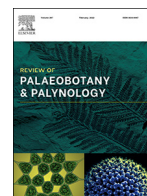




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Dispersed spore assemblages from the Lower Devonian Rañeces - La Vid groups of Northern Spain: Palaeogeographical implications

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ABSTRACT

Dispersed spore assemblages are described from the Early Devonian (late Lochkovian-late Emsian) Rañeces Group (Asturias) and equivalent La Vid Group (Leon) of Northern Spain. The lower part of both groups consists predominantly of limestone and yields only impoverished palynological assemblages. However, the upper parts contain more clastic sediments and yield rich assemblages of well preserved palynomorphs. These are dominated by marine forms but also include abundant spores. Sixty-two spore taxa are reported from the Valporquero Formation (Leon). These all belong to a single assemblage that can be equated with the *lindlarensis-sextantii* Assemblage Zone (mid-early late Emsian age) erected in northern Gondwana. The sequences are independently age constrained by conodont and invertebrate macrofossil evidence and the ages derived from these studies are concordant with the assigned spore zones. The Spanish spore assemblages are from deposits that accumulated around the Armorican Terrane Assemblage (ATA), a group of islands that lay between the continents of Laurussia and Gondwana. Jacaard Index analysis indicates that the Valporquero Formation spore assemblage is endemic, and not closely related to those previously described from Laurussia or Gondwana, although it has more in common with the latter. This suggests that the Armorican Terrane Assemblage was widely separated from both Laurussia and Gondwana, but was located closer to and had more connectivity with Northern Gondwana.

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1. Introduction

Northern Spain (Cantabrian Zone) hosts an extensive outcrop of Devonian deposits that represent a near complete stratigraphical sequence through the Devonian (reviewed in [García-Alcalde et al., 2002](#)) (Figs. 1, 2). The outcrop extends across a shelf from nearshore marine (Asturias Province) to shallow mid shelf (Leon Province) to deep offshore shelf-basin (Palencia Province) (Fig. 1). These deposits are of particular interest because they accumulated around an isolated land mass known as the Armorican Terrane Assemblage (ATA) ([Torsvik and Cocks, 2017](#)). Throughout the Devonian the ATA was situated between the supercontinents Gondwana (to the southeast) and Laurussia (to the northwest) with significant tracts of ocean believed to have separated the ATA from these continents ([Askew and Wellman, 2020](#)) (Fig. 3). The stratigraphical sequences of the Northern Spanish Devonian have been well documented (e.g. [Barrois, 1882](#);

[Comte, 1959](#); [García-Alcalde et al., 2002](#); [García-López, 2002](#)) and are well age-constrained using macrofossil and conodont evidence (e.g. [García-López and Bastida, 2002](#)) (Fig. 2). A growing body of research suggests that the Silurian-Devonian terrestrial vegetation of the ATA, as evidenced by dispersed spore assemblages, was highly endemic due to this isolation ([Askew and Wellman, 2019](#)). This paper reviews the dispersed spore assemblages from the Lower Devonian (Lochkovian-Emsian) Rañeces - La Vid groups and discusses their significance in terms of palaeophytogeography. These dispersed spore floras have not been revised since the preliminary work of Cramer and colleagues in the 1960s–1970s (e.g. [Cramer, 1967a](#)). Historically these were some of the earliest works on Lower Devonian dispersed spores and consequently have some significance regarding Early Devonian spore taxonomy.

2. Geological setting

Northern Spain together with some other parts of modern Europe constitute a group of relatively small landmasses known as the ATA ([Torsvik and Cocks, 2017](#)). The ATA separated from Gondwana during the Cambrian. By Devonian times the ATA formed an isolated group of islands that were separated by relatively large tracts of ocean from the

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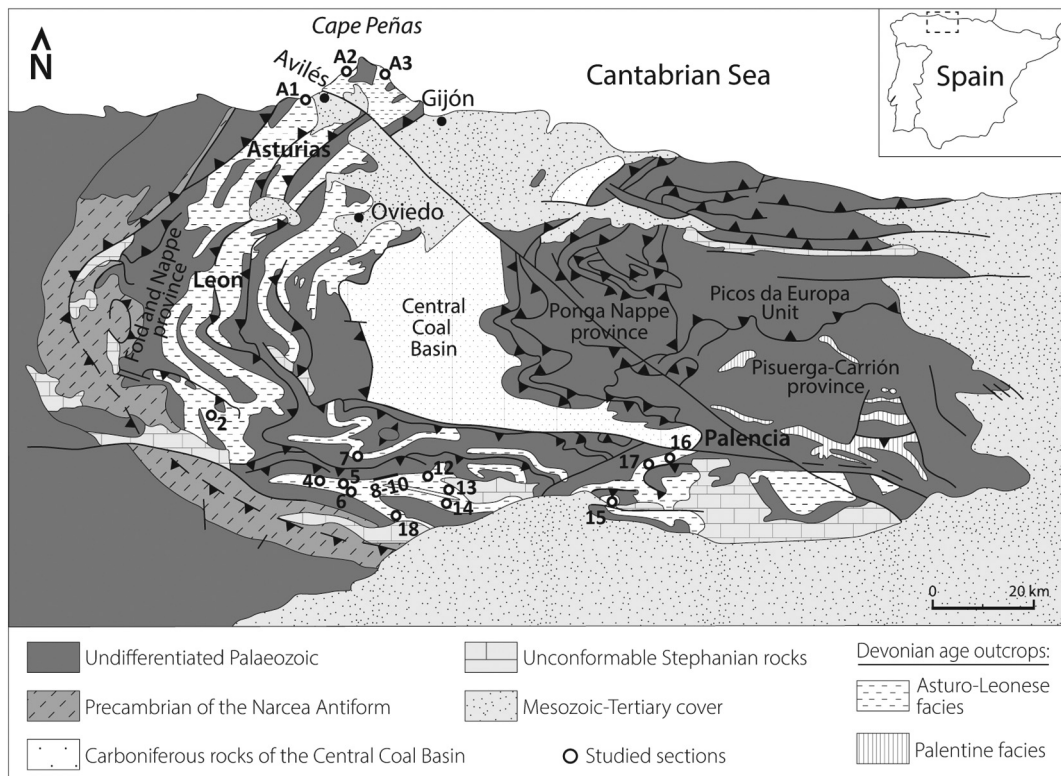


Fig. 1. Outline map of Northern Spain showing the outcrop of Devonian deposits with the location of sampled sections. Numbered localities/sections are from Appendix A.

Chronostratigraphic Units	Lithostratigraphic Units		
	Asturias	León	Palencia
390 m.y. Eifelian	Moniello Fm.	Santa Lucía Fm.	Polentinos Fm.
400 m.y. Emsian	Rañeces Group Aguión Fm. Ferroñes Fm.	La Vid Group Coladilla Fm. Valporquero Fm. La Pedrosa Fm.	Abadía Fm.
			Lebanza Fm.
Pragian	Bañugues Fm.	Felmín Fm.	
Lochkovian	Nieva Fm.		
410 m.y. Pridoli	Furada Fm.	San Pedro Fm.	Carazo Fm. Upper Member Lower Member

Fig. 2. Stratigraphical sequence of the Lower Devonian deposits of Northern Spain and their age and correlation.

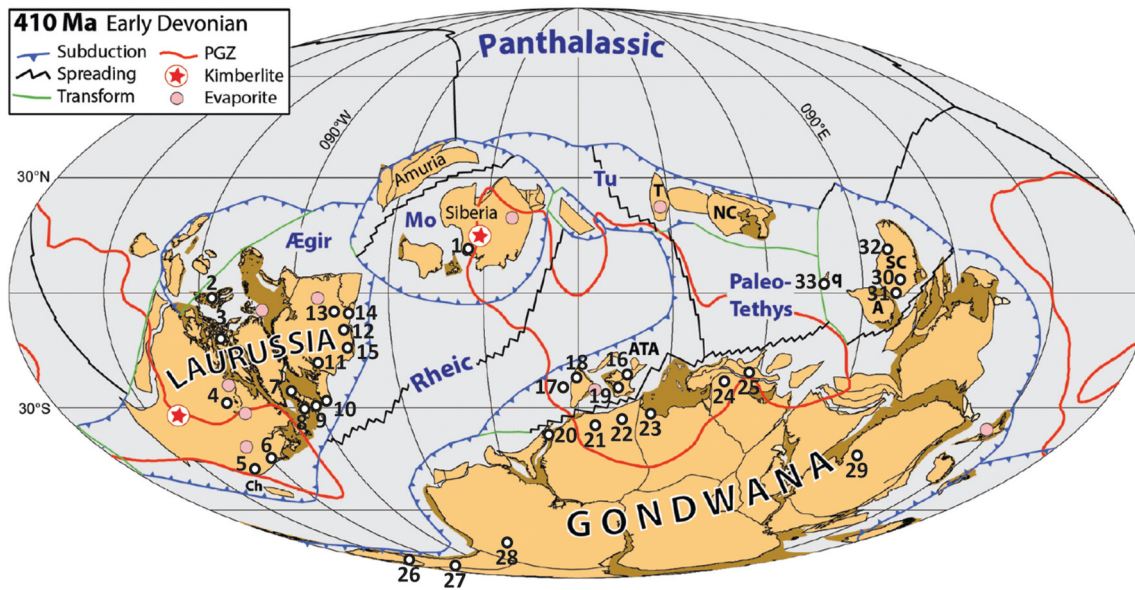
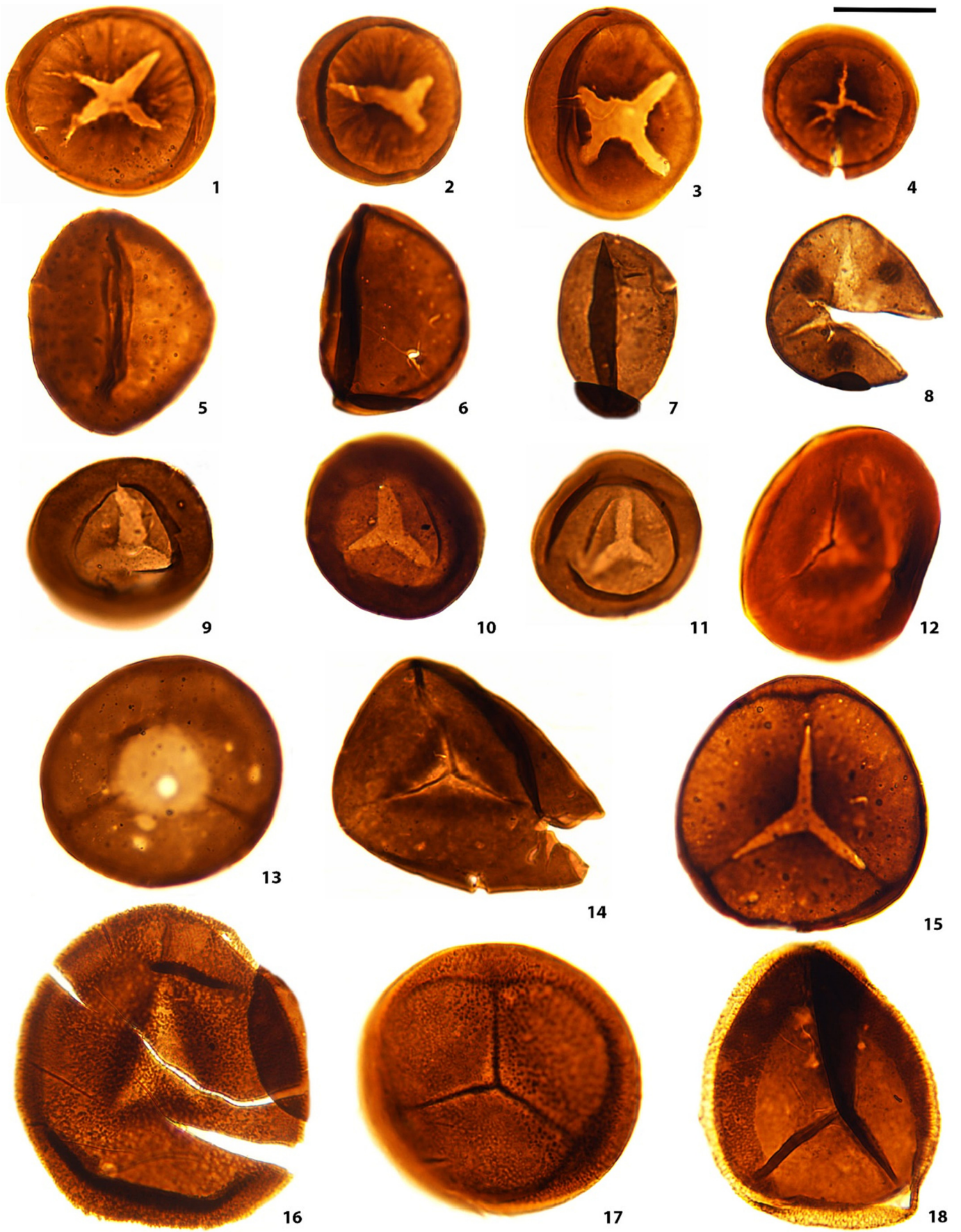


Fig. 3. Palaeocontinental reconstruction of the Early Devonian with the position of the Armorican Terrane Assemblage indicated. Palaeocontinental reconstruction from Torsvik and Cocks (2017) with permission. Numbers refer to previously described Emsian spore assemblages (see Table 7).

Table 1

Spore taxa previously reported from the Rañeces - La Vid groups and their interpretation with respect to the taxonomy utilised in the current work.

Taxon	Description	Designation
<i>Leiotriletes bonitus</i> Cramer 1967 (1967-Plate II, fig. 32; 1969-Plate I, fig. 9)	Triangular, laevigate, darkened around periphery and along trilete mark	<i>Camarazontriletes</i> sp. A
<i>Retusotriletes barbatus</i> Cramer 1967 (1967-Plate II, fig. 38)	Retusoid, scabrate; contact areas dark	<i>Retusotriletes</i> spp.
<i>Dictyotriletes gorgoneus</i> Cramer 1967 (1967-Plate III, figs. 69,72)	Reticulate with irregular polygonal lumina 2–3 µm wide	Widely reported taxon not identified herein.
<i>Acanthotriletes espinositus</i> Cramer 1967 (1967-Plate II, fig. 49; 1969-Plate II, fig. 18)	Densely packed slender spines 2.5 µm tall	<i>Dibolisporites</i> spp. (Plate II, fig. 4 in this paper)
<i>Acanthotriletes</i> cf. <i>tenuispinosus</i> Naumova 1953 (1967-Plate II, fig. 44; Plate III, fig. 68)	Densely packed slender spines 1–2 µm tall	<i>Dibolisporites tuberculatus?</i> Breuer and Steemans, 2013
<i>Anapiculatisporites abrepunius</i> Cramer 1967 (1967-Plate II, fig. 47)	Widely dispersed cones 1 µm tall	<i>Apiculiretusispora</i> spp.
<i>Anapiculatasporites chistosus</i> Cramer 1967 (1967-Plate II, fig. 45)	A <i>Dibolisporites</i> with widely dispersed spines 2–3 µm tall	<i>Dibolisporites</i> spp.
<i>Anapiculatisporites matagallegus</i> Cramer 1967 (1967-Plate II, fig. 46; Plate III, fig. 50; 1976-Plate IV, fig. 54)	Densely packed cones up to 2 µm tall	Probably <i>Dibolisporites eifeliensis</i> (Lanning) McGregor 1973
<i>Anapiculatasporites picantus</i> Cramer 1967 (1967-Plate II, fig. 36)	Densely packed cones 1 µm tall	<i>Apiculiretusispora</i> spp.
<i>Anapiculatasporites tojoides</i> Cramer 1967 (1967-Plate II, fig. 48; 1969-Plate II, fig. 20, Plate III, fig. 34)	Sparsely packed cones	Steenmans (1989) transferred to <i>Aneurospora</i> (<i>Anapiculatasporites</i>) <i>tojoides</i> (Cramer 1967) Steemans 1989
<i>Anapiculatisporites</i> cf. <i>Lophotriletes subverrucosus</i> Jush. 1953 (1967-Plate II, figs. 42–43)	Sparsely packed baculae	<i>Dibolisporites</i> spp.
<i>Emphanisporites mcgregorii</i> Cramer 1967 (1967-Plate III, fig. 59; 1969-Plate I, fig. 13)	Herringbone proximal radial muri	Widely reported taxon identified herein.
<i>Emphanisporites obscurus</i> McGregor 1961 (1967-Plate III, fig. 56)	Indistinct proximal muri	?Corroded <i>E. rotatus</i> or <i>E. biradiatus</i>
<i>Emphanisporites rotatus</i> McGregor 1961 (1967-Plate III, figs. 57,58,62)	Simple proximal radial muri.	Widely reported taxon identified herein.
<i>Cyclogranisporites finus</i> Cramer 1967 (1967-Plate III, fig. 54)	Interradial thickenings and distally packed granulate	<i>Apiculiretusispora</i> (but too small for <i>A. arabiansis</i>).
<i>Cyclogranisporites zumbonus</i> Cramer 1967 (1967-Plate III, fig. 67)	Distal ornament of sparsely packed grana/spines.	? <i>Apiculiretusispora</i> .
<i>Cyclogranisporites</i> sp. 1 Cramer & Diez 1976 (1976-Plate IV, fig. 52)	Widely dispersed grana-coni	<i>Dibolisporites</i> spp.
<i>Perotriletes gordianus</i> Cramer 1967 (1967-Plate III, fig. 64; 1976-Plate IV, figs. 47,51,53)	Triangular with smooth perispore	Possibly <i>Zonotriletes brevivelatus</i> B&S(13).
<i>Hymenozonotriletes aterciopeladus</i> Cramer 1967 (1967-Plate IV, fig. 78)	Inner body with separating granulate outer layer	<i>Rhabdosporites minutus</i> Tiwari & Schaarschmidt 1975
<i>Rhabdosporites</i> (<i>Hymenozonotriletes</i>) <i>butifarrus</i> (Cramer 1967) Cramer 1969 (1967-Plate IV, fig. 79)	Cones form a reticulum	<i>Acinosporites</i> (<i>Verrucosporites</i>) <i>apiculatus</i> (Stree) Stree 1967
<i>Rhabdosporites</i> (<i>Hymenozonotriletes</i>) <i>prosperus</i> Cramer 1967 (1967-Plate IV, figs. 76,81; 1969-Plate II, figs. 21,23,24,25)	Reticulate-verrucate	<i>Acinosporites lindlarensis</i> Riegel 1968



supercontinents of Gondwana (to the southeast) and Laurussia (to the northwest) (Fig. 3). However, palaeocontinental/palaeogeographical reconstructions are controversial and differ regarding the size and extent of the oceans with either open ocean separating Gondwana and Laurussia (Scotese, 2008; Torsvik and Cocks, 2017) or a land bridge to the west of the Rheic Ocean joining the two supercontinents (Scotese, 2016). Nonetheless, in most recent palaeocontinental/palaeogeographical reconstructions the ATA is situated opposite to the North African part of Northern Gondwana (Scotese, 2008, 2016; Torsvik and Cocks, 2017).

The Devonian deposits of Northern Spain crop out in a large arc from the northern Coast near Gijón, south through Asturias Province, before veering into an east–west orientation across León and into Palencia Province. The deposits represent a transect across a marine shelf from nearshore (Asturias), across the shelf (León) and into an offshore deep basinal setting (Palencia). The sedimentary sequence represents a near continuous sequence through the Devonian and has been well documented regarding stratigraphical correlation, sedimentology, palaeontology and biostratigraphy (e.g. García-Alcalde et al., 2002; Gutiérrez-Marco et al., 2019). The sediments are entirely marine in origin and exhibit a broad alternation between calcareous and clastic deposition.

One of the calcareous-clastic alternations is the Rañeces Group and equivalent La Vid Group of late Lochkovian to late Emsian age. Different stratigraphical classifications developed in Asturias, Leon and Palencia for these coeval strata: Rañeces Group (Asturias); La Vid Group (Leon); Lebanza and Abadia formations (Palencia) (e.g., Gutiérrez-Marco et al., 2019) (Fig. 2). The Rañeces - La Vid groups are between

400 and 600 m in thickness and consists predominantly of limestones, dolomites and shales.

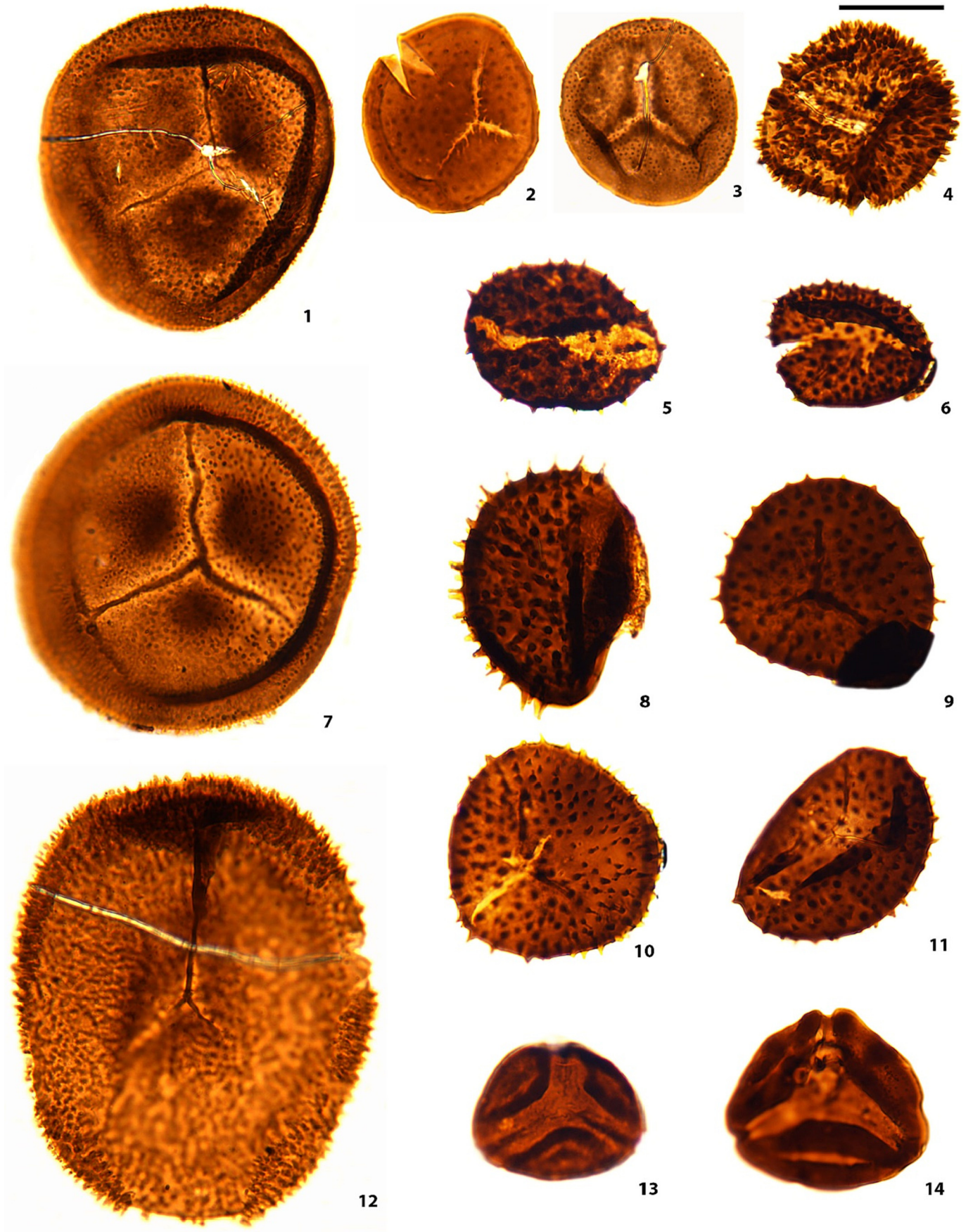
In Asturias the Rañeces Group is divided into four formations. The contact with the underlying Furada Formation is not exposed. The lowermost strata belongs to the Nieva Formation (Barrois, 1882; Llopis Llado, 1961; Radig, 1962; Arbizu, 1972; Zamarreño, 1976; Vera de la Puente, 1989; García-Alcalde, 1992). The Nieva Formation consists of 335 m of alternating thick-bedded bioclastic limestone, argillaceous bioturbated limestones and thin calcareous siltstones-shales. At the top of the formation limited reef building commences. Brachiopods from the basal part indicate a Lochkovian Age (Arbizu, 1972; García-Alcalde, 1996) and middle-late Lochkovian conodonts are present (García-López and Sanz-López, 2000, 2002a). Towards the top of the formation early Pragian conodonts have been reported along with age-diagnostic brachiopods (García-Alcalde, 1996). The Lochkovian/Pragian boundary has been identified based on conodont evidence (García-López and Arbizu, 1993).

The Bañugues Formation (Zamarreño, 1976; García-Alcalde, 1992) comprises 150–200 m of dolostones and limestones. The brachiopod fauna from the uppermost part of this formation and the lowermost part of the succeeding formation was related to the 'faune des monstres' of the Armorican Massif (García-Alcalde, 1992) that derives from strata thought to include the Pragian/Emsian boundary.

The Ferroñes Formation (Barrois, 1882) is 120 m in thickness and consists of shales, shelly marls and bioclastic limestones. Rich conodont and brachiopod faunas have been recovered from the formation

Plate I. Dispersed spores from the Valporquero Fm of northern Spain. Scale bar = 20 µm.

1. *Artemopyra reticosta* Breuer et al. 2007 (Sample 17SPAIN31; Slide 2; E.F.no. C44).
2. *Artemopyra reticosta* Breuer et al. 2007 (Sample 2000LV01; Slide 1; E.F.no. S41/1).
3. *Laevolancis (Archaeozonotriletes) divellomedium* (Chibrickova) Burgess & Richardson 1991 (Sample 17SPAIN31; Slide 2; E.F.no. E36).
4. *Laevolancis (Archaeozonotriletes) divellomedium* (Chibrickova) Burgess & Richardson 1991 (Sample 17SPAIN35; Slide 1; E.F.no. U41/3).
5. Ornamented monolet spore (Sample 17SPAIN43; Slide 2; E.F.no. L51.4). Solitary occurrence.
6. *Latosporites ovalis* Breuer et al. 2007 (Sample 2000LV04; Slide 1; E.F.no. C46/1).
7. *Latosporites ovalis* Breuer et al. 2007 (Sample 2000LV01; Slide 1; E.F.no. X43).
8. *Retusotriletes maculatus* McGregor & Camfield 1976 (Sample 2000LV01; Slide 3; E.F.no. H47).
9. *Retusotriletes* sp. A (Sample 2000LV20; Slide 1; E.F.no. S43).
10. *Retusotriletes* sp. A (Sample 2000LV01; Slide 1; E.F.no. R28).
11. *Retusotriletes* sp. A (Sample 2000LV04; Slide 1; E.F.no. N28).
12. *Retusotriletes (Phyllothecotriletes) rotundus* (Stree) Stree emend. Lele & Stree 1969 (Sample 17SPAIN48; Slide 2; E.F.no. N27/4).
13. *Retusotriletes tenerimedium* Chibrickova 1959 (Sample 17SPAIN46; Slide 2; E.F.no. L33/1).
14. *Retusotriletes (Phyllothecotriletes) triangulatus* (Stree) Stree 1967 (Sample 2000LV04; Slide 1; E.F.no. M28/1).
15. *Retusotriletes goensis* Lele & Stree 1969 (Sample 2000LV01; Slide 1; E.F.no. Q39/4).
16. *Apiculiretusispora brandtii* Stree 1964 (Sample 2000LV04; Slide 1; E.F.no. E44/4).
17. *Apiculiretusispora (Cyclogranisporites) plicata* (Allen) Stree 1967 (Sample 17SPAIN47; Slide 2; E.F.no. J52/4).
18. *Apiculiretusispora (Cyclogranisporites) plicata* (Allen) Stree 1967 (Sample 17SPAIN31; Slide 2; E.F.no. G50).



indicative of an Emsian age (Alvarez, 1990; García-Alcalde, 1992; García-López and Arbizu, 1993; García-Alcalde and Truyols-Massoni, 1994; Truyols-Massoni and García-Alcalde, 1994).

The Aguión Formation (Radig, 1962) consists of ca. 160 m of red marls and crinoidal limestones. The lower part comprises 20 m of crinoidal limestone that is utilised as a marker horizon for recognising the base of the formation. At the classic fossiliferous locality at the Arnao platform the palaeontology and sedimentology of this horizon has been the subject of intense study (e.g. Alvarez-Nava and Arbizu, 1986). This reefal build up has been equated to the second reefal episode of the León area. Conodonts recovered from the formation indicate a late Emsian age (García-López and Arbizu, 1993; García-López and Sanz-López, 2002a). The Aguión Formation is overlain by the distinctive limestones of the Moniello Formation.

In León the La Vid Group is approximately 400 m in thickness and is also divided into four formations. The basal contact with the San Pedro Formation is transitional, with alternating siltstones, sandstones and dolomites, and represents a general change from siliciclastic to carbonate sedimentation (Keller, 1988; Keller and Grötsch, 1988). This change has been related to a deepening episode. The lowest formation of the La Vid Group is the Felmín Formation (Vilas-Minondo, 1971) that is laterally equivalent to the Nieva and Bañugues formation of Asturias (Fig. 2). It is 114 m in thickness and is composed of dolomites, calcareous

sandstone and shales. Vera de la Puente (1989) interprets the Felmín Formation deposits as littoral to lagoonal in transition to tidal flats.

La Pedroso Formation (Vera de la Puente, 1989) is 107 m in thickness and comprises bioclastic limestones, silty limestones and shales. It is equivalent to the lower part of the Ferroñes Formation of Asturias. It is interpreted as reflecting a progressive deepening from an inner to mid ramp environment to the outer or deep ramp (Vera de la Puente, 1989; Keller, 1988).

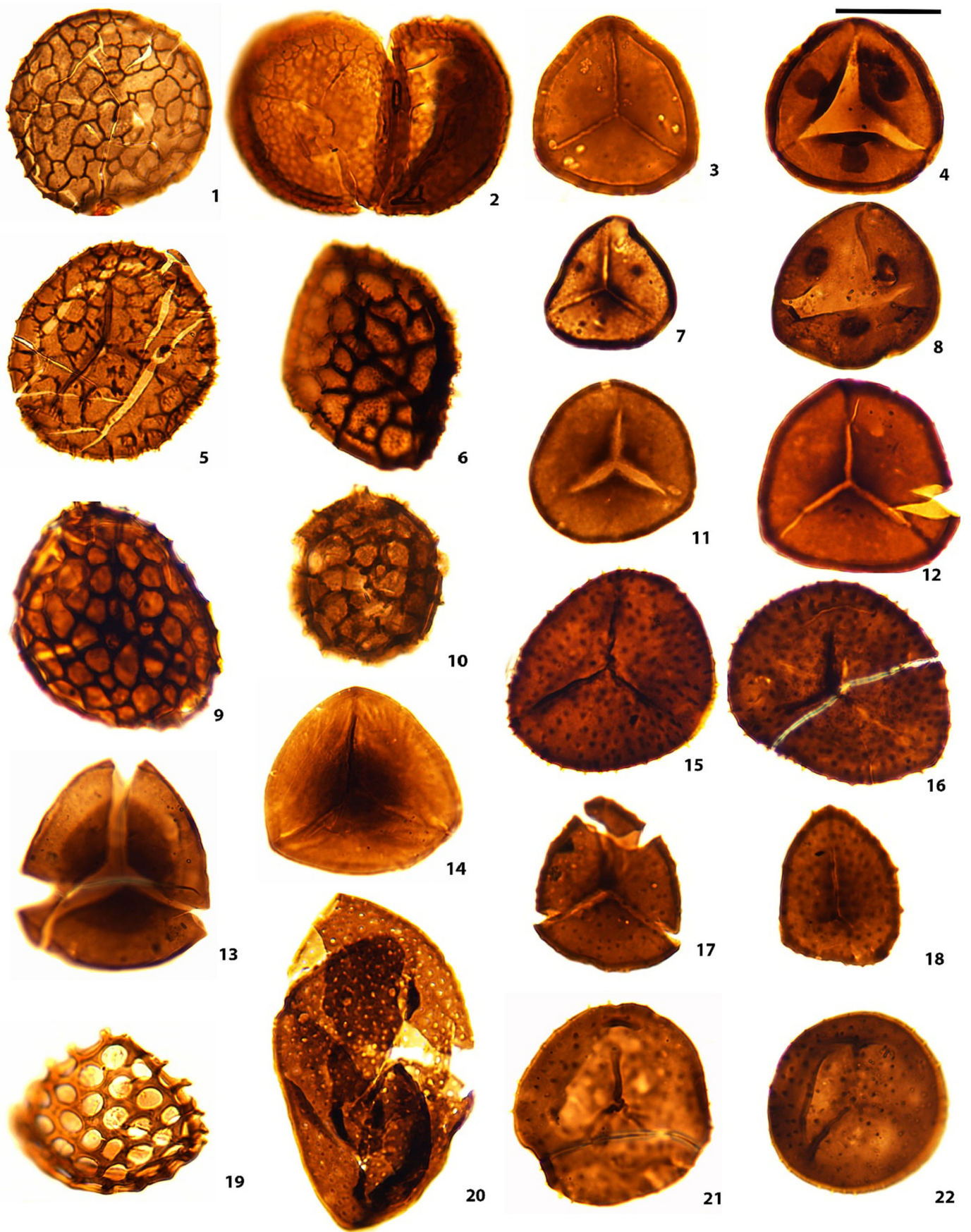
The Valporquero Formation (Vilas-Minondo, 1971) is 169 m in thickness and consists of shales with occasional limestones (Fig. 2). It is equivalent to the upper part of the Ferroñes Formation of Asturias. These sedimentary rocks are interpreted as accumulating as deep ramp or distal ramp shales.

The Coladilla Formation (Vera de la Puente, 1989) is 35 m in thickness and is comprised of red marls with shales and bioclastic carbonate lenses followed by crinoidal limestones intercalated among shales. It is equivalent to the Aguión Formation of Asturias (Fig. 2). The limestones are believed to represent small biostromes. The La Vid Group is overlain by the distinctive limestone unit known as the Santa Lucía Formation.

Conodonts from the La Vid Group have been studied by Grötsche (1988), García-López and Alonso-Menéndez (1994) and García-López and Sanz-López (2002b). Conodont faunas from the lower part of the Felmín Formation indicate a middle Lochkovian age (Grötsche, 1988;

Plate II. Dispersed spores from the Valporquero Fm of northern Spain. Scale bar = 20 µm.

1. *Apiculiretusispora arabiensis* Al-Ghazi 2009 (Sample 17SPAIN35; Slide 1; E.F.no. K52/4).
2. *Apiculiretusispora* sp. (Sample 17SPAIN31; Slide 2; E.F.no. Y48/1).
3. *Apiculiretusispora* sp. (Sample 17SPAIN31; Slide 2; E.F.no. D37).
4. *Dibolisporites* spp. in tetrad configuration (Sample 17SPAIN26; Slide 1; E.F.no. K52/1).
5. *Dibolisporites* (*Bullatisporites*) *bullatus* (Allen) Riegel 1973 (Sample 2000LV01; Slide 1; E.F.no. E35).
6. *Dibolisporites* (*Bullatisporites*) *bullatus* (Allen) Riegel 1973 (Sample 2000LV01; Slide 1; E.F.no. D40/2).
7. *Apiculiretusispora arabiensis* Al-Ghazi 2009 (Sample 17SPAIN43; Slide 2; E.F.no. N51).
8. *Dibolisporites tuberculatus* Breuer & Steemans 2013 (Sample 18SPAIN18; Slide 1; E.F.no. V39.1).
9. *Dibolisporites tuberculatus* Breuer & Steemans 2013 (Sample 2000LV04; Slide 1; E.F.no. C32/4).
10. *Dibolisporites* (*Anapiculatisporites*) *eifeliensis* (Lanninger) McGregor 1973 (Sample 17SPAIN26; Slide 3; E.F.no. K28/2).
11. *Dibolisporites* (*Anapiculatisporites*) *eifeliensis* (Lanninger) McGregor 1973 (Sample; Slide 2000LV04; Slide 3; E.F.no. S30).
12. *Dibolisporites* (*Triletes*) *echinaceus* (Eisenack) Richardson 1965 (Sample 17SPAIN42; Slide 1; E.F.no. T42/2).
13. *Coronospora inornata* Breuer & Steemans 2013 (Sample 2000LV04; Slide 3; E.F.no. K39).
14. *Coronospora inornata* Breuer & Steemans 2013 (Sample 18SPAIN08; Slide 2; E.F.no. R25).



García-López and Sanz-López, 2002b). Those from the upper part of the formation suggest a Pragian or earliest Emsian age (García-López and Alonso-Menéndez, 1994). The same fauna continues into the lower part of the La Pedrosa Formation (García-López and Alonso-Menéndez, 1994). A conodont fauna of early Emsian age is reported higher in the formation (García-López and Sanz-López, 2002b). Conodont faunas from the uppermost part of the formation García-López and Sanz-López (2002b) are of late Emsian age. Conodont data are sparse for the upper part of the Valporquero and Coladilla formations, but those that do occur suggest a late Emsian age (García-López and Sanz-López, 2002b).

The Rañeces - La Vid groups consist predominantly of calcareous deposits with small reefal build-ups common. This suggests accumulation in a warm tropical setting, which is consistent with palaeocontinental reconstructions for the ATA. In terms of palaeoenvironments (e.g. García-López, 2002), the Nieva Formation is interpreted as accumulating in an open marine platform. However, the laterally equivalent Bañugues-Felmin formations accumulated, at least in part, on tidal flats. The La Pedrosa Formation was deposited under open marine conditions, which were probably some distance from the coastline, with water depth gradually increasing over time. The fine siliciclastic deposits higher in the formations probably accumulated in deep waters under calm conditions. The Aguión-Coladilla formations also accumulated in open marine conditions relatively far from the coast. However, there is evidence for shallowing in some areas.

3. Previous palynological studies

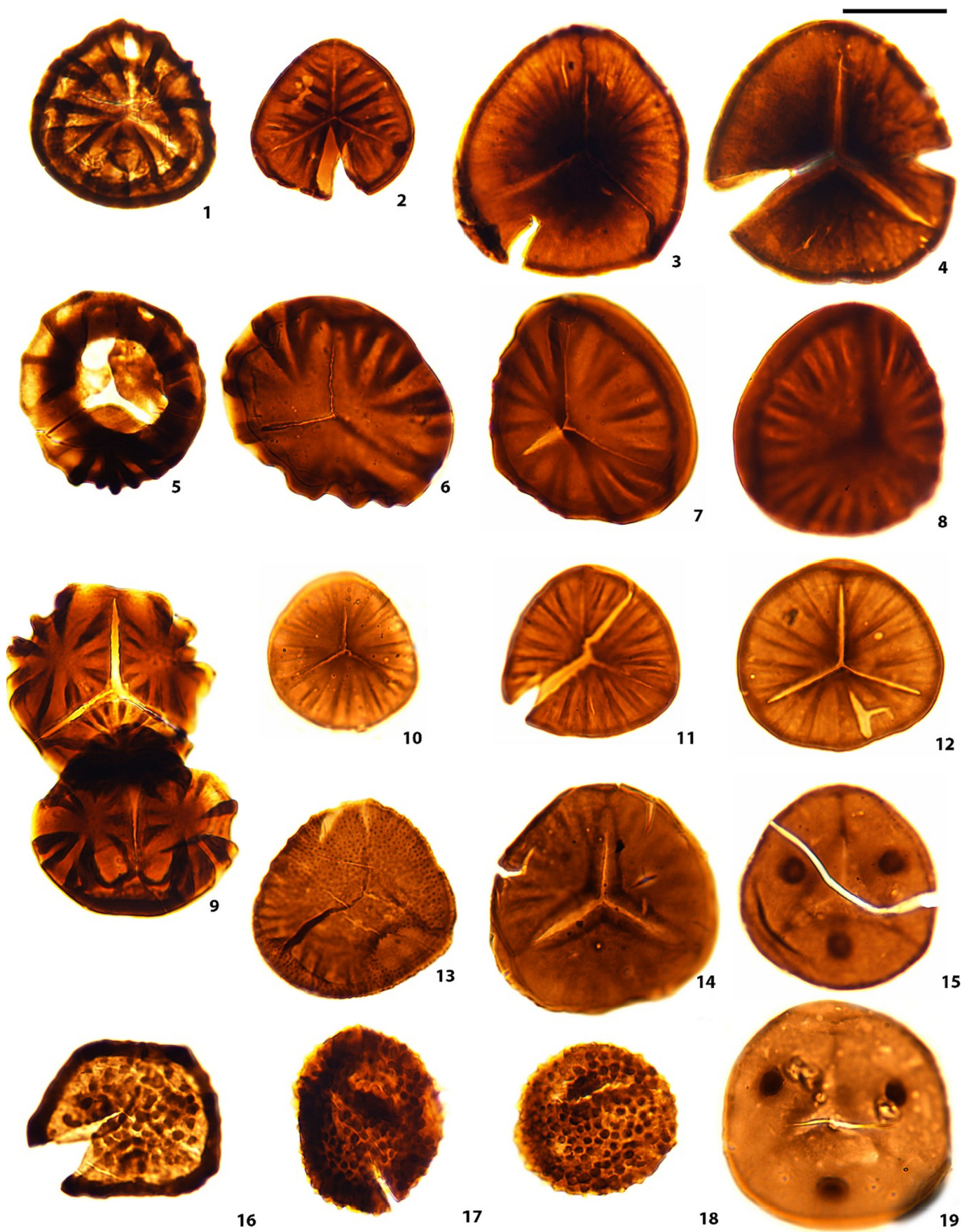
The first research on the palynology of the Devonian sequences of Northern Spain (Cantabrian Zone) was undertaken by Cramer and colleagues in a series of classic studies early in the history of palynological research. Those on the 'La Vid Group' focused primarily on the marine palynomorphs: acritarchs, prasinophycean cysts and chitinozoans (Cramer, 1964, 1967a, 1967b; Cramer et al., 1976; Diez and Cramer, 1978). However, Cramer also reported briefly on land plant dispersed spores that co-occurred with these marine palynomorphs (Cramer, 1967b) and erected a number of new taxa. Despite the fact that these studies on dispersed spores occurred early in the history of this endeavour, many of these taxa have slipped into obscurity, probably because the descriptions were brief, based on few specimens and they were scantily illustrated. Table 1 lists the taxa reported by Cramer (1967b) and suggests a modern taxonomic determination.

4. Sampling and methods

Since 2000 numerous field excursions to the Northern Spanish Devonian sequences have been undertaken by CHW during which 83 samples were collected for palynological analysis from 17 sections. These are listed in Appendix A and the location of the sections illustrated in Fig. 1. Samples were processed at the University of Sheffield using standard HCl-HF-HCl palynological acid macerations techniques. Samples

Plate III. Dispersed spores from the Valporquero Fm of northern Spain. Scale bar = 20 µm.

1. *Dictyotriletes kerpilii* Wellman 2006 (Sample 17SPAIN21; Slide 2; E.F.no. H44).
2. *Dictyotriletes kerpilii* Wellman 2006 (Sample 17SPAIN50; Slide 2; E.F.no. R27/3).
3. *Ambitisporites avitus* Hoffmeister 1959 (Sample 17SPAIN46; Slide 2; E.F.no. M40/4).
4. *Ambitisporites (Retusotriletes) eslae* (Cramer & Diez) Richardson et al. 2001 (Sample 2000LV04; Slide 1; E.F.no. P34).
5. *Dictyotriletes subgranifer* McGregor 1973 (Sample 18SPAIN35; Slide 2; E.F.no. M32).
6. *Dictyotriletes subgranifer* McGregor 1973 (Sample 2000LV04; Slide 1; E.F.no. U36).
7. *Ambitisporites tripapillatus* Moreau-Benoit 1976 (Sample 2000LV01; Slide 1; E.F.no. S33/1).
8. *Ambitisporites (Retusotriletes) eslae* (Cramer & Diez) Richardson et al. 2001 (Sample 2000LV01; Slide 1; E.F.no. K30/1).
9. *Dictyotriletes (Reticulatisporites) emsiensis* (Allen) McGregor 1973 (Sample 17SPAIN08; Slide 2; E.F.no. L37).
10. *Dictyotriletes subgranifer* McGregor 1973 (Sample 2000LV04; Slide 1; E.F.no. W30/1).
11. *Ambitisporites* sp. A (Sample 2000LV04; Slide 1; E.F.no. X37/4).
12. *Ambitisporites* sp. A (Sample 2000LV20; Slide 1; E.F.no. C30).
13. *Concentricosisporites (Stenozonotriletes) sagittarius* (Rodríguez) Rodríguez 1983 (Sample 18SPAIN35; Slide 2; E.F.no. P38/4).
14. *Concentricosisporites (Stenozonotriletes) sagittarius* (Rodríguez) Rodríguez 1983 (Sample 17SPAIN31; Slide 2; E.F.no. T52/3).
15. *Aneurospora (Anapiculatasporites) tojooides* (Cramer 1967) Steemans 1989 (Sample 2000LV20; Slide 1; E.F.no. R42/3).
16. *Aneurospora (Anapiculatasporites) tojooides* (Cramer 1967) Steemans 1989 (Sample 17SPAIN21; Slide 2; E.F.no. V30/3).
17. *Aneurospora* sp. A (Sample 2000LV04; Slide 1; E.F.no. C45/1).
18. *Aneurospora* sp. A (Sample 2000LV04; Slide 1; E.F.no. J35).
19. *Brochotriletes foveolatus* Naumova 1953 (Sample 17SPAIN47; Slide 2; E.F.no. H51).
20. *Brochotriletes* sp. A (Sample 17SPAIN08; Slide 2; E.F.no. N33).
21. *Aneurospora* sp. B (Sample 17SPAIN43; Slide 2; E.F.no. E34/1/2).
22. *Aneurospora* sp. B (Sample 18SPAIN40; Slide 2; E.F.no. H35/1).



were sieved using a 20 µm mesh, subjected to a heavy liquid separation using ZnCl₂, and further sieved using a 20 µm mesh. The residues were then oxidised using fresh Schultz solution for varying periods of time before strew mounting onto glass coverslips and glued to glass slides using epoxy resin. Slides were examined using standard light microscopy techniques (Olympus BH2 microscope) and images captured using a Q Imaging MicroPublisher 3.3 RTV camera.

Sample recovery was extremely variable and largely dependent on lithology. Limestones were often barren or yielded very low organic matter content. Palynomorphs, where present, were usually poorly preserved and often dark and opaque. Calcareous mudstones and shales, often interbedded with the limestones, were also often barren. Some yielded low quantities of organic matter, but the palynomorphs (if present) were often poorly preserved, dark in colour and of moderate to high opacity. Only very few calcareous samples oxidised well enough to produce moderate to light coloured palynomorphs that were translucent and could be adequately studied using a light microscope (see Appendix A). Shales, present in thick units such as the Valporquero Formation, often yielded large quantities of organic matter containing abundant well preserved palynomorphs. Organic matter yield is highly variable and seems to relate to weathering of the shales. As noted by Cramer (1967b) these shales weather rapidly in the climate of Northern Spain and it is difficult to obtain fresh rock. Where present it can yield vast quantities of organic material. In more weathered material organic yield diminishes considerably and the preservation of the palynomorphs deteriorates. Thermal maturity also varies considerably

depending on location (in general decreasing eastwards) and local tectonics. Some samples oxidise extremely well yielding yellow-orange translucent palynomorphs. Other samples fail to clear on oxidation.

Productive slides were scanned through and qualitative assessment was made through presence-absence data sheets (Tables 3–6). The data generated was analysed using the Jaccard Similarity Coefficient (e.g. Izsack and Price, 2001) (On-line data Appendix 1).

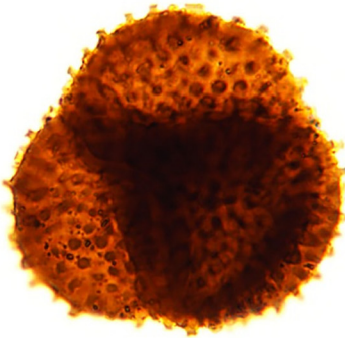
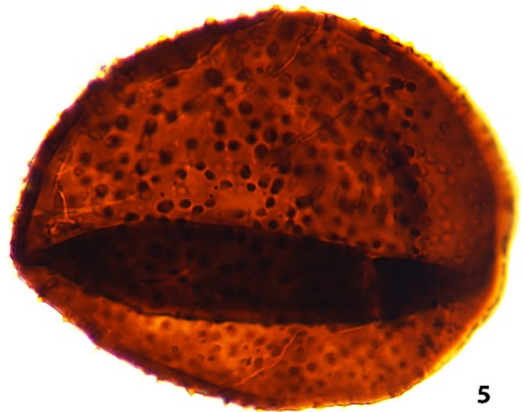
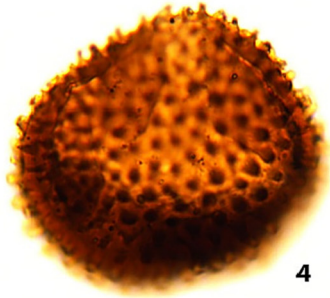
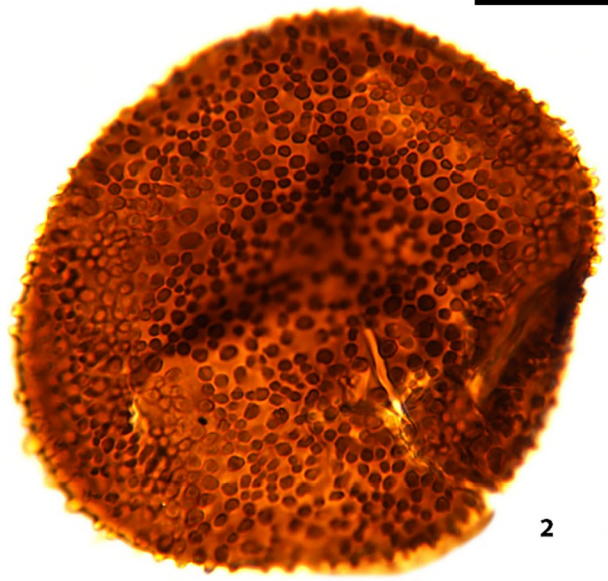
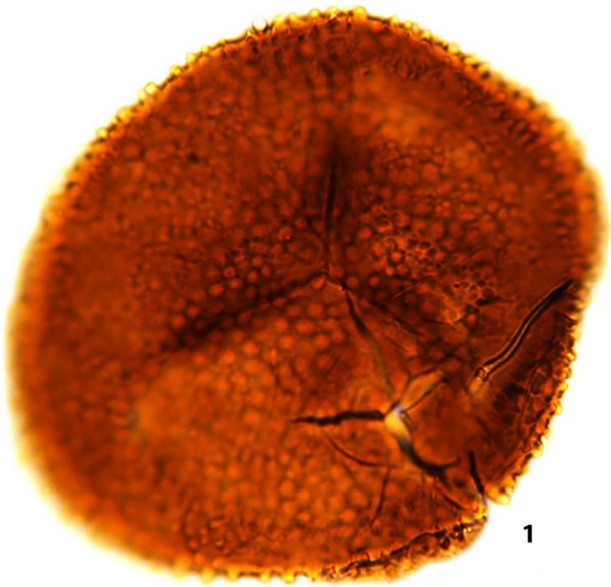
All materials (rock, residues, slides) are housed in the collections of the Centre for Palynology of the School of Biosciences, University of Sheffield, UK. Figured specimens are located using England Finder Coordinates (Plates I–VII).

5. Results

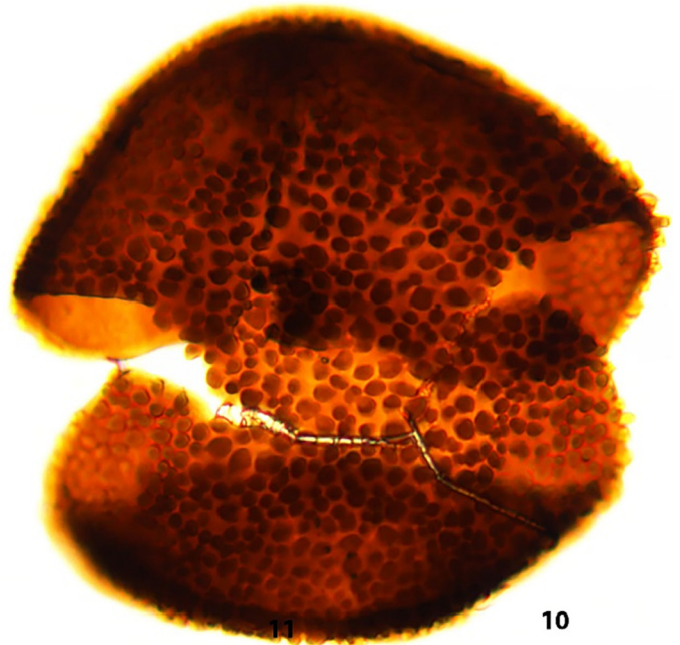
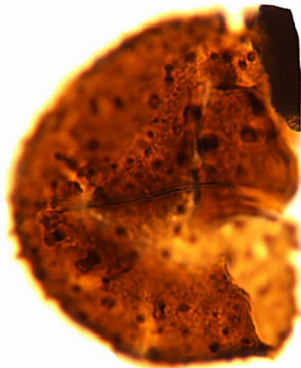
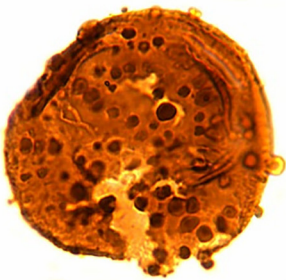
All of the recovered assemblages are from marine deposits and dominated by marine palynomorphs (acritarchs, prasinophycean cysts, chitinozoans and scolecodonts). Spores are present in all but in varying quantities (herein identified as rare, moderate abundance or common). The palynomorphs recovered from the Asturian coastal sections are often of high thermal maturity (opaque) and poor preservation and the spores are difficult to identify. Inland the palynomorphs are of lower thermal maturity (although variable) and many assemblages contain well preserved palynomorphs of low thermal maturity that are easily identifiable. Table 2 lists all of the dispersed spore taxa identified. The distribution of spores is documented in the Asturias sequences

Plate IV. Dispersed spores from the Valporquero Fm of northern Spain. Scale bar = 20 µm.

1. *Emphanisporites annulatus* McGregor 1961 (Sample 17SPAIN35; Slide 1; E.F.no. L46/2).
2. *Emphanisporites mcgregorii* Cramer 1966 (Sample 2000LV20; Slide 3; E.F.no. D32).
3. *Emphanisporites edwardsiae* Wellman 2006 (Sample 17SPAIN35; Slide 1; E.F.no. D53/1).
4. *Emphanisporites edwardsiae* Wellman 2006 (Sample 2000LV04; Slide 1; E.F.no. R46/3).
5. *Emphanisporites (Triletes) erraticus* (Eisenack) McGregor 1961 (Sample 2000LV04; Slide 1; E.F.no. U40/1).
6. *Emphanisporites (Triletes) erraticus* (Eisenack) McGregor 1961 (Sample 18SPAIN08; Slide 2; E.F.no. O52).
7. *Emphanisporites biradiatus* Steemans 1989 (Sample 17SPAIN43; Slide 2; E.F.no. X27).
8. *Emphanisporites biradiatus* Steemans 1989 (Sample 17SPAIN43; Slide 2; E.F.no. S40/3).
9. *Emphanisporites schultzei* McGregor 1973 (Sample 17SPAIN47; Slide 2; E.F.no. M43/1).
10. *Emphanisporites rotatus* McGregor emend. McGregor 1973 (Sample 17SPAIN46; Slide 2; E.F.no. M31).
11. *Emphanisporites rotatus* McGregor emend. McGregor 1973 (Sample 17SPAIN31; Slide 2; E.F.no. G38/2).
12. *Emphanisporites rotatus* McGregor emend. McGregor 1973 (Sample 17SPAIN31; Slide 2; E.F.no. O52).
13. *Emphanisporites micromatus* Richardson & Lister 1969 (Sample 2000LV04; Slide 3; E.F.no. G29/4).
14. *Emphanisporites* sp. A (Sample 2000LV04; Slide 1; E.F.no. F36/4).
15. *Scylaspora elegans* Richardson et al. 2001 (Sample 18SPAIN35; Slide 2; E.F.no. R38/3).
16. *Synorisporites tripapillatus* Richardson & Lister 1969 (Sample 2000LV04; Slide 3; E.F.no. E44/2).
17. *Synorisporites* spp. (Sample 17SPAIN47; Slide 2; E.F.no. G38/2).
18. *Synorisporites* spp. (Sample 17SPAIN47; Slide 2; E.F.no. P47/4).
19. *Scylaspora elegans* Richardson et al. 2001 (Sample 17SPAIN10; Slide 1; E.F.no. W36).



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(Table 3), La Vid Type Section (Table 4), Argovejo section (Table 5) and all other sections (Table 6).

5.1. Rañeces Group: Nieva Formation

Eight samples of the Nieva Fm were collected from Sections A1 (Santa Maria del Mar: Playa de Bahinas) and A2 (Xago-Verdicio: Playa de Xago east) (Appendix A). The single sample from Section A1 contained only rare highly coalified spores that were indeterminate. The seven samples from Section A2 were either barren or contained only rare highly coalified spores that were indeterminate, except for a single sample, which contained abundant spores, but unfortunately these were also highly coalified and indeterminate.

5.2. Rañeces Group: Bañugues Formation

Two samples were collected from the Bañugues Fm from Section A3 (Bañugues: playa east) (Appendix A). One was barren and the other yielded an assemblage containing spores in moderate abundance, although these were of moderate thermal maturity and poorly preserved. Only five taxa were identifiable (*Ambitisporites* spp., *Apiculiretusispora* spp., *Dictyotriletes* spp., *Emphanisporites rotatus*, *Retusotriletes* spp.) (Table 3), and this assemblage is consequently of little help in age designation.

5.3. Rañeces Group: Ferroñes Formation

Four samples from the Ferroñes Fm were collected from two sections: A1 (Santa Maria del Mar: Ensenada) and A3 (Bañugues: playa

west) (Appendix A). The palynomorph assemblages from two samples from Section A1 contained only very rare spores. One assemblage is notable in being dominated by chitinozoans and scolecodonts with extremely rare smooth-walled spores (*Ambitisporites* spp., *Retusotriletes* spp.) and a single specimen of *Emphanisporites*. Both samples collected from Section A3 were barren.

5.4. Rañeces Group: Aguión Formation

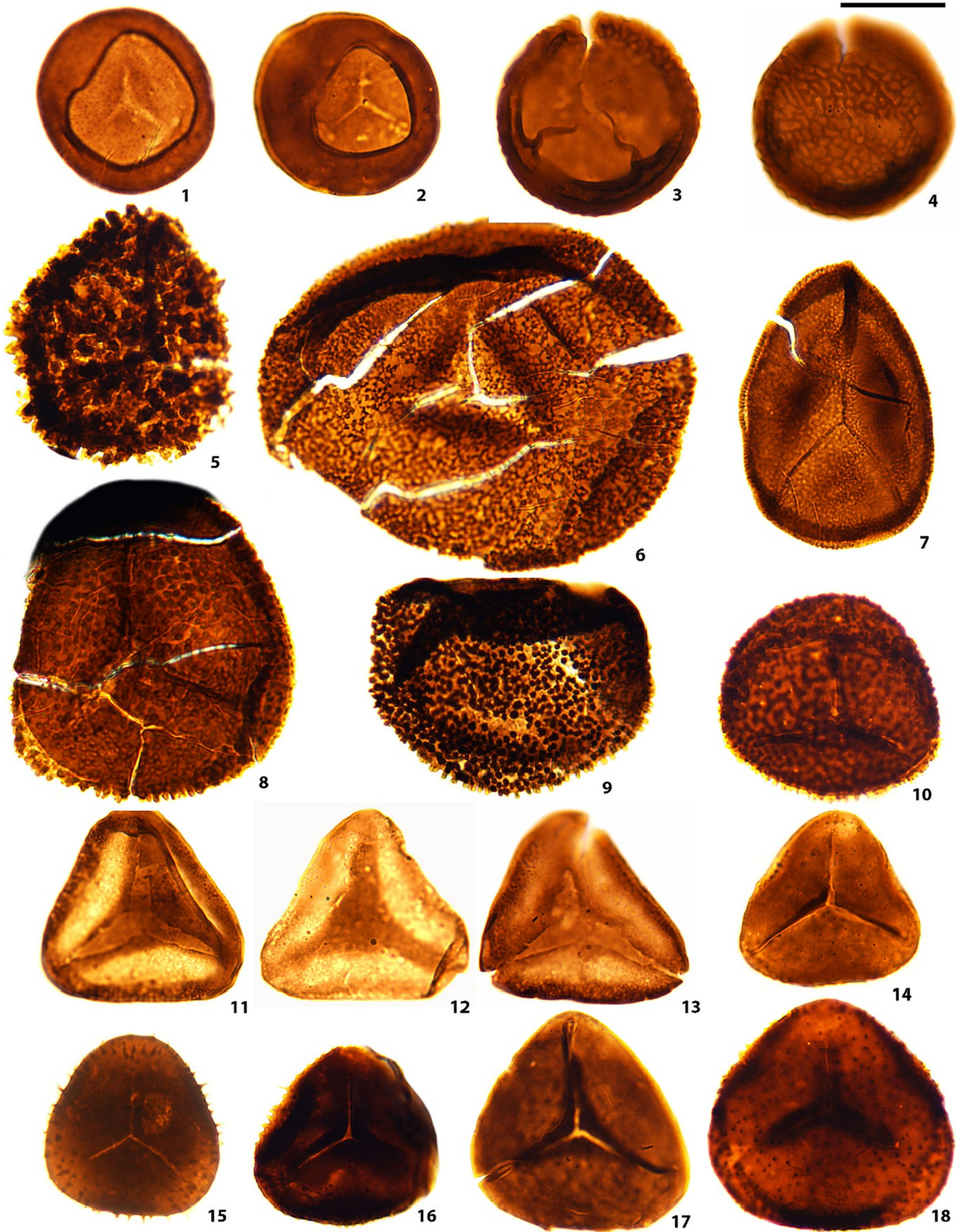
Four samples were collected from the Aguión Fm from Section A1 (Santa Maria del Mar: Arnao) (Appendix A). One was barren but the other three yielded rich assemblages of well preserved spores of relatively low thermal maturity. All three samples were logged and included 20 spore taxa (Table 3). This depauperate assemblage is consistent with the late Emsian age for the formation indicated by conodonts (García-López and Arbizu, 1993; García-López and Sanz-López, 2002a).

5.5. La Vid Group: Felmín Formation

Two samples were collected from the L8-L10 section at the LE473 Roadcut and five samples were collected from rare shales/limey shales from the Felmín Fm in the road cutting that is the La Vid Type section (Appendix A). Both of the LE473 samples were barren. From La Vid one sample yielded an assemblage of reasonably abundant palynomorphs of moderate preservation and thermal maturity. It is dominated by marine elements with chitinozoans particularly abundant. Spores are extremely rare and only represented by simple

Plate V. Dispersed spores from the Valporquero Fm of northern Spain. Scale bar = 20 µm.

- 1, 2. *Verrucosporites polygonalis* Lanninger 1968 (Sample 17SPAIN48; Slide 2; E.F.no. Q43/2).
3. *Archaeozonotriletes* (*Retusotriletes*) *chulus* (Cramer) Richardson & Lister 1969 (Sample 17SPAIN47; Slide 2; E.F.no. K41).
4. *Cymbosporites dammamensis* Steemans 1995 tetrad (Sample 18SPAIN08; Slide 1; E.F.no. K53/1).
5. *Verrucosporites polygonalis* Lanninger 1968 (Sample 17SPAIN31; Slide 2; E.F.no. V25/3).
6. *Cymbosporites dammamensis* Steemans 1995 tetrad (Sample 17SPAIN42; Slide 1; E.F.no. T54/1).
7. *Cymbosporites dammamensis* Steemans 1995 (Sample 17SPAIN46; Slide 2; E.F.no. C24/3).
8. *Verruciretusispora* (*Triletes*) *dubia* (Eisenack) Richardson & Rasul 1978 (Sample 17SPAIN47; Slide 2; E.F.no. V24).
9. *Verruciretusispora* (*Triletes*) *dubia* (Eisenack) Richardson & Rasul 1978 (Sample 17SPAIN25; Slide 2; E.F.no. P50/2).
10. *Verrucosporites polygonalis* Lanninger 1968 (Sample 17SPAIN43; Slide 2; E.F.no. W51).



laevigate forms (*Retusotriletes* spp.). The other samples were either barren or contained very rare coalified palynomorphs.

5.6. La Vid Group: La Pedrosa Formation

The La Pedrosa Fm was sampled from three sections (10 samples in total): L8-L10 (the LE473 road cutting); L13 (the road cutting that is the Type Section for the La Vid Group); L16 (the Argovejo locality) (Appendix A). All three samples from L8-L10 were barren. Of the six samples from L13 four contained only very rare and coalified palynomorphs. Two contained better preserved palynomorphs of lower thermal maturity but the spores were only rare to moderate in abundance. The two samples from L16 contained well preserved palynomorphs of low thermal maturity but spores were again only of low to moderate abundance. The depauperate spore assemblages are difficult to age date but nothing in them disagrees with the late Pragian-mid Emsian age suggested by conodonts (Grötsche, 1988; García-López and Alonso-Menéndez, 1994; García-López and Sanz-López, 2002b). The occurrence of the age diagnostic taxon

Camarozonotriletes sextantii may indicate an Emsian age for samples located higher in the formation (Table 5).

5.7. La Vid Group: Valporquero Formation

Numerous sections of the Valporquero Fm were sampled (39 samples) (Appendix A). Eight of these yielded assemblages of abundant and extremely well preserved palynomorphs of moderate thermal maturity that cleared during oxidation. Many of the palynomorph assemblages included abundant spores. The spore assemblages are all similar in composition and can be treated as a single assemblage that can be dated as mid to late (but not latest) Emsian in age (see Section 6). Fig. 4 represents a composite log showing the relative position of the productive samples that were logged. The distribution of spore taxa reported is outlined in Tables 4–6.

5.8. La Vid Group: Coladilla Formation

The Coladilla Fm was examined but no lithologies suitable for palynomorph preservation were identified and collected.

Plate VI. Dispersed spores from the Valporquero Fm of northern Spain. Scale bar = 20 µm.

1. *Archaeozonotriletes* sp. A (Sample 2000LV04; Slide 3; E.F.no. Q33).
2. *Archaeozonotriletes* sp. A (Sample 2000LV04; Slide 3; E.F.no. N37).
- 3–4. *Chelinospora* spp. (Sample 18SPAIN08; Slide 3; E.F.no. V48/4).
5. *Acinosporites lindlarensis* Riegel 1968 (Sample 2000LV04; Slide 3; E.F.no. P43/4).
6. *Acinosporites (Verrucosisorites) apiculatus* (Streel) Streel 1967 (Sample 2000LV04; Slide 3; E.F.no. G46/4).
7. *Cymbosporites asymmetricus* Breuer et al. 2007 (Sample 2000SPAIN04; Slide 3; E.F.no. Q48/4).
8. *Acinosporites lindlarensis* Riegel 1968 (Sample 17SPAIN26; Slide 1; E.F.no. X46/1).
9. *Acinosporites lindlarensis* Riegel 1968 (Sample 17SPAIN47; Slide 2; E.F.no. K40).
10. *Acinosporites lindlarensis* Riegel 1968 (Sample 2000LV01; Slide 1; E.F.no. J29/1).
11. *Camarozonotriletes* sp. A (Sample 2000LV04; Slide 3; E.F.no. V38/3).
12. *Camarozonotriletes* sp. A (Sample 17SPAIN43; Slide 2; E.F.no. K34).
13. *Camarozonotriletes* sp. A (Sample 2000LV04; Slide 3; E.F.no. K30/3).
14. *Camarozonotriletes* sp. (Sample 17SPAIN46; Slide 2; E.F.no. M53/1).
15. *Camarozonotriletes sextantii* McGregor & Camfield 1976 (Sample 2000LV04; Slide 1; E.F.no. C36/1).
16. *Camarozonotriletes sextantii* McGregor & Camfield 1976 (Sample 2000LV04; Slide 1; E.F.no. U31).
17. *Camarozonotriletes sextantii* McGregor & Camfield 1976 (Sample 17SPAIN20; Slide 2; E.F.no. Y42).
18. *Camarozonotriletes sextantii* McGregor & Camfield 1976 (Sample 18SPAIN18; Slide 1; E.F.no. M37/3).

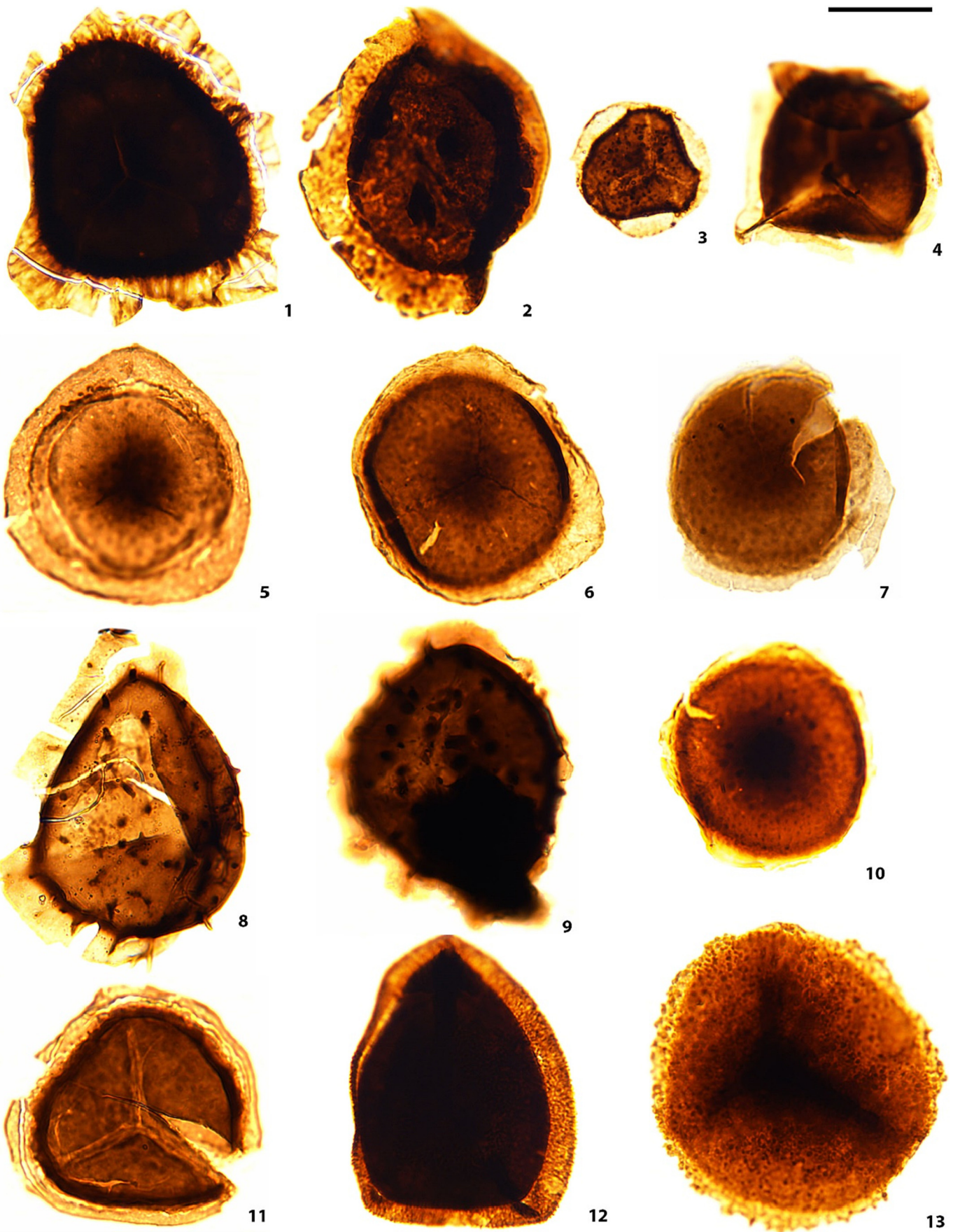


Table 2

Dispersed spore taxa reported.

HILATE CRYPTOSPORES	
<i>Artemopyra reticosta</i> Breuer et al. 2007	[Plate I, figs. 1–2; Valp. Fm 12 samples in 8 sections]
<i>Laevolancis</i> (<i>Archaeozonotrilletes</i>) <i>divellomedia</i> (Chibrickova) Burgess & Richardson 1991	[Plate I, figs. 3–4; Valp. Fm. 12 samples in 7 sections]
MONOLETE SPORES	
<i>Latosporites ovalis</i> Breuer et al. 2007	[Plate I, figs. 6–7; Valp. Fm 9 samples in 4 sections]
TRILETE SPORES: RETUSOID LAEVIGATE	
<i>Retusotrilletes goensis</i> Lele & Streeel 1969	[Plate I, fig. 15; Valp. Fm 2 samples in 2 sections]
<i>Retusotrilletes maculatus</i> McGregor and Camfield, 1976	[Plate I, fig. 8; Valp. Fm 9 samples in 6 sections]
<i>Retusotrilletes</i> (<i>Phyllothecotrilletes</i>) <i>rotundus</i> (Streeel) Streeel emend. Lele & Streeel 1969	[Plate I, fig. 12; Valp. Fm 7 samples in 4 sections]
<i>Retusotrilletes tenerimedium</i> Chibrickova 1959	[Plate I, fig. 13; Valp. Fm 9 samples in 6 sections]
<i>Retusotrilletes</i> (<i>Phyllothecotrilletes</i>) <i>triangulatus</i> (Streeel) Streeel 1967	[Plate I, fig. 14; Valp. Fm 26 samples in 8 sections]
<i>Retusotrilletes</i> sp. A	[Plate I, figs. 9–11; Valp. Fm 10 samples in 5 sections]
TRILETE SPORES: RETUSOID ORNAMENTED	
<i>Apiculiretusispora arabiensis</i> Al-Ghazi 2009	[Plate II, figs. 1, 7; Valp. Fm 12 samples in 4 sections]
<i>Apiculiretusispora brandtii</i> Streeel 1964	[Plate I, fig. 16; Valp. Fm 22 samples in 8 sections]
<i>Apiculiretusispora</i> (<i>Cyclogranisporites</i>) <i>plicata</i> (Allen) Streeel 1967	[Plate I, figs. 17–18; Valp. Fm 19 samples in 8 sections]
<i>Apiculiretusispora</i> spp.	[Plate II, figs. 2–3]
<i>Dibolisporites</i> (<i>Bullatisporites</i>) <i>bullatus</i> (Allen) Riegel 1973	[Plate II, figs. 5–6; Valp. Fm 4 samples in 3 sections]
<i>Dibolisporites</i> (<i>Triletes</i>) <i>echinaceus</i> (Eisenack) Richardson 1965	[Plate II, fig. 12; Valp. Fm 12 samples in 5 sections]
<i>Dibolisporites</i> (<i>Anapiculatisporites</i>) <i>eifeliensis</i> (Lanninger) McGregor 1973	[Plate II, figs. 10–11; Valp. Fm 5 samples in 3 sections]
<i>Dibolisporites tuberculatus</i> Breuer and Steemans, 2013	[Plate II, figs. 8–9; Valp. Fm 11 samples in 6 sections]
<i>Dictyotrilletes</i> (<i>Reticulatisporites</i>) <i>emsiensis</i> (Allen) McGregor 1973	[Plate III, fig. 9; Valp. Fm 4 samples in 4 sections]
<i>Dictyotrilletes kerprii</i> Wellman 2006	[Plate III, figs. 1–2; Valp. Fm 13 samples in 6 sections]
<i>Dictyotrilletes subgranifer</i> McGregor 1973	[Plate III, figs. 5–6,10; Valp. Fm 12 samples in 7 sections]
TRILETE SPORES: CRASSITATE LAEVIGATE	
<i>Ambitisporites avitus</i> Hoffmeister 1959	[Plate III, fig. 3; Valp. Fm 18 samples in 7 sections]
<i>Ambitisporites</i> (<i>Retusotrilletes</i>) <i>eslae</i> (Cramer & Diez) Richardson et al. 2001	[Plate III, figs. 4, 8; Valp. Fm 3 samples in 2 sections]
<i>Ambitisporites tripapillatus</i> Moreau-Benoit 1976	[Plate III, fig. 7; Valp. Fm 3 samples in 3 sections]
<i>Ambitisporites</i> sp. A	[Plate III, figs. 11–12; Valp. Fm 4 samples in 3 sections]
TRILETE SPORES: CRASSITATE ORNAMENTED	
<i>Aneurospora</i> (<i>Anapiculatasporites</i>) <i>tojooides</i> (Cramer 1967) Steemans 1989	[Plate III, figs. 15–16; Valp. Fm 10 samples in 7 sections]
<i>Aneurospora</i> sp. A	[Plate III, figs. 17–18; Valp. Fm 1 sample in 1 section]
<i>Aneurospora</i> sp. B	
	[Plate III, figs. 21–22; Valp. Fm 5 samples in 4 sections]
<i>Brochotrilletes foveolatus</i> Naumova 1953	[Plate III, fig. 19; Valp. Fm 5 samples in 3 sections]
<i>Brochotrilletes</i> sp. A	[Plate III, fig. 20; 1 sample in 1 section (Asturias only)]
<i>Camarozonotrilletes sextantii</i> McGregor and Camfield, 1976	[Plate VI, figs. 15–18; Valp. Fm 4 samples in 2 sections]
<i>Camarozonotrilletes</i> sp. A	[Plate VI, figs. 11–13; Valp. Fm 4 samples in 2 sections]
<i>Concentricosporites</i> (<i>Stenozonotrilletes</i>) <i>sagittarius</i> (Rodriguez) Rodriguez 1983	[Plate III, figs. 13–14; Valp. Fm 3 samples in 2 sections]
<i>Coronospora inornata</i> Breuer and Steemans, 2013	[Plate II, figs. 13–14; Valp. Fm 2 samples in 2 sections]
<i>Emphanisporites annulatus</i> McGregor 1961	[Plate IV, fig. 1; Valp. Fm 1 sample in 1 section]
<i>Emphanisporites biradiatus</i> Steemans 1989	[Plate IV, figs. 7–8; Valp. Fm 5 samples in 3 sections]
<i>Emphanisporites edwardsiae</i> Wellman 2006	[Plate IV, figs. 3–4; Valp. Fm 13 samples in 7 sections]
<i>Emphanisporites</i> (<i>Triletes</i>) <i>erraticus</i> (Eisenack) McGregor 1961	[Plate IV, figs. 5–6; Valp. Fm 4 samples in 3 sections]
<i>Emphanisporites mcgregorii</i> Cramer 1966	[Plate IV, fig. 2; Valp. Fm 5 samples in 3 sections]
<i>Emphanisporites micromnatus</i> Richardson & Lister 1969	[Plate IV, fig. 13; Valp. Fm 1 sample in 1 section]
<i>Emphanisporites rotatus</i> McGregor emend. McGregor 1973	[Plate IV, figs. 10–12; Valp. Fm 22 samples in 7 sections]
<i>Emphanisporites schultzei</i> McGregor 1973	[Plate IV, fig. 9; Valp. Fm 1 sample in 1 section]
<i>Emphanisporites</i> sp. A	[Plate IV, fig. 14; Valp. Fm 1 sample in 1 section]
<i>Scylaspora elegans</i> Richardson et al. 2001	[Plate IV, figs. 15,19; Valp. Fm 3 samples in 3 sections]
<i>Synorisporites tripapillatus</i> Richardson & Lister 1969	[Plate IV, fig. 16; Valp. Fm 1 sample in 1 section]
<i>Synorisporites</i> spp.	[Plate IV, figs. 17–18; Valp. Fm 5 samples in 3 sections]
<i>Verruciretusispora</i> (<i>Triletes</i>) <i>dubia</i> (Eisenack) Richardson and Rasul, 1978	[Plate V, figs. 8,12; Valp. Fm 3 samples in 3 sections]
<i>Verrucosporites polygonalis</i> Lanninger 1968	[Plate V, figs. 1–6; Valp. Fm 16 samples in 6 sections]
TRILETE SPORES: PATINATE LAEVIGATE	
<i>Archaeozonotrilletes</i> (<i>Retusotrilletes</i>) <i>chulus</i> (Cramer) Richardson & Lister 1969	[Plate V, fig. 9; Valp. Fm 5 samples in 4 sections]
<i>Archaeozonotrilletes</i> sp. A	[Plate VI, figs. 1–2; Valp. Fm 2 samples in 2 sections]
TRILETE SPORES: PATINATE ORNAMENTED	
<i>Chelinospora</i> spp.	[Plate VI, figs. 3–4; Valp. Fm 1 sample in 1 section]
<i>Cymbosporites asymmetricus</i> Breuer et al. 2007	[Plate VI, fig. 4; Valp. Fm 7 samples in 4 sections]
<i>Cymbosporites dammamensis</i> Steemans 1995	[Plate V, figs. 10–11; Valp. Fm 8 samples in 5 sections]
TRILETE SPORES: BILAYERED, SACCATE AND ZONATE	
<i>Acinosporites</i> (<i>Verrucosporites</i>) <i>apiculatus</i> (Streeel) Streeel 1967	[Plate VI, fig. 6; Valp. Fm 1 sample in 1 section]
<i>Acinosporites lindlarensis</i> Riegel 1968	[Plate VI, figs. 5, 8–10; Valp. Fm 7 samples in 6 sections]
<i>Camptozonotrilletes</i> sp.	[Plate VII, fig. 1; Valp. Fm 2 samples in 2 sections]
<i>Cirratiradites diaphanus</i> Steemans 1989	

Plate VII. Dispersed spores from the Valporquero Fm of northern Spain. Scale bar = 20 µm.

- Camptozonotrilletes* sp. (Sample 17SPAIN21; Slide 2; E.F.no. E36/3).
- Cirratiradites diaphanus* Steemans 1989 (Sample 18SPAIN18; Slide 3; E.F.no. L52/2).
- Craspedispora* sp. A (Sample 2000LV01; Slide 3; E.F.no. r34).
- Perotrilletes* spp. (Sample 17SPAIN35; Slide 1; E.F.no. C39).
- Zonate Spore sp. A (Sample 2000LV04; Slide 1; E.F.no. L30/4).
- Zonate Spore sp. A (Sample 2000LV04; Slide 3; E.F.no. L35/1).
- Zonate Spore sp. A (Sample 17SPAIN31; Slide 2; E.F.no. Y34).
- Stalicospora trewinii* Wellman 2006 (Sample 18SPAIN18; Slide 3; E.F.no. S47).
- Stalicospora trewinii* Wellman 2006 (Sample 2000LV04; Slide 1; E.F.no. N39).
- Zonate Spore sp. A (Sample 2000LV04; Slide 3; E.F.no. T36).
- Zonitilletes brevivelatus* Breuer & Steemans 2013 (Sample 17SPAIN47; Slide 2; E.F.no. L43).
- Rhabdosporites minutus* Tiwari & Schaarschmidt 1975 (Sample 2000LV04; Slide 3; E.F.no. Y36).
- Zonate Spore spp. (Sample 17SPAIN50; Slide 2; E.F.no. W38).

[Plate VII, fig. 2; Valp. Fm 3 samples in 2 sections]
Craspedispora sp. A
 [Plate VII, fig. 3; Valp. Fm 1 sample in 1 section]
Perotrilites spp.
 [Plate VII, fig. 4; Valp. Fm 1 sample in 1 section]
Rhabdosporites minutus Tiwari & Schaarschmidt 1975
 [Plate VII, fig. 12; Valp. Fm 5 samples in 3 sections]
Stalicospora trewinii Wellman 2006
 [Plate VII, figs. 8–9; Valp. Fm 2 samples in 1 section]
Zontriletes breivelatus Breuer and Steemans, 2013
 [Plate VII, fig. 11; Valp. Fm 5 samples in 4 sections]
Zonate Spore sp. A
 [Plate VII, figs. 5–7, 10; Valp. Fm 3 samples in 2 sections]

6. Age and biostratigraphical correlation of the Valporquero Fm dispersed spore assemblage

6.1. Introduction

The dispersed spore assemblages recovered from the Valporquero Fm are all very similar in composition differing mainly in the presence/absence of taxa that are rare in the assemblages. Table 2 lists the taxa encountered and shows how many samples and sections they were recorded in (semi-quantitative count data is of limited value because the individual samples contain widely varying abundances of spores transported into the marine environment). Tables 3–6 outline the stratigraphical distribution of spore taxa in the different sections examined.

6.2. Biostratigraphy

Previous biostratigraphical evidence (based chiefly on conodont assemblages) indicates that the Valporquero Fm is of Emsian age, more specifically mid to late (but not latest) Emsian age (see above). Because of the location of the ATA, between Laurussia and Gondwana, the spore assemblages from this terrane are best compared with biostratigraphical schemes developed on both palaeocontinents.

In terms of the scheme of Richardson and McGregor (1986), developed for Laurussia (the Old Red Sandstone continent), the Valporquero Fm assemblage best correlates with the *annulatus-sextantii* (AS) Spore

Table 3

Distribution of dispersed spores in the Asturias sequence. Ordering of spore taxa follows the scheme in Table 2.

Sample Formation	17/02 Banugues	17/12 Ferrones	17/10 Aguion	17/08 Aguion	17/07 Aguion
Taxon					
<i>Retusotrilites maculatus</i>			X		
<i>Retusotrilites rotundus</i>			X	X	X
<i>Retusotrilites triangulatus</i>			X	X	X
<i>Retusotrilites</i> spp.	X	X	X	X	X
<i>Apiculiretusispora arabiensis</i>					X
<i>Apiculiretusispora brandtii</i>			X	X	X
<i>Apiculiretusispora plicata</i>			X		
<i>Apiculiretusispora</i> spp.	X	X	X	X	X
<i>Dibolisporites tuberculatus</i>			X	X	
<i>Dictyotrilites kerprii</i>				X	
<i>Dictyotrilites</i> spp.	X				
<i>Ambitisporites avitus</i>					X
<i>Ambitisporites tripapillatus</i>				X	
<i>Ambitisporites</i> spp.	X	X	X	X	X
<i>Brochosporites</i> sp. A				X	
<i>Concentricosporites sagittarius</i>			X		
<i>Emphanisporites edwardsiae</i>					X
<i>Emphanisporites rotatus</i>	X	X	X	X	X
<i>Synorisporites</i> spp.			X		
<i>Verrucosisporites polygonalis</i>			X		
<i>Zonate</i> spp.					X

Assemblage Biozone of early (but not earliest) to early late Emsian age (Fig. 5). Both nominal species are present (*Emphanisporites annulatus* and *Camarazonotrilites sextantii*) as are many of the listed characteristic species.

In terms of the scheme of Streel et al. (1987), developed in the Ardenne-Rhenish region of Laurussia, the Valporquero Fm assemblage best correlates with the FD Opperl Zone of late early to early late Emsian age. The presence of *Rhabdosporites minutus* refines this to the Min Interval Zone, potentially suggesting the upper bracket of this age range. However, the presence of rare *Acinosporites apiculatus* towards the top of the type section may suggest the incoming of the succeeding AP Opperl Zone of late (but not latest) Emsian age.

In terms of the scheme of Breuer and Steemans (2013), developed in Saudi Arabia and Libya in northern Gondwana, the Valporquero Fm assemblage best correlates with the *lindlarensis-sextantii* Assemblage Zone based on the presence of the diagnostic species *Acinosporites lindlarensis* and *Camarazonotrilites sextantii*. This zone indicates a mid-early late Emsian age.

6.3. Palaeophytogeography

Dispersed spore assemblages provide evidence for palaeophytogeographical differentiation from at least the Early Devonian (Lochkovian) (e.g. Wellman et al., 2022). In assessing palaeophytogeographical differentiation among Emsian dispersed spore assemblages it should be noted that they are well documented in both Laurussia and Gondwana, although they are less well known beyond these two supercontinents. Table 7 lists the localities from which assemblages of abundant and diverse spores have been studied. Fig. 3 illustrates the palaeogeographical distribution of these dispersed spore assemblages.

In order to make comparisons with previously reported Emsian spore assemblages a database was created of all Emsian spore taxa reported from the best known Emsian spore assemblages from close to the ATA in Laurussia (Canada, the Anglo-Welsh Basin, the Ardenne-Rhenish region) and Gondwana (North Africa and the Arabian Plate) (On Line Data – Appendix 1). For each region the different local spore zones were differentiated. The Spanish assemblage was then compared with each of these regions/zones by calculating the Jaccard Index (Jaccard Similarity Coefficient). Results are illustrated in Table 8.

It is evident from the Jaccard Index data in Table 8 that the Spanish Assemblage is more similar to those from Gondwana (North Africa and the Arabian Plate) than Laurussia. Jaccard Index calculated for all of the Laurussian zones vary from 0.13–0.16. Jaccard Index calculated for all of the Gondwana zones are considerably higher varying from 0.24–0.34. The *lindlarensis-sextantii* Assemblage Zone and *annulatus-protea* Assemblage Zone show the highest similarities with the *lindlarensis-sextantii* Assemblage Zone scoring 0.31 in North Africa and 0.34 on the Arabian Plate and the *annulatus-protea* Assemblage Zone scoring 0.28 in North Africa and 0.34 on the Arabian Plate. However, it should be noted that the similarity indexes for both regions are relatively low, indicating possible endemism in the floras present in the ATA. It is also clear that there are large differences between Laurussian and Gondwanan dispersed spore assemblages. Of the 240 taxa reported from Laurussia and Gondwana only 49 are common to both, with 105 reported only from Laurussia and 86 reported only from Gondwana.

Whilst it is clear that the Spanish assemblage has most in common with those from Gondwana it also contains 16 taxa that appear to be either: (i) endemic; or (ii) previously reported but with a different age range. Taxa that appear to be undescribed and are potentially endemic are: *Ambitisporites* sp. A, *Aneurospora* sp. A, *Aneurospora* sp. B, *Archaeozonotrilites* sp. A, *Brochotrilites* sp. A, *Camarazonotrilites* sp. A., *Camarazonotrilites* sp., *Craspedispora* sp. A, *Emphanisporites* sp. A, *Retusotrilites* sp. A, *Zonate Spore* sp. A (although it should be noted that these taxa are relatively rare and occur in too few numbers to officially name and describe). There are also a number of previously described taxa that have not previously been reported from the Emsian

Table 4

Distribution of dispersed spores in the La Vid Type Section. Ordering of spore taxa follows the scheme in Table 2.

Sample Formation	17/33 Felmin	00LV07 La Pedrosa	00LV06 La Pedrosa	18/18 Valporqu.	00LV04 Valporqu.	17/31 Valporqu.	00LV01 Valporqu.	00LV20 Valporqu.
Taxon								
<i>Artemopyra reticosta</i>				X	X	X	X	
<i>Laevolancis divellomedia</i>				X	X	X		
<i>Latosporites ovalis</i>				X	X		X	
<i>Retusotriletes goensis</i>							X	
<i>Retusotriletes maculatus</i>				X	X		X	
<i>Retusotriletes tenerimedium</i>							X	
<i>Retusotriletes triangulatus</i>			X	X	X	X	X	X
<i>Retusotriletes</i> sp. A				X	X		X	X
<i>Retusotriletes</i> spp.	X	X	X	X	X	X	X	X
<i>Apiculiretusispora arabiensis</i>				X	X		X	X
<i>Apiculiretusispora brandtii</i>				X	X	X	X	X
<i>Apiculiretusispora plicata</i>			X	X	X	X		
<i>Apiculiretusispora</i> spp.	X	X	X	X	X	X	X	
<i>Dibolisporites bullatus</i>	X						X	
<i>Dibolisporites echinaceus</i>				X	X		X	X
<i>Dibolisporites eifeliensis</i>				X	X		X	
<i>Dibolisporites tuberculatus</i>				X	X			X
<i>Dibolisporites wetteldorfensis</i>				X	X			
<i>Dictyotriletes emsiensis</i>							X	
<i>Dictyotriletes kerpilii</i>					X			X
<i>Dictyotriletes subgranifer</i>				X	X	X		
<i>Ambitisporites avitus</i>		X	X	X		X		X
<i>Ambitisporites eslae</i>							X	X
<i>Ambitisporites tripapillatus</i>							X	
<i>Ambitisporites</i> sp. A					X			X
<i>Aneurospora tojooides</i>				X	X			X
<i>Aneurospora</i> sp. A					X			
<i>Brochosporites foveolatus</i>					X		X	
<i>Brochotriletes hudsonii</i>					X			
<i>Concentricosporites sagittarius</i>					X	X		
<i>Coronospora inornata</i>					X			
<i>Emphanisporites biradiatus</i>					X	X		
<i>Emphanisporites edwardsiae</i>					X	X	X	X
<i>Emphanisporites erraticus</i>					X			
<i>Emphanisporites mcgregorii</i>					X	X		X
<i>Emphanisporites micromnatus</i>					X			
<i>Emphanisporites rotatus</i>				X	X	X	X	X
<i>Emphanisporites</i> sp. A					X			
<i>Scylaspora elegans</i>					X			
<i>Synorisporites tripapillatus</i>					X			
<i>Synorisporites</i> spp.				X				
<i>Verruciretusispora dubia</i>			X					
<i>Verrucosporites polygonalis</i>					X	X	X	X
<i>Archaeozonotriletes chulus</i>				X				
<i>Archaeozonotriletes</i> sp. A					X			
<i>Cymbosporites asymmetricus</i>				X	X		X	
<i>Cymbosporites dammamensis</i>			X	X				
<i>Acinosporites apiculatus</i>					X			
<i>Acinosporites lindlarensis</i>				X				
<i>Camarozonotriletes sextantii</i>				X	X			
<i>Camarozonotriletes</i> sp. A					X		X	X
<i>Cirratiradites diaphanous</i>				X				
<i>Craspedispora</i> sp. A							X	
<i>Rhabdosporites minutus</i>					X		X	X
<i>Rhaldospora trewinii</i>				X	X			
<i>Zontriletes brevivellatus</i>					X		X	
<i>Zonate spore</i> sp. A					X	X		

Table 5
Distribution of dispersed spores in the Argovejo section. Ordering of spore taxa follows the scheme in Table 2.

SAMPLE FORMATION	18/05 La Pedrosa	18/06 La Pedrosa	17/48 Valporquero	17/50 Valporquero	17/51 Valporquero	17/47 Valporquero
TAXON						
<i>Artemopyra reticosta</i>						X
<i>Laevolancis divellomedia</i>				X	X	
<i>Latosporites ovalis</i>					X	X
<i>Retusotriletes rotundus</i>			X	X		
<i>Retusotriletes tenerimedium</i>						X
<i>Retusotriletes triangulatus</i>	X	X	X	X	X	X
<i>Retusotriletes</i> spp.	X	X	X	X	X	X
<i>Apiculiretusispora brandtii</i>		X		X	X	X
<i>Apiculiretusispora plicata</i>		X		X	X	X
<i>Apiculiretusispora</i> spp.	X	X	X	X	X	X
<i>Dibolisporites echinaceus</i>		X		X	X	X
<i>Dibolisporites eifeliensis</i>				X		
<i>Dibolisporites tuberculatus</i>					X	
<i>Dictyotriletes emsiensis</i>					X	
<i>Dictyotriletes kerprii</i>		X		X	X	
<i>Dictyotriletes subgranifer</i>				X		
<i>Ambitisporites avitus</i>		X	X	X	X	X
<i>Aneurospora tojooides</i>					X	
<i>Aneurospora</i> sp. B				X		
<i>Brochosporites foveolatus</i>		X				X
<i>Emphanisporites edwardsiae</i>				X		X
<i>Emphanisporites erraticus</i>		X				
<i>Emphanisporites rotatus</i>	X	X	X	X	X	X
<i>Emphanisporites schultzi</i>						X
<i>Synorisporites</i> spp.		X				X
<i>Verruciretusispora dubia</i>						X
<i>Verrucosporites polygonalis</i>	X	X	X			X
<i>Archaeozonotriletes chulus</i>				X		X
<i>Cymbosporites asymmetricus</i>					X	
<i>Cymbosporites dammamensis</i>				X	X	
<i>Acinosporites lindlarensis</i>					X	X
<i>Camazonotriletes sextantii</i>		X	X			
<i>Rhabdosporites minutus</i>					X	
<i>Zontriletes brevivellatus</i>						X

Table 6
Distribution of dispersed spores in the remaining Valporquero Fm sections. Ordering of spore taxa follows the scheme in Table 2.

Sample Formation Section	17/24 Valporqu. L8-L10	17/25 Valporqu. L8-L10	17/26 Valporqu. L8-L10	18/08 Valporqu. L15	17/19 Valporqu. L2	17/20 Valporqu. L2	17/35 Valporqu. L12	18/39 Valporqu. L2	18/40 Valporqu. L2	17/46 Valporqu. L15	17/42 Valporqu. L15	17/43 Valporqu. L15	17/35 Valporqu. L7	17/21 Valporqu. L4
<i>Artemopyra reticosta</i>			X				X	X	X			X	X	X
<i>Laevolancis divellomedia</i>				X	X	X	X	X			X	X	X	X
<i>Latosporites ovalis</i>				X										
<i>Retusotriletes goensis</i>							X							
<i>Retusotriletes maculatus</i>								X						
<i>Retusotriletes rotundus</i>				X										
<i>Retusotriletes tenerimedium</i>		X	X		X	X	X	X	X	X	X	X	X	X
<i>Retusotriletes triangularis</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Retusotriletes</i> sp. A				X	X	X	X	X	X	X	X	X	X	X
<i>Retusotriletes</i> spp.		X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Apiculiretusispora arabiensis</i>				X	X	X	X	X	X	X	X	X	X	X
<i>Apiculiretusispora brandtii</i>				X	X	X	X	X	X	X	X	X	X	X
<i>Apiculiretusispora plicata</i>				X	X	X	X	X	X	X	X	X	X	X
<i>Apiculiretusispora</i> spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Dibolisporites bullatus</i>				X			X							
<i>Dibolisporites echinaceus</i>						X		X						
<i>Dibolisporites epheliensis</i>			X		X			X						
<i>Dibolisporites tuberculatus</i>			X	X				X	X				X	
<i>Dictyotriletes emsiensis</i>			X		X	X		X	X				X	X
<i>Dictyotriletes kerpji</i>			X		X	X		X	X				X	X
<i>Dictyotriletes subgranifer</i>			X		X	X		X	X				X	X
<i>Ambitisporites avitus</i>		X	X		X	X		X		X				
<i>Ambitisporites eslae</i>														
<i>Ambitisporites tripapillatus</i>														
<i>Ambitisporites</i> sp. A							X						X	
<i>Aneurospora tojoides</i>			X		X		X	X	X				X	X
<i>Aneurospora</i> sp. B														
<i>Brochosporites foveolatus</i>														
<i>Concentricosporites sagittarius</i>	X									X				
<i>Coronospora inornata</i>													X	
<i>Emphanisporites annulatus</i>													X	X
<i>Emphanisporites biradiatus</i>												X	X	X
<i>Emphanisporites edwardsiae</i>			X			X		X	X				X	X
<i>Emphanisporites erraticus</i>												X		
<i>Emphanisporites mcgregorii</i>								X	X					
<i>Emphanisporites rotatus</i>								X	X					X
<i>Scylaspora elegans</i>														
<i>Scylaspora</i> spp.		X												
<i>Verruciretusispora dubia</i>														
<i>Verrucosporites polygonalis</i>														
<i>Archaeozonotriletes chilus</i>													X	X
<i>Archaeozonotriletes</i> sp. A														
<i>Chelinospora</i> spp.														
<i>Cymbosporites asymmetricus</i>			X								X			
<i>Cymbosporites dammamensis</i>											X			
<i>Acinosporites lindlarensis</i>											X			
<i>Canarozonotriletes</i> sp. A			X											
<i>Campozonotriletes</i> sp.						X								X
<i>Cirratiradites diaphanous</i>														
<i>Perotriletes</i> spp.														
<i>Rhabdosporites minutus</i>								X						
<i>Zonitrites brevivellatus</i>			X										X	
<i>Zonate spore</i> sp. A						X								

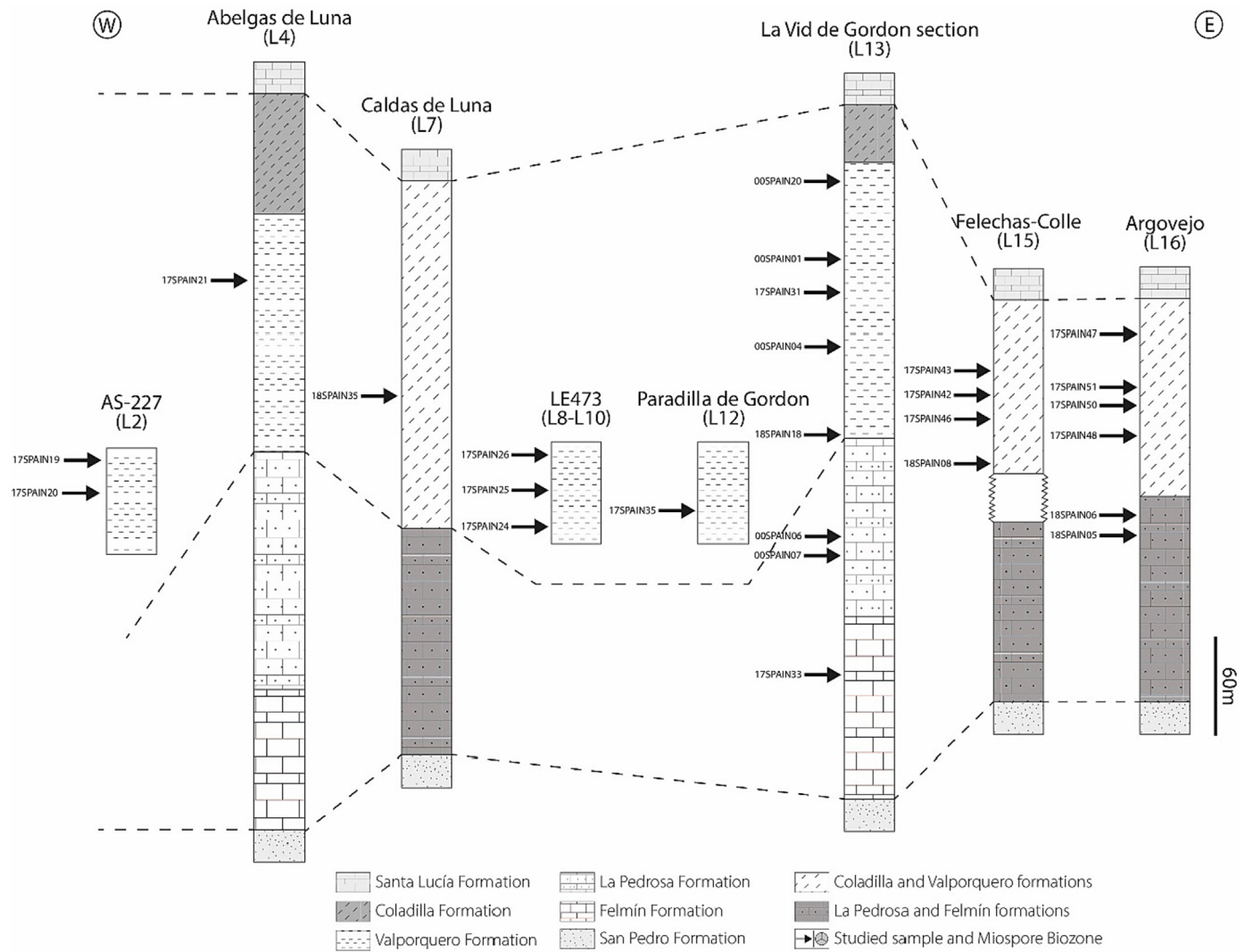


Fig. 4. Stratigraphical sections of the main localities illustrating the position of logged spore samples. The dashed lines show the correlation of the main formations within the different sections.

Chronostrat. Units	Richardson and McGregor (1986)	Streel et al. (1987)	Breuer & Steemans (2013)	
Eifelian	<i>douglstownensis eurypterota</i>	AP	Pro <i>svalbardiae</i> <i>eximius</i>	
			Cor <i>annulatus</i> <i>protea</i>	
Emsian	<i>annulatus sextantii</i>	FD	Min <i>lindlarensis</i> - <i>sextantii</i>	
			Pra Fov	<i>ovalis</i> <i>milleri</i>
			AB	<i>biornatus</i> <i>ovalis</i>
Pragian	<i>polygonalis emsiensis</i>	PoW	Su <i>papillensis</i> - <i>baqaensis</i>	
			Paβ	
			Paα	
			W	
Lochkovian	<i>breconensis - zavallatus</i>	BZ	Po E Z	
			MN	G
				Stβ
Stα				
Mβ				
Mα				
R				
Lochkovian	<i>micror-natus newportensis</i>	MN	Nβ	
			Nα	

Fig. 5. Early Devonian spore biostratigraphical schemes and correlation of the dispersed spore assemblages from the Valporquero Formation.

Table 8

Comparison using the Jaccard Index between the spore assemblage from the Valporquero Formation described herein and other well-known Emsian assemblages.

Locality/local spore zone	Number of taxa	Jaccard index
Canada (AS Spore Assemblage Biozone)	82	0.15
Canada (DE Spore Assemblage Biozone)	60	0.16
Anglo-Welsh Basin (AS Spore Assemblage Biozone)	23	0.13
Ardenne-Rhenish region (AB Opper Zone)	51	0.15
Ardenne-Rhenish region (FD Opper Zone; Fov. Interval Zone)	14	0.15
Ardenne-Rhenish region (FD Opper Zone; Pra. Interval Zone)	15	0.14
Ardenne-Rhenish region (FD Opper Zone; Min. Interval Zone)	15	0.16
Ardenne-Rhenish region (AP Opper Zone; Cor. Interval Zone)	13	0.13
Ardenne-Rhenish region (AP Opper Zone; Pro. Interval Zone)	26	0.14
North Africa (OB Assemblage Zone; O Subzone)	44	0.29
North Africa (OB Assemblage Zone; M Subzone)	46	0.28
North Africa (OB Assemblage Zone; A Subzone)	50	0.32
North Africa (LS Assemblage Zone)	59	0.31
North Africa (AP Assemblage Zone)	42	0.28
Arabian Plate (OB Assemblage Zone; O Subzone)	81	0.24
Arabian Plate (OB Assemblage Zone; M Subzone)	76	0.26
Arabian Plate (OB Assemblage Zone; A Subzone)	82	0.31
Arabian Plate (LS Assemblage Zone)	87	0.34
Arabian Plate (AP Assemblage Zone)	48	0.34

of Gondwana or Laurussia (e.g. *Synorisporites tripapillatus*) although these are generally represented only by rare specimens. These potentially have different age ranges on the ATA, rather than being reworked, as there is little evidence for reworking in this assemblage (e.g. highly distinctive spores well known from the underlying San Pedro Formation, such as *Iberoespora*, are absent). Despite evidence that the Valporquero Fm assemblage is somewhat endemic, it is interesting to

Table 7

Previously reported Emsian dispersed spore assemblages (only an example of key references are provided).

Locality	Continent	Spore zone	Key references
1 Russia (Kuznets Basin)	Siberia	DE	Chibrikova (1977)
2 Spitsbergen	Laurussia	AS + DE	Allen (1967)
3 Ellesmere Island	Laurussia	AS	McGregor (1974)
4 Canada (Ontario)	Laurussia	AS	McGregor and Camfield (1976)
5 Eastern Canada	Laurussia	AS + DE	McGregor (1977); Wellman (2018)
6 Maine, USA	Laurussia	DE	Andrews et al. (1977)
7 Scotland	Laurussia	AS	Wellman (2009, 2014)
8 Ireland	Laurussia	AB	Higgs (1999)
9 Southern England	Laurussia	AS	Richardson and Rasul (1978)
10 Ardenne-Rhenish	Laurussia	AS + DE	Streel et al. (1987)
11 Lithuania	Laurussia	AS	Arkhangelskaya (1980)
12 Poland	Laurussia	DE	Turnau (1986); Filipiak (2011); Filipiak et al. (2022)
13 Russia (south Urals)	Laurussia	AS + DE	Chibrikova (1977, 1978)
14 Russia (south central)	Laurussia	AS	Andreeva (1973)
15 Romania	Laurussia	AS	Beju (1967)
16 Czech Republic	ATA	AS	McGregor (1979)
17 Portugal	ATA		Pereira et al. (1999)
18 Spain	ATA		Cramer (1967a); this paper
19 France	ATA		Le Hérisse (1983)
20 Morocco	Gondwana	AS	Rahmani-Antari and Lachkar (2001)
21 Algeria	Gondwana		Kermandji et al. (2008); Bougara et al. (2017)
22 Tunisia	Gondwana	AB-FD	Loboziak et al. (1992)
23 Libya	Gondwana	AS + DE	Moreau-Benoit (1988); Streel et al. (1990)
24 Saudi Arabia	Gondwana	OB + LS + AP	Breuer and Steemans (2013)
25 Iran	Gondwana		Ghavidel-Syooki (2003)
26 Argentina	Gondwana		Rubinstein and Steemans (2007); García-Muro et al. (18); Noetinger and Di Pasquo (2013)
27 Uruguay	Gondwana		Rubinstein et al. (2018); Daners et al. (2017)
28 Brazil	Gondwana	OB(a) + LS	García-Muro et al. (2020)
29 Antarctica	Gondwana	AS	Kemp (1972)
30 China (Guizhou)	South China		Gao and Hou (1975); Gao (1983)
31 China (Yunnan)	South China	ES	Gao (1983); Wang (1994)
32 China (Sichuan)	South China		Huang et al. (2016)
33 China (Qinling)	?South China		Gao and Ye (1987)

note that differences are largely at the species level with no major differences in terms of higher taxa (i.e. at spore generic level). A possible exception is the absence of spores with bifurcating processes (e.g. *Ancyrospora*) from both the ATA and Northern Gondwana (Breuer et al., 2009) indicating that such spores had not arrived at these regions by this time.

7. Conclusions

- A rich spore assemblage comprising 62 taxa is reported from the Valporquero Fm that has been age constrained using conodonts and invertebrates as mid-late Emsian in age.
- The Valporquero Fm spore assemblage can be equated with the *lindlarensis-sextantii* Assemblage Zone, of mid to late Emsian age, developed in northern Gondwana (Saudi Arabia and Libya) by Breuer and Steemans (2013). In terms of Laurussia spore zones this is equivalent to the AS Spore Assemblage Biozone of early (but not earliest) to early late Emsian age in the scheme of Richardson and McGregor (1986) and the FD Opper Zone (Min. Interval Zone) of early late Emsian age in the scheme of Streel et al. (1987).
- Analyses using the Jaccard Index (Jaccard Similarity Coefficient) indicates that the Valporquero Fm spore assemblages is most similar to coeval spore assemblages from Northern Gondwana.
- The Valporquero Fm spore assemblages contains a number of taxa that are either endemic or from outside their usual age range.

Appendix A

Samples from the Raneces – La Vid groups that were palynologically processed. PALY = palynological recovery (where B = barren, R = rare spores, M = moderate abundances of spores, A = abundant spores, C = coalified, (L) = logged sample).

Section	Fm	Sample	Co-ordinates	Paly
A1. Santa Maria del Mar (Playa de Bahinas)	Nieva Fm.	17SPAIN13	N43°34'40.9" W006°00'15.0" (+/- 19 m)	RC
Santa Maria del Mar (Ensenada SMDM)	Ferroñes Fm.	17SPAIN11	N43°34'19.8" W005°59'47.0" (+/- 34 m)	R
Santa Maria del Mar (Ensenada SMDM)	Ferroñes Fm.	17SPAIN12	N43°34'23.1" W005°59'51.7" (+/- 14 m)	R (L)
Santa Maria del Mar (Arnao)	Aguión Fm.	17SPAIN07	N43°34'44.5" W005°59'04.7" (+/- 12 m)	M (L)
Santa Maria del Mar (Arnao)	Aguión Fm.	17SPAIN08	N43°34'44.5" W005°59'04.7" (+/- 12 m)	M (L)
Santa Maria del Mar (Arnao)	Aguión Fm.	17SPAIN09	N43°34'44.5" W005°59'04.7" (+/- 12 m)	B
Santa Maria del Mar (Arnao)	Aguión Fm.	17SPAIN10	N43°34'44.5" W005°59'04.7" (+/- 12 m)	M (L)
A2. Xago-Verdicio (Playa de Xago east)	Nieva Fm.	17SPAIN05	N43°36'25.7" W005°54'50.1" (+/- 10 m)	RC
Xago-Verdicio (Playa de Xago east)	Nieva Fm.	17SPAIN06	N43°36'21.2" W005°54'51.5" (+/- 5 m)	AC
Xago-Verdicio (Playa de Verdicio west)	Nieva Fm.	17SPAIN14	N43°35'57.6" W005°55'44.2" (+/- 10 m)	B
Xago-Verdicio (Playa de Verdicio west)	Nieva Fm.	18SPAIN55	N43°37'24.3" W005°52'56.9" (+/- 6 m)	B
Xago-Verdicio (Playa de Verdicio east)	Nieva Fm.	17SPAIN03	N43°37'43.4" W005°52'35.8" (+/- 9 m)	B
Xago-Verdicio (Playa de Verdicio east)	Nieva Fm.	17SPAIN04	N43°37'44.7" W005°52'34.8" (+/- 6 m)	RC
Xago-Verdicio (Playa de Verdicio east)	Nieva Fm.	17SPAIN15	N43°36'35.8" W005°54'48.6" (+/- 10 m)	B
A3. Bañugues (playa east)	Bañugues Fm.	17SPAIN01	N43°37'57.8" W005°48'25.0" (+/- 11 m)	B
Bañugues (playa east)	Bañugues Fm.	17SPAIN02	N43°37'58.9" W005°48'23.3" (+/- 6 m)	R (L)
Bañugues (playa west)	Ferroñes Fm.	18SPAIN53	N43°37'55.1" W005°48'39.5" (+/- 7 m)	B
Bañugues (playa west)	Ferroñes Fm.	18SPAIN54	N43°37'55.1" W005°48'39.5" (+/- 7 m)	B
L2. AS-227 roadcut (La Peral to El Puerto)	Valporquero Fm.	17SPAIN19	N43°02'25.6" W006°14'36.5" (+/- 5 m)	A (L)
AS-227 roadcut (La Peral to El Puerto)	Valporquero Fm.	17SPAIN20	N43°02'27.8" W006°14'58.8" (+/- 17 m)	A (L)
AS-227 roadcut (La Peral to El Puerto)	Valporquero Fm.	18SPAIN39	N43°02'17.3" W006°14'32.0" (+/- 18 m)	A (L)
AS-227 roadcut (La Peral to El Puerto)	Valporquero Fm.	18SPAIN40	N43°02'17.3" W006°14'32.0" (+/- 18 m)	A (L)
L4. Abelgas de Luna	Valporquero Fm.	17SPAIN21	N43°53'17.2" W005°58'38.5" (+/- 18 m)	M (L)
Abelgas de Luna	Valporquero Fm.	17SPAIN22	N43°53'17.2" W005°58'38.5" (+/- 18 m)	R (L)
L5. CL-626 roadcut Barrios de Luna	Valporquero Fm.	00-C623-4	4207/9236	R
CL-626 roadcut Barrios de Luna	Valporquero Fm.	00-C623-5	4207/9236	B
CL-626 roadcut Barrios de Luna	Valporquero Fm.	00-C623-6	4214/9235	B
CL-626 roadcut Barrios de Luna	Valporquero Fm.	00-C623-7	4214/9235	B
CL-626 roadcut Barrios de Luna	Valporquero Fm.	00-C623-10	4218/9224	RC
CL-626 roadcut Barrios de Luna	Valporquero Fm.	17SPAIN37	N43°53'44.7" W005°52'54.5" (+/- 10 m)	B
L6. CL-626 roadcut Barrios de Luna	Valporquero Fm.	17SPAIN38	N43°53'16.9" W005°52'26.2" (+/- 5 m)	B
CL-626 roadcut Barrios de Luna	Valporquero Fm.	17SPAIN39	N43°51'24.9" W005°51'37.8" (+/- 12 m)	B
L7. Caldas de Luna	Valporquero Fm.	18SPAIN35	N42°56'20.5" W005°50'47.5" (+/- 10 m)	A (L)
L8-L10. LE473 roadcut	La Pedrosa Fm.	17SPAIN23	N42°54'17.1" W005°49'53.3" (+/- 11 m)	B
L8-L10. LE473 roadcut	Valporquero Fm.	17SPAIN24	N42°54'10.1" W005°51'90.7" (+/- 10 m)	R (L)
L8-L10. LE473 roadcut	Valporquero Fm.	17SPAIN25	N42°54'08.6" W005°51'13.4" (+/- 7 m)	R (L)
L8-L10. LE473 roadcut	Valporquero Fm.	17SPAIN26	N42°54'06.7" W005°51'26.8" (+/- 5 m)	M (L)
L8-L10. LE473 roadcut	La Pedrosa Fm.	17SPAIN29	N42°54'18.6" W005°48'54.2" (+/- 7 m)	B
L8-L10. LE473 roadcut	La Pedrosa Fm.	17SPAIN30	N42°54'16.1" W005°49'04.7" (+/- 10 m)	B
L8-L10. LE473 roadcut	Valporquero Fm.	18SPAIN30	N42°53'35.4" W005°46'42.9" (+/- 12 m)	R
L8-L10. LE473 roadcut	Felmin Fm.	18SPAIN31	N42°54'22.1" W005°49'26.2" (+/- 5 m)	B

However, at the generic level no major groups present in Laurussia or Northern Gondwana are absent.

- The evidence suggests that the ATA was relatively isolated with a somewhat endemic flora but was probably closer and had greater connectivity with Northern Gondwana as opposed to Laurussia.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2022.104825>.

Data availability

Data will be made available on request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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(continued)

Section	Fm	Sample	Co-ordinates	Paly
L8-L10. LE473 roadcut	Felmin Fm.	18SPAIN33a	N42°54'22.1" W005°49'26.2" (+/- 5 m)	B
L12. Paradilla de Gordon	Valporquero Fm.	17SPAIN35	N42°52'59.3" W005°44'31.9" (+/- 4 m)	A (L)
L13. Roadcut east of La Vid de Gordon.	Valporquero Fm.	00LV20	N42°53' W005°37'	M (L)
L13. Roadcut east of La Vid de Gordon.	Valporquero Fm.	00LV01	N42°53' W005°37'	A (L)
L13. Roadcut east of La Vid de Gordon.	Valporquero Fm.	00LV02	N42°53' W005°37'	AC
L13. Roadcut east of La Vid de Gordon.	Valporquero Fm.	00LV03	N42°53' W005°37'	B
L13. Roadcut east of La Vid de Gordon.	Valporquero Fm.	00LV04	N42°53' W005°37'	A (L)
L13. Roadcut east of La Vid de Gordon.	Valporquero Fm.	17SPAIN31	N42°53' W005°37'	M (L)
L13. Roadcut east of La Vid de Gordon.	Valporquero Fm.	18SPAIN18	N42°53'38.2" W005°37'33.2" (+/- 9 m)	M (L)
L13. Roadcut east of La Vid de Gordon.	La Pedrosa Fm.	00LV05	N42°53' W005°37'	RC
L13. Roadcut east of La Vid de Gordon.	La Pedrosa Fm.	00LV06	N42°53' W005°37'	R (L)
L13. Roadcut east of La Vid de Gordon.	La Pedrosa Fm.	00LV07	N42°53' W005°37'	R (L)
L13. Roadcut east of La Vid de Gordon.	La Pedrosa Fm.	00LV08	N42°53' W005°37'	RC
L13. Roadcut east of La Vid de Gordon.	La Pedrosa Fm.	00LV09	N42°53' W005°37'	RC
L13. Roadcut east of La Vid de Gordon.	Felmin Fm.	17SPAIN32	N42°53'41.0" W005°37'31.8" (+/- 12 m)	RC
L13. Roadcut east of La Vid de Gordon.	Felmin Fm.	18SPAIN19	N42°53'" W005°37'" (+/- m)	B
L13. Roadcut east of La Vid de Gordon.	Felmin Fm.	17SPAIN34	N42°53'45.8" W005°37'30.2" (+/- 6 m)	RC
L13. Roadcut east of La Vid de Gordon.	Felmin Fm.	17SPAIN33	N42°53'47.9" W005°37'28.6" (+/- 7 m)	R (L)
L13. Roadcut east of La Vid de Gordon.	Felmin Fm.	18SPAIN20	N42°53'47.3" W005°37'29.9" (+/- 9 m)	B
L14. Santa Lucia de Gordon	Limestone	18SPAIN17	N42°52'34.9" W005°38'18.9" (+/- 5 m)	B
L15. Felechás-Colle	Valporquero Fm.	17SPAIN42	N42°51'10.0" W005°15'30.9" (+/- 7 m)	A (L)
L15. Felechás-Colle	Valporquero Fm.	17SPAIN43	N42°51'10.0" W005°15'30.9" (+/- 7 m)	A (L)
L15. Felechás-Colle	Valporquero Fm.	17SPAIN44	N42°51'03.6" W005°15'34.3" (+/- 6 m)	B
L15. Felechás-Colle	Valporquero Fm.	17SPAIN45	N42°51'03.6" W005°15'34.3" (+/- 6 m)	B
L15. Felechás-Colle	Valporquero Fm.	17SPAIN46	N42°50'56.1" W005°15'26.2" (+/- 6 m)	A (L)
L15. Felechás-Colle	Valporquero Fm.	18SPAIN08	N42°51'11.7" W005°13'31.8" (+/- 8 m)	A (L)
L16. Argovejo	Valporquero Fm.	17SPAIN47	N42°54'04.5" W005°06'37.2" (+/- 4 m)	A (L)
L16. Argovejo	Valporquero Fm.	17SPAIN48	N42°54'05.7" W005°07'21.5" (+/- 5 m)	R (L)
L16. Argovejo	Valporquero Fm.	17SPAIN49	N42°54'05.1" W005°07'19.2" (+/- 6 m)	R (L)
L16. Argovejo	Valporquero Fm.	17SPAIN50	N42°54'04.7" W005°07'04.1" (+/- 5 m)	M (L)
L16. Argovejo	Valporquero Fm.	17SPAIN51	N42°54'04.7" W005°07'04.1" (+/- 5 m)	M (L)
L16. Argovejo	Valporquero Fm.	18SPAIN04	N42°54'02.3" W005°07'03.2" (+/- 5 m)	B
L16. Argovejo	La Pedrosa Fm.	18SPAIN05	N42°54'05.6" W005°07'03.3" (+/- 5 m)	R (L)
L16. Argovejo	La Pedrosa Fm.	18SPAIN06	N42°54'05.6" W005°07'03.3" (+/- 5 m)	M (L)
L17. Vinayo	Valporquero Fm.	18SPAIN34	N42°48'39.9" W005°46'10.0" (+/- 11 m)	MC
L18. Cremenés C621		00 N621/A/01		
L18. Cremenés C621		00 N621/A/15		
P01. Labanza-Abadía	Abadía Fm.	17SPAIN52	N42°57'48.9" W005°32'40.5" (+/- 6 m)	B
P01. Labanza-Abadía	Abadía Fm.	17SPAIN53	N42°57'50.9" W005°32'18.1" (+/- 7 m)	B
P01. Labanza-Abadía	Abadía Fm.	17SPAIN54	N42°57'54.6" W005°32'06.5" (+/- 5 m)	RC
P01. Labanza-Abadía	Labanza Fm.	17SPAIN55	N42°58'05.3" W005°31'46.4" (+/- 7 m)	B
P01. Labanza-Abadía	Labanza Fm.	17SPAIN56	N42°58'05.3" W005°31'46.4" (+/- 7 m)	RC

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