in certain beds on quite a large scale, probably due to its SE-facing aspect.

This site is located in a different habitat than the other sampled sections, as reflected in its palynomorph log (fig. 32). The lower part of the section, up to sample S, is generally defined by a predominance of phytoplankton. They are superabundant in samples Y and T, producing the richest samples seen in this study by a large margin, driven almost entirely by the abundance of *Gorgonisphaeridium cumulatum*. This is a common and often abundant taxon but reaches its acme here. Following this period of phytoplankton dominance the rest of the log contains a majority of spores, possibly reflecting a fall in sea level and a progradation of the shoreline, placing it nearer this once further offshore site and facilitating the dispersal of land-derived spores. The assemblage also shows a gradual decline in richness, the reasons for which are unclear. Chitinozoans are never common in this section, with a small assemblage seen only in sample D.

7.1.4 - Mirantes de Luna

The section at Mirantes de Luna (fig. 29) is extremely fragmented, being composed of nine separate exposures. The lithology of the section is primarily sandstone and clay grade shale and mudstone with a significant component of limestone interspersed with the sandstones and mudstones at the section’s southern extremity. The deposits dip at an angle of 42° to 84°, initially to the south, then to the north in the exposure shown as lowest in fig. 29, reflecting the fact that this section exists in the nose of a syncline (see Chapter 2). The vertical scale in fig. 29 is not representative of the stratigraphic relationship between parts of this section; the Huergas formation is partially doubled here, with the two parts being mirror images of each other and the top of the formation is absent, being found at the very tip of the syncline and not exposed here. The frequency of faults and breaks in exposure prevent the confident reconstruction of the whole formation based on this section. The shale and mudstone layers in this exposure were found to be practically barren, with very few recognisable palynomorphs (see Appendix I), possibly related to the considerable tectonic distortion evident at this site.

7.2 - Palynomorph assemblage and biostratigraphy

This study has found a larger palynomorph assemblage than any previously described from the Naranco, Huergas and Gustalapiedra formations. Brief overviews of the three main fossil groups are given in Chapter 5. The below sections will compare the present assemblage with other contemporary ones and detail the biostratigraphical interpretations possible using this enhanced dataset, relating them to the conclusions arrived at in Chapter 4 with the previously known assemblage.

7.2.1 - Phytoplankton

The composition of the phytoplankton assemblage shows a lack of temporal variation. The sampled sections contain almost all species seen in the assemblage as a whole, with the only exceptions being *Comasphaeridium hirsutum* ?, *C. silesiense* ?, *Cymatiosphaera octoplana* ?, *Dictyotidium variatum*, *Ozotobrachion* cf. *furcillatus* and *Villosacapsula cazurra* ?. *D. variatum* and *O. furcillatus* occur across the stratigraphic range of the formation elsewhere, while the remaining species are all known exclusively from much older deposits. Separating any outcrop sites from the rest of the assemblage based on this data is difficult, given the close similarity of the individual assemblages. The sampled sections show few new taxa appearing through their length, with no pattern evident in which taxa occur later, with none becoming significant components of the assemblage.

7.2.1.1 - Assemblage comparison

A cluster analysis of Middle Devonian phytoplankton assemblages (see figure 33) shows the present community to be a sister group to all others except the Australian assemblage of Colbath (1990). Further Gondwanan assemblages are close to the present one, with most of

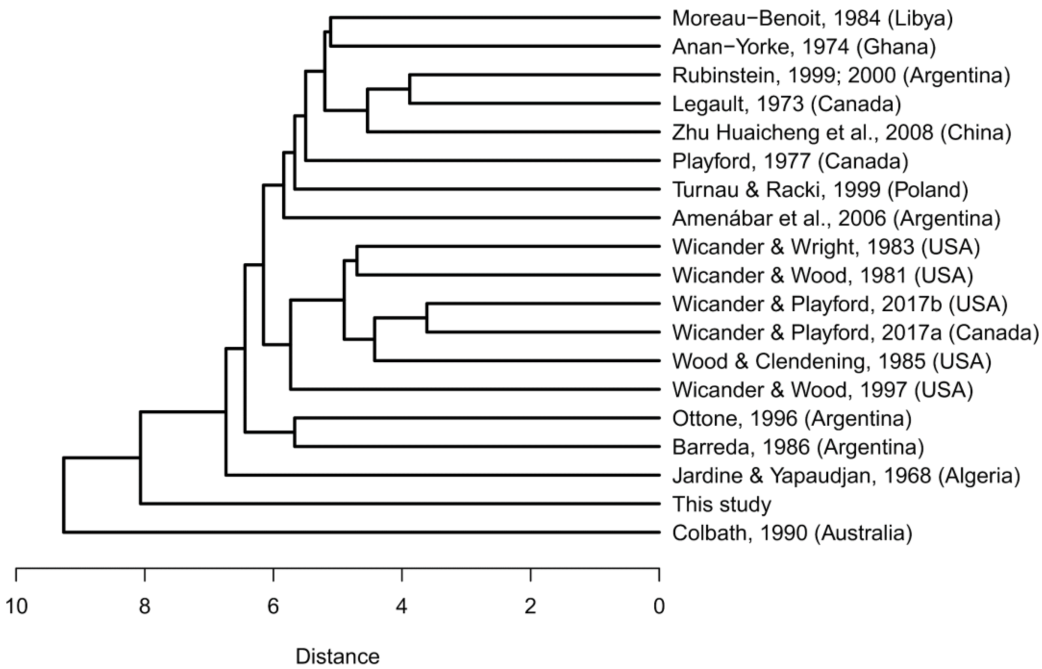


Figure 33. Dendrogram of a cluster analysis of Middle Devonian phytoplankton assemblages, with locations indicated. Distances calculated using Euclidean distance. Hierarchical clustering used the UPGMA method.

the Laurussian assemblages forming a distinct group within the dendrogram, though this could be related to authorship, with inconsistent use of taxonomic concepts between authors.

Those species this assemblage does share with others tend to be wide-ranging ones. Many of the species that are most-often reported in contemporary assemblages occur here, including *Duvernaysphaera angelae*, *Dictyotidium variatum*, *Navifusa bacilla*, *Polyedryxium pharaone* and *Stellinium micropolygonale*. However, various other widespread species are entirely absent here. Most notable among these are *Arkonites bilixus* and *Tyligmasoma alargada*, known from most of the studies mentioned in table 5, particularly in Laurussia, but not seen at all in this Spanish assemblage. The three areas of Laurussia, Gondwana and Spain seem to broadly share a suite of widespread taxa reported from many areas, with minor continental differences. Major differences are evident in the rare taxa that serve to characterise the assemblages. The Spanish assemblage is shown to be endemic to a large degree, with its characterising rare taxa differing from both Laurussia and Gondwana.

7.2.1.2 - Biostratigraphy

The use of phytoplankton in Devonian stratigraphy is hampered by a distinct lack of comprehensive study (Le Hérissé et al., 2000). Various papers have attempted to construct range charts of phytoplankton taxa through the Devonian period, which vary in size and utility here. Species recorded here and mentioned in the chart of Wicander & Wood (1997) all range through the entire Middle Devonian. The range chart of Le Hérissé et al. (2000) is much larger, yet still the majority of species it mentions which have been found here are long ranging. The only exceptions to this are *Palacanthus tripus* and *Villosacapsula globosa*, both of which are Frasnian to Famennian species. Their appearance here is perplexing, as they are both identified confidently. The relative lack of previous research on Spanish phytoplankton, combined with Iberia's isolation at the time, may be the reason for this discrepancy.

The scheme of Jardiné et al. (1974) can be better applied to the assemblage found here than to the previously known assemblage, given the greater number of species. *Duvernaysphaera angelae*, *Navifusa bacilla*, *Polyedryxium* (*Crameria*) *pharaone* and *Stellinium micropolygonale* (*S. octoaster*) have all been found in the present study with *P. decorum*, *P. fragosulum* (formerly *Crameria pyramis*) and *Pterospermella* (*Pterospermopsis*) *hermosita* identified tentatively, indicating affinity to the L1 and L2 zones. Concerning representatives of the L3 zone, *P.* "*talum*" has a complicated taxonomic history, ultimately being invalid owing to being a thesis taxon (Fensome et al., 1990). As the description for '*P.* cf. *talus* Deunff, 1966', cited by Jardiné et al. (1974), is a part of that thesis and the present author has been unable to view it, no stratigraphic conclusions have been drawn from it. The only remaining representative of the L3 zone recorded in this assemblage is *Veryhachium stelligerum*, found only in the Crémenes-Las Salas section. It ranges from the 6th sample, 18.91 m into the section, through to the uppermost sample taken. This indicates slightly younger sediment than is found elsewhere, deposited higher in the Givetian. In contrast with this interpretation, *V. valiente* is not recorded as occurring later than the Ludlow.

Some taxa recorded here have previously only been reported from rocks older than the Middle Devonian in age, namely *Comasphaeridium hirsutum*, *C. silesiense*, *Cymatiosphaera octoplana*, *Micrhystridium cortracumense*, *Multiplicisphaeridium rochesterense*, *Polyedryxium primarium*, *Pterospermella benardinae* (though this species is reported from the Emsian in Spain), *Villosacapsula cazurra* (also known from the Emsian in Spain) and *Visbysphaera pirifera*. Combined with *Palacanthus tripus* and *Villosacapsula globosa*, both mentioned above as being younger taxa, and *Estiastra culcita,* which is also only known from later than the Middle Devonian, a mixed picture is evident. Reworking is a possibility, though it would have to have been quite selective; no discernible pattern can be seen in where the older species occur, they co-occur with an otherwise typical Middle Devonian community and reworking does not explain the younger species recovered here.

7.2.2 - Chitinozoans

This study represents the first attempt to catalogue the chitinozoan assemblage of the Naranco, Huergas and Gustalapiedra formations at specific level. 32 types are identified, though 8 of these are only identified to genus level and only 8 are identified confidently. The assemblage seems to cluster within a few samples, beyond simple marine versus terrestrial dominated sediment. Certain samples at the Playa del Tranqueru site are very rich in *H.* cf. *glabra*, while the assemblage in one sample taken at the Aguasmestas-Pigüeña site consists of more than 10% chitinozoans but is otherwise notable for its diverse assemblage of large spores and complete lack of phytoplankton. Speculative reasons for this pattern include preferential preservation or local ecological refugia.

7.2.2.1 - Assemblage comparison

When the interrelatedness between Middle Devonian chtinizoan assemblages is assessed by cluster analysis the present assemblage is seen to nest within them, most closely related to a Laurussian assemblage from Ohio and a Gondwanan assemblage from Brazil (see figure 34), and without any clear groupings of Laurussian or Gondwanan assemblages. This is potentially a taxonomic or authorship artefact or may indicate a lack of provinciality in chitinozoan faunas in the Devonian.

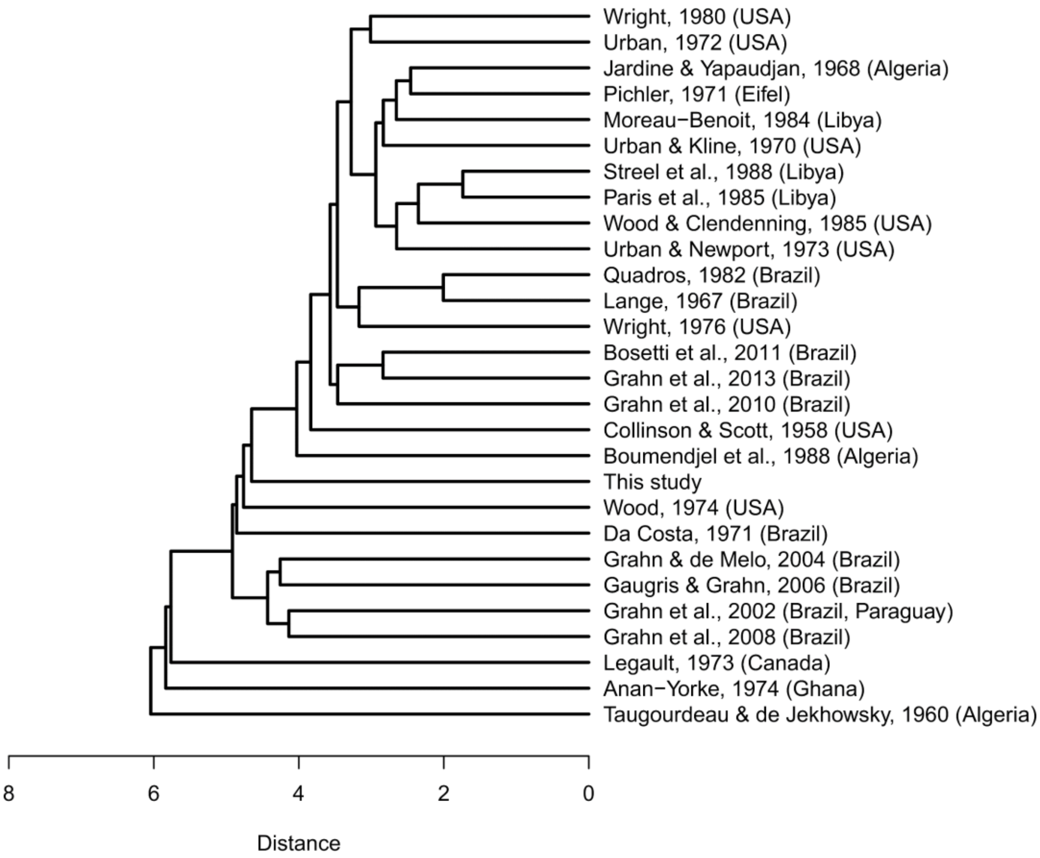


Figure 34. Dendrogram of a cluster analysis of Middle Devonian chitinozoan assemblages, with locations indicated. Distances calculated using Euclidean distance. Hierarchical clustering used the UPGMA method.

It is harder to identify commonly shared species among the chitinozoan assemblages than the phytoplankton ones, possibly owing to a less consistent use of taxonomy. Various common species in other assemblages, such as *Alpenachitina eisenacki, Ancyrochitina ancyrea, Angochitina devonica, A. milanensis, Hoegisphaera glabra* and *Fungochitina pilosa* are represented here. That being said, it is unusual to have a complete lack of species belonging to genera such as *Eisenackitina* and *Urochitina*, both of which are common in the Middle Devonian (Paris et al., 1999). Indeed, only one species of Desmochitinid, *Hoegisphaera* cf. *glabra*, was recovered and that form is long ranging. In addition, the Spanish material is still missing some very widespread taxa, such as *Ancyrochitina cornigera, A. desmea, A. langei, A. morzadeci, A. spinosa* and *Ramochitina ramosi*.

7.2.2.2 - Biostratigraphy

The species identified, both confidently and tentatively, are generally Middle Devonian species, though the lack of previous research prevents comparison on a geographically local level. Certain species not previously recorded in the Middle Devonian are detailed here. *Ramochitina corniculata* is known from the Silurian, while *R. derbyi* is known from the

Frasnian, but both these species are identified tentatively here owing to damage and may represent homeomorphs. *Saharochitina* sp. A Oulebsir & Paris, 1993 is recorded only from the Ordovician, though it is a very simple form with few distinguishing features and only represented here by a single specimen. *Sphaerochitina compactilis* is also a simple form found in the Ordovician, with something of a disconnect between its description and the original figured specimens, also only identified tentatively here. *S. ricardi* is reported up to the early Eifelian in Spain, close to the age of the present material and in the same area. The same is true of the specific form of *S. sphaerocephala* found here, though the species as a whole ranges from the Ordovician to Famennian.

Unfortunately, as detailed above, biozonation schemes for Middle Devonian chitinozoans are not widely applicable and often do not agree in different areas. The depositional period of the formation is divided into three biozones in the global scheme of Paris et al. (2000). Lowermost is the *Alpenachitina eisenacki* interval zone, also characterised by *Angochitina callawayensis* and *Eisenackitina turgifunda*. The next biozone, straddling the Eifelian-Givetian boundary, is the *Eisenackitina aranea* interval zone, which also includes *A. callawayensis* and *E. turgifunda* as well as being marked by the appearance of *Linochitina santullanensis* and *Ancyrochitina langei*. The *Ancyrochitina cornigera* interval zone occurs in the Givetian, including *A. eisenacki*, *E. aranea*, *Fungochintina pilosa* and several species of *Ramochitina*. Of these, only *A. eisenacki* and *F. pilosa* have been recorded from this Spanish assemblage. The presence of *F. pilosa* could indicate an age corresponding to the *A. cornigera* interval zone which begins in the late middle *Polygnathus varcus* conodont zone (Paris et al., 2000), however conodont data show that this is younger than the top of the formation.

This global scheme of Paris et al. (2000) presents a somewhat confusing picture. *Hoegisphaera* cf. *glabra* is reported as occurring in the Middle Devonian, possibly as a homeomorph of the true species as discussed above. *Fungochitina lata* is described as occurring only in the Lochkovian, *Ramochitina magnifica* in only the Emsian to early Eifelian and *Angochitina mourai* in the Frasnian to Famennian, openly contradicting their reported occurrences in the literature as detailed under their taxonomic entries above.

7.2.3 - Spores

The spore assemblage found in this study is large, yet not especially variable. Only *Dibolisporites* sp. A, *Retusotriletes* cf. *microgranulatus* ? and *Zonotriletes simplicissimus* are not found in the sampled sections. In addition, the sections do not show many inceptions of new taxa, with most usually already occurring at the base of the section. Of the taxa that first appear higher up the sections only *Devonomonoletes* cf. sp. 1 and three species of

Emphanisporites in the San Pedro de Nora site become significant components of the assemblage. Neither are of stratigraphic importance.

7.2.3.1 - Assemblage comparison

The dispersed spore assemblage can give some impression of the macrofossil community from which it came, though such interpretations are tentative, as detailed in Chapter 4. Table 5 lists the genera recovered here with which macrofossil groups are associated, based on Allen (1980), Gensel (1980) and Balme (1995). This reveals a varied plant community, though this is influenced disproportionately by certain genera such as *Granulatisporites* and *Retusotriletes* being associated with many parent plant groups, possibly due to their simple form. The community includes a significant progymnosperm component, evidenced by the presence of *Geminospora* and *Rhabdosporites*.

When this Spanish assemblage is compared with contemporary ones from around the world it is found to be a sister group to all other assemblages except McGregor and Camfield (1982) from Canada (see figure 35). There is undoubtedly an 'authorship effect' in this analysis, with some authors' work appearing to cluster independently of their locality, presumably because of the taxonomic concepts they embrace (Marshall, 1996a). However, overall the impression is clear. The Spanish assemblage is not particularly similar to any other Middle Devonian spore assemblage. It is most closely related to the composite assemblage of Breuer and Steemans (2013) from Saudi Arabia and North Africa, followed by two other Gondwanan

Table 5. Macrofossil groups associated with the spore genera found in this study.

Genus	**Associated macrofossil group(s)**
Acinosporites	Lycopsida
Ambitisporites	Rhyniopsida
Anapiculatisporites	Lycopsida
Apiculatasporites	Filicopsida
Apiculatisporis	Equisetopsida, Filicopsida, Zosterophyllopsida
Apiculiretusispora	Rhyniopsida, Trimeropsida, Zosterophyllopsida
Deltoidospora	Filicopsida
Dibolisporites	Cladoxylopsida, Filicopsida
Dictyotriletes	Filicopsida
Geminospora	Progymnospermopsida
Grandispora	Filicopsida
Granulatisporites	Cycadopsida, Equisetopsida, Filicopsida, Lycopsida, Rhyniopsida
Raistrickia	Filicopsida
Retusotriletes	Barinophytopsida, Lycopsida, Rhyniopsida, Trimeropsida, Zosterophyllopsida
Rhabdosporites	Progymnospermopsida
Verrucosisporites	Cycadopsida, Filicopsida, Lycopsida

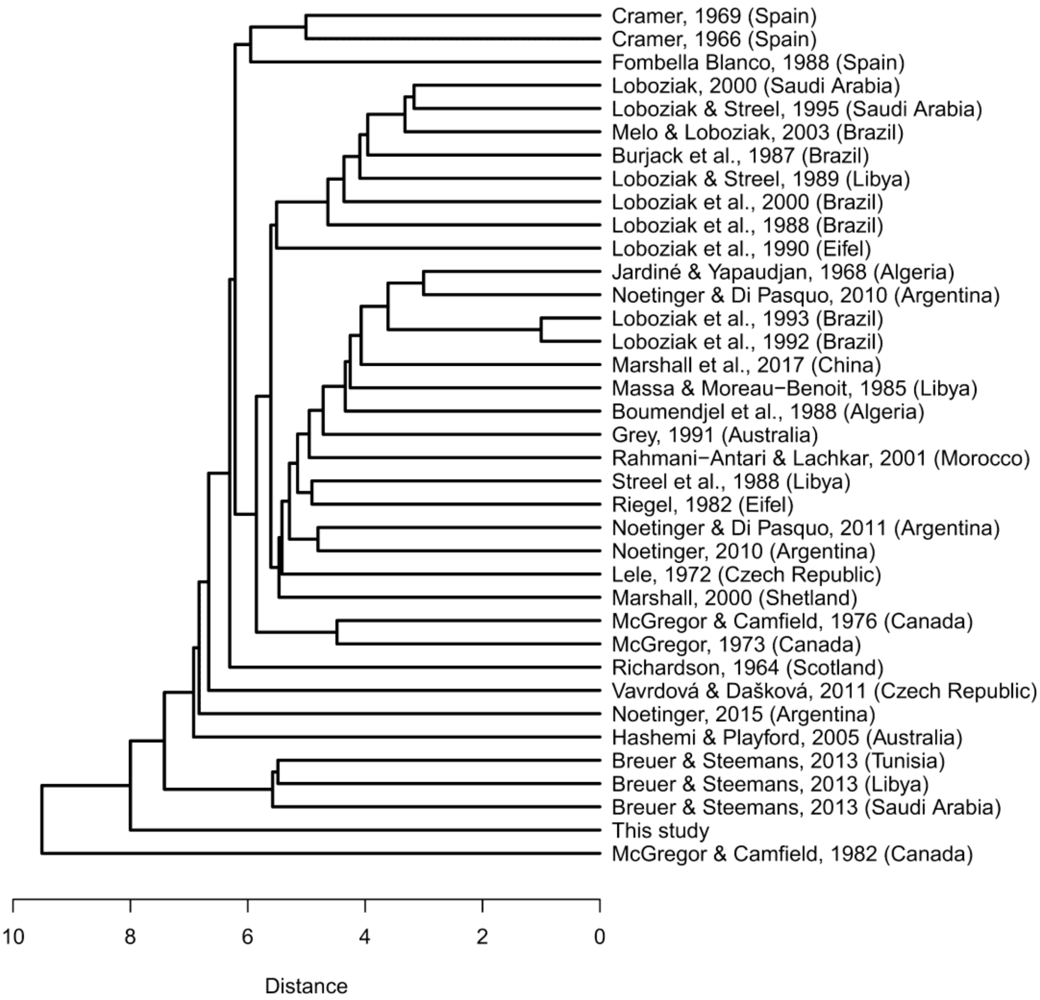


Figure 35. Dendrogram of a cluster analysis of Middle Devonian spore assemblages, with locations indicated. Distances calculated using Euclidean distance. Hierarchical clustering used the UPGMA method.

floras from Australia and Argentina, so a slight bias towards a Gondwanan affinity is indicated.

This study did not recover *Ancyrospora* or *Rhabdosporites langii* from the studied assemblage, despite them being common and widespread members of Old Red Sandstone continent assemblages at the time (Wellman, 2002, 2009). *Ancyrospora* is unknown in previous reports from the formations (Cramer, 1966, 1969a; Fombella Blanco, 1988; Gill, 2001), while Breuer & Steemans (2013) report an absence of *Ancyrospora* in Saudi Arabia and North Africa during the middle Givetian interval. *R. langii* has only been previously reported in this material as a rare taxon by Gill (2001), however a re-interpretation of Gill's material by the present author has determined this to be a misidentification. The figured specimen is more closely referable to *R. minutus*.

7.2.3.2 - Biostratigraphy

The major factor influencing the biostratigraphic interpretation of the spore assemblage found in this study is the widespread occurrence of *G. lemurata*. This defines a biozone in the earliest Givetian in all three main spore biozonation schemes used in this study.

The scheme of Richardson & McGregor (1986) includes some other taxa which corroborate the placement of the studied formations in the *lemurata-magnificus* zone, namely *Acinosporites acanthomammillatus* (identified tentatively here), *Apiculiretusispora brandtii* (identified tentatively here), *Emphanisporites annulatus*, *Grandispora inculta* (identified tentatively here), *G.* (*Calyptosporites*) *protea*, *G.* (*C.*) *velata* and *Verrucosisporites scurrus*. However, this assemblage also includes various taxa indicated as becoming extinct much earlier. The range chart of Richardson & McGregor (1986) shows *Ambitisporites avitus* becoming extinct in the Přídolí, *Emphanisporites micrornatus* (identified tentatively here) in the middle Emsian, *Dictyotriletes gorgoneus* in the late Emsian, *Apiculiretusispora plicata* in the middle Eifelian and *Grandispora douglastownensis* (identified tentatively here) becoming extinct in the late Eifelian, in the previous biozone. It should be noted that this scheme refers to the Old Red Sandstone continent and adjacent basins in North America and Central Europe with only a single section in North Africa.

G. lemurata also defines an interval zone within the AD Oppel zone in the scheme of Streel et al. (1987). Further taxa mentioned in the scheme and recorded here are *A. acanthomammillatus*, *E. annulatus*, *G.* (*C.*) *protea*, *G.* (*C.*) *velata* and *Rhabdosporites minutus*. These species are not mentioned as disappearing before the Lem. zone, though no true range chart is given. The late Emsian to early Givetian part of this scheme is based on the work of Riegel on the Eifel region of the Rhenish Massif, summarised in Riegel (1982). The range chart of selected taxa given therein records *A. acanthomammillatus, A. lindlarensis, A. brandtii*, *E. annulatus, E. rotatus* and *G.* (*C.*) *velata* as occurring on the Eifelian-Givetian boundary. However, it also records *Brochotriletes* cf. *foveolatus* (identified tentatively here) as disappearing in the late Emsian. This is the only other taxon found here mentioned in this selected range chart.

The placement of this assemblage in the *lemurata* zone of Breuer & Steemans (2013) is supported by 39 species shared in both studies, including *A. acanthomammillatus, A. lindlarensis, A. brandtii, Camarozonotriletes*? *concavus, E. annulatus, G. douglastownensis, G. permulta*, *G. stolidota* (identified tentatively here), *G. velata*, *R. minutus*, and *V. scurrus*. However this still leaves 49 species in the former study and 60 in the current one that are not shared, including common forms like *A. avitus*, *A. picantus, A. plicata*, *E.* cf. *orbicularis* (var.

A) and *Planisporites* cf. *minimus*. Various taxa also appear out of place here, relative to the scheme of Breuer & Steemans (2013). *A. plicata* and *Retusotriletes tenerimedium* do not exist after the Emsian while *C. parvus* occurs later in the Givetian and *E. laticostatus* does not appear until the Frasnian in this northwestern Gondwanan assemblage.

In addition to these schemes, *G. lemurata* also appears at the same time in the Devonian succession of the South Portuguese zone (Pereira et al., 2008), with *V. scurrus* found at the same level. This is the only study found which considers Iberia in detail, however the succession does not extend far below the first appearance of *G. lemurata*.

7.2.4 - Biostratigraphical synthesis

The palynological assemblage found in this study presents a number of difficulties. Spores are the most useful of these fossil groups for biostratigraphy and the occurrence of *G. lemurata* at key points in this assemblage indicates an early Givetian age. As *G. lemurata* ranges almost throughout all three sampled sections in this study, yet *Samarisporites triangulatus* from the overlying zone is not seen, it must be concluded that the entire sampled range of the formation was deposited in the *lemurata* biozone. *G. lemurata* does not occur in the lowermost two samples of the Playa del Tranqueru, however these two samples contain a very poor palynomorph assemblage in general (see Appendix I).

Various spore taxa in this assemblage refute this interpretation, as they do not range into the *lemurata* zone and do not co-occur with *G. lemurata* at all in many cases, according to the above schemes. This does not necessitate a reconsideration of the formations' age; rather it indicates the imperfect applicability of these existing schemes to this assemblage. A certain endemism probably prevailed in the floral assemblage of Middle Devonian Iberia, also evidenced by the lack of *Ancyrospora* and *R. langii*. As the assemblage is not particularly variable and covers only a single biozone it is considered impractical to attempt to create a new zonation for this material.

Chitinozoans do not add much to this interpretation. *A. eisenacki* can indicate an Eifelian or Givetian age, agreeing with the spore record, though it is only identified tentatively here. Similarly to the spores, unexpected taxa occur, adding to Iberia's provincial nature.

Phytoplankton provide similar information. Mostly they indicate an Eifelian-Givetian age, with only one outlier, again contributing to Iberia's idiosyncratic nature. The existence of *V. stelligerum* in the Crémenes-Las Salas section indicates that this material may be somewhat younger, extending further up the *lemurata* spore zone but not into the *triangulatus* zone. This is the only indication of a progression in the age of any of this sediment and indicates a certain amount of diachronism. The Crémenes-Las Salas section in the southeast appears to be younger than the other sections, suggesting a northern location for the sediment source and refining the interpretation of García-Alcalde et al. (2002).

The conodont dating of this formation has been detailed in Chapter 2 and it is very important in developing the full picture of the formation's stratigraphy. The top of the formation dates to the lower *Polygnathus varcus* subzone, placing it in the early Givetian (see fig. 1). The inception of *G. lemurata* is determined to be "slightly above the base of the Givetian" by Loboziak & Melo (2002) and is dated to ca. 385.5-387.7 Ma by other studies (Marshall et al., 2007; Turnau & Narkiewicz, 2011; Becker et al., 2012). This gives only a small interval of time within which the sampled interval of the formation can have been deposited, only slightly over 1.5 million years between 386 and 387.7 Ma.

7.3 - Palaeogeographical interpretations

The analysis presented above raises various questions around how such an unusual, to some degree endemic assemblage of flora and fauna could arise in this area. Possible solutions to these questions are discussed here.

7.3.1 - Terrestrial flora

Geminospora lemurata is considered to have arisen from *Rhabdosporites langii* and originated with the archaeopteridalean progymnosperms (Marshall, 1996b). The presence of *G. lemurata*, in the absence of its progenitor, suggests a restriction on dispersal. *R. langii* is significantly larger than *G. lemurata*, therefore the latter will be better able to disperse to more remote areas. Furthermore, the commensurate lack of *G. lemurata*'s associated megaspore, *Contagisporites optivus*, supports the idea of the Cantabrian Zone being geographically isolated during the Middle Devonian. This provides palaeophytogeographical support for some of the palaeocontinental reconstructions presented in Chapter 2, those which depict Spain in an isolated setting during the Middle Devonian.

7.3.2 - Marine plankton

The distribution of marine phyto- and zooplankton raises a similar question to the one posed by the terrestrial flora: how did such an endemic assemblage arise in the oceans around the isolated landmasses of Iberia? Although the seas were continuous, isolation may have arisen because of ocean currents. Evidence for such currents may come in the form of contourites, sedimentary features produced by currents in deep water. Contourites are fairly well known in the Middle Devonian, with evidence for them being found in Germany, Morocco, Australia, Canada and the Carnic Alps (Du et al., 2008; Hüneke, 2006, 2013; Knapp et al., 2017). Reconstructions of ocean currents based on these deposits indicate a north easterly current flowing past Iberia into the narrowing Rheic Ocean to the west (Hüneke, 2006). This would place Iberia upstream of the locations of the other microphytoplankton assemblages it is compared with here (see figure 36). This would have presented a serious barrier to the dispersal of all but the most widespread taxa, those found on both major continents. Species more limited in their distribution would have been unable to disperse to Iberia across these currents.

It should be noted that, as discussed in Chapter 2, palaeocontinental reconstructions disagree on the position of Gondwana and the extent and continuity of the Rheic Ocean in the Middle Devonian. Scotese (2008) depicts a land bridge across the Rheic Ocean in the Givetian, possibly impeding the flow of ocean currents, while Torsvik and Cocks (2016) reconstruct an open seaway. The ocean current reconstruction of Hüneke (2006) includes an open Rheic Ocean but with Gondwana in a similar rotational position to Scotese (2008). These findings concerning plankton support the existence of strong ocean currents in an open Rheic Ocean unimpeded by land bridges.

7.3.3 - Palaeogeographical synthesis

The results presented here indicate the Cantabrian Zone was sufficiently isolated during the Middle Devonian for a significantly endemic assemblage of dispersed spores and marine plankton to arise. Ocean currents provide a plausible mechanism for functional isolation to arise in the marine realm, preventing the dispersal of many planktonic species to the area. This does not, of course, account for the presumably wind-based dispersal of land plant spores to

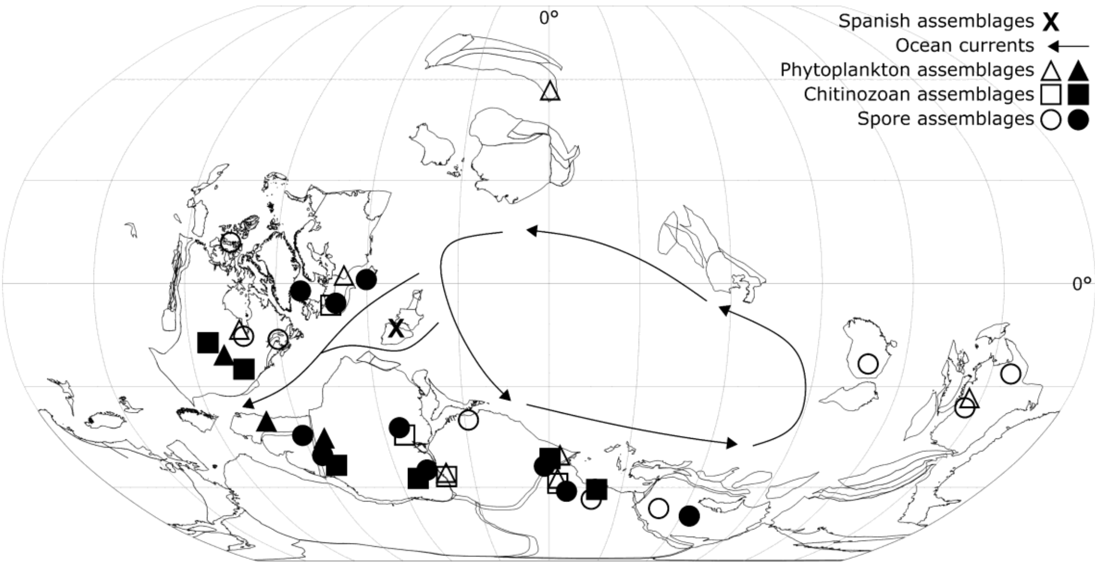


Figure 36. Palaeocontinental reconstruction of the Middle Devonain world, with modern continents indicated. The location of Spain is marked and some palaeocurrents indicated. Symbols indicate the locations of assemblages mentioned in figures 33-35. Filled-in symbols represent locations with multiple assemblages very close to one another. Base map after Torsvik & Cocks (2016). Palaeocurrent reconstruction after Hüneke (2006).

this region. This must, instead, be accounted for by geographical distance from the spores' point of origin.

Different palaeogeographic reconstructions differ on the distance between the ATA and both Gondwana and Laurussia. Some favour a larger distance, particularly from Laurussia (Scotese, 2001, 2008), some depict a position close to Laurussia and far from Gondwana (e.g. Stampfli et al., 2002) and others favouring less separation from both continents (e.g. Cocks & Torsvik, 2006; Torsvik & Cocks, 2013a). The presence of *Geminospora lemurata* in this assemblage, in the absence of the related *Rhabdosporites langii* and *Contagisporites optivus*, indicates only the microspore was able to subaerially disperse to the Cantabrian Zone. This, in turn, implies a significant separation from Laurussia, where the archaeopteridalean lineage is presumed to have arisen (Marshall, 1996a).

The endemic palynomorph assemblages of the Cantabrian Zone support early Givetian reconstructions with a large separation between the ATA and both Laurussia and Gondwana, along with a probably open Rheic Ocean through which strong currents could flow. The final closing of this ocean and the collision between the ATA and Laurussia (featured in all published palaeogeographic reconstructions) cannot have occurred until much later.

7.4 - Stratigraphical and lithological interpretations

7.4.1 - Sedimentary dynamics

It is evident that the formation was not deposited throughout the conodont-controlled time interval it is constrained by. The upper, interbedded part with preserved palynomorphs (see fig. 26) must have been deposited quickly, after the inception of *G. lemurata*. It is disingenuous to suppose that the uninterrupted sand making up the lower part of the formation was deposited slowly; more parsimonious is the idea that the entire formation was deposited quickly, with disconformities present within at least the lower part of the formation. The base of the formation may also be erosional under these circumstances; it is certainly unconformable with the underlying limestone. The reports of conodonts from the base of the Huergas formation may represent reworked material.

Supporting this interpretation of a rapid period of deposition is the existence of various sedimentary structures at a number of exposures in the formation. The Playa del Tranqueru site preserves obvious flame structures, formed by pressure on soft sediments that had not yet fully consolidated. The San Pedro de Nora site preserves ball and pillow structures on the bases of some sand beds towards the top of the formation, at a variety of sizes, again indicating unconsolidated sediment. Rapid deposition of sediment is conducive to the formation of these structures; the sediment did not have time to solidify before pressure from younger sediments caused distortion. Bed folding is also seen at some sites in the Huergas formation, principally the Mirantes de Luna and Crémenes-Las Salas sections, though this could be the result of later tectonic distortion, more severe here than in Asturias. These structures are detailed in Appendix II.

7.4.2 - Correlation with Devonian sea level changes

The pattern of sedimentary change observed here may be related to Devonian sea level changes. The Euramerican transgression-regression curve of Johnson et al. (1985) places the conodont-defined period in which the Naranco, Huergas and Gustalapiedra formations were deposited (see section 2) in the Ic to If zones, with each zone representing a transgression-regression cycle. The present author deems it unlikely that all these cycles are represented (or can be identified) in the Spanish sequence. The most complete and best described Spanish section is at the Playa del Tranqueru, which includes the entire thickness of the formation. The lower half of the formation is entirely composed of a thick, undifferentiated, sandy unit, as per García-Ramos (1978). The upper part of the formation shows interbedding with finer clay- and siltstones. Based on spore biostratigraphy the present author suggests that the upper part falls entirely within the If zone of Johnson et al. (1985). It is possible that the formation represents the regression of the Ie zone (the lower sandstone unit) and the transgression of the If zone (the interbedded upper unit), with a possible disconformity at the base of the formation representing the Ic and Id zones.

The finer scale sea level reconstructions of Brett et al. (2007, 2011) for eastern North America resolve three or four transgression-regression cycles within the time period represented by the upper part of the Naranco, Huergas and Gustalapiedra formations. Four relatively thick units, with a higher than average proportion of fine sedimentary rock layers and possibly representing periods of higher sea level, can be seen at the Playa del Tranqueru section. However, beds of clay- and siltstone are distributed throughout the upper part of the formation fairly evenly, rendering any correlation with the North American curve speculative at best.

Fine scale studies of marine transgressions linked to palynological markers have also been carried out in Brazilian basins. The Spanish rock’s age corresponds to the top of zone C and zones D and E of Grahn et al. (2013). Zone E is of a more transgressive character than the two lower zones, represented by a distinct change from sandy to shaly deposits, and it is tempting to align this change with the boundary between the lower and upper parts of the Naranco, Huergas and Gustalapiedra formations. Unfortunately, few of the palynomorphs used to calibrate this Brazilian sequence are found in Spain, and the specific early Givetian markers are absent.

A further Brazilian scheme describes regressions at an even finer scale of 4th/5th order (Young, 2006; Young & Borghi, 2006). This scheme has been applied in late Eifelian-early Givetian rocks in the Parnaíba Basin which contain abundant palynomorphs, allowing potential marker species to be identified (Grahn et al., 2008). Again, the Spanish material can be likened on purely lithological grounds to the sandy sequence B followed by the much finer grained sequences C and D. In this basin the chitinozoan *A. eisenacki* is found in both sequences C and D, while *Ancyrochitina flexuosa* and *Fungochitina pilosa* are only found in sequences C and D, respectively. These species occur in the Playa del Tranqueru section in this same sequence, with *F. pilosa* first appearing about 27 m above *A. flexuosa*. Grahn et al. (2008) indicate the Eifelian-Givetian boundary as being at the boundary between sequences C and D, however, in Spain *G. lemurata* occurs at the same level as *A. flexuosa*, suggesting a Givetian age. If sequence C is represented in the Spanish material it must be much thinner than in Brazil.

The paucity of useful palynomorphs, particularly chitinozoans, prevents any serious attempt to correlate these Spanish strata with Brazil. Many studies report a transgressive episode in the earliest Givetian (e.g. Grahn and de Melo, 2004; Grahn et al., 2010), but without key palynomorph marker species any link between the Spanish and Brazilian sequences, or any of these regional schemes, must remain speculative. Another possible confounding factor is the short time in which the Spanish material was deposited; there was insufficient time for many transgression-regression cycles to take place before carbonate deposition resumed following a fall in clastic input, possibly resulting from climatic changes.

7.5 - The Kačák Event

The information presented here can be used to comment on the Kačák Event. The event is known to occur within the depositional interval of the Naranco, Huergas and Gustalapiedra formations, however the sampled, fossiliferous levels were deposited after the event had concluded. Previous studies on South American material have recorded the event ceasing before the inception of *G. lemurata* (Troth et al., 2011; Marshall, 2016), therefore the sampled part of the studied formations does not contain the Kačák Event as it is usually defined, though its duration is far from certain as discussed in Chapter 2.

The effects of the event on the local flora and fauna cannot be determined, as no strata from directly before the event are available in northern Spain. Other intervals known to contain the Kačák Event in other parts of the world consist of black or dark grey limestones or shales representing an anoxic or hypoxic environment (House, 1996). The Naranco and Huergas formations contain organic-rich, grey silt- and mudstones, representing less intense hypoxia and possibly a longer period of environmental disruption following the Kačák Event than is recorded elsewhere. The Man Member of the Gustalapiedra formation may represent greater hypoxia, though this cannot be said to represent the Kačák Event with certainty owing to the formation's poor palynomorph assemblage.

The monsoonal hypothesis for the cause of the Kačák Event put forward by Marshall et al. (2007) and detailed in Chapter 2 is supported by evidence recovered in this study. Monsoons would be expected to cause a large amount of terrestrial runoff, producing a large amount of deposition in a short space of time. This is seen here, supported by biostratigraphical and lithological evidence. It is conceivable that in a nearshore environment the sea would be too shallow to produce the hypoxia recognised as the Kačák Event elsewhere, even with a marine transgression. Instead the terrigenous sediment would predominate and produce a thick, rapidly deposited sedimentary unit.

Considered together, the deposits of the Naranco, Huergas and Gustalapiedra formations clearly represent a relatively long period of clastic sedimentation, interrupting background carbonate deposition. Presumably, this was the result of increased terrigenous input of clastic sediment. Either the Kačák Event is a rapid, discrete event that lies somewhere within this sequence, or it can be considered a more prolonged, possibly polyphased, event representing an extended period of environmental perturbation, manifested in increased terrigenous input from the land. Recognising this environmental cause of the Kačák Event, though, does raise questions about how it would manifest around the world. Euxinic shales alone may not necessarily be sufficient for recognising the event, especially if the depositional environment was shallow. The event may, in fact, appear in different ways in different places, leaving a variety of sedimentary signatures. There is also no guarantee the 'event' happened simultaneously around the world, it may have occurred over a varying length of time in different places, depending on how long benthic anoxia persisted. The Kačák Event possibly represents a prolonged climatic event, with the black shales reported from some areas simply representing discrete horizons when oceanic anoxia occurred in certain places.

8 - Conclusions

- A rich assemblage of marine and land-derived palynomorphs has been recorded from the Naranco, Huergas and Gustalapiedra formations of northern Spain.
- The assemblage presents a number of anomalous occurrences or absences of certain taxa, indicating a degree of endemism in Iberia at the time.
- The unique characteristics of the terrestrial spore assemblage suggest the Cantabrian Zone, within the ATA, was a significant distance offshore by the Middle Devonian, enough to prevent subaerial dispersal of larger spore taxa (including megaspores) and many widespread species.
- The marine plankton assemblage may have been isolated by ocean currents preventing the dispersal of many planktonic species to the ATA.
- The endemic nature of this palynomorph assemblage, and hence the lack of species used as stratigraphic markers elsewhere, make it difficult to correlate the Spanish sequence with sea level curves or transgression-regression schemes defined in other regions.
- The Middle Devonian palynomorph assemblages and sedimentary record of the Cantabrian Zone support a large separation between the ATA and the supercontinents of Laurussia and Gondwana, with an open Rheic Ocean containing strong ocean currents.
- The assemblage's biostratigraphy, combined with known occurrences of conodonts in surrounding formations, indicates at least the sampled interval of the formations was deposited rapidly, in a period of around 1.5 million years.
- The sampled interval was deposited entirely after the Kačák Event as it is usually defined but supports the hypothesis of the event being caused by an increasingly monsoonal climate causing increased nearshore deposition.
- This environmental cause raises questions as to how the Kačák Event can be recognised around the world. Anoxic sediments may only have occurred sporadically and in certain areas, while the event may have been a more drawn-out, possibly polyphasic period caused by continued environmental perturbation.

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10 - Plates

10.1 - Phytoplankton

Plate descriptions include taxon, slide and England finder reference for each specimen.

Plate I

A 10 µm scale bar is shown.

1. *Ammonidium microfurcatum* ?; AJA2-7R-O2; S50
2. *Chomotriletes* ?*bistchoensis* ?; AJA2-3C-O2; V43/3
3. *Comasphaeridium hirsutum* ?; AJA4B-O2; O33/2 [best specimen found; large bubble unavoidable]
4. *C. silesiense* ?; AJA2-20B-2-O2; L50/4
5. *Crameria duplex*; AJA3A-O1; V42/3
6. *Dateriocradus* sp. A; AJA2-GI-O1; C48
7. *Diexallophasis remota*; AJA7A-O1; S28/4
8. *D. remota*; AJA2-GD-O1; U47
9. *D.* cf. *remota*; AJA3A-O1; F43/2
10. cf. *Estiastra* sp. A; AJA2-7O-O1; O43/3
11. *E.* cf. *culcita*; AJA2-GH-O1; P38/2
12. *Gorgonisphaeridium* cf. *absitum*; AJA2-GX-O1; W30 [crystalline artefacts unavoidable]
13. *G. cumulatum*; AJA2-GY-O1; X36/1
14. *G. cumulatum*; AJA2-GY-O1; X47
15. *G. evexispinosum*; AJA2-GT-O2; X44/2
16. *Micrhystridium cortracumense*; AJA2-20A-O1; H29
17. *M. stellatum*; AJA7A-O1; T46/2
18. *Exochoderma arca*; AJA3A-O1; K43
19. *Gorgonisphaeridium disparatum* ?; AJA2-GA-O1; W48
20. *Micrhystridium* cf. *adductum*; AJA2-3A-O1; U39/4

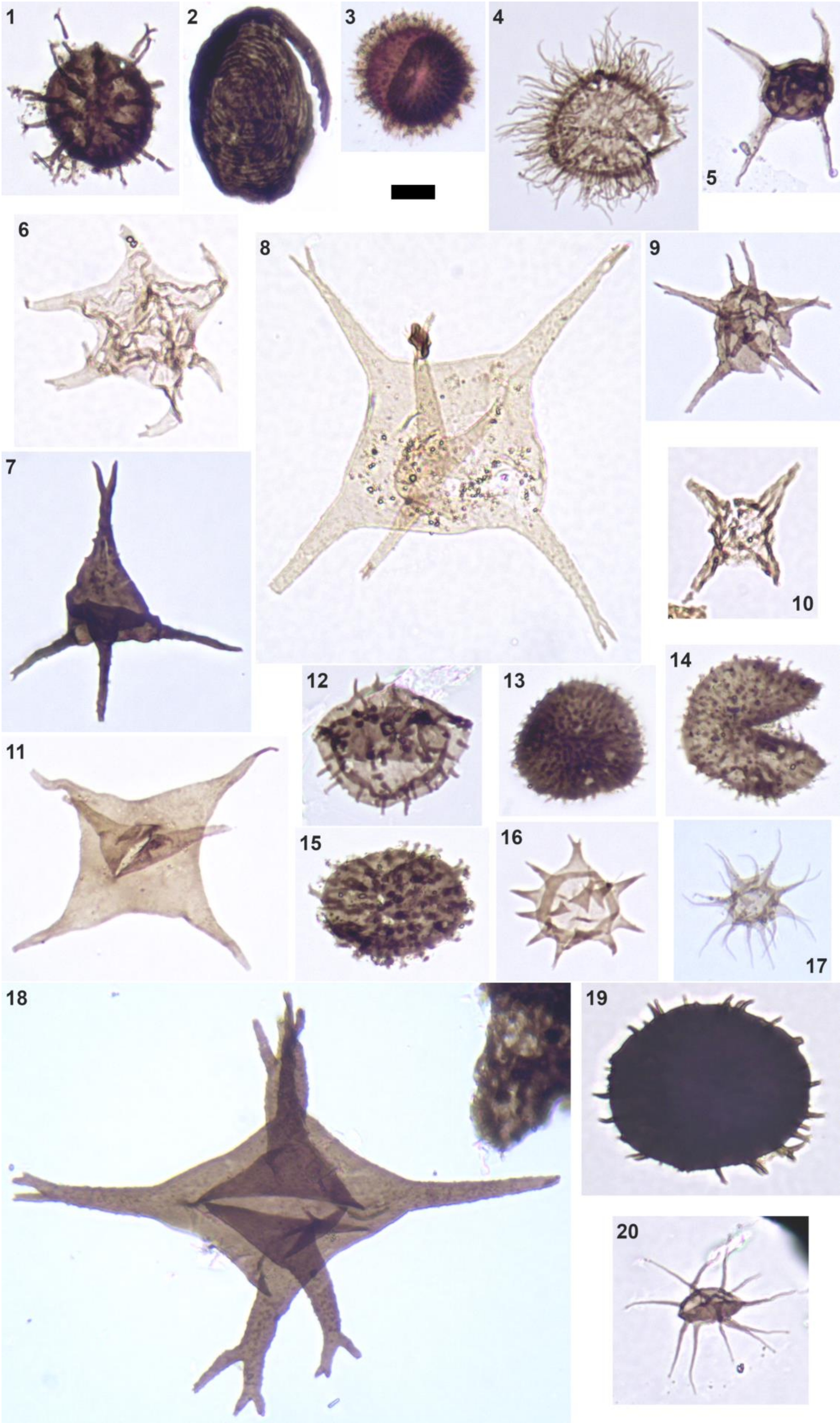
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Plate II

A 10 µm scale bar is shown.

1. *Exochoderma triangulata*; AJA2-3C-O2; U39
2. *Micrhystridium* cf. *stellatum*; AJA7A-O1; X44/2
3. *Ozotobrachion* cf. *furcillatus*; AJA2-20B-2-O2; P42
4. *O.* cf. *furcillatus*; AJA2-20B-2-O2; R35
5. *Micrhystridium* sp. A; AJA2-GY-O1; X35
6. *Multiplicisphaeridium* cf. *rochesterense*; AJA2-GI-O1; V33/4
7. *M. ramispinosum*; AJA120A-O2; O35/3
8. *Tunisphaeridium caudatum*; AJA2-GI-O1; S51
9. *Navifusa bacilla*; AJA2-GZ-O1; O44/3
10. *Solisphaeridium* cf. *inaffectum*; AJA3A-O1; B33/3
11. *Stellechinatum* cf. *spiciferum* (var. C); AJA2-GV-O2; V46/1
12. *Tylotopalla* sp. A; AJA2-GZ-O1; J39/4
13. *T.* sp. A; AJA2-GAA-O2; X47
14. *Veryhachium* cf. *arcarium*; AJA2-3F-O1; B46/3
15. *V. downiei*; AJA11A-O1; H44/4

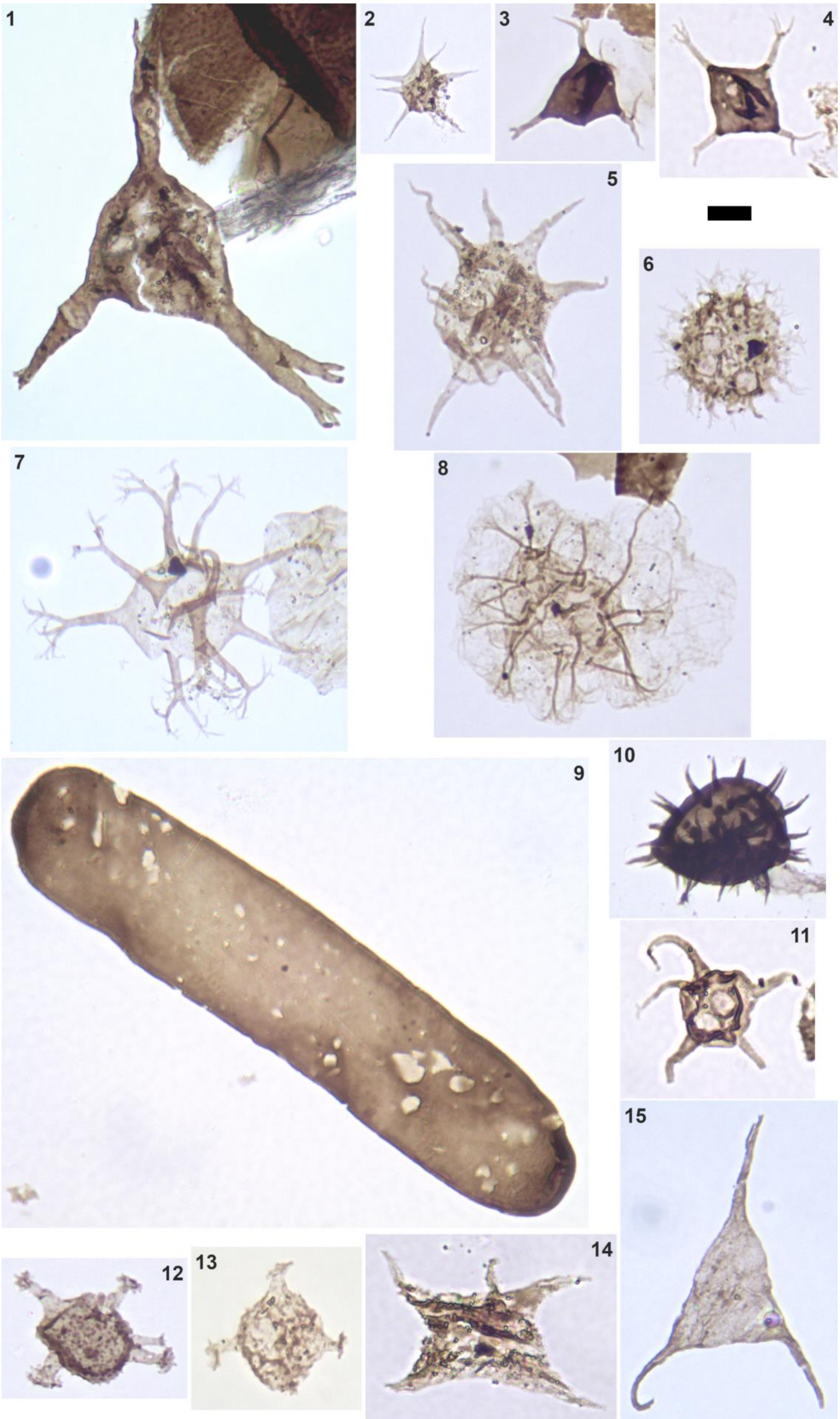
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Plate III

A 10 µm scale bar is shown.

1. *Stellechinatum spiciferum*; AJA3A-O1; X44 [specimen shows pyrite damage]
2. *S.* cf. *spiciferum* (var. A); AJA3A-O1; T44/1 [specimen shows pyrite damage]
3. *S.* cf. *spiciferum* (var. B); AJA2-GA-O1; F33
4. *Veryhachium arcarium*; AJA3A-O1; H39
5. *V. europaeum*; AJA3A-O1; X46/1 [specimen shows pyrite damage]
6. *V. polyaster*; AJA120A-O2; L35/4

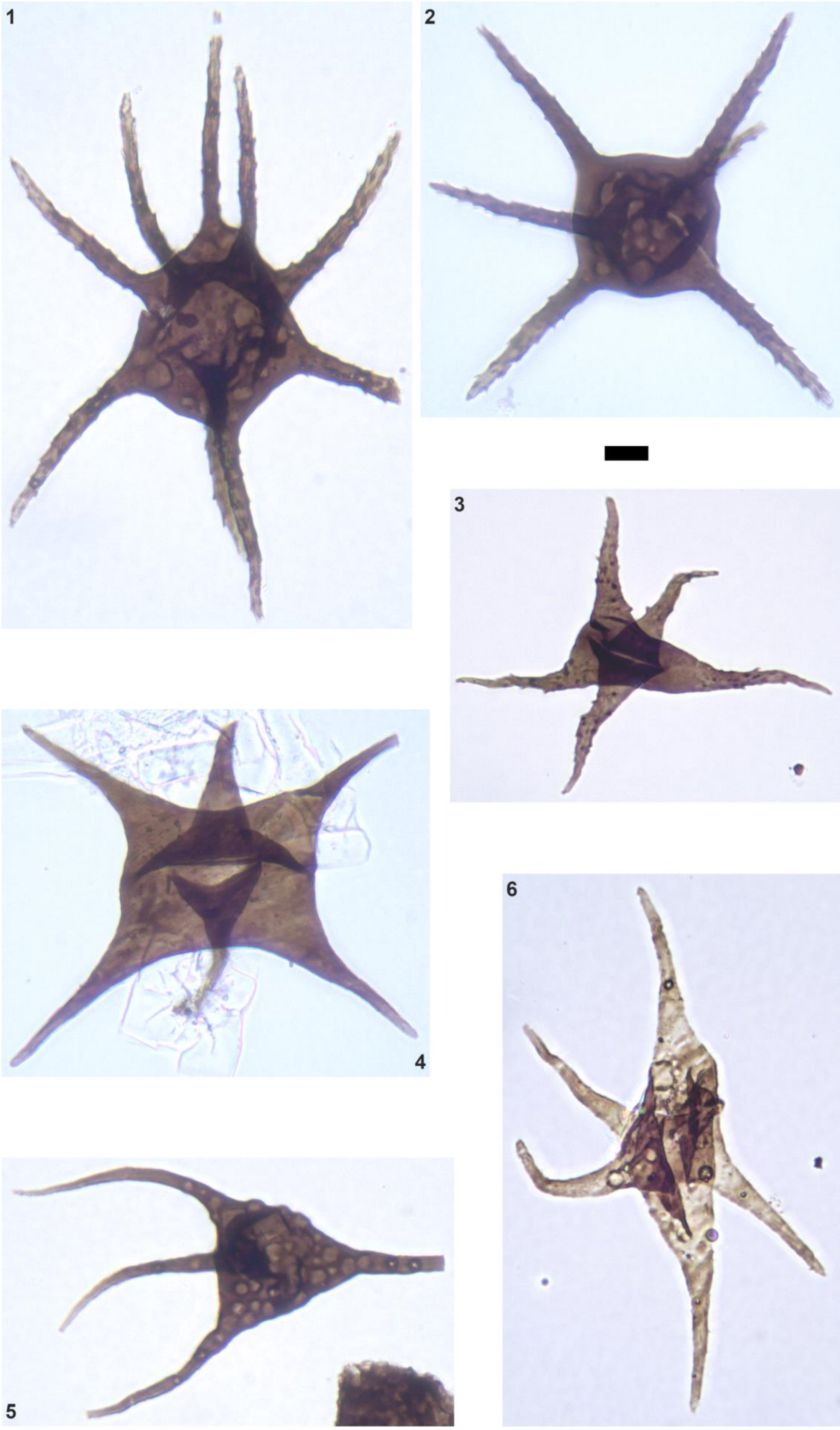
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Plate IV

A 10 µm scale bar is shown.

1. *Veryhachium polyaster* var. *hexaster*; AJA3A-O1; P39/4 [specimen shows pyrite damage]
2. *V. polyaster* cf. var. *hexaster*; AJA2-GA-O1; V51
3. *Visbysphaera* cf. *pirifera*; AJA2-GD-O1; Q31/4
4. *Veryhachium stelligerum*; AJA11A-O1; D32
5. *V.* cf. *trispininflatum*; AJA3A-O1; Q40
6. *V. valiente*; AJA3A-O1; M34/3 [specimen damaged]
7. *V. valiente* ?; AJA7A-O1; G48/2 [specimen damaged]
8. *Villosacapsula cazurra* ?; AJA2-PD-O1; R46/4 [specimen damaged]
9. *V. globosa*; AJA2-GI-O1; E37
10. *V. globosa*; AJA3A-O1; U32 [specimen damaged; spine base visible in centre of vesicle]
11. *Cymatiosphaera cuba*; AJA2-PC-O1; C36/1
12. *C. cuba*; AJA3A-O1; P41 [specimen shows possible pyrite damage]
13. *C. pavimenta*; AJA2-GZ-O1; K43
14. *C.* cf. *pavimenta*; AJA2-7F-O1; V33/2

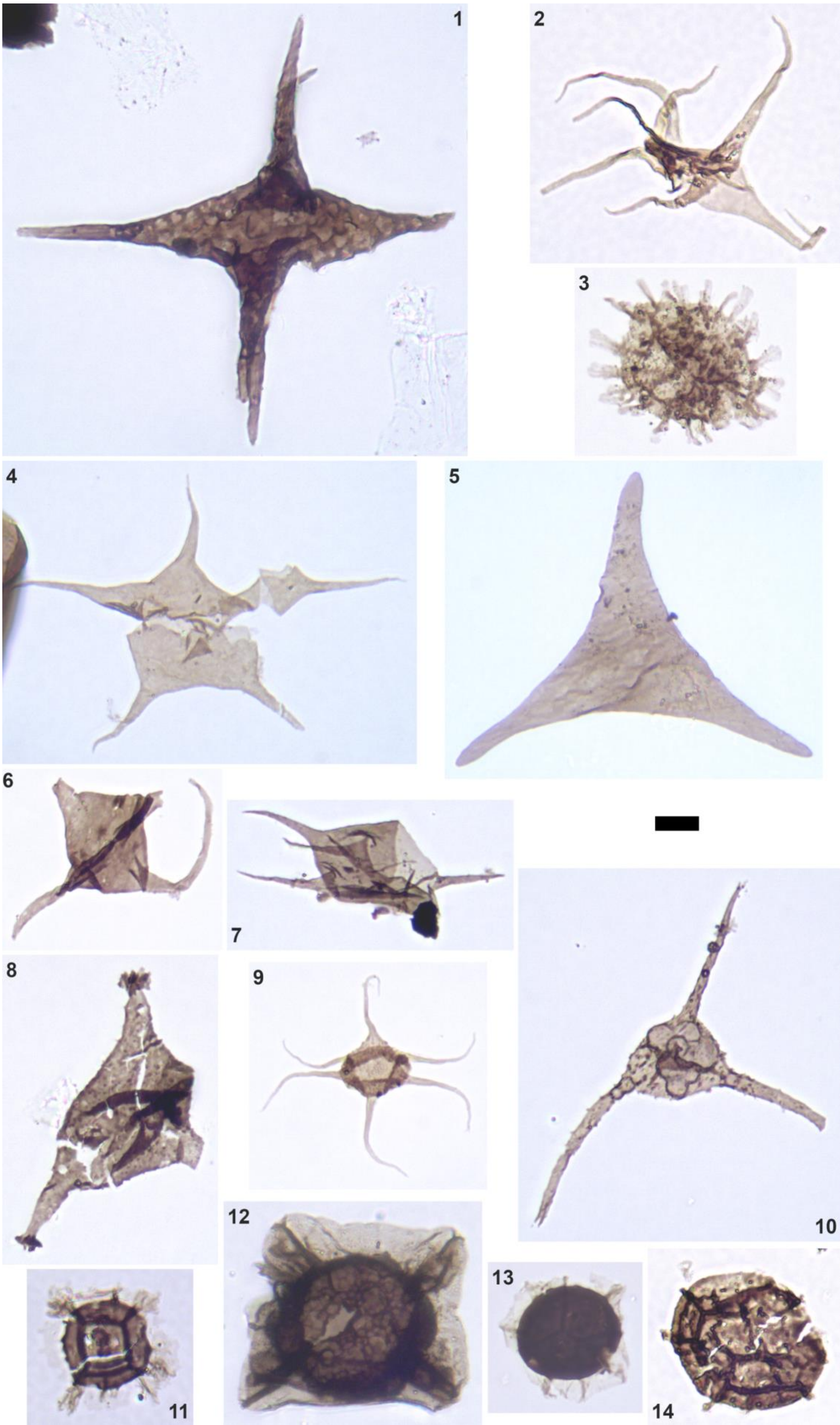
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Plate V

A 10 µm scale bar is shown.

1. *Cymatiosphaera octoplana* ?; AJA2-20A-O1; U36/2 [crystalline artefacts and phytodebris in lower part of image unavoidable]
2. *C.* cf. *perimembrana*; AJA2-3R-O1; V32/1
3. *C.* cf. *vespertilio* (var. A); AJA2-GG-O1; P41/1
4. *C.* cf. *vespertilio* (var. B); AJA3A-O1; B36/4
5. *Dictyotidium variatum*; AJA2A-O1; W35
6. *Duvernaysphaera tenuicingulata* ?; AJA2-GAA-O2; S45/4
7. *D. angelae*; AJA2-GF-O1; R42
8. *D. angelae*; AJA2-GI-O1; X34/3
9. *D.* cf. *angelae*; AJA2-3D-O2; U46 [crystalline artefacts unavoidable]
10. *Palacanthus* cf. *ledanoisii*; AJA7A-O1; G31/1
11. *Polyedryxium mirum*; AJA2-GI-O1; Y34/3
12. *Palacanthus signum*; AJA2-3A-O1; J46
13. *P.* cf. *ledanoisii*; AJA2-20A-O1; S38/4
14. *P.* cf. *ledanoisii*; AJA3A-O1; T33
15. *Polyedryxium deflandrei*; AJA2-GH-O1; Q44/1
16. *P.* cf. *accuratum*; AJA2-GZ-O1; V31 [crystalline artefacts unavoidable]
17. *Palacanthus tripus*; AJA2-GD-O1; X49
18. *Polyedryxium* cf. *decorum*; AJA120A-O2; D30
19. *P.* cf. *fragosulum*; AJA3A-O1; K30/1
20. *P. primarium* ?; AJA2-GT-O2; U31

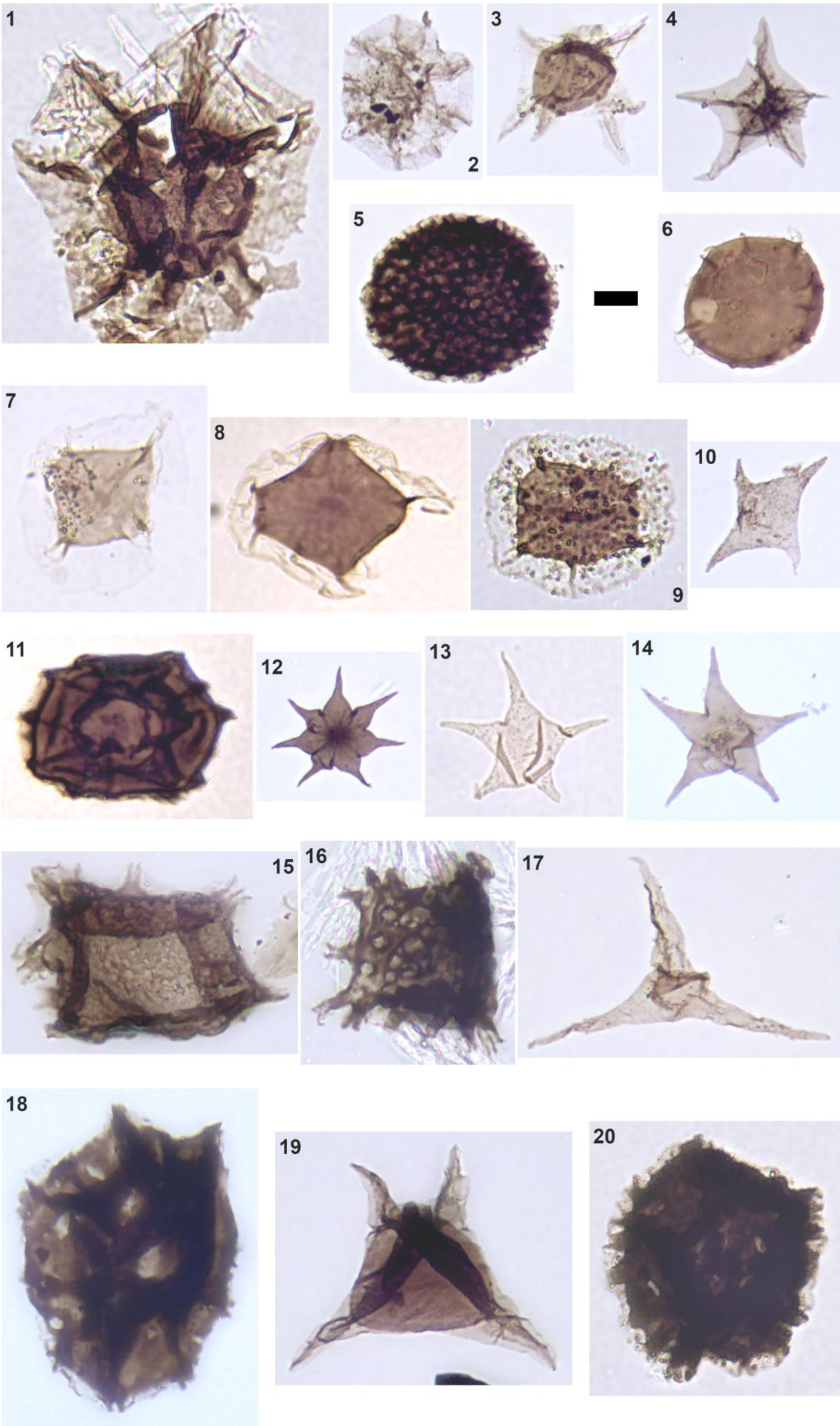
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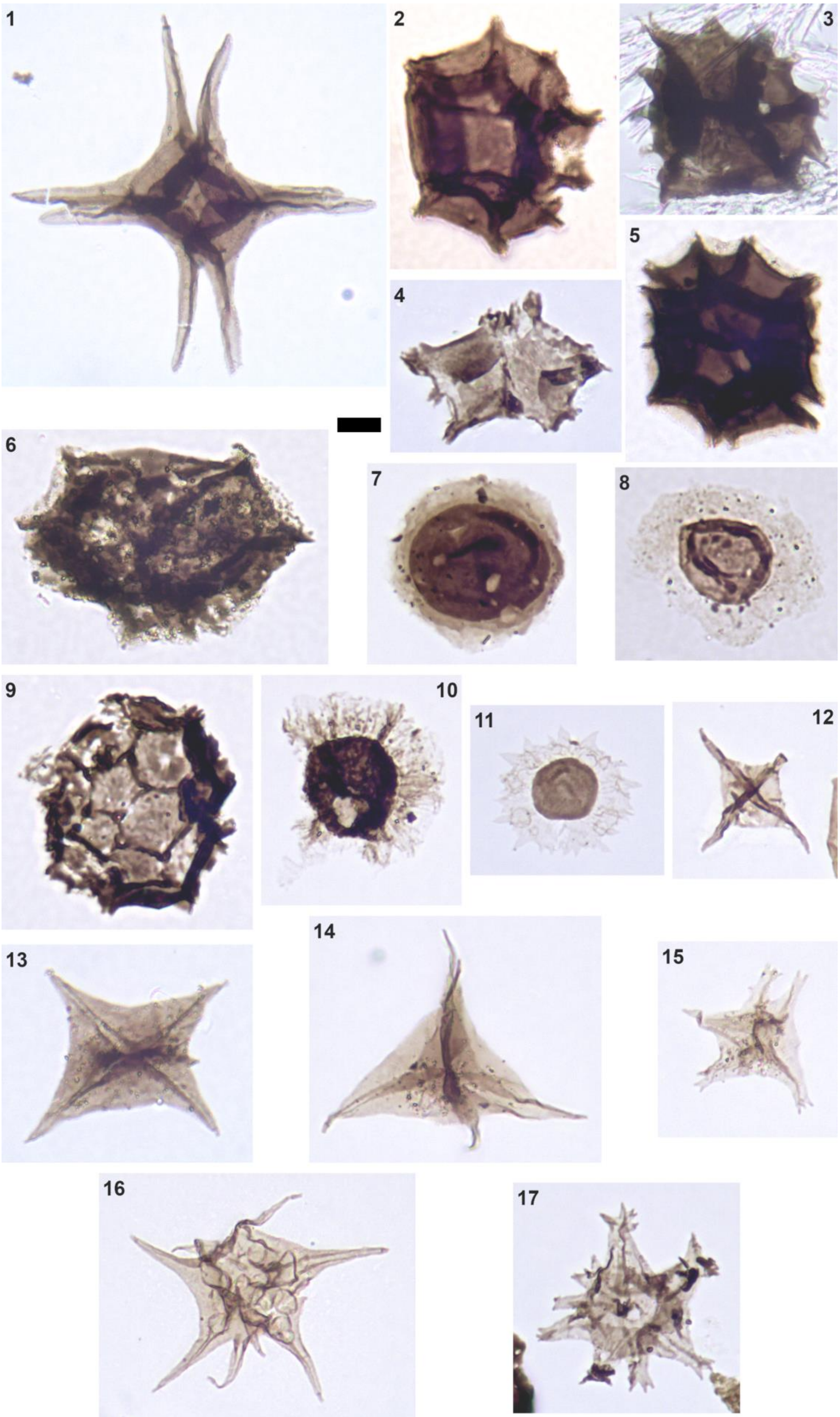
Plate VI

A 10 µm scale bar is shown.

1. *Polyedryxium pharaone*; AJA3A-O1; W40
2. *P. robustum*; AJA2-GH-O1; Z49/1
3. *P.* “*talum*”; AJA2-GZ-O1; O51 [crystalline artefacts unavoidable]
4. *P.* sp. C; AJA2-GZ-O1; R32/3
5. *P.* sp. A; AJA2-GB-O1; H45
6. *P.* sp. B; AJA2-GP-O2; F31/2
7. *Pterospermella* cf. *hermosita*; AJA2-20B-2-O2; X33
8. *P.* cf. *hermosita*; AJA2-20B-2-O2; X35/3
9. *Polyedryxium* sp. D; AJA2-GZ-O1; M48/4
10. *Pterospermella bernardinae*; AJA2-7O-O1; T38/3
11. *P. rajada*; AJA2-GI-O1; U36/3
12. *Stellinium* ?*tetrahedroide*; AJA2-7D-O1; W39/3
13. *S. comptum*; AJA3A-O1; R42
14. *S.* cf. *comptum*; AJA2-GD-O1; N40/1
15. *S.* sp. A; AJA2-GD-O1; D36
16. *S. micropolygonale*; AJA2-GA-O1; D47/4
17. *S.* sp. B; AJA2-GW-O1; R38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10.2 - Chitinozoans

Plate descriptions include taxon, slide and England finder reference for each specimen. All images are taken at 40× or 100× magnification, indicated in the plate description, with all images adjusted to the same scale.

Plate VII

A 20 µm scale bar is shown.

1. *Alpenachitina eisenacki*; AJA2-3C-O2; T39; 40×
2. *Ancyrochitina ancyrea* ?; AJA2-GI-O1; H52/4; 40×
3. *A. taouratinensis*; AJA11A-O1; Y33/1; 40×
4. *A.* cf. *flexuosa* (var. C); AJA2-3S-O2; Z42/2; 40×
5. *A.* cf. *flexuosa* (var. B); AJA3A-O1; H34/3; 40×
6. *A.* cf. *flexuosa* (var. A); AJA2-GB-O1; N48; 40×
7. *A.* cf. *tomentosa*; AJA2-7L-O1; V43/3; 100×
8. *Angochitina* cf. *capillata*; AJA10B-O1; S30/3; 40×
9. *A. devonica*; AJA2-3T-O1; N35; 40×
10. *A. devonica* ?; AJA2-3G-O2; E37; 40×
11. *A. milanensis*; AJA10B-O2; K29; 40×
12. *A. mourai*; AJA11A-O1; O45/3; 40×
13. *A.* sp. A; AJA2-7E-O1; H35; 40×
14. *A.* sp. B; AJA2-GY-O1; U43/2; 100×
15. *A.* sp. C; AJA10B-O2; X29/1; 100×
16. *A.* sp. D; AJA10B-O1; S40/4; 40×
17. *A.* sp. E; AJA3A-O1; W44/1; 100×
18. *Clavachitina* ? sp. A; AJA2-3H-O2; T33; 100×
19. *Fungochitina* cf. *lata*; AJA2-7B-O1; J39; 100×
20. *F. pilosa*; AJA10B-O1; G45/2; 100×


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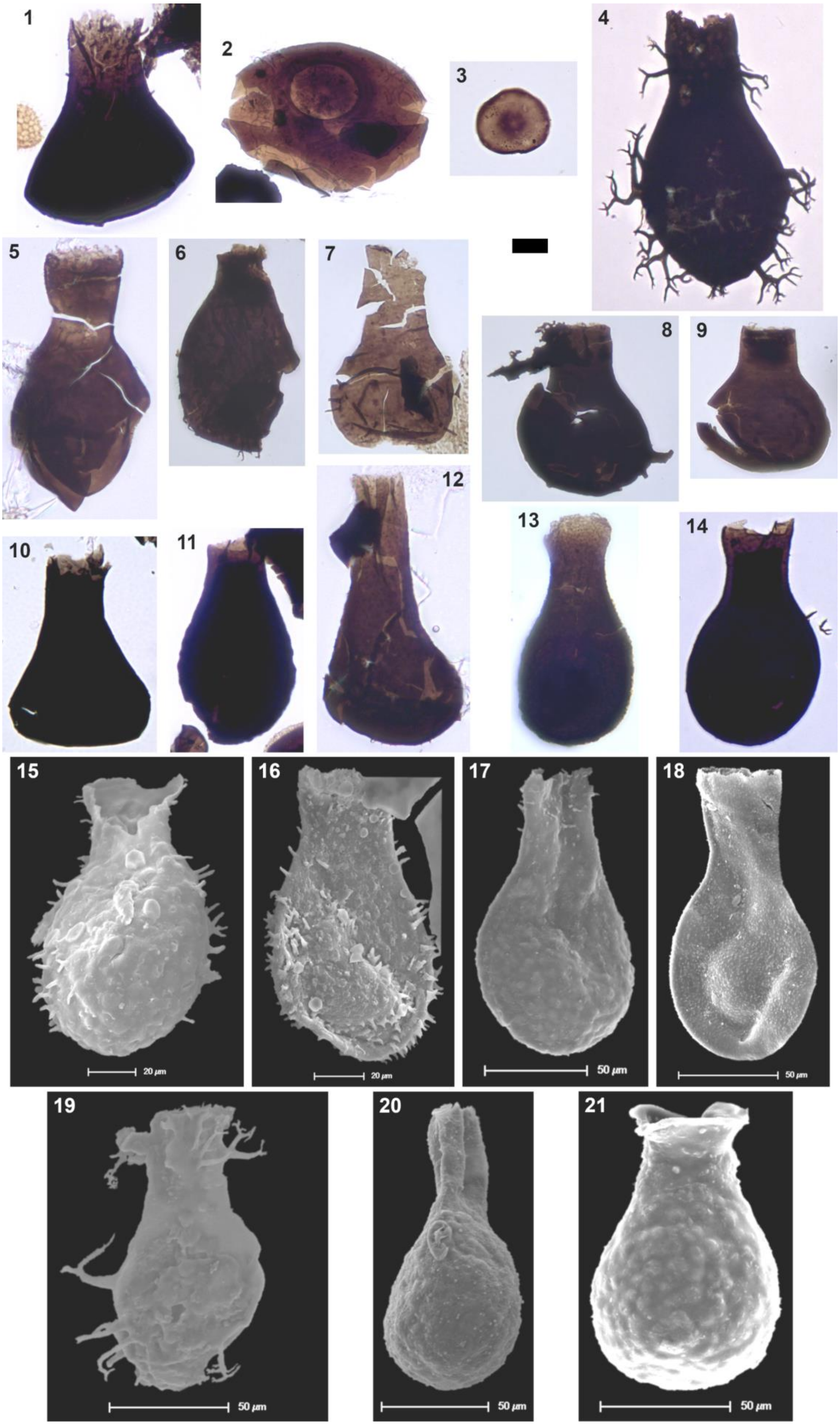
Plate VIII

A 20 µm scale bar is shown.

1. *Fungochitina* cf. *pistilliformis*; AJA2-7L-O1; V37/3; 40×
2. *Hoegisphaera* cf. *glabra*; AJA120A-O2; T40; 100×
3. *H.* cf. *glabra*; AJA2-GY-O1; X47; 100× [detached annular ring]
4. *Ramochitina* cf. *magnifica*; AJA2-3C-O2; M46; 40×
5. *Lagenochitina* sp. A; AJA10B-O2; R44; 40×
6. *Ramochitina* sp. A; AJA2-GQ-O1; F33; 100×
7. *R. derbyi* ?; AJA2-GX-O1; T46/4; 100×
8. *R. corniculata* ?; AJA3A-O1; L48; 100×
9. *R. corniculata* ?; AJA2-3B-O2; G37; 100×
10. *Saharochitina* sp. A; AJA2-PC-O1; O38/3; 100×
11. *Sphaerochitina* cf. *compactilis*; AJA10B-O1; W34; 40×
12. *S.* cf. *ricardi*; AJA10B-O2; R45; 40×
13. *S. cuvillieri*; AJA10B-O1; H37/2; 100×
14. *S. sphaerocephala sensu* Díez & Cramer, 1978; AJA10B-O1; S45/1; 40×

The following SEM images are taken at a variety of magnifications, given in the plate description along with the stub and specimen numbers. Individual scale bars are given for each specimen.

15. *Angochitina devonica*; ER1C8; 832×
16. *A. milanensis*; ER2C5; 947× [debris in upper right of image unavoidable]
17. *A.* sp. D; ERP1C2; 548×
18. *Sphaerochitina cuvillieri*; ERP1C7; 723×
19. *Ramochitina* cf. *magnifica*; ER1C11; 674×
20. *Sphaerochitina* cf. *ricardi*; ERP1C4; 609×
21. *S. sphaerocephala sensu* Díez & Cramer, 1978; ERP1C5; 675×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10.3 - Spores

Plate descriptions include taxon, slide and England finder reference for each specimen. All images are taken at 100× magnification except where indicated. Some figures indicated in the plate descriptions and surrounded by a border are taken at a different scale with their own scale bars shown.

Plate IX

A 10 µm scale bar is shown.

1. *Acinosporites acanthomammillatus* ?; AJA2-GZ-O1; R31 [best specimen found]
2. *A. lindlarensis*; AJA2-7A-O1; W40/4
3. *Ambitisporites avitus*; AJA3A-O1; X34/3
4. *A. dilutus*; AJA2-PC-O1; G46/3 [open trilete form]
5. *A.* sp. A; AJA598C-O1; N39/1 [open trilete form]
6. *A.* cf. sp. A; AJA120A-O2; S31/1 [open trilete form]
7. *A.* sp. B; AJA3A-O1; Y34/2
8. *A.* sp. C; AJA11A-O1; M33/1
9. *Anapiculatisporites carminae*; AJA598C-O1; D46/4
10. *A. picantus*; AJA598C-O1; D26
11. *Apiculatasporites perpusillus*; AJA3A-O1; R34/2
12. *Anapiculatisporites abrepunius*; AJA598C-O1; J27 [open trilete form]
13. *Apiculatisporis* cf. *elegans*; AJA598C-O1; L33/1 [open trilete form]
14. *Apiculiretusispora* cf. *brandtii*; AJA598C-O1; T37/2
15. *A. plicata*; AJA10B-O1; V37/4
16. *A.* cf. *plicata*; AJA2-3V-O2; V31/3
17. *Brochotriletes foveolatus* ?; AJA2-7E-O1; O33
18. *Camarozonotriletes*? *concavus*; AJA2-7Q-O1; W41/2

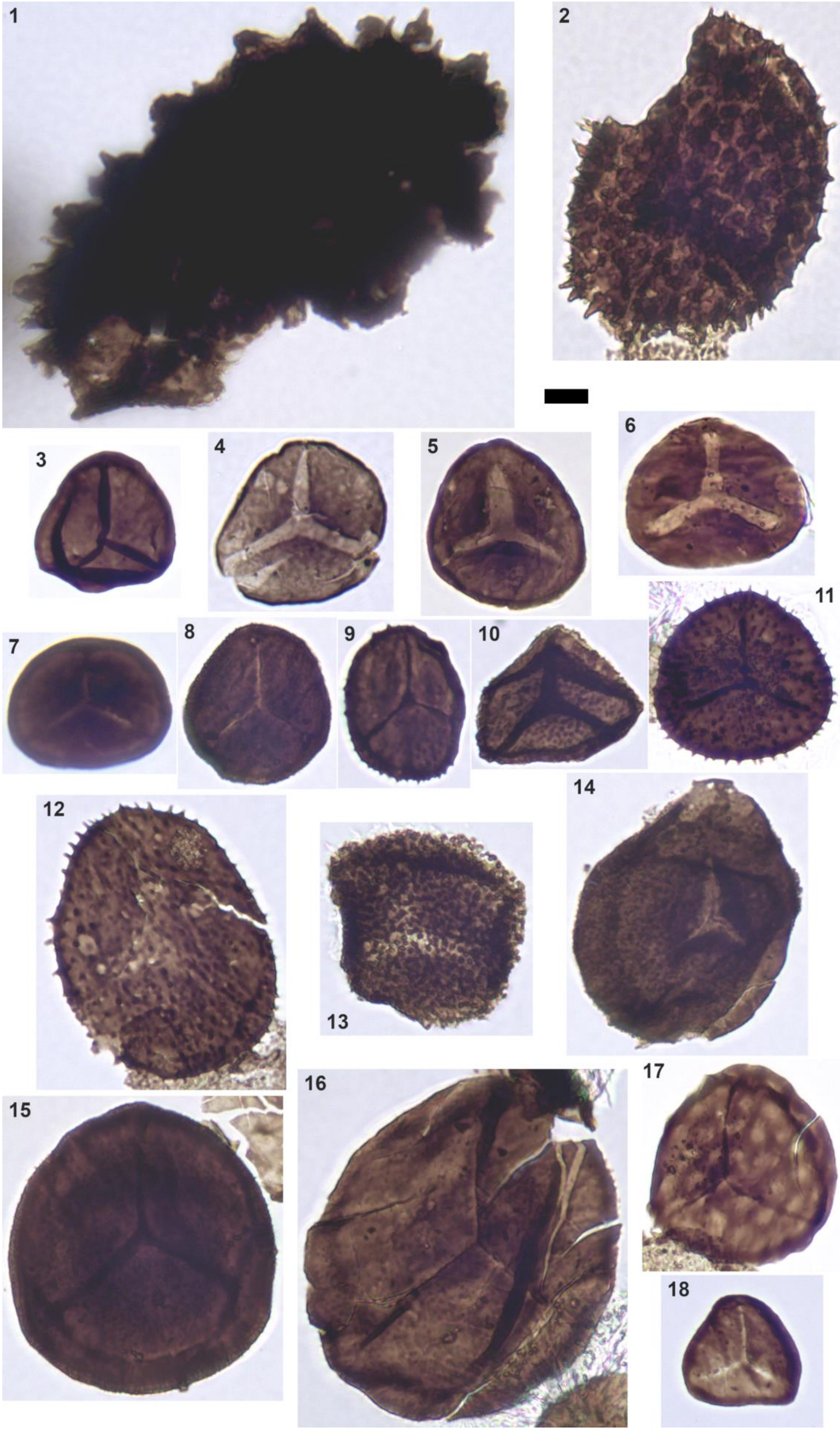
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Plate X

A 10 µm scale bar is shown.

1. *Apiculiretusispora* ? sp. A; AJA2-GZ-O1; U44 [specimen distorted]
2. *A.* ? sp. A; AJA2-GA-O1; X33 [specimen damaged]
3. cf. *A.* sp. B; AJA2-GP-O2; S37 [40× magnification; 20 µm scale bar shown]
4. *Camarozonotriletes parvus*; AJA2-7G-O1; W30/2 [open trilete form]
5. *Concavisporites* ? sp. A; AJA7A-O1; Y37/2
6. *Deltoidospora priddyi*; AJA2-7B-O1; V44/4
7. *Diatomozonotriletes* cf. *franklinii*; AJA598C-O1; J33/1
8. *Deltoidospora* sp. A; AJA11A-O2; U35
9. *Corystisporites* cf. sp.; AJA2-GD-O1; R45/3
10. *Devonomonoletes* cf. sp. 1; AJA2-7E-O1; H46/3
11. *Dictyotriletes gorgoneus*; AJA2-3R-O1; X41/4
12. *Dibolisporites* sp. A; AJA10B-O2; W42/3
13. *D. tuberculatus*; AJA3A-O1; P40
14. *D. tuberculatus*; AJA3A-O1; V28
15. *Dictyotriletes* cf. *hemeri*; AJA598C-O1; H31/4 [open trilete form]
16. *D.* cf. *hemeri*; AJA2-7D-O1; W33/2 [open trilete form]

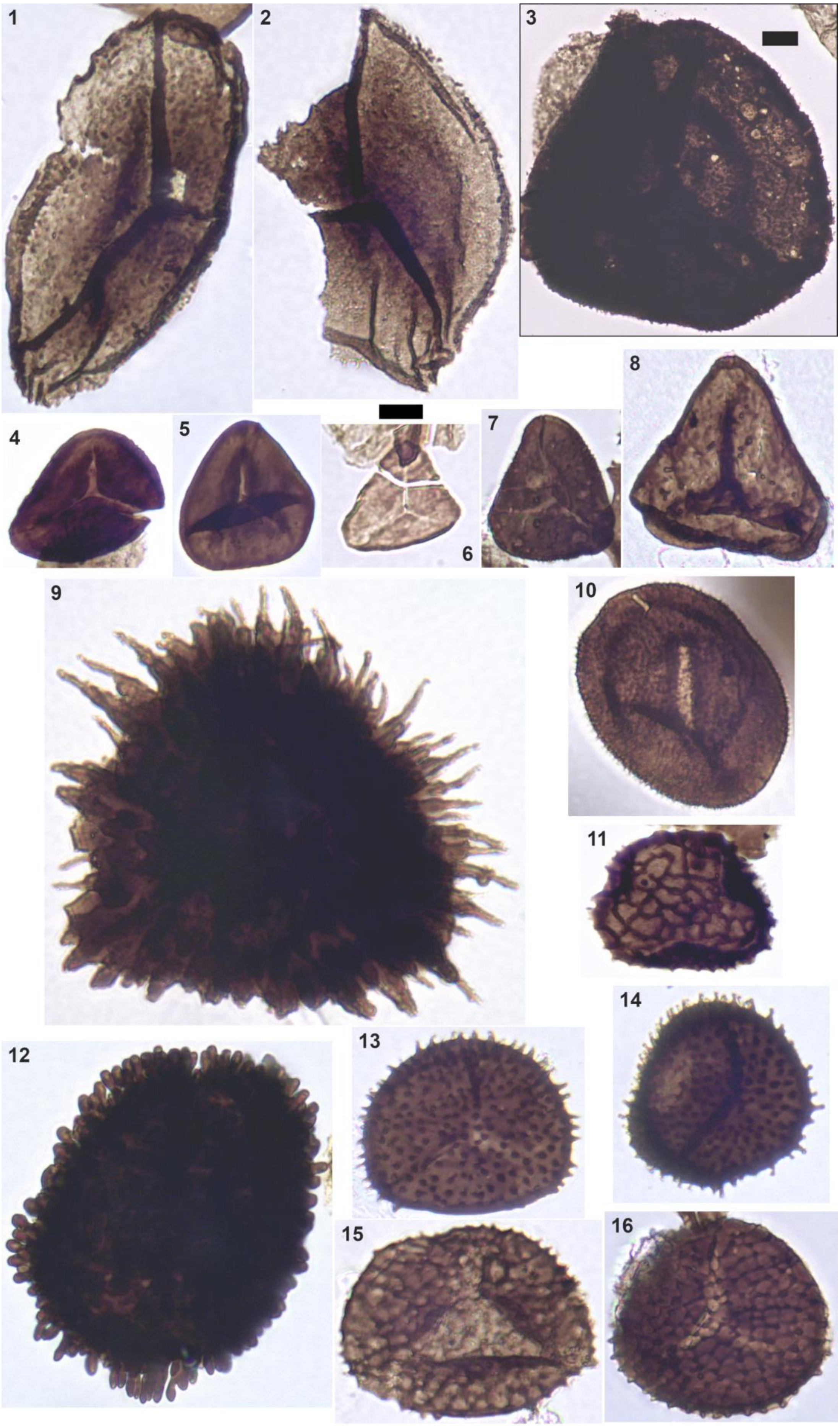

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Plate XI

A 10 µm scale bar is shown.

1. *Emphanisporites annulatus*; AJA2-20B-2-O2; O42/4
2. *E.* cf. *annulatus* (var. A); AJA2-7A-O1; B43/3
3. *E.* cf. *annulatus* (var. B); AJA7A-O1; X42/4
4. *E.* cf. *annulatus* ?; AJA598C-O1; L32/1
5. *E. augusta*; AJA2-7F-O1; W39/1
6. *E*. cf. *hoboksarensis*; AJA120A-O2; N43/2
7. *E*. *mcgregorii*; AJA2-3R-O1; Y49
8. *E*. cf. *augusta*; AJA598C-O1; C26/2
9. *E*. cf. *laticostatus*; AJA120A-O2; L35/4
10. *E.* cf. *micrornatus* (var. A); AJA2-GE-O1; T30
11. *E.* cf. *micrornatus* (var. B); AJA2-GF-O1; S40
12. *E. orbicularis*; AJA2-GE-O1; S43/2
13. *E*. cf. *orbicularis* (var. C); AJA2-PC-O1; N41
14. *E*. cf. *orbicularis* (var. B); AJA2-7A-O1; M50/1
15. *E*. cf. *orbicularis* (var. A); AJA10B-O1; M33
16. *E*. *protoannulatus*; AJA2-GH-O1; S33/3
17. *E*. *rotatus*; AJA7A-O1; C42/3
18. *E*. cf. *rotatus* (var. A); AJA3A-O1; Y32/3 [open trilete form]
19. *E*. cf. *rotatus* (var. B); AJA7A-O1; U42/1
20. *E.* sp. A; AJA2-7C-O1; V46/4
21. *E.* sp. B; AJA2-7C-O1; H29
22. *E.* sp. C; AJA2-7G-O1; Y43/2 [specimen damaged]
23. *E.* sp. G; AJA2-GP-O2; F31
24. *E.* sp. E; AJA2-GH-O1; Y42/3 [specimen damaged]
25. *E.* sp. H; AJA2-GX-O1; Q35
26. *E.* sp. D; AJA2-7O-O1; V35
27. *E.* sp. F; AJA2-GH-O1; U43

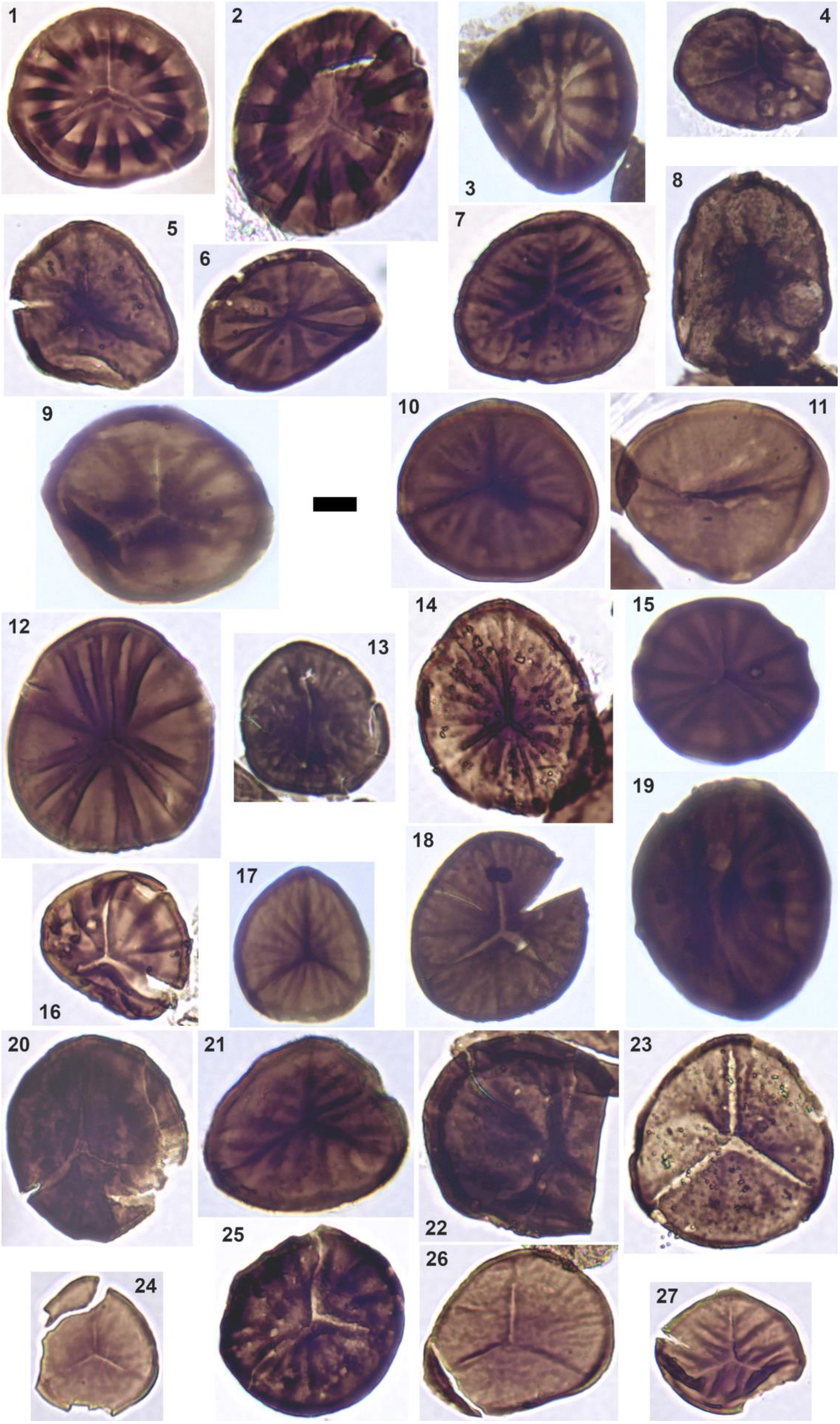
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Plate XII

A 10 µm scale bar is shown.

1. *Geminospora lemurata*; AJA2-3C-O2; E43/3
2. *G. lemurata*; AJA2-GE-O1; R49/2
3. *G. lemurata*; AJA2-GAB-O2; P29/3 [specimen damaged]
4. *G. lemurata*; AJA2-7A-O1; O49/3
5. *G. lemurata*; AJA2-7Q-O1; V50 [specimen damaged]
6. *G. lemurata*; AJA2-7A-O1; N39/2
7. *G.* cf. *svalbardiae*; AJA2-7A-O1; N32
8. *G.* cf. *svalbardiae*; AJA11A-O1; T46/4
9. *G.* cf. *svalbardiae*; AJA2A-O1; V42 [specimen damaged]
10. *Grandispora douglastownensis* ?; AJA2-GE-O1; M49/4 [40× magnification; 20 µm scale bar shown]
11. *G.* cf. *inculta*; AJA7A-O1; C28/4 [40× magnification; 20 µm scale bar shown]
12. *G*. *velata*; AJA10B-O1; D28/2 [40× magnification; 20 µm scale bar shown]
13. *Granulatisporites concavus*; AJA3A-O1; W36
14. *G.* cf. *concavus* (var. A); AJA10B-O1; O38
15. *G.* cf. *concavus* (var. B); AJA13B-O2; M40
16. *G.* cf. *muninensis*; AJA7A-O1; W39/2
17. *Latosporites* sp. 1; AJA10B-O1; R28
18. *Planisporites* cf. *minimus*; AJA598C-O1; K34
19. *Retusotriletes atratus*; AJA2-3R-O1; E42/1
20. *R.* cf. *atratus*; AJA120A-O2; X37/3 [open trilete form]
21. *Latosporites* cf. sp. 1; AJA598C-O1; V31/2

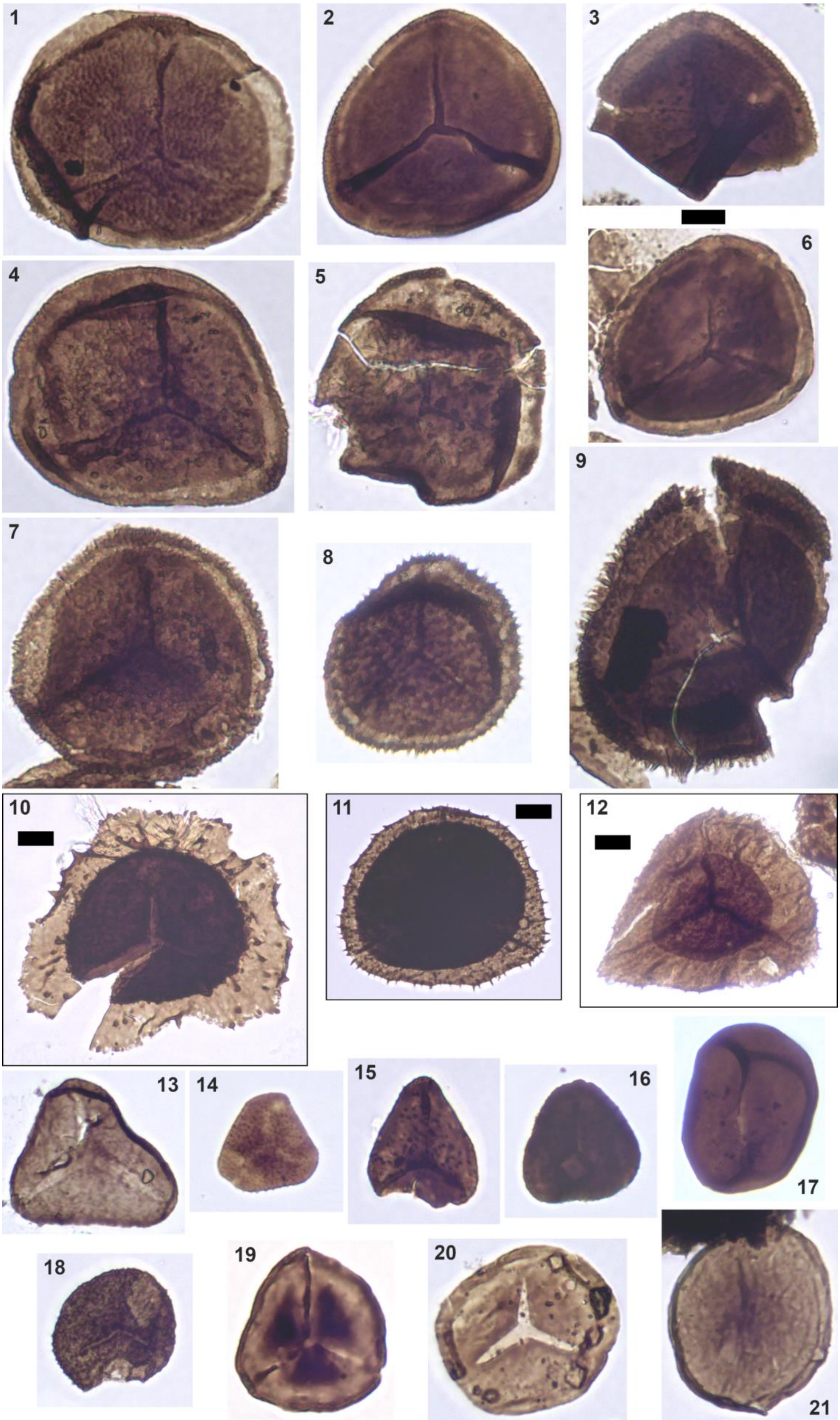
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Plate XIII

A 10 µm scale bar is shown.

1. *Grandispora permulta*; AJA2-GI-O1; U46/4
2. *G. protea*; AJA2-20A-O1; P48
3. *G.* cf. *stolidota*; AJA2-7O-O1; W37
4. *Raistrickia* ? sp. A; AJA2-7J-O1; R34/1 [surrounding phytodebris unavoidable]
5. *Retusotriletes goensis*; AJA11A-O1; W39/4
6. *'Grandispora' (Hymenozonotriletes) argutus*; AJA10B-O1; U33/3
7. *Retusotriletes* cf. *microgranulatus* ?; AJA2A-O1; Y32
8. *R. tenerimedium*; AJA2-7M-O1; J37/2
9. *R.* sp. A; AJA11A-O1; M37

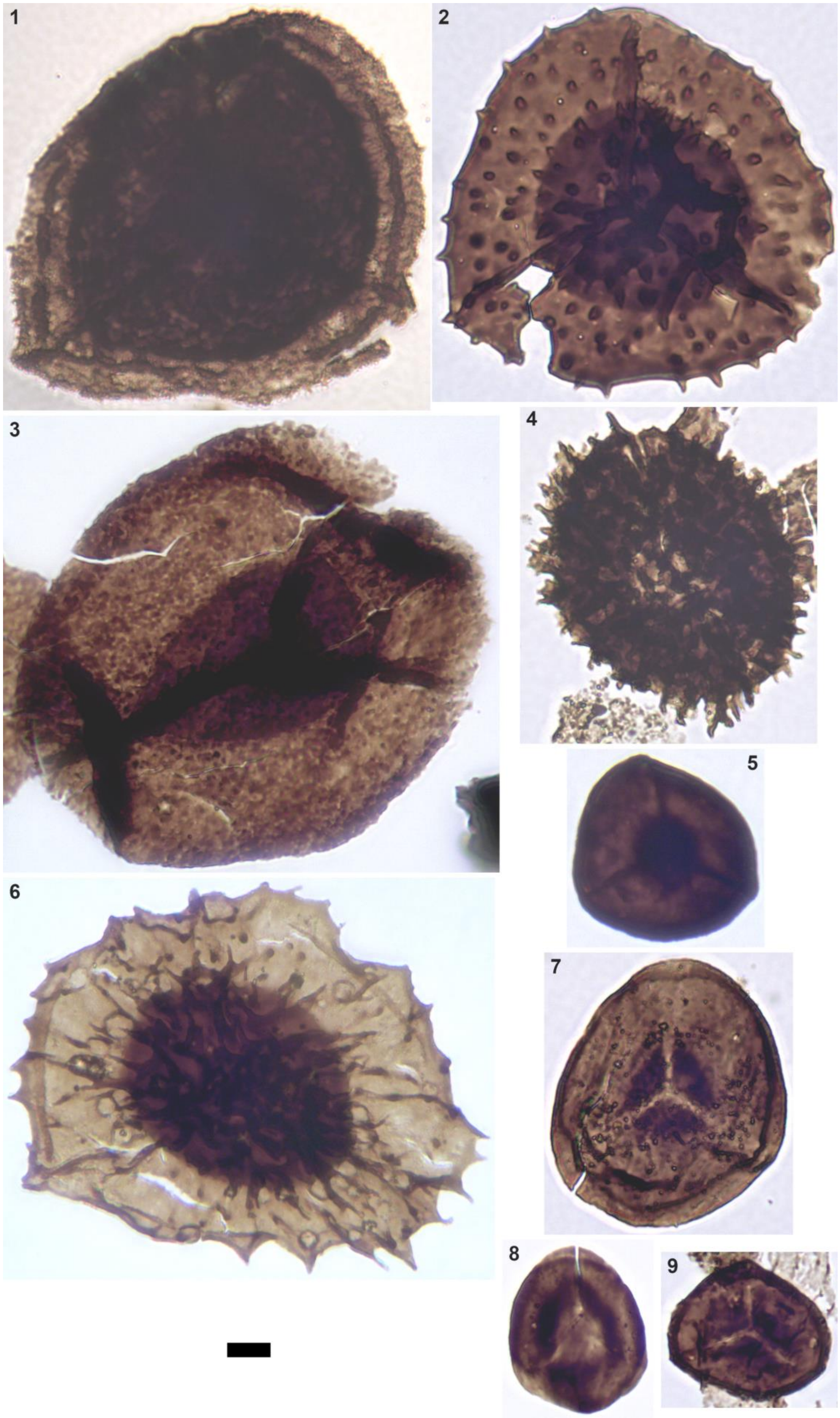
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Plate XIV

A 10 µm scale bar is shown.

1. *Retusotriletes pychovii*; AJA7A-O1; L27
2. *R*. cf. *pychovii*; AJA2-7I-O1; O44
3. *R. semizonalis*; AJA2-7H-O1; O39
4. *R. rotundus*; AJA7A-O1; T33/3
5. *R.* cf. *rotundus*; AJA598C-O1; M35/2 [specimen damaged]
6. *R. triangulatus*; AJA11A-O1; M36
7. *R.* sp. B; AJA3A-O1; D34/4
8. *R.* sp. C; AJA2A-O1; L39/2 [phytodebris in left of image unavoidable]
9. *Rhabdosporites minutus*; AJA11A-O1; B45/4
10. *Retusotriletes* cf. *triangulatus*; AJA2-7H-O1; U35
11. *Rhabdosporites* cf. *minutus*; AJA2-GAA-O2; S32 [specimen damaged; best specimen found]
12. *Samarisporites* cf. *praetervisus*; AJA2-7K-O1; U33/3 [specimen damaged; best specimen found]
13. *Verrucosisporites scurrus*; AJA2-GAB-O2; P44/2

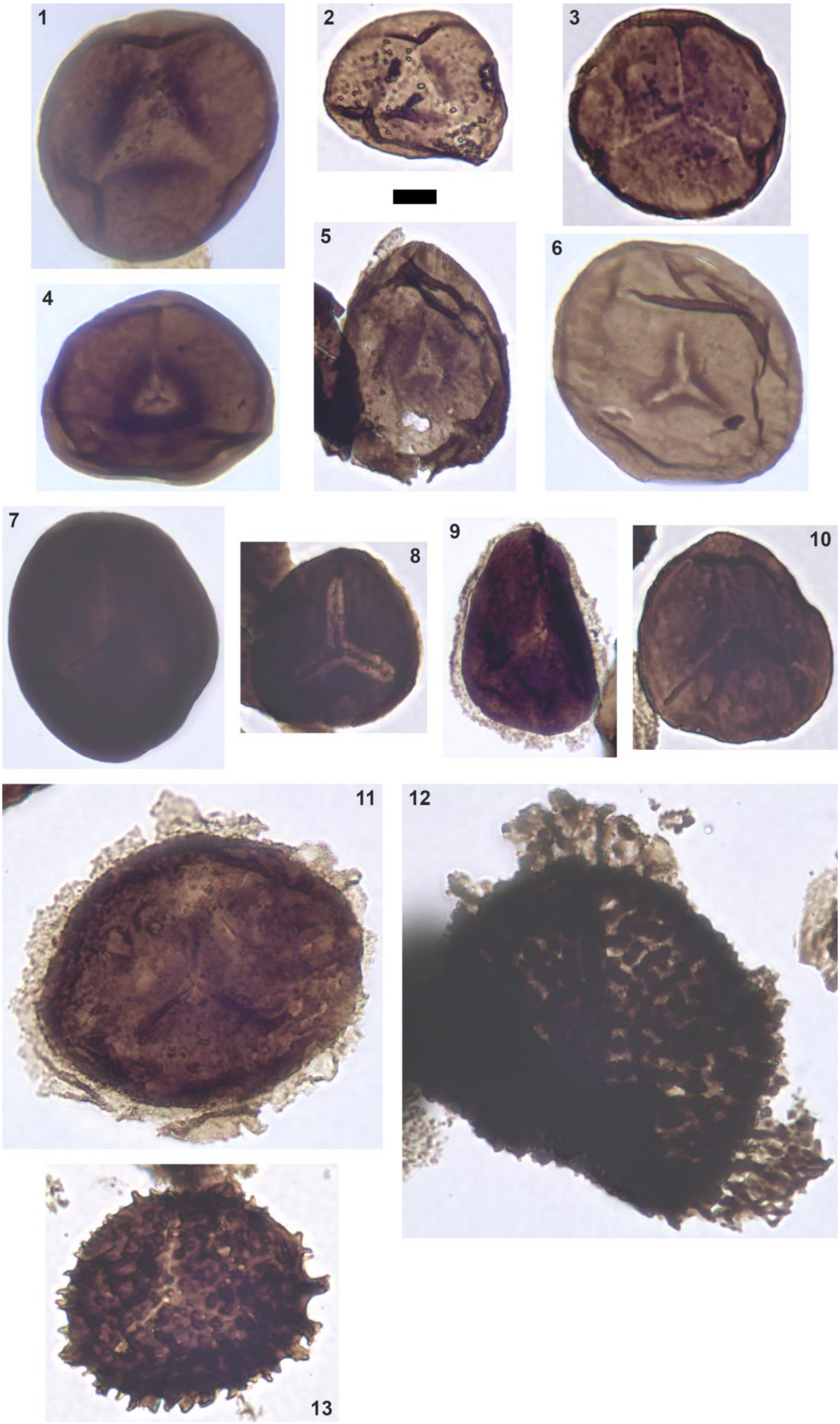
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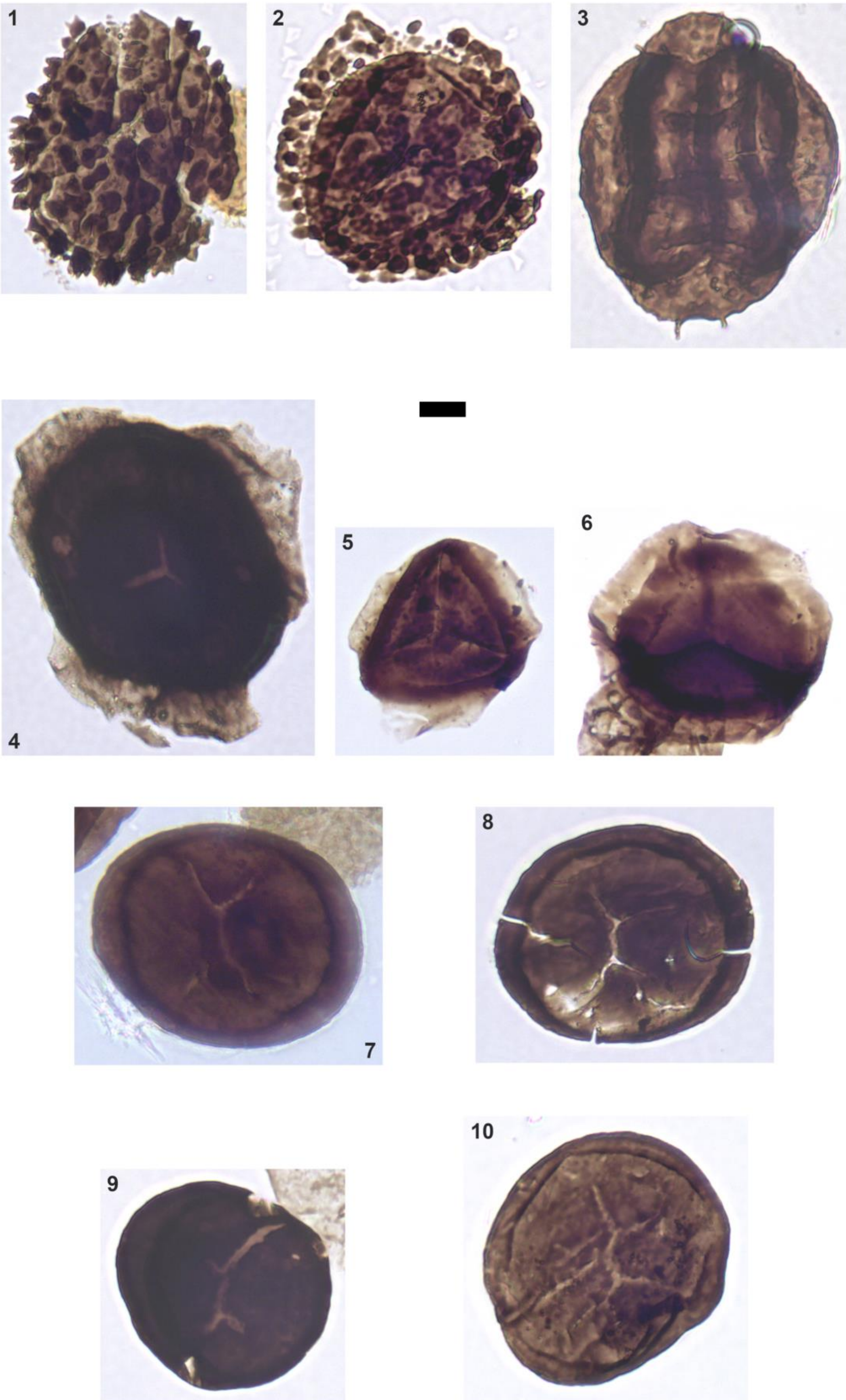
Plate XV

A 10 µm scale bar is shown.

1. *Verrucosisporites tumulentis*; AJA2-3N-O1; Q41
2. *V. tumulentis*; AJA2-3E-O2; E33/2 [specimen damaged; crystalline artefacts unavoidable]
3. Tetrad; AJA2-7B-O1; U46/2
4. *Zonotriletes armillatus*; AJA598C-O1; L28/3
5. *Z. armillatus*; AJA120A-O1; Q38
6. *Z. simplicissimus*; AJA120A-O1; U29
7. Unidentified spore A; AJA7A-O1; N37/3
8. Unidentified spore A; AJA2-7R-O2; K49
9. Unidentified spore A; AJA2-GO-O2; O43
10. Unidentified spore A; AJA2-3C-O2; L46/2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Appendix I: Sample details

'Yield' is the volume of residue following heavy liquid centrifugation, approximately measured in ml; 'Lyc' is the number of *Lycopodium* tablets added; 'TAI'=Thermal Alteration Index; 'TO'=Time in Schulze's solution, given in minutes unless otherwise stated. In the 'Palynology' column, 'PS'=plant structures; 'AOM'=Amorphous Organic Matter; 'Int'-Inertinite.

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2A	Medium grey, some minor oxidation, visible grains under light, slightly gritty, fine siltstone	2	2	PS, spores, AOM, some phytoplankton, preservation generally good, sparse palys	2+	~15
AJA3A	Medium grey, laminate, imperfect planes, fine mudstone with some visible grains under light, some evidence of oxidation, clay-like feel	1	1	Int, some AOM, numerous spores and phytoplankton, chitinozoan, preservation excellent	3 – 3+	10
AJA3B	Medium grey, somewhat laminate, imperfect planes, fine mudstone with some visible grains under light, evidence of oxidation with reddening, clay-like feel	1	1	Int, some PS and AOM, numerous spores and phytoplankton, preservation very good	≥3	25
AJA3C	Medium grey, imperfect laminae, oxidation seen on and between planes-pale or faint red, visible grains under light, gritty, siltstone	1*	2	AOM, PS, int, spores, phytoplankton, chitinozoan, preservation intermediate – degradation	≥3	~30
AJA3Di	Medium-dark grey, some indication of lamination, numerous grains visible to eye, some of 500µm scale, smooth texture, mudstone	3*	2	AOM, int, rare PS, spores and debris, rare phytoplankton, preservation poor – degradation	3-	~10
AJA3Dii	Medium-dark grey, laminate, numerous grains visible to eye, some of 500µm scale, smooth texture, layers differ slightly in colour, mudstone	3	3	AOM, int, spores and spore debris, preservation intermediate	2+ – 3	~40
AJA3Diii	Medium grey, very irregular lamination, obvious grains, some minor surface oxidation, very slightly gritty, mudstone	2	2	AOM, int, occasional PS, occasional spores, rare phytoplankton, preservation intermediate	3 – 3+	20

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA3E	Medium-pale grey, little outside evidence of lamination, yet quite fissile, no grains visible to eye, some ~250µm black and brown inclusions and some platy minerals seen with lens, smooth texture, mudstone	1	1	Int, some AOM, occasional spores, preservation good?	≥3-	50
AJA3F	Medium-dark grey, evidence of lamination, some oxidation, numerous particles visible to eye, gritty, siltstone	3	3	AOM, int, rare PS, numerous spores, preservation generally good	2+ – 3	30
AJA4A	Medium grey, somewhat laminate, imperfect planes, fine mudstone with some visible grains under light, evidence of oxidation with reddening, clay-like feel	1	1	Int, AOM, very rare spores, preservation intermediate	2 – 2+	20
AJA4B	Medium grey with some pale laminae, paling and reddening seen, few visible grains under light, tends to break into blocky chunks, mudstone	1	1	AOM, int, some PS, rare spores, some recognisable fragments, preservation generally poor – degradation	2+ – 3-	25
AJA4C	Medium grey with some pale laminae, marked reduction and oxidation seen, few visible grains under light, weathers pale brown, tends to break into blocky chunks, mudstone	2	2	Abundant int, AOM, sparse spores, preservation generally good	2 – 2+	~15
AJA5A	Pale grey-green, laminated, marked oxidation on some planes, some visible grains, smooth texture, mudstone	0	1	Int, AOM, PS, spores, preservation good, palys sparse	2+	5
AJA7A	Medium-dark grey, some irregular bedding, little evidence of oxidation, very few grains visible, smooth texture, mudstone	2	2	Some int, AOM & PS, abundant spores, numerous phytoplankton, preservation good	2+ – 3+	~20
AJA7B	Medium-dark grey, somewhat laminate, oxidation seen on and between planes, many grains visible to eye, gritty, siltstone	2	2	Int, AOM, PS, rather sparse spores, preservation variable – degradation	2- – 2	20
AJA7C	Medium grey, some minor oxidation, laminate, comparatively soft, grains visible to eye, slightly gritty, fine siltstone	2	2	PS, int, some AOM, somewhat sparse spores, preservation good	2 – 2+	~25

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA7D	Pale grey, very few grains visible, platy minerals abundant, gritty, calcareous siltstone	1	1	Occasional AOM and int, very rare spores, barren? (v. low org. C)	~3	~60
AJA7E	Pale-medium grey, some grains visible, irregular lamination, smooth texture, mudstone	<1	NA	Rare AOM, no recognisable spores or phytoplankton, barren (v. low org. C/degradation)	NA	NA
AJA10A	Medium grey, laminate, oxidation visible on and between planes, many grains visible to eye, somewhat gritty, siltstone	3*	2	PS, AOM, sparse spores, preservation good	2 – 3-	~20
AJA10B	Grey-brown, no visible laminae, some oxidation on surfaces, grains visible to eye, quite blocky, gritty, siltstone	2	2	Int, AOM, spores, various chitinozoans, preservation generally good	3- – 3	~40
AJA11A	Medium-dark grey, very little evidence of lamination, some oxidation, grains visible, slightly gritty, fine siltstone	2*	1	AOM, PS, int, abundant spores, preservation generally good	2+ – 3	10
AJA13A	Dark grey-brown, no obvious laminae, purplish-black inclusions, grains visible to eye, sand visible under lens, very gritty, sandy siltstone	<1	NA	Int, rare AOM, very rare possible spore fragments, possible chitinozoan, preservation poor – degradation, functionally barren?	NA	NA
AJA13B	Medium-dark grey, no obvious lamination, grains visible to eye, very gritty, siltstone, possibly containing some sand	1	1	Int, AOM, rare spores, preservation intermediate	2+ – 3	60
AJA15A	Medium grey, irregular lamination, some fissility, oxidation on and between planes, grains visible to eye, very slightly gritty, fine siltstone	3	NA	Int, AOM, some spores and phytoplankton, possible scolecodonts, preservation very poor – degradation	4- – 4	NA
AJA15B	Black, very finely laminated, very fissile, 250-375µm orange inclusions, smooth texture, black shale	1	1	Much int, some AOM, very rare spores, barren?	2	60
AJA120A	Medium grey, some oxidation, some laminae, some grains visible under light, slightly gritty, fine siltstone	2	2	AOM, int, PS, many spores and phytoplankton, preservation good to excellent	2 – 2+	~20

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA598A	Pale grey-green, laminated, marked oxidation on some planes, visible grains, gritty texture, siltstone	2*	1	Int, rare AOM, rare spores, preservation intermediate – degradation	3-	20
AJA598B	Pale grey, finely laminate, some oxidation, visible grains, gritty, siltstone	3*	1	Int, rare AOM, sparse spores, preservation intermediate – degradation	2+ – 3-	~20
AJA598C	Pale-medium grey, large purplish-black areas, some visible grains, gritty, siltstone	2-3*	2	Int, AOM, PS, spores, preservation generally good	2+ – 3-	~13
AJA599A	Very dark grey-brown, very fissile, some visible grains, somewhat gritty, fine shale, possibly organic rich	1	NA	Barren – AOM, int	NA	NA
AJA599B	Medium-pale grey, some lamination, some alignment of platy mineral, some minor reduction, slightly gritty, siltstone, possibly with some limestone	<1	1	AOM, int, occasional spores, preservation good	2+ – 3	~25
AJA600A	Dark grey, finely laminate but not fissile, some visible grains, very gritty, siltstone	1	1	Int, AOM, some PS, no recognisable spores, barren (AOM?)	NA	60
AJA2-3A	Copper green colour, widespread oxidation, some visible grains, somewhat gritty bite, siltstone	<1	1	Int, some AOM, rare spores, rare phytoplankton, preservation good	2+	8
AJA2-3B	Pale grey with greenish tinge, quite fissile, oxidation, some visible grains, somewhat gritty bite, fine siltstone	<1	1	Int, some AOM, some PS, rare spores, chitinozoan, scolecodont, preservation quite good	3- - 3	15
AJA2-3C	Very deep red colour, fissile, some lamination, some oxidation, some visible grains, somewhat gritty bite, fine siltstone	1	1	PS, AOM, spores, phytoplankton, chitinozoans, preservation quite good	3- - 3	18
AJA2-3D	Dark grey, some irregular lamination, quite fissile, some platy alignment, some oxidation, some visible grains, smooth bite, coarse mudstone	1	1	AOM, PS, some Int, spores, some phytoplankton, chitinozoan, preservation quite good	3- - 3	15

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-3E	Medium-dark grey, platy alignment, somewhat fissile, some minor oxidation, smooth bite, mudstone	1	1	PS, some Int, spores, some phytoplankton, chitinozoans, scolecodont, preservation quite good	2+ - 3	10
AJA2-3F	Dark-medium grey, fissile, lamination, slight oxidation, ever so slightly gritty bite, mudstone	1	1	AOM, PS, spores, some phytoplankton, preservation quite good	3- - 3	13
AJA2-3G	Dark grey, slight oxidation, some visible grains, gritty bite, siltstone	1	1	Much AOM, some spores, some phytoplankton, preservation intermediate	3-	13
AJA2-3H	Dark grey, somewhat fissile, slight oxidation, some visible grains, gritty bite, siltstone	1	1	AOM, PS, rare spores, phytoplankton, many chitinozoans, scolecodont, preservation intermediate	2+ - 3-	9
AJA2-3I	Dark grey, slight oxidation, visible grains, gritty bite, siltstone	1	1	AOM, PS, some spores, possible phytoplankton, preservation intermediate	2+ - 3-	10
AJA2-3J	Dark grey, slight oxidation, visible grains, gritty bite, siltstone	1	1	Much AOM, spores, some possible phytoplankton, scolecodont, preservation good	2+ - 3	11
AJA2-3K	Dark grey, visible grains, gritty bite, siltstone	3	3	Much AOM, some PS, rare spores, preservation good	2	10
AJA2-3L	Medium-dark grey, some oxidation, some visible grains, gritty bite, siltstone	1	1	Int, PS, some AOM, some spores, some phytoplankton, preservation good	3- - 3	18
AJA2-3M	Medium-dark grey, some platy alignment, slight oxidation, some visible grains in places, slightly gritty bite in places, coarse mudstone	<1	1	AOM, Int, spores, some phytoplankton, preservation good	2+ - 3	8
AJA2-3N	Dark grey, some lamination, decidedly fissile, visible grains, somewhat gritty bite, siltstone	<1	1	AOM, PS, spores, some phytoplankton, preservation very good	2+ - 3	8
AJA2-3O	Dark grey, lamination, slight oxidation, visible grains, somewhat gritty bite, siltstone	2	2	Int, PS, some AOM, spores, some phytoplankton, preservation good	3 - 3+	20

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-3P	Medium-dark grey, platy alignment, some vague lamination, slightly gritty bite, coarse mudstone	<1	1	PS, AOM, spores, chitinozoan, preservation good	3- - 3	18
AJA2-3Q	Medium-dark grey, some lamination, some oxidation/mineral invasion, visible grains in places, gritty bite, siltstone	<1	1	PS, Int, AOM, spores, scolecodont, preservation good	3 - 3+	17
AJA2-3R	Medium-dark grey, some platy alignment, decidedly blocky, some oxidation, some visible grains, ever so slightly gritty bite, fine siltstone	1	1	AOM, PS, spores, phytoplankton, a chitinozoan, preservation good	3- – 3	13
AJA2-3S	Dark grey, distinct, non-continuous pale lamination, visible grains, somewhat gritty bite, siltstone	1	1	Int, PS, some AOM, comparatively sparse spores, chitinozoans, preservation good	3 – 3+	23
AJA2-3T	Medium grey, some oxidation, visible grains, gritty bite, siltstone	1	1	PS, Int, some AOM, comparatively sparse spores, possible phytoplankton, chitinozoan, preservation quite good	3 – 3+	20
AJA2-3U	Medium-dark grey, some vague lamination, somewhat fissile, slight oxidation, few visible grains, slightly gritty bite, fine siltstone	1	1	PS, Int, some AOM, various spores, preservation good	3- – 3	15
AJA2-3V	Dark grey, lamination, somewhat fissile, slight oxidation, some visible grains, somewhat gritty bite, fine siltstone	2	2	Int, AOM, some PS, rare spores, very rare possible phytoplankton, chitinozoans, preservation quite good	3- – 3+	20
AJA2-3W	Dark grey, some lamination, some visible grains, somewhat gritty bite, fine siltstone	2	2	AOM, PS, some Int, some spores, preservation quite good	3- – 3	20
AJA2-3X	Medium grey, lamination, some platy alignment, some oxidation, visible grains, somewhat gritty bite, siltstone	2	2	Int, AOM, some PS, rare spores, preservation quite good	2+ – 3+	20
AJA2-3Y	Medium-dark grey, lamination, platy alignment, oxidation, few visible grains, ever so slightly gritty bite, fine siltstone	2	2	AOM, Int, some PS, quite rare spores, preservation quite good	3-	20

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-3Z	Medium-dark grey, lamination, visible grains, less in places, gritty bite, less in places, siltstone	2	2	AOM, some PS, some spores, preservation quite good	3- – 3	21
AJA2-3AA	Medium grey, some lamination, oxidation, some visible grains, slightly gritty bite, fine siltstone	2	2	AOM, some PS, some spores, preservation quite good	3 – 3+	22
AJA2-3AB	Medium grey, some lamination, slight oxidation, some visible grains, slightly gritty bite, fine siltstone	2	2	AOM, some PS, some spores, chitinozoan, preservation quite good	3	18
AJA2-3AC	Medium grey, lamination, somewhat fissile, oxidation, some visible grains, smooth bite, coarse mudstone	3	3	AOM, some PS, some spores, preservation moderate	2+ – 3	15
AJA2-3AD	Medium grey, lamination, some visible grains, ever so slightly gritty bite, fine siltstone	1	1	PS, Int, some AOM, spores, preservation quite good	3	17
AJA2-3AE	Dark grey, irregular lamination, oxidation, some visible grains, slightly gritty bite, fine siltstone	2	2	PS, some AOM, some spores, preservation quite good	3- – 3+	18
AJA2-3AF	Dark grey, irregular lamination, oxidation, some visible grains, slightly gritty bite, fine siltstone	2	2	PS, AOM, some spores, possible chitinozoan, preservation moderate	3- – 3	12
AJA2-3AG	Dark grey, irregular lamination, oxidation, some visible grains, slightly gritty bite, fine siltstone	1	1	AOM, some PS, some spores, preservation poor	3- – 3	20
AJA2-7A	Pale brownish-grey, visible grains, smooth bite, coarse mudstone?	1	1	AOM, PS, many spores, preservation very good	2+ - 3	13
AJA2-7B	Pale brownish-grey, visible grains, smooth bite, coarse mudstone?	1	1	AOM, PS, Int, spores, preservation good	2+ - 3	9
AJA2-7C	Pale grey-green, some oxidation, visible grains, gritty bite, siltstone	1	1	AOM, PS, many spores, some phytoplankton, preservation very good	3- - 3	13
AJA2-7D	Medium-dark grey, lamination, some oxidation, some visible grains, slightly gritty bite, fine siltstone	1	1	AOM, PS, spores, phytoplankton, preservation good	2+ - 3	7
AJA2-7E	Dark grey, some lamination, smooth bite, mudstone	1	1	AOM, PS, many spores, some phytoplankton, preservation good	3- - 3+	14

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-7F	Dark grey, lamination, fissile, visible grains, gritty bite, siltstone	2	2	Much AOM, PS, some spores, preservation good	2+ - 3	10
AJA2-7G	Dark grey, some lamination, somewhat shard-ey, fissile, visible grains, gritty bite, siltstone	2	2	AOM, some PS, some Int, spores, preservation good	3- - 3	15
AJA2-7H	Dark grey, some oxidation, visible grains, slightly gritty bite, fine siltstone	2	2	PS, AOM, spores, some phytoplankton, preservation good	2+ - 3	14
AJA2-7I	Medium-dark grey, some oxidation, many visible grains, gritty bite, siltstone	1	1	AOM, PS, spores, phytoplankton, scolecodont, preservation good	2+ - 3-	13
AJA2-7J	Dark grey, some lamination, visible grains, somewhat gritty bite, fine siltstone	2	2	AOM, PS, some spores, preservation quite good	3- - 3	14
AJA2-7K	Dark grey, lamination with paler layers, many visible grains, gritty bite, siltstone	1	1	Much AOM, PS, some Int, rare spores, preservation quite good	3- - 3+	21
AJA2-7L	Dark grey, some oxidation, some visible grains, somewhat gritty bite, fine siltstone	1	1	AOM, PS, some spores, some phytoplankton, chitinozoan, preservation quite good	2+ - 3-	8
AJA2-7M	Dark grey, irregular lamination, oxidation, visible grains, gritty bite, siltstone	2	2	PS, AOM, various spores, preservation quite good	3 – 3+	15
AJA2-7N	Dark grey, some irregular lamination, oxidation, visible grains in places, gritty bite in places, coarse mudstone?	1	1	AOM, Int, rare spores, preservation quite good	3 - 3+	15
AJA2-7O	Dark grey, significant oxidation, gritty bite in places, coarse mudstone?	1	1	AOM, PS, many spores, some phytoplankton, preservation good	2+ - 3	8
AJA2-7P	Dark grey, some oxidation, ever so slightly gritty bite, mudstone	2	2	PS, AOM, some spores, preservation quite good	3 – 3+	21
AJA2-7Q	Dark grey, oxidation, visible grains, slightly gritty bite, fine siltstone	2	2	AOM, Int, some PS, spores, some phytoplankton, preservation quite good	2+ - 3	13
AJA2-7R	Dark grey, rather fissile, some oxidation, visible grains, slightly gritty bite, fine siltstone	1	1	AOM, PS, spores, preservation quite good	3- – 3	12

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-7S	Dark grey, slight oxidation, some visible grains, gritty bite, siltstone	2	2	AOM, rare spores, preservation generally poor	3+	29
AJA2-13A	Medium grey, common oxidation, some grains visible, gritty, siltstone	<1	1	PS, Int, AOM, some spores, preservation not good	3- - 3+	24
AJA2-13B	Dark grey, decidedly blocky, some oxidation, some visible grains, gritty bite, siltstone	<1	1	Much Int, PS, AOM, rare spores, rare phytoplankton, preservation not good	3- - 3	13
AJA2-14A	Medium-pale grey, some tendency towards lamination, some oxidation, some visible grains, somewhat gritty, fine siltstone	1	1	AOM, Int, some PS, rare spores, preservation medium	3- - 3	15
AJA2-15A	Yellow-brown sandstone	N/A	N/A	N/A	N/A	N/A
AJA2-15B	Grey, some oxidation, slightly gritty bite, fine siltstone?	N/A	N/A	N/A	N/A	N/A
AJA2-15C	Grey, significant oxidation, gritty bite, siltstone	N/A	N/A	N/A	N/A	N/A
AJA2-16A	Medium grey, irregular texture, somewhat gritty, fine siltstone?	N/A	N/A	N/A	N/A	N/A
AJA2-16B	Dark grey, occasional particles, smooth texture, mudstone	1	1	Much AOM, some PS, some Int, sparse palys, scolecodont, preservation uncertain	2+?	12
AJA2-16B-2	See AJA2-16B	2	2	See AJA2-16B		12
AJA2-16C	Dark grey, some suggestion of lamination, smooth texture, mudstone	1	1	AOM, some PS, no definite palys	3-?	14
AJA2-16C-2	See AJA2-16C	2	2	See AJA2-16C		19
AJA2-19A	Pale grey-green colour, quite fissile, some oxidation, some visible grains, clay-ey feel and smooth texture, fine siltstone?	<1	1	Int, some AOM, some spores, preservation not good	3- - 3	15
AJA2-19B	Similar to 19A, very fissile, without visible grains, fine siltstone?	<<1	1	Int, some PS, very rare palys, preservation poor	3	15
AJA2-20A	Dark grey, prominent orange laminations (oxidation?), some visible grains, gritty bite, siltstone	<1	1	Much AOM, PS, spores, phytoplankton, preservation very good [processed 10g]	2+ - 3-	9

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-20B	Dark grey, fissile, gritty bite, fine siltstone?	<1	1	Int, AOM, some spores, phytoplankton, preservation quite good	2+ - 3-	9
AJA2-20B-2	See AJA2-20B	<1	1	See AJA2-20B [processed 18g]		9
AJA2-20C	Dark grey, many visible grains, gritty bite, siltstone	<1	1	Much Int, very rare palys, preservation poor?	3-?	10
AJA2-20C-2	See AJA2-20C	<1	1	See AJA2-20C		10
AJA2-22A	Grey, some paler laminations (oxidation?), visible grains, gritty bite, siltstone	1	1	Int, AOM, rare spores, preservation good	3- - 3	14
AJA2-22A-2		1	1	See AJA2-22A		14
AJA2-22B	Medium-dark grey, slight oxidation, some visible grains, gritty bite, siltstone	1	1	Int, AOM, some spores, some phytoplankton, scolecodont, preservation OK	3- - 3	13
AJA2-22C	Medium-dark grey, slight oxidation, some visible grains, gritty bite, siltstone	1	1	Int, AOM, some PS, very rare palys, scolecodont, preservation unknown	2+ - 3?	10
AJA2-22C-2	See AJA2-22C	<1	1	See AJA2-22C		10
AJA2-22D	Medium-dark grey, slight oxidation, some visible grains, gritty bite, siltstone	1	1	Int, AOM, PS, rare spores, preservation OK	3	18
AJA2-22D-2	See AJA2-22D	<1	1	See AJA2-22D		18
AJA2-22E	Medium-dark grey, occasional oxidation, some visible grains, gritty bite, siltstone	1	1	Int, AOM, rare spores and phytoplankton, preservation quite good	2+ - 3	9
AJA2-22E-2	See AJA2-22E	1	1	See AJA2-22E		9
AJA2-GA	Dark grey, orange coloured oxidation present, coarse appearance, very gritty bite, coarse siltstone	1	1	Int, PS, numerous phytoplankton, some spores, preservation OK	3- - 3	18
AJA2-GB	Medium-dark grey, numerous visible grains, gritty bite, siltstone	1	1	Int, PS, some spores, phytoplankton, preservation quite good	2+ - 3-	10
AJA2-GC	Yellowish sandstone	N/A	N/A	N/A	N/A	N/A
AJA2-GD	Pale grey, some oxidation, visible grains, somewhat gritty bite, siltstone	2	2	PS, Int, spores, chitinozoan, preservation good	2+ - 3	15

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-GE	Grey, oxidation, visible grains, gritty bite, siltstone	2	2	PS, spores, phytoplankton, preservation good	2+ - 3-	9
AJA2-GF	Grey, some hints of lamination, some oxidation, visible grains, very gritty, siltstone	2	2	Much PS, spores, some phytoplankton, preservation good	2+ - 3	11
AJA2-GG	Grey, varied oxidation, some visible grains, slightly gritty bite, fine siltstone	2	2	Much PS, spores, some phytoplankton, preservation good	2+ - 3-	10
AJA2-GH	Grey, varied oxidation, possible alignment of platy minerals, some visible grains, slightly gritty bite, fine siltstone	2	2	PS, spores, rare phytoplankton, preservation good	2+ - 3	18
AJA2-GI	Medium-dark grey, orange oxidation, quite fissile, some lamination, smooth bite, mudstone	2	2	PS, phytoplankton, some spores, chitinozoan, preservation quite good	3 – 3+	19
AJA2-GJ	Medium-dark grey, platy alignment, some oxidation, very slightly gritty bite, very fine siltstone	2	2	AOM, PS, some spores, some phytoplankton, preservation OK	2 – 3-	16
AJA2-GK	Dark grey, tends to break into shards, many visible grains, gritty bite, siltstone	2	2	AOM, PS, spores, some phytoplankton, preservation generally good	2+ – 3	12
AJA2-GL	Medium grey, significant platy alignment, some oxidation, some visible grains in places, gritty bite in places, fine siltstone?	2	2	AOM, some PS, some spores, preservation not good	2+ - 3	19
AJA2-GM	Dark grey, some platy alignment, many visible grains, gritty bite, siltstone	1	1	AOM, PS, some Int, quite numerous phytoplankton, rare spores, preservation medium	3-	13
AJA2-GN	Grey-brown, some oxidation, some visible grains, gritty bite, siltstone	2	2	Int, AOM, some PS, rare spores, some phytoplankton, possible chitinozoan, preservation not good	2+ - 3	15
AJA2-GO	Dark grey, occasional platy alignment, slightly gritty bite, fine siltstone	1	1	AOM, PS, some Int, rare spores, possible phytoplankton, chitinozoan, preservation quite good	2+ - 3	13

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-GP	Blue-grey, some oxidation, quite shard-ey, very few visible grains, smooth bite, coarse mudstone	2	2	AOM, some PS, spores, possible phytoplankton, preservation quite good	2+ - 3	16
AJA2-GQ	Medium grey, some oxidation, some platy alignment, many visible grains, slightly gritty bite, siltstone	3	3	AOM, numerous spores, preservation medium	2+ – 3-	17
AJA2-GR	Grey, orangey oxidation, many visible grains, gritty bite, siltstone	2	2	AOM, some PS, some spores, possible phytoplankton, preservation medium	3-	21
AJA2-GS	Dark grey, significant oxidation, smooth bite, mudstone	2	2	AOM, some spores, possible phytoplankton, preservation medium	2+ - 3	14
AJA2-GT	Grey, some lamination, somewhat shard-ey, oxidation, some visible grains, somewhat gritty bite, siltstone	2	2	AOM, phytoplankton, some spores, chitinozoan, preservation variable (sometimes medium)	2+ - 3-	8
AJA2-GU	Medium-dark grey, some platy alignment, some lamination, some visible grains, somewhat gritty bite, siltstone	2	2	AOM, numerous phytoplankton, some spores, a chitinozoan, preservation medium	3-	13
AJA2-GV	Medium-dark grey, some lamination, oxidation, some visible grains, slightly gritty bite, siltstone	2	2	AOM, phytoplankton, rare spores, preservation quite good	3- - 3	14
AJA2-GW	Dark grey, fissile, oxidation, some platy alignment, smooth bite, mudstone	1	1	AOM, rare PS, various phytoplankton, rare spores, preservation medium	3-	12
AJA2-GX	Dark grey, oxidation, gritty bite, fine siltstone	1	1	AOM, spores, phytoplankton, preservation medium-good	3- – 3	20
AJA2-GY	Medium-dark grey, lamination, oxidation, some visible grains, gritty bite, siltstone	1	1	AOM, phytoplankton, some spores, preservation quite good	3- - 3	15
AJA2-GZ	Dark grey, lamination, quite fissile, red oxidation, some visible grains, very slightly gritty bite, fine siltstone	1	1	AOM, phytoplankton, rare spores, preservation medium-good	3-	11

Sample	Lithology	Yield	Lyc	Palynology	TAI	TO
AJA2-GAA	Grey, red oxidation, some lamination, some visible grains, somewhat gritty bite, siltstone	1	1	AOM, some spores, some phytoplankton, preservation quite good	3- - 3	13
AJA2-GAB	Dark grey, platy alignment, very few visible grains, very slightly gritty bite, fine siltstone	2	2	Much AOM, some PS, some spores, preservation medium-good	3 – 3+	16
AJA2-PA	Dark grey, some lamination, some minor oxidation, smooth bite, mudstone (limey?)	<1	1	Int, occasional possible spore fragment, preservation poor, functionally barren (v. low org. C/degradation)	2 – 4	19h 22m
AJA2-PA-2	See AJA2-PA	<<1	1	See AJA2-PA		19h
AJA2-PB	Dark grey, some lamination, some minor oxidation, smooth bite, mudstone (limey?)	<1	1	Int, some AOM, no discernible palys, barren (v. low org. C/degradation)	4	19h 30m
AJA2-PB-2	See AJA2-PB	<<1	1	See AJA2-PB		19h 1m
AJA2-PC	Dark grey, very smooth, regular texture, smooth bite, mudstone	<1	1	Int, AOM, some possible spores, preservation poor	4- – 4	19h 3m
AJA2-PC-2	See AJA2-PC	<<1	1	See AJA2-PC		19h 2m
AJA2-PD	Dark grey, smooth bite, mudstone (limey?)	<1	1	Int, rare AOM, some possible spores, preservation poor	4- – 4	19h 12m
AJA2-PD-2	See AJA2-PD	<<1	1	See AJA2-PD		19h 3m

Appendix II: Macrofossils and sedimentary structures

A II.1 - Macrofossils

Various macrofossils were observed at outcrop as well as a small number taken in hand specimen. These are detailed below, organised by their site of origin.

A II.1.1 - Playa del Tranqueru

AJA2-3A preserved a possible shell impression. AJA2-3H bears the well-preserved impression of a bryozoan. In addition, possible bioturbation was seen in outcrop on the bases of two beds.

A II.1.2 - Mirantes de Luna

A total of three fossil hand specimens were obtained from this site. AJA2-15A is quite a large specimen bearing remains of several bryozoans. AJA2-15B bears a possible shell impression, though it is mostly obscured. AJA2-15C contains a number of mineralised crinoid fragments. Additional bryozoans, crinoid fragments and shells were observed in outcrop including two major depositional horizons with fossils outcropping across the entire surface of a boulder.

A II.1.3 - Geras

AJA2-16A is a hand specimen bearing the impression of a bivalve or brachiopod shell. A shell was also observed in AJA2-16C. A crinoid fragment was observed in outcrop.

A II.1.4 - Crémenes-Las Salas

AJA2-GC is a hand specimen bearing the impression of a crinoid ossicle or possibly a mollusc such as a limpet. Possible shell cross-sections were also observed in outcrop.

A II.2 - Sedimentary structures

Some sites included interesting sedimentary structures, briefly described below.

A II.2.1 - Playa del Tranqueru

This site displayed some ripple marks on two sand beds, indicating a relatively shallow sea. The site is particularly notable for its unique red and white sand beds. These seem to occur in two main types. One involves a very pale sand with flame structures seen in an orange sediment. These flame structures always point towards what was the top of the beds during deposition and it is speculated that they represent pockets of mud or other sediment trapped within a large, possibly swiftly deposited sand bed which have then intruded upwards into the sand before becoming fully consolidated. The different sediments have then gained different colours through differential responses to oxidation and weathering. The other main type involves a very pale, usually white sand with bands of dark red on it, both across beds, seen edge on or fully exposed, or between beds. This is interpreted as the result of oxidising fluids infiltrating the sand bed, as evidenced by the pattern seen on some beds; this is the pattern of spread of the fluids. This dark red banding is also seen in a very small number of dark grey siltstone beds, similarly spreading across beds and occasionally between them. The site's location on the coast and its exposure to the sea has probably contributed to this phenomenon.

A II.2.2 - San Pedro de Nora

This site is notable for displaying obvious ball and pillow structures on the bases of some sand beds in the upper part of the formation. These structures are seen at a variety of sizes.

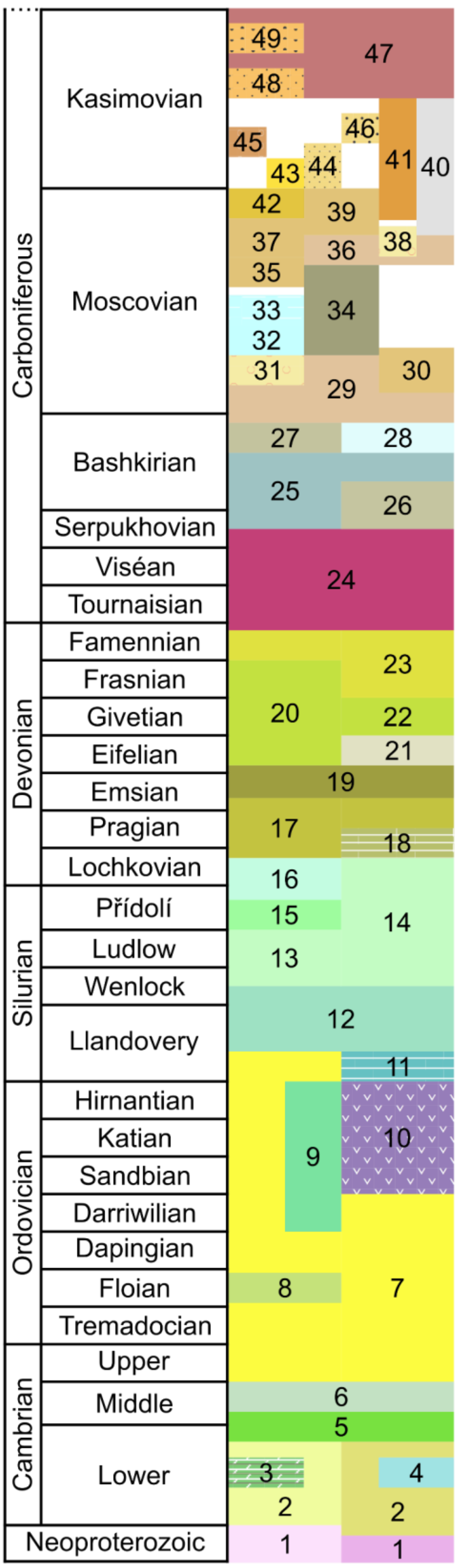
A II.2.3 - Mirantes de Luna

This site showed an unusual bed of reddish-coloured shale containing round nodules; possibly constituting a conglomerate. In addition, beds were seen to be folded at multiple locations, often quite severely and occasionally sinuously, indicating significant distortion.

A II.2.4 - Crémenes-Las Salas

This site is unique in displaying large nodules within some sandstone beds which had weathered in an onion-skin fashion. These structures were seen in numerous beds and at various scales. Some local faulting was also observed, in one location enclosing a unit of finely interbedded dark red and pale sands, of a clearly different character to surrounding strata.

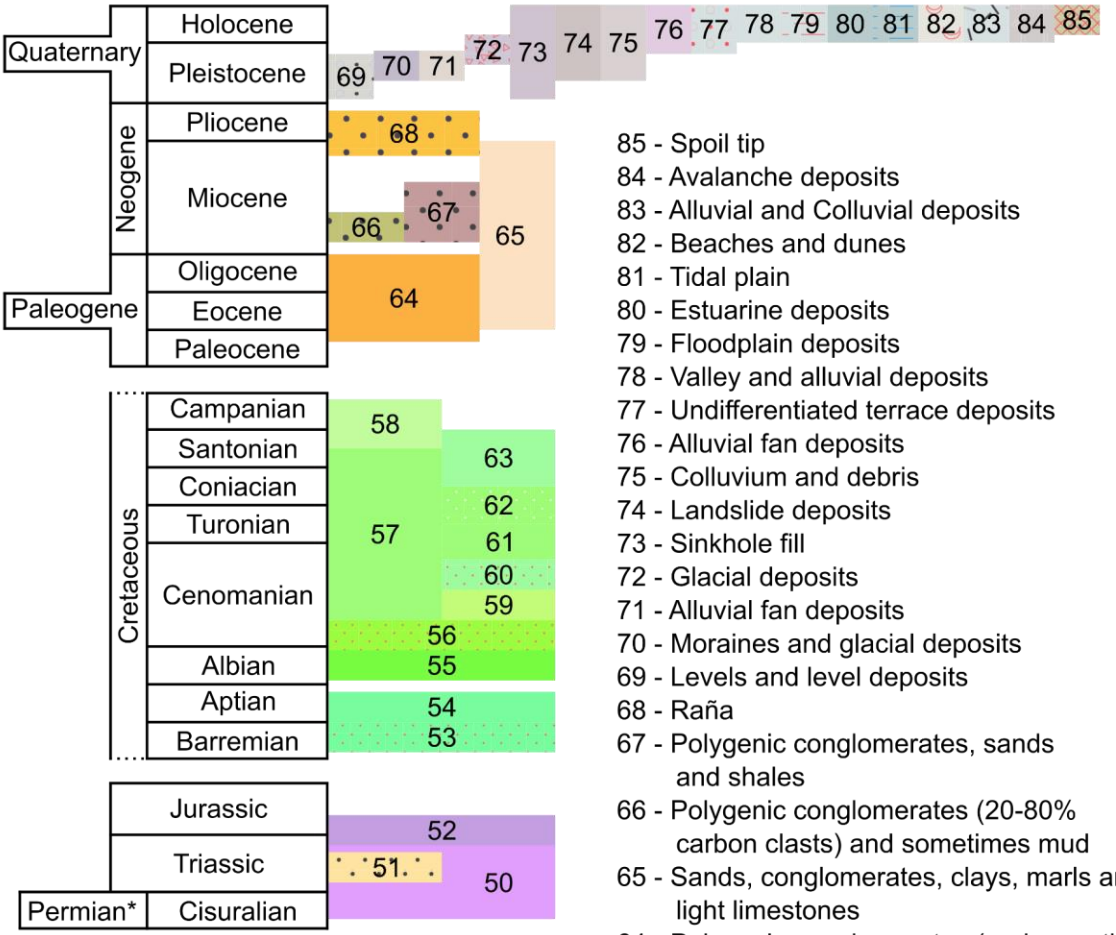
Key to Figures 12-19 - Neoproterozoic to Carboniferous deposits



49 - Sabero (polymictic conglomerates)
48 - Sabero (quartzitic conglomerates)
47 - Sabero
46 - Cea group
45 - Cuenca Puerto de Ventana
44 - Cea group
43 - Cea group
42 - Conjas-Mental group
41 - Canseco-Rucayo; Reyero-Salamón; Cea group; Cuenca de Ciñera-Matallana; Cuenca de la Magdalena; Cuenca de Villablino
40 - Brañosera*; Mélange del Porma; Maraña
39 - San Salvador; Verdeña*
38 - Olloniego; Ablanedo
37 - Anciles
36 - Vergaño*
35 - Dueñas
34 - Ferreras
33 - Bachende, Middle Mbr.
32 - Bachende, Lower Mbr.
31 - Curavadas*
30 - San Emiliano, Candemuela Mbr.
29 - San Emiliano, La Majúa Mbr.
28 - Valdetega
27 - San Emiliano
26 - Cuevas; Olleros
25 - Barcallente
24 - Alba; Vegamián; Cándamo-Baleas
23 - Nocedo; Fueyo; Ermita; Piñeres
22 - Portilla; Candás
21 - Naranco; Huergas
20 - Gustalapiedra*; Cardaño*
19 - Moniello; Santa Lucía; Polentinos*
18 - Lebanza; Felmín; Valporquero; Coladilla
17 - Abadía; La Vid group; Rañeces group
16 - Upper Carazo*
15 - Lower Carazo*
14 - Furada; San Pedro
13 - Las Arroyacas*
12 - Formigoso
11 - Castro, Viodo Mbr.
10 - Castro
9 - Pajares
8 - Barrios (clay and slate intercalations)
7 - Barrios
6 - Oville
5 - Láncara
4 - Calcareous levels
3 - Herrería (dolomite intercalations)
2 - Herrería
1 - Narcea; Mora

*Fig. 19 only

Key to Figures 12-19 - Permian to Holocene deposits and igneous units



85 - Spoil tip
84 - Avalanche deposits
83 - Alluvial and Colluvial deposits
82 - Beaches and dunes
81 - Tidal plain
80 - Estuarine deposits
79 - Floodplain deposits
78 - Valley and alluvial deposits
77 - Undifferentiated terrace deposits
76 - Alluvial fan deposits
75 - Colluvium and debris
74 - Landslide deposits
73 - Sinkhole fill
72 - Glacial deposits
71 - Alluvial fan deposits
70 - Moraines and glacial deposits
69 - Levels and level deposits
68 - Raña
67 - Polygenic conglomerates, sands and shales
66 - Polygenic conglomerates (20-80% carbon clasts) and sometimes mud
65 - Sands, conglomerates, clays, marls and light limestones
64 - Polygenic conglomerates (and sometimes calcareous breccias) with sands, silts and red clays
63 - Oviedo
62 - La Argañosa
61 - San Lázaro
60 - Latores
59 - La Manjoya
58 - Boñar, Upper Mbr.
57 - Boñar, Lower Mbr.
56 - El Caleyu; Utrillas
55 - Ullaga
54 - Antromero
53 - Peñaferruz
52 - Gijón
51 - Gravels, sandstones and clays
50 - Sotres; Cabranes; Caravia; Fuentes

a - Mafic dykes and sills
b - Granodiorites and post-kinematic biotite granites

*Guadalupian and Lopingian not represented

Playa del Tranqueru - 3

San Pedro de Nora - 7

Crémenes-Las Salas - G