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A palynological investigation of the Early-Middle Devonian transition and associated Choteč Event in Northern Spain

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ABSTRACT

In Northern Spain there is a near complete sequence of Devonian rocks that accumulated around a relatively isolated land mass, the Armorican Terrane Assemblage, which was separated from Gondwana to the south and Laurussia to the north. The Lower to Middle Devonian transition records a dramatic facies change from carbonate to siliciclastic sedimentation. The Choteč Event, a global anoxic pulse that occurs just above the Lower-Middle Devonian boundary (392.5–393.1 Ma), has been identified within this transition. These strata are included in the Moniello and Naranco fms in Asturias and the equivalent Santa Lucía and Huergas fms in Leon. They are independently age-contrained based on conodont and invertebrate biotas. For the first time we describe palynomorph assemblages recovered from the Lower to Middle Devonian transition in Northern Spain. The assemblages contain terrestrial (spores) and marine (acritarchs, prasinophycean cysts, chitinozoans) elements, thus recording primary productivity on both the land and in the oceans. The older assemblages belong to the *annulatus–sextantii* Spore Zone and the younger assemblages the *douglastownensis–eurypterota* Spore Zone, which is concordant with the independent age constraints. Our analysis of the distribution and diversity of marine and terrestrial palynomorphs supports interpretations of the facies change associated with the Choteč Event as being related to a change to increased rainfall and terrestrial runoff. However, this change is associated with only limited taxon turnover in both land plant spores and marine phytoplankton and chitinozoans.

1. Introduction

The Devonian sequence of Northern Spain exhibits dramatic facies changes as the carbonates of the Moniello and equivalent Santa Lucía fms transition into the siliciclastic deposits of the Naranco and equivalent Huergas fms (Figs. 1, 2). This transition has been related to the Basal Choteč Event, a global anoxic pulse that occurs just above the Lower-Middle Devonian boundary (García-Alcalde, 1998; Brocke et al., 2016; van Loevezijn and Raven, 2017; Becker et al., 2020). Herein we describe rare palynological assemblages recovered from the carbonate platform deposits of the Moniello/Santa Lucía fms and more common assemblages from the transitional beds around the contact with the overlying Naranco/Huergas fms. Palynomorph assemblages have not previously been reported from the Moniello/Santa Lucía and basal Naranco/Huergas fms, although rich palynological assemblages from the upper part of the Naranco/Huergas fms have recently been described (Askew

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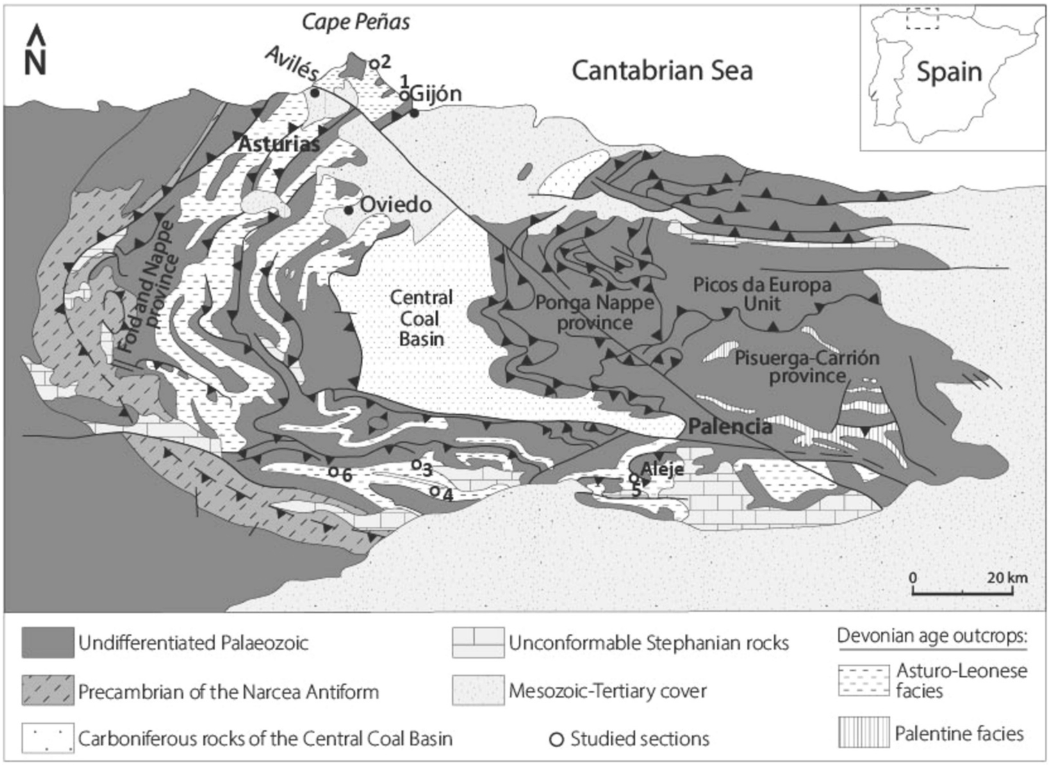
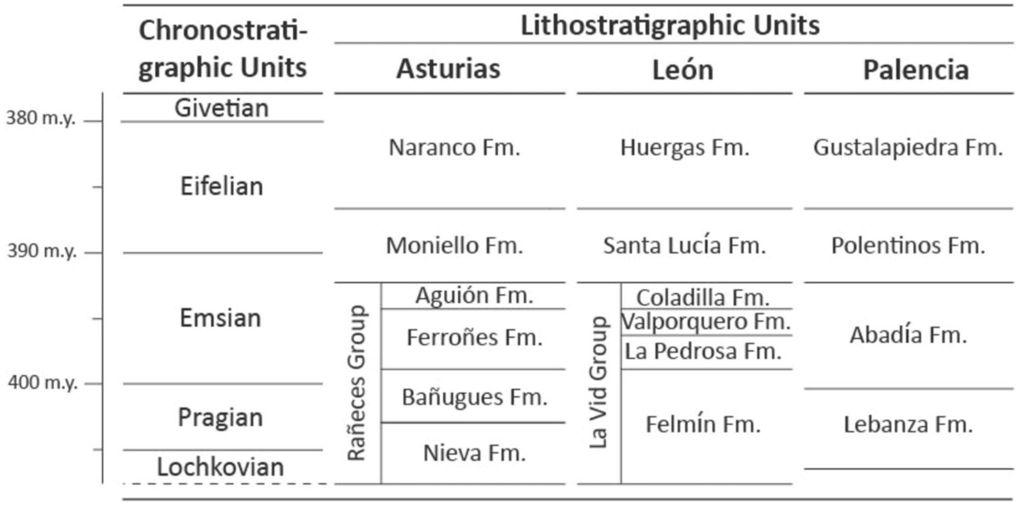


Fig. 1. Outline map of Northern Spain showing the outcrop of Devonian deposits with the location of sampled sections. Numbered localities/sections are from Appendix A.



	Chronostratigraphic Units	Lithostratigraphic Units		
		Asturias	León	Palencia
380 m.y.	Givetian	Naranco Fm.	Huergas Fm.	Gustalapiedra Fm.
	Eifelian			
390 m.y.		Moniello Fm.	Santa Lucía Fm.	Polentinos Fm.
	Emsian	Rañeces Group: Aguión Fm.	La Vid Group: Coladilla Fm.	Abadía Fm.
		Rañeces Group: Ferroñes Fm.	La Vid Group: Valporquero Fm.	
			La Vid Group: La Pedrosa Fm.	
400 m.y.	Pragian	Rañeces Group: Bañugues Fm.	La Vid Group: Felmín Fm.	Lebanza Fm.
	Lochkovian	Rañeces Group: Nieva Fm.		

Fig. 2. Stratigraphical sequence of the Lower-Middle Devonian deposits of Northern Spain and their age and correlation (after Garcia-López, 2002).

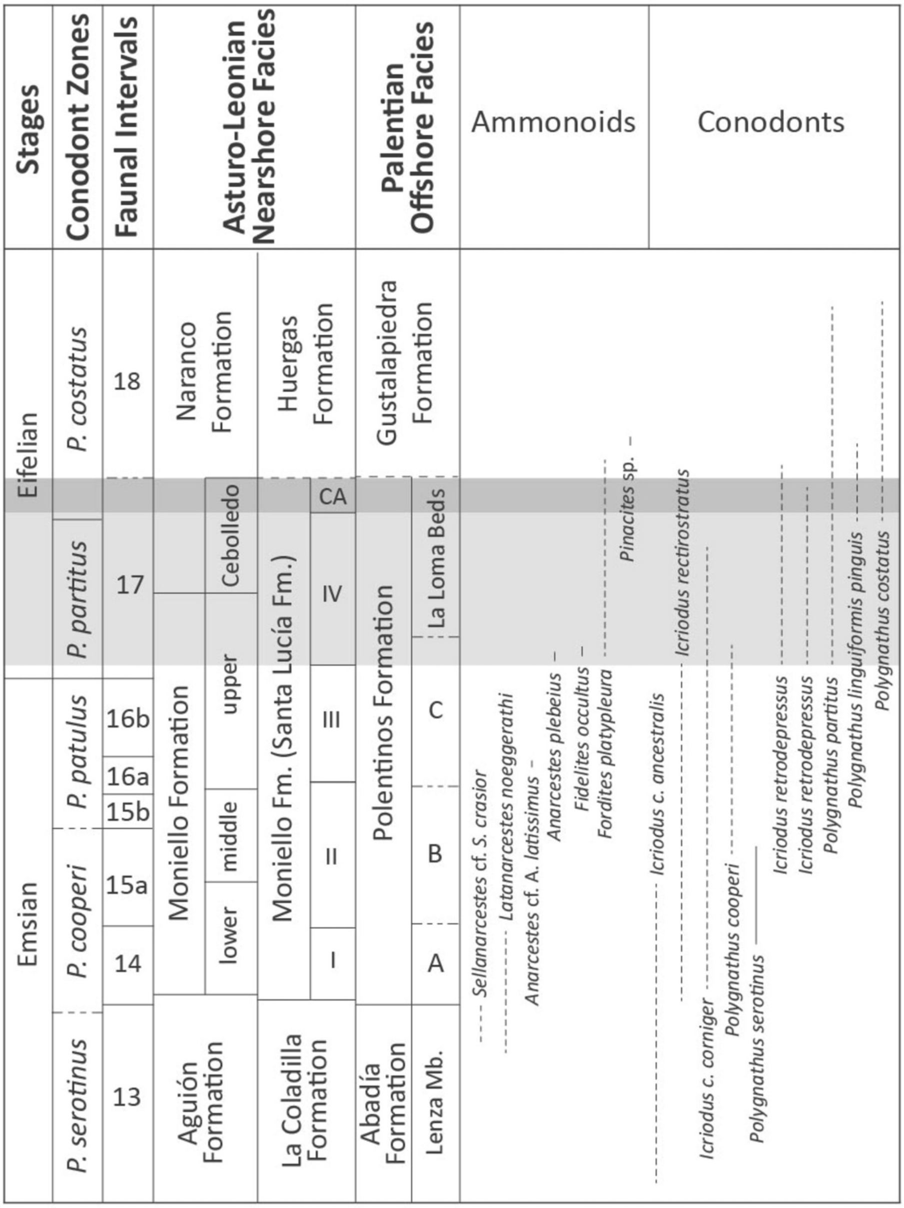


Fig. 3. Stratigraphical distribution of important zonal fossils used in age dating of the formations. Grey areas refer to the Choteč Event. See the text for references.

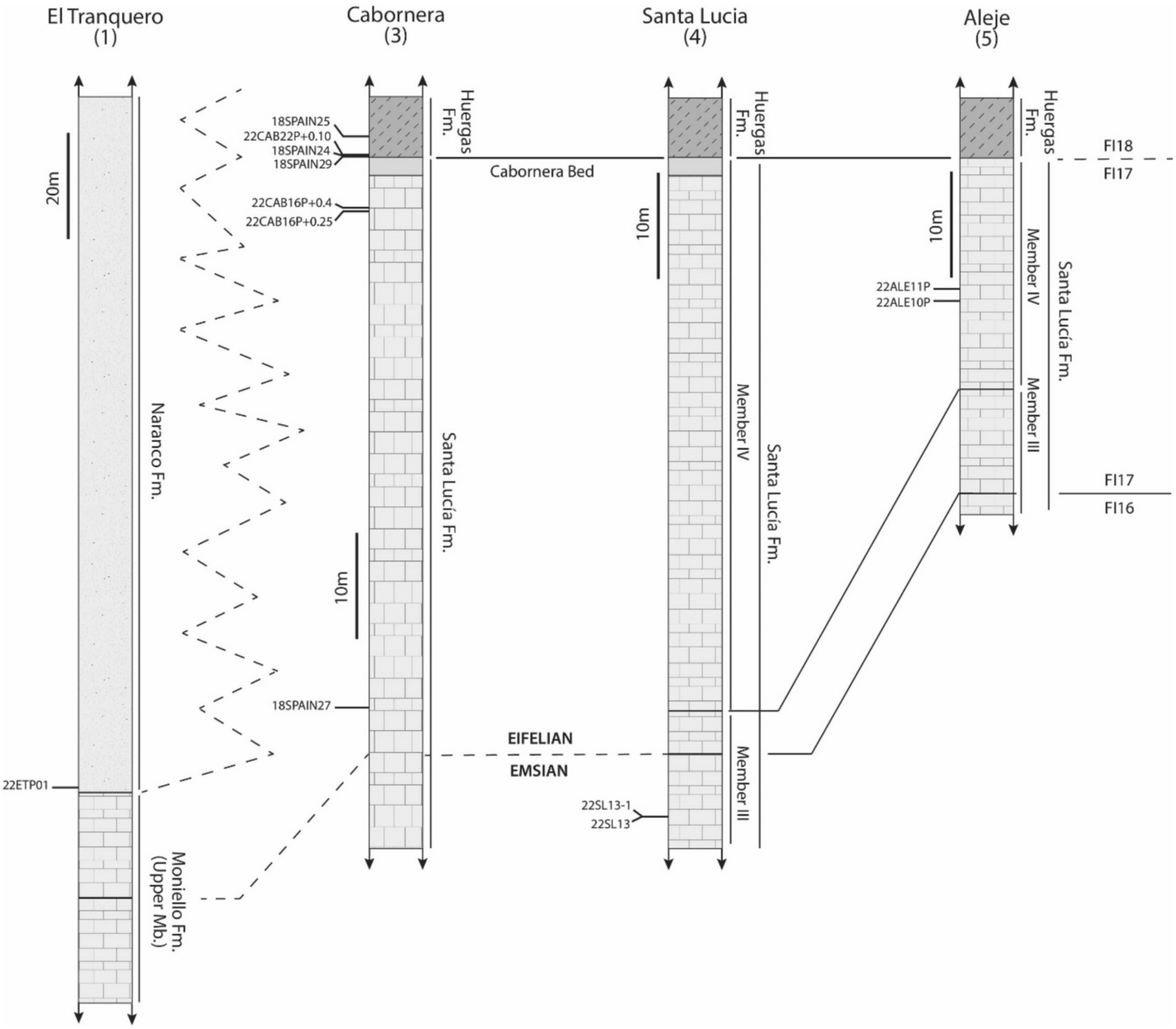


Fig. 4. Stratigraphical sections of the main localities illustrating the position of logged spore samples. The dashed lines show the correlation of the main formations within the different sections according to evidence form palynology (this paper) and conodonts and faunal intervals of marine macrofauna.

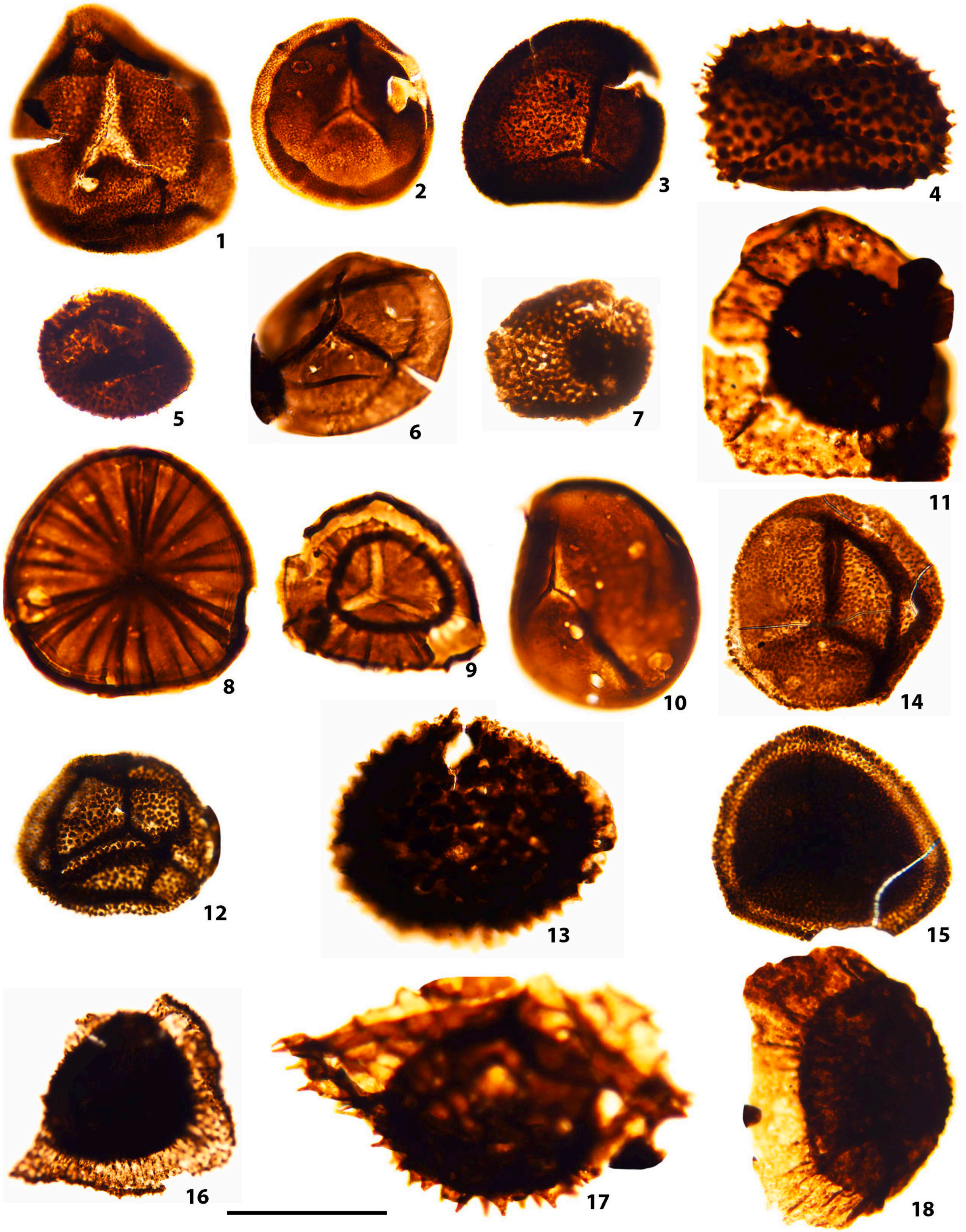


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Plate I. Dispersed spores from the Santa Lucía Fm of Northern Spain. Scale bar = 30 μm (5,8,9,10), =45 μm (1,2,3,4,6,7,12,13,14,15), = 60 μm (11,16,17,18).
1. *Apiculiretusispora brandtii* (Sample 22SL13.1; Slide 1; E.F.no. L36/2).
2. *Apiculiretusispora plicata* (Sample 22SL13.1; Slide 1; E.F.no. J45).
3. *Dibolisporites echinaceus* (Sample 22SL13.1; Slide 1; E.F.no. M33/1).
4. *Dibolisporites tuberculatus* (Sample 18SPAIN27; Slide A; E.F.no. W27).
5. *Dibolisporites* with short, wide, flat-topped pila (Sample 22SL13; Slide 1; E.F.no. V31/3).
6. Spore with crenulate folding along the trilete mark (Sample 22SL13; Slide 1; E.F.no. J31).
7. *Brochotriletes* sp. (Sample 22SL13; Slide 1; E.F.no. U45).
8. *Emphanisporites rotatus* (Sample 18SPAIN27; Slide A; E.F.no. H51).
9. *Emphanisporites annulatus* (Sample 18SPAIN27; Slide A; E.F.no. O44).
10. *Retusotriletes* sp. (Sample 22SL13; Slide 1; E.F.no. F50/3).
11. *Grandispora protea* (Sample 22SL13; Slide 1; E.F.no. E34).
12. *Acinosporites lindlarensis* (Sample 18SPAIN27; Slide A; E.F.no. U43/2).
13. *Acinosporites acanthomammillatus* (Sample 18SPAIN27; Slide A; E.F.no. F42/1).
14. *Geminospora svalbardiae* (Sample 18SPAIN27; Slide A; E.F.no. L50).
15. *Geminospora convoluta* (Sample 18SPAIN27; Slide A; E.F.no. S42).
16. *Grandispora* sp. 1 (Sample 22SL13; Slide 1; E.F.no. G45).
17. *Ancyrospora nettersheimensis?* (Sample 18SPAIN27; Slide A; E.F.no. H49/2).
18. *Samarisporites praetervisus* (Sample 22SL13; Slide 1; E.F.no. Q40/3).

and Wellman, 2018; Askew, 2019; Askew and Russell, 2019). The new palynological assemblages include diverse terrestrial (spores) and marine (acritarchs, prasinophytes and chitinozoans) forms that record concurrent primary productivity on the land and in the oceans. They are notable because they are independently age-constrained by conodonts and other biota and they straddle the Choteč Event. The Choteč Event is considered to represent a global anoxic pulse (Becker et al., 2020). Here it is identified in an isolated island setting (Armorican Terrane Assemblage) separated from the main Devonian continents by large tracts of ocean (Askew and Wellman, 2020). In this palaeogeographical context we consider potential causes for the global anoxic pulse based on our palynological observations.

2. Geological setting

In the Cantabrian Mountains (Cantabrian Zone) of Northern Spain the late Emsian to early Eifelian (Lower-Middle Devonian) is characterised by the extensive development of a carbonate ramp (Figs. 1, 2, 3). It corresponds to the most important and extended reefal growth in the Devonian passive margin sedimentation of this area (named reefal episode IV by Fernández-Martínez et al., 2006). The limestones, argillaceous limestones and shales attain 250 m in thickness (ranging between 175 and 310 m) and corresponds to the Moniello Fm, first described by Barrois (1882) in the Moniello inlet of the Asturian coast. It was subsequently redefined by Arbizu et al. (1979). Lateral equivalents were named the Santa Lucía Fm for the southern side of the Cantabrian Mountains in León (Comte, 1936) and the Otero Fm eastwards in the Palencia area (Koopmans, 1962). These strata yield a rather abundant and diverse fauna of corals, brachiopods, bryozoans, crinoids, ostracods, trilobites and echinoderms with occasional tentaculitids, nautiloids, fish remains and conodonts.

The Moniello Fm developed above multi-coloured shales, marls and pinkish limestones included in the Aguión and Coladilla fms (north and south sides of the Cantabrian Mountains, respectively) (Radig, 1962; Vera de la Puente, 1989). Vera de la Puente (1989) and Hofmann and Keller (2006) suggested a short, time lateral replacement between the Coladilla and the Moniello fms.

The Moniello Fm is succeeded by the laterally equivalent Naranco Sandstone (Adaro and Junquera, 1916) and Huergas Shale (Comte, 1936). The Naranco Fm corresponds to 450–500 m of sandstone with interbedded shale, with ferruginous sandstones in the northern part of the Cantabrian Mountains. It yields brachiopods, bryozoans, corals and bivalves. The Naranco Fm corresponds to a wave-dominated siliciclastic platform with storms, shoal development and local beach deposits (García-Ramos, 1978; García-Ramos et al., 1984). Ferruginous sandstones and enriched-iron ooids are common in the Naranco succession and are interpreted as deriving from iron supplied through weathering of Cambrian-Ordovician volcanic rocks (García-Ramos et al., 1987). The siliciclastic supply decreases in the upper part of the formation where tidal and wave influenced deposits occur. Southwards, distal sedimentation prevailed with dark sandstones and sandy limestones in the Huergas Fm (230–400 m in thickness). This formation yields brachiopods, bivalves, trilobites, ostracods, ammonoids and dacryoconarid tentaculitids, showing the distal components of the siliciclastic supply including horizons with abundant deep-water fauna.

Successions of the Santa Lucía Fm are subdivided into four informal members: Members I–IV (Evers, 1968; García-Alcalde et al., 1979) whereas at the Asturian coast only three members are present in the Moniello Fm (Méndez-Bedia, 1976; García-Alcalde et al., 1979). Locally, abundant echinoderm limestone and brachiopods from the upper half of the upper member suggest correlation with Member IV. Sedimentary cycles from several centimetres to a few metres are present with eight sedimentary sequences 30–40 m in thickness (Hofmann and Keller, 2006; García-Alcalde, 2017). Three or four facies zones (or facies associations) were recognised in the spatial distribution of the Moniello Fm that occur in longitudinal belts (Coo et al., 1971; Coo, 1974; Méndez-Bedia, 1976; Buggisch et al., 1982; Hofmann and Keller, 2006). They crop out approximately parallel to the Asturian oroclinal structure,

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Plate II. Dispersed spores from the Cabornera Bed (Santa Lucía Fm) of Northern Spain. Scale bar = 30 μm (except 4 where scale bar = 60 μm).
1. *Retusotriletes triangulatus* (Sample 22CAB16P.40; Slide 1; E.F.no. U34/4).
2. *Apiculiretusispora plicata* (Sample 22CAB16P.40; Slide 1; E.F.no. M41/4).
3. *Dibolisporites eifeliensis* (Sample 22CAB16P.25; Slide 1; E.F.no. P49).
4. *Dibolisporites echinaceus* (Sample 22CAB16P.40; Slide 1; E.F.no. H51.1).
5. *Apiculiretusispora arabiensis* (Sample 22CAB16P.25; Slide 1; E.F.no. G46/4).
6. *Dictyotriletes hemeri* (Sample 22CAB16P.25; Slide 1; E.F.no. J32/2).
7. *Ambitisporites* sp. (Sample 22CAB16P.40; Slide 1; E.F.no. K40/2).
8. *Emphanisporites rotatus* (Sample 22CAB16P.40; Slide 1; E.F.no. X45/1).
9. *Emphanisporites mcgregorii* (Sample 22CAB16P.40; Slide 1; E.F.no. O36/2).
10. *Cymbosporites senex* (Sample 22CAB16P.25; Slide 1; E.F.no. W39/3).
11. *Verrucosisporites* sp. (Sample 22CAB16P.25; Slide 1; E.F.no. P44).
12. *Lophotriletes devonicus* (Sample 22CAB16P.25; Slide 1; E.F.no. M32/2).
13. *Lophotriletes devonicus* (Sample 22CAB16P.40; Slide 1; E.F.no. R40/3).
14. *Camarazonotriletes sextantii* (Sample 22CAB16P.25; Slide 1; E.F.no. Q35).
15. *Lophotriletes devonicus* (Sample 22CAB16P.25; Slide 1; E.F.no. P42/1).
16. *Diatomozonotriletes franklinii* (Sample 22CAB16P.40; Slide 1; E.F.no. K37/2).

which folded older Variscan structures during the late Carboniferous-early Permian (Weil et al., 2019). Interpretational 'unfolding' of the oroclinal structures allows recognition that the facies associations run parallel to a north–south palaeo-coastline (current geographic coordinates) and an eastern uplifted Cantabrian block, where Devonian deposits are lacking.

The sublitoral and offshore belt corresponds to outer ramp bioclastic deposits reworked by storms. Biostromes of stromatoporoid sponges and tabulate corals are well developed. Incipient bioherms, as framestones of stromatoporoids, up to a maximum 2 m in height occur between common biostromes, although locally the Arnao development attained 140 m in thickness (Méndez-Bedia and Soto, 1984; Méndez Bedia et al., 1994). Reef growth protected lagoonal back-reef communities, particularly during sedimentation of the middle member, where the gently west-dipping ramp developed locally, forming a rim that protected multiple construction sites. Small sequences of reefal communities extended to the lagoon area. Proximal facies correspond to lagoon intertidal to supratidal facies with rarer fauna. Peloid and finely laminated mudstones contains bird's-eyes and laminoid-fenestral fabrics (Coo, 1974; Méndez-Bedia, 1976; Hofmann and Keller, 2006). Ostracods and calcispheres represent the autochthonous fauna with rarer auloporids, gastropods, brachiopods and crinoids. Marl and siltstone-shale beds are present, particularly in the middle member. Casts of evaporite minerals and polygonal desiccation cracks in dolomitic beds corresponds to desiccation horizons.

Deposition of encrinitic limestones of Member IV on the outer part of the ramp represents the end of the reefal biostromes, with an increase on siliciclastic supply and a decreasing abundance and diversity of fauna. Here brachiopods show large size and crinoids and blastoids were abundant. García-Alcalde (2017) recently defined the Cebolledo Mb for alternating beds of reddish crinoidal limestones, carbonated sandstones and sandy shales (83 m thick) in the upper part of the Moniello Fm. He suggested that the brown and reddish limestones, above encrinitic limestones of Member IV in the southeastern sections, are equivalent to the Cebolledo Mb. Furthermore, a transitional interval of alternating limestone and dark shale, between the Santa Lucía/Huergas fms exposed in the Esla nappe (Aleje and Arbejal sections), is usually included in Member IV of the Santa Lucía Fm (García-Alcalde, 2011) and is also equivalent to the Cebolledo Mb. Finally, García-Alcalde (2017) recognised the Cebolledo Mb in the lowermost part of the Naranco Fm (130 m) at the Moniello inlet section, where prevailing sandstones with shales and siltstones include several intervals of dolomitic sandy limestones with macrofauna of Faunal Interval 17. Consequently, lateral intertonguing between the Naranco and Moniello fms existed, despite sharp isochronous boundaries often being illustrated in lithostratigraphic schemes (e.g. García-Muro and Rubinstein, 2022).

Van Loevezijn and Raven (2017) differentiated the Cabornera Bed in the basal Huergas Fm of the particularly well exposed rocks on the road from Beberino to Buiza along the tributary of the Casares River (called Folledo creek). The grey limestones of the Santa Lucía Fm gives way to 1.6–1.7 m thick of alternating dark shaly mudstones and wackestones with a few bioclastic intercalations. An iron mineralisation crust occurs immediately above the light-grey limestones of the Santa Lucía Fm (Van Loevezijn and Raven, 2017). Coo (1974) and Hofmann and Keller (2006) differentiated a similar bed in several sections in the Bernesga Valley (León), but they included it at the top of the Santa Lucía Fm. Chamosite or iron oolites occur in a thin bed. Fernández Martínez et al. (2003) described heterocorals from this bed near Geras de Gordón.

The Santa Lucía Fm is coeval with the Polentinos Fm in the Palentian nappes (Van Veen, 1965), where tectonically displaced units allow investigation of the Palentian deep-water facies (Brower, 1964), from the basin beyond the Cantabrian Zone. In the deep basin, the condensed sedimentation (30–60 m thick) is associated with mixed pelagic and benthic faunas, including locally dacryoconarids and ammonoids, as well as mixed icriodid and polygnathid conodont faunas. The Polentinos Fm consists of limestones with interbedded shales divided into three informal members (A-C after Jahnke et al., 1983). Furthermore, García-Alcalde et al. (1988) included in the Polentinos Fm the lower part of the La Loma Mb (La Loma beds), which comprise a few metres of alternating shales, limestones and marls that were originally included in the overlying Gustalapiedra Fm. The Polentinos Fm is above shales and marls with rare limestones of the Lezna Mb (Jahnke et al., 1983) of the Abadía

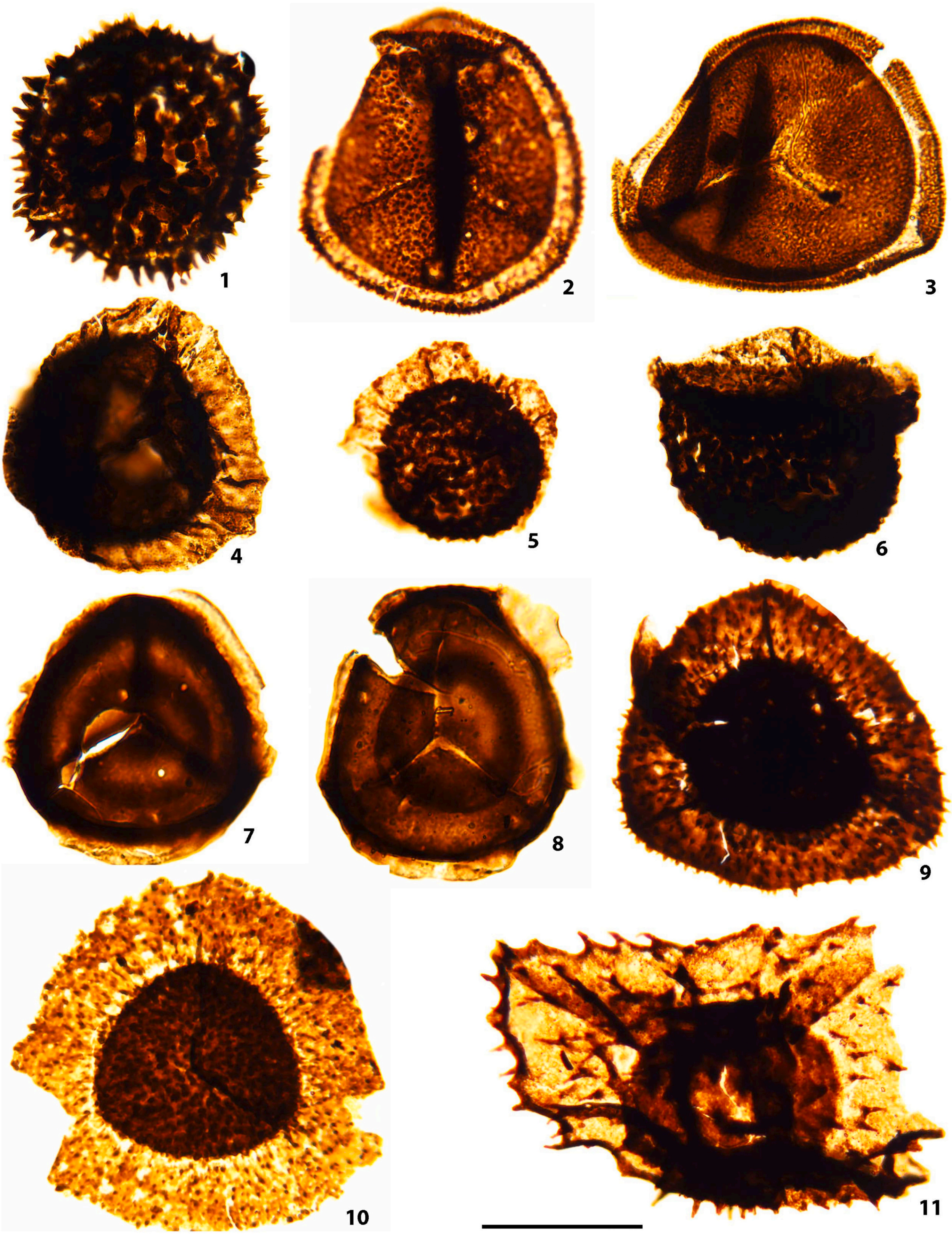

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Plate III. Dispersed spores from the Cabornera Bed of Northern Spain. Scale bar = 30 μm (2,3,7,8), =45 μm (1,4,5,6,10) = 60 μm (9,11).
1. *Acinosporites acanthomammillatus* (Sample 22CAB16P.25; Slide 1; E.F.no. U47).
2. *Geminospora svalbardiae* (Sample 22CAB16P.40; Slide 1; E.F.no. V49).
3. *Geminospora svalbardiae* (Sample 22CAB16P.25; Slide 1; E.F.no. K37/1).
4. *Samarisporites praetervisus* (Sample 22CAB16P.25; Slide 1; E.F.no. U29/2).
5. *Samarisporites praetervisus* (Sample 22CAB16P.40; Slide 1; E.F.no. H45).
6. *Samarisporites praetervisus* (Sample 22CAB16P.25; Slide 1; E.F.no. C49/2).
7. *Zonotriletes armillatus* (Sample 22CAB16P.25; Slide 1; E.F.no. L38/2).
8. *Zonotriletes armillatus* (Sample 22CAB16P.25; Slide 1; E.F.no. S34).
9. *Grandispora douglastownensis* (Sample 22CAB16P.40; Slide 1; E.F.no. D44/2).
10. *Grandispora* spp. (Sample 22CAB16P.25; Slide 1; E.F.no. N44/2).
11. *Ancyrospora nettersheimensis* (Sample 22CAB16P.40; Slide 1; E.F.no. K34/2).

Fm (Van Veen, 1965). The La Loma beds are succeeded by 50 m of shales of the Gustalapiedra Fm (Van Veen, 1965; redefined by García-Alcalde et al., 1988).

Biostratigraphy of the Moniello, Naranco and Huergas fms is based on invertebrate faunas, particularly brachiopods. Studies of these successions has focussed on the type sections of the Moniello inlet and the El Puerto Creek section (type section of the Santa Lucía Fm). García-Alcalde (1996) defined informal biozones (named faunal intervals: FI), with imprecise boundaries between them, characterised by the distribution of species (García-Alcalde, 2017). The Moniello Fm extends from FI14 to FI17. The local occurrences of conodonts, particularly shallow water icriodid faunas, allows global correlation based on García-López (1987), García-López and Sanz-López (2002a, 2002b). However, the first occurrences of marker species are discrete, and the lowermost occurrences may be younger than their inception globally.

Icriodus corniger ancestralis is present in the Coladilla Fm and the basal beds of the Santa Lucía Fm, where it co-occurs with *I. culicellus* and *I. leptus* in the informal *I. c. ancestralis* Zone (García-López and Sanz-López, 2002b). This zone is correlated with the upper Emsian *I. fusiformis* Zone (Aboussalam et al., 2015) and the *Polygnathus laticostatus* to *P. serotinus* zones (García-López and Sanz-López, 2002a). The first occurrences of *Icriodus rectirostratus* and *I. corniger corniger* in the upper beds of FI14 and in FI15a (*I. c. corniger* Zone) is correlated with beds of the *Polygnathus serotinus* Zone or with the overlying *Polygnathus patulus* Zone (Bultynck, 2003). However, these taxa are known from below the *P. serotinus* Zone in Morocco (Aboussalam et al., 2015). The occurrence of the brachiopod *Zdimir* cf. *hercynicus* from FI15b may be close to the lower boundary of the *P. patulus* Conodont Zone, according to the Rhenish distribution reported by Weddige et al. (1979).

In the Palentian nappes, Henn (1985) correlated the Lezna Mb with the *Polygnathus serotinus* Zone, although conodont evidence was also limited to *Icriodus culicellus* and *I. leptus*. The occurrence of the ammonoid *Latanarcestes noeggerathi*, together with *Sellanarcestes* cf. *S. crassior*, in the uppermost beds of the Lezna Mb (Montesinos, 1988), suggests correlation with the upper part of the *P. serotinus* Zone, later differentiated in the overlying *P. cooperi* Zone by Aboussalam et al. (2015). The disappearance of the genus *Sellanarcestes* at the base of the Polentinos Fm suggests correlation with the *P. cooperi* Zone according to ranges in Becker and House (1994). This correlation is more accurate than that obtained from the basal Moniella/Santa Lucía fms. Member A of the Polentinos Fm yields scarce dacryoconarids, *Nowakia richteri*, *N. holyocera* and *N.* ex gr. *sulcata*, and conodonts, *P. serotinus* and *I. culicellus* (Henn, 1985). Furthermore, the occurrence of the dacryoconarid *Nowakia holynensis* in the upper part of Member A suggests that these beds are close to the upper boundary of the *P. cooperi* Zone. Member B yields *P. cooperi* (Henn, 1985).

The *Polygnathus partitus* Zone and the lower Eifelian was correlated on the basis of the occurrence of *Icriodus retrodepressus* from the basal bed of the Member IV in the El Puerto Creek section (García-López, 1987) and at the top of the Moniello Fm at the Aralla section (Buggisch et al., 1982). However, both findings are potentially younger than expected and related to facies restrictions, based on Ellwood et al. (2006) who located the lower boundary of the Eifelian in the biostromal limestone of the member III at 4.2 m below the first *I. retrodepressus* occurrence. This correlation is based on the comparison of the magnetic susceptibility records of the El Puerto Creek section and the GGSP for the lower boundary of the Eifelian. It coincides exactly with the lower boundary of FI17 based on articulate brachiopods. FI17 is recognised in Member IV, the Cebolledo Mb and the lower part of the Naranco Fm (García-Alcalde, 2017). Buggisch et al. (1982) studied conodonts at the top of the Moniello Fm at the Piedrasecha section, including *Icriodus* sp. E Weddige, 1977 and *Polygnathus linguiformis pinguis* that occurred from the upper beds of the *P. partitus* Zone according to the distribution in Weddige (1977). The occurrence of *Icriodus* cf. *I. regularicrescens* could indicate the *P. costatus* Zone. García-López (1987) reported *P. costatus* and *P. patulus* close the top of the Santa Lucía Fm in the Beberino-Cabornera roadcut, and based on this occurrence the top of the formation is correlated with the basal *P. costatus* Zone. A conodont association correlated with the *Polygnathus costatus* Zone, including the polygnathids *P. costatus* and *P. partitus*, is known from a bioclastic packstone in the Cabornera Bed at the El Puerto creek section (García-López and Sanz-López, 2002b).

The Huergas Fm yields pelagic faunas of ammonoids, trilobites, dacryoconarid tentaculitids and ostracods included in FI18 (García-Alcalde, 1996). The ammonoids *Foordites platypleura* and *Werneroceras constrictum* occur in the lowermost beds at the Pola de Gordon and Barrios de Luna sites (Montesinos, 1989). *Anarcestes* sp., *Holzapfeloceras* sp. A and *Werneroceras* sp. are present in the lowermost 20 m of the formation, whereas *Subanarcestes marcocephalus*, *Agoniatites bicanaliculatus*, *Werneroceras constrictum* and *Holzafeloceras* sp. occur in the lower part of the Huergas Fm. Trilobite faunas show a sharp change in the lower part of the Huergas Fm, where Smeenk (1983) differentiated their

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Plate IV. Dispersed spores from the Huergas Fm of Northern Spain. Scale bar = 30 μm.
1. *Retusotriletes* sp. (Sample 22CAB22P; Slide 1; E.F.no. E41).
2. *Retusotriletes triangulatus* (Sample 22CAB22P; Slide 1; E.F.no. K48).
3. *Apiculiretusispora plicata* (Sample 22CAB22P; Slide 1; E.F.no. S40/3).
4. *Apiculatasporites perpussilus* (Sample 22CAB22P; Slide 1; E.F.no. Q35/3).
5. *Apiculatisporis* cf. *elegans* (Sample 22CAB22P; Slide 1; E.F.no. P35/1).
6. *Apiculiretusispora* spp. (Sample 18SPAIN24; Slide 1; E.F.no. E30/1).
7. *Apiculiretusispora arabiensis* (Sample 18SPAIN29; Slide 1; E.F.no. N36/2).
8. *Apiculiretusispora plicata* (Sample 18SPAIN24; Slide 1; E.F.no. N27/3).
9. *Ambitisporites* sp. (Sample 22CAB22P; Slide 1; E.F.no. H42/1).
10. *Cymbosporites* spp. (Sample 22CAB22P; Slide 1; E.F.no. K41/1).
11. *Acinosporites lindlarensis* (Sample 18SPAIN24; Slide 1; E.F.no. K38/3).
12. *Brochotriletes hudsonii* (Sample 22CAB22P; Slide 1; E.F.no. R44).
13. *Emphanisporites rotatus* (Sample 18SPAIN29; Slide 1; E.F.no. U36).
14. *Verrucosisporites* spp. (Sample 18SPAIN25A; Slide 1; E.F.no. H30).
15. *Lophotriletes devonicus* (Sample 18SPAIN24; Slide 1; E.F.no. W32/1).
16. *Lophotriletes devonicus* (Sample 18SPAIN24; Slide 1; E.F.no. G34/2).
17. *Devonomonoletes* sp. (Sample 22CAB22P; Slide 1; E.F.no. Q43).
18. *Latosporites* sp. 1 (Sample 22CAB22P; Slide 1; E.F.no. Q41/3).

units VII to IX.

Polygnathus partitus and *Icriodus* cf. *I. retrodepressus*, indicating the basal Eifelian, occur in the upper part of Member C of the Polentinos Fm in the deep basin. Above there is an increase in faunal diversity together with the occurrence of the dacryoconarid *Nowakia sulcata sulcata* (Henn, 1985). The La Loma beds yield ammonoids of the *Fidelites* Genozone (Henn, 1985; Montesinos, 1987a, 1987b, 1989), such as *Anarcestes plebeius*, *Foordites platypleura*, *Fidelites occultus* and *Fidelites* cf. *F. vernathenanum*. Henn (1985) correlated these beds with the upper part of the *P. partitus* Zone and recognised the *P. costatus* Zone in the uppermost La Loma beds, based only on the occurrence of *Icriodus* cf. *I. amabilis*. The inception of the ammonoids *Pinacites* sp. and *Pinacites juegleri* in the overlying beds of the Gustalapiedra Fm correlate with the upper part of the *P. costatus* Zone (Montesinos, 1989).

3. Materials and methods

Six sections of the Moniello/Santa Lucía and Naranco/Huergas formations were investigated in the Cantabrian Mountains and samples collected for palynological analysis (Figs. 1, 4). Details of the collected samples are provided in Appendix A and briefly summarised below.

The type section of the Moniello Fm is exposed in the coastal cliffs along Moniello inlet in the north coast of Asturias (1 in Fig. 1). The sequence comprises predominantly massive limestones unsuitable for palynological analysis. However, three samples of thin layers of dark, muddy limestone were discovered and collected for palynological analysis.

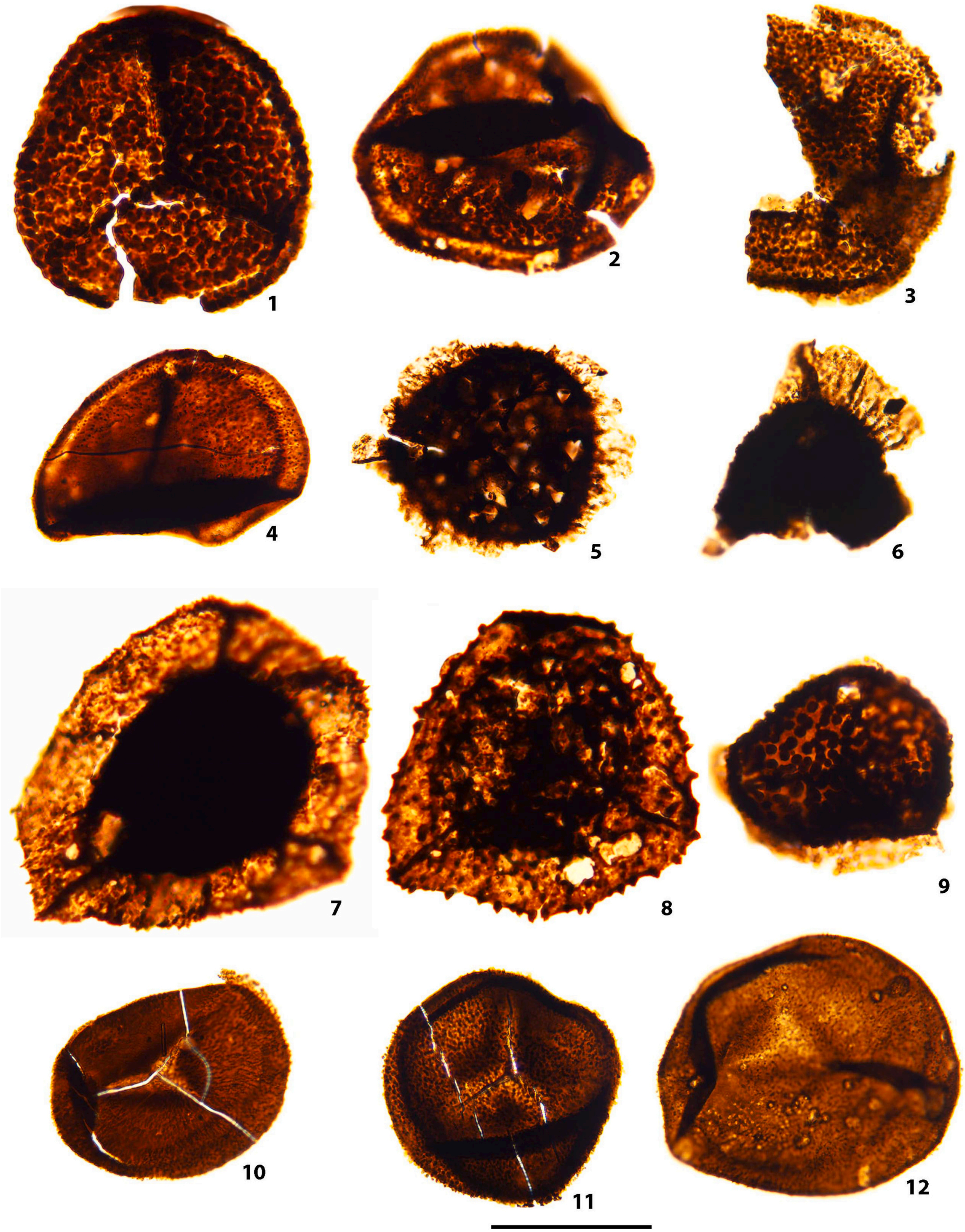
The type section of the Santa Lucía Fm crops out in El Puerto creek near the village of Santa Lucía in the southern side of the Cantabrian Mountains (García-López and Sanz-López, 2002a; 3 in Fig. 1). The sequence comprises predominantly massive limestones unsuitable for palynological analysis. However, a number of thin intercalations of darker calcareous mudstones were located and ten samples collected for palynological analysis.

Another investigated sequence of the Santa Lucía Fm is exposed in roadcuts along the CL-626 road that follows the east shore of Los Barrios de Luna (6 in Fig. 1). Again, the sequence comprises predominantly massive limestones unsuitable for palynological analysis. However, a number of thin muddy limestone intercalations were located in five discrete horizons in the sequence and sampled for palynological analysis.

In the coastal exposures of Asturias, the contact between the Moniello Fm and Naranco Fm was studied at El Tranquero (2 in Fig. 1). The lower part of the sequence consists of massive sandstones unsuitable for palynological investigation. However, a thin shale parting between two thick sandstone beds was sampled.

The contact between the Santa Lucía and Huergas fms was studied in two sections: Cabornera and near Aleje (4 and 5 in Fig. 1). The road cuts along the Cabornera to Buiza road and the main LE473 road branching from this reveals an excellent section exhibiting the contact between the Santa Lucía and Huergas fms (van Loevezijn and Raven, 2017). Two samples were collected from thin calcareous mudstones in the Santa Lucía Fm, five samples from the Cabornera Bed at the contact, and four samples from the basal shales of the Huergas Fm. At Aleje, the upper part of Member IV of the Santa Lucía Fm shows a transition with intercalations of massive limestone and siltstone before passing into siltstones of the Huergas Fm. Samples of the siltstone intercalations of Member IV were collected for palynological analysis.

Samples were palynologically processed at the University of Sheffield using standard HCl-HF palynological acid maceration. Samples were sieved using a 20 μm mesh, subjected to a heavy liquid separation using $ZnCl_2$, and further sieved using a 20 μm mesh. The residues are highly variable in thermal maturity depending on location of the section (see below and Appendix A), varying from Thermal Alteration Index 2+ to 4- (using the colour scheme published in Traverse, 2007). They were then oxidised using fresh Schultz solution for varying periods of time, until translucent, before being strew mounted onto glass coverslips and fixed to glass slides using epoxy resin. Slides were examined using



(caption on next page)

Plate V. Dispersed spores from the Huergas and Naranco fms of Northern Spain. Scale bar = 30 μm (1,2,3,6), =45 μm (4,5,7,8,9,10,11,12).
1. *Geminospora convoluta* (Sample 22CAB22P; Slide 1; E.F.no. G36).
2. *Geminospora svalbardiae* (Sample 22CAB22P; Slide 1; E.F.no. O34/4).
3. *Geminospora svalbardiae* (Sample 22CAB25A; Slide 1; E.F.no. M37/4).
4. *Geminospora svalbardiae* (Sample 22CAB22P; Slide 1; E.F.no. Y50).
5. *Samarisporites praetervisus* (Sample 22CAB22P; Slide 1; E.F.no. B41/4).
6. *Samarisporites praetervisus* (Sample 18SPAIN25A; Slide 1; E.F.no. S49).
7. *Grandispora velata* (Sample 22CAB22P; Slide 1; E.F.no. Y30).
8. *Grandispora douglastownensis* (Sample 22CAB22P; Slide 1; E.F.no. L30/4).
9. *Samarisporites praetervisus* (Sample 22CAB22P; Slide 1; E.F.no. O31/4).
10. *Apiculiretusispora brandtii* (Sample ETP01; Slide 1; E.F.no. V37).
11. *Apiculiretusispora arabiensis* (Sample ETP01; Slide 1; E.F.no. P49).
12. *Dibolisporites echinaceus* (Sample ETP01; Slide 1; E.F.no. T50/2).

standard light microscopy techniques and images captured using a Q Imaging MicroPublisher 3.3 RTV camera. All materials (rock, residues, slides) are housed in the collections of the Centre for Palynology of the University of Sheffield, UK. Figured specimens are located using England Finder Co-ordinates.

4. Results

The three samples from the type section of the Moniello Fm in coastal Asturias (1 in Fig. 1) included two barren samples and one that yielded palynomorphs. However, palynomorphs from the productive sample were too thermally mature (opaque and dark brown-black in colour) to usefully analyse.

Most of the ten samples collected from the type section of the Santa Lucía Fm (3 in Fig. 1) in the southern side of the Cantabrian Mountains were either barren or yielded only very rare, poorly preserved palynomorphs. However, two samples from the same calcareous mudstone horizon in Member III (samples 22SL13 and 22SL13–1) yielded palynomorphs that were moderately preserved and of low thermal maturity and were suitable for logging. These are both dominated by spores, with acritarchs and prasinophytes being rare and of low diversity, chitinozoans represented by only a few specimens, although scolecodonts are relatively common (see Tables 2–3 and Plates I–X). All five samples of the Santa Lucía Fm from roadcuts along the CL-626 (6 in Fig. 1) yielded very low quantities of organic residue that contained very rare coalified palynomorphs (opaque and black) unsuitable for detailed palynological analysis.

Samples from the road cuts along the Cabornera to Buiza road and adjacent main LE473 road (4 in Fig. 1) were very variable regarding both preservation and thermal maturity. One of the samples from the Santa Lucía Fm was barren whilst the other yielded a highly interesting assemblage of moderately preserved palynomorphs of moderate thermal maturity. The latter sample (18SPAIN27a) was logged and notable for the abundance of the spore *Emphanisporites annulatus*. Along with spores, the acritachs, prasinophytes, chitinozoans and scolecodonts are abundant and moderately diverse (Tables 2–3 and Plates I–X). All four samples from the Cabornera Bed yielded abundant palynomorphs, although these varied in preservation from good to poor and thermal maturity from low to moderate. Two of the samples were sufficiently preserved for detailed palynological analysis (22CAB16P + 0.25 and 22CAB16P + 0.40). These rich palynomorph assemblages yeilded abundant and diverse spores, acritachs, prasinophytes, chitinozoans and scolecodonts (Tables 2–3 and Plates I–X). Of the five samples collected from the basal Huergas Fm one was barren and the others yielded abundant and diverse spores that were moderately preserved and of low thermal maturity and suitable for logging (22CAB22P + 0.10, 18SPAIN29, 18SPAIN24, 18SPAIN25). All were dominated by spores with acritachs, prasinophytes, chitinozoans and scolecodonts rare (Tables 2–3 and Plates I–X).

From the Aleje section two samples (22ALE10P and 22ALE11P) from the upper part of Member IV of the Santa Lucía Fm (García-Alcade, 2014) yielded excellent assemblage of well preserved palynomorphs of low thermal maturity. The single sample (ETP01) obtained from the lower part of the Naranco Fm (correlated with the Cebolledo Mb) of the El-Tranquero section yielded an excellent assemblage of well preserved palynomorphs of low thermal maturity. All three were logged.

Table 1 lists all palynomorphs recovered and Tables 2–3 outlines their distribution in the studied samples.

5. Discussion

5.1. Biostratigraphy of the palynomorph assemblages

In terms of dispersed spore zonation two schemes have been developed for Laurussia (Richardson and McGregor, 1986; Streel et al., 1987) and two for Gondwana (Loboziak and Melo, 2002; Breuer and Steemans, 2013) (Fig. 5). Examination of the spore assemblages reported herein reveals that they have much more in common with those from northwestern Gondwana. The dispersed spore assemblages from Member III of the Santa Lucía Fm from the type section and from the lower part of the Santa Lucía Fm in the Cabornera section belong with the *annulatus-protea* Assemblage Zone of Breuer and Steemans (2013) that is of late Emsian age. This assemblage includes both of the nominal species of the zone and other characteristic species. In the Santa Lucía Fm type section Member III has yielded the late Emsian *Polygnathus patulus* Conodont Zone, although Ellwood et al. (2006) correlated the lower boundary of the Eifelian at 4.2 m below the top of Member III using

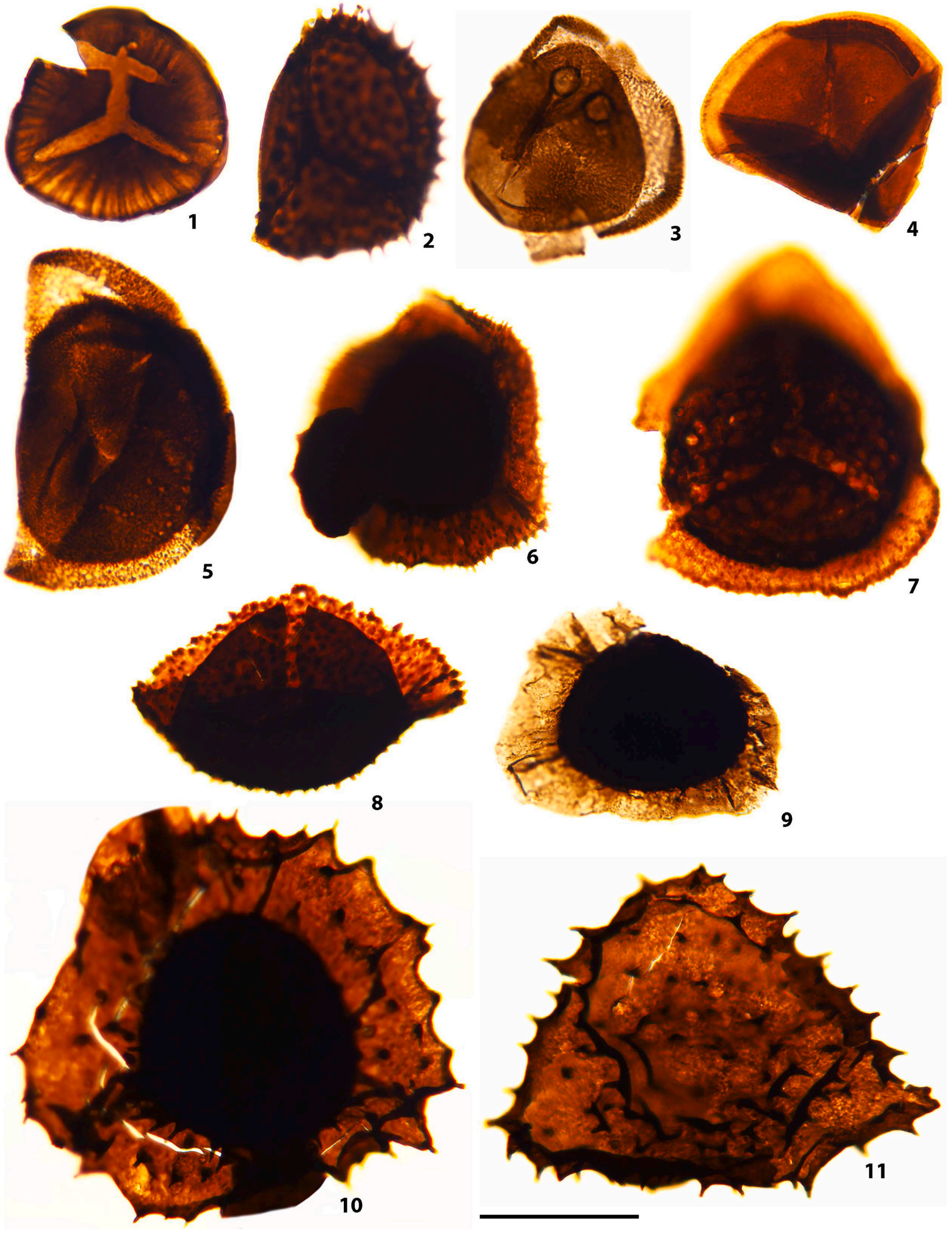


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Plate VI. Dispersed spores from the Naranco Fm of Northern Spain. Scale bar = 30 μm (1,2,3,4,5), =60 μm (6,7,8,9,10,11)..
1. *Emphanisporites rotatus* (Sample ETP01; Slide 1; E.F.no. M37/4).
2. *Dibolisporites tuberculatus* (Sample ETP01; Slide 1; E.F.no. U45/3).
3. *Rhabdosporites minutus* (Sample ETP01; Slide 1; E.F.no. B40/3).
4. *Geminospora svalbardiae* (Sample ETP01; Slide 1; E.F.no. G44/4).
5. *Rhabdosporites minutus* (Sample ETP01; Slide 1; E.F.no. E50/4).
6. *Grandispora velata* (Sample ETP01; Slide 1; E.F.no. F42).
7. Zonate spore with reticulum over the inner body (Sample ETP01; Slide 1; E.F.no. C32/2).
8. *Grandispora douglastownensis* (Sample ETP01; Slide 1; E.F.no. C36/1).
9. *Grandispora* sp. (Sample ETP01; Slide 1; E.F.no. M43/4).
10. *Ancyrospora nettersheimensis* (Sample ETP01; Slide 1; E.F.no. K33/3).
11. *Ancyrospora nettersheimensis* (Sample ETP01; Slide 1; E.F.no. K30/3).

magnetostratigraphy susceptibility.

The remainder of the assemblages from Member IV, the Cabornera Bed, the Cebolledo Mb and the basal Naranco/Huergas formations are younger and belong to the *svalbardiae-eximius* Assemblage Zone of Breuer and Steemans (2013). They contain one of the nominal species (*Geminospora svalbardiae*) whose First Appearance Datum is at the base of this zone in Northern Gondwana (Breuer and Steemans, 2013). Other characteristic species of this zone reported in Northern Spain include *Ancyrospora nettersheimensis* (previously referred to as *Grandispora argutus* Naumova, 1953 sensu Askew and Wellman, 2018 in Spanish studies), *Grandispora velata* and *Acinosporites acanthomammillatus*. Other taxa reported in the Northern Spain assemblage are entirely consistent with this designation according to taxon ranges provided by Breuer and Steemans (2013). The age of the *svalbardiae-eximius* Assemblage Zone is early Eifelian according to Breuer and Steemans (2013). This is in concordance with independent biostratigraphical data from conodonts and brachiopods that indicate an early Eifelian age for the strata under consideration.

Regarding chitinozoans, the biozonal scheme used for dating the assemblages was the global biozonation scheme developed by Paris et al. (2000). Significant chitinozoan ranges, where relevant, are also discussed in comparison to different regions of Gondwana. When correlated with the ages provided by the conodonts and the spores (late Emsian-early Eifelian), the studied assemblages are part of a “not yet defined” biozone of Paris et al. (2000). This interval does not show any important taxon ranges that start or end within it, except for the upper part of *Bursachitina riclonensis*, a taxon that was not observed in our samples.

The two productive samples from the type section of the Santa Lucía Fm provide only rare chitinozoans that are placed in open nomenclature. One specimen of *Angochitina devonica*, a wide-ranging taxon, was observed in one of the samples. However, a few poorly preserved specimens of *Angochitina* cf. *A. daemoni*, a taxon that is observed in the late Emsian of Western Gondwana (Grahn, 2005), were observed. This taxon potentially corroborates the conodonts and spore age for the Santa Lucía Fm, but realistically more evidence is needed to date the upper part of the Santa Lucía Fm based on chitinozoans.

The assemblages recovered from the younger Cabornera Bed contain a more diverse chitinozoan assemblage that includes *Angochitina daemoni* (sample 22CAB16P + 0.40). This taxon is recognised in the Eifelian of Western Gondwana (Grahn, 2005), including Brazil and Paraguay (Grahn et al., 2000). The assemblage from the Naranco Fm (ETP01) and the two samples from Member IV (22ALE10P and 22ALE11P) provided the most diverse assemblages. These include broad-ranging taxa (e.g. *Angochitina devonica* and *Hoegisphaera* cf. *H. gabra*), *Angochitina daemoni* and a typical late early Eifelian species in Western Gondwana: *Fungochitina pilosa* (Grahn, 2005). *Alpenachitina eisenacki*, the key species of the first Eifelian biozone of Paris et al. (2000), is not recorded herein. This suggests, as expected, that these strata are older than the Naranco and Huergas sections studied by Askew and Russell (2019), which start in the *A. eisenacki* Biozone. Common species to both studies include: *Ancyrochitina* cf. *A. taouratinensis*, *Angochitina devonica, A. capillata, Fugochitina pilosa*, *Hoegisphaera* cf. *H. glabra* and *Ramochitina* cf. *R. magnifica*. According to Paris et al. (2000), the range of *Ramochitina magnifica* extends to the early Eifelian in southwestern Gondwana. However, due to poor preservation we could not accurately measure our specimens, although they seem smaller than the overall size from the original description, as also noted by Askew and Russell (2019) in their Givetian specimens from the Huergas Fm.

The range of *Ancyrochitina taouratinensis* is reported to start in the late Givetian (Grahn, 2005). However, similar specimens were observed in this study in older rocks (basal Huergas Fm), indicating a possible earlier inception in the early Eifelian and continuing through out the Givetian in this region, as also observed in Askew and Russell (2019). Another important taxon is *Angochitina capillata* that has a worldwide distribution with a broad stratigraphical range. However, as mentioned by Camina et al. (2024) Middle Devonian records are scarce. Askew and Russell (2019) have records of specimens from the early Givetian Naranco, Huergas and Gustalapiedra fms. In this study we confirm the appearance of this species from the early Eifelian. *Angochitina calcarata* was reported by Diez and Cramer (1978) from the La Vid Group as having a range that extends to the early Emsian. A few specimens observed in this study are similar to *A. calcarata* suggesting its range may extend to the early Eifelian. More studies are needed to confirm this information.

In terms of acritarchs and prasinophytes there is a limited amount of

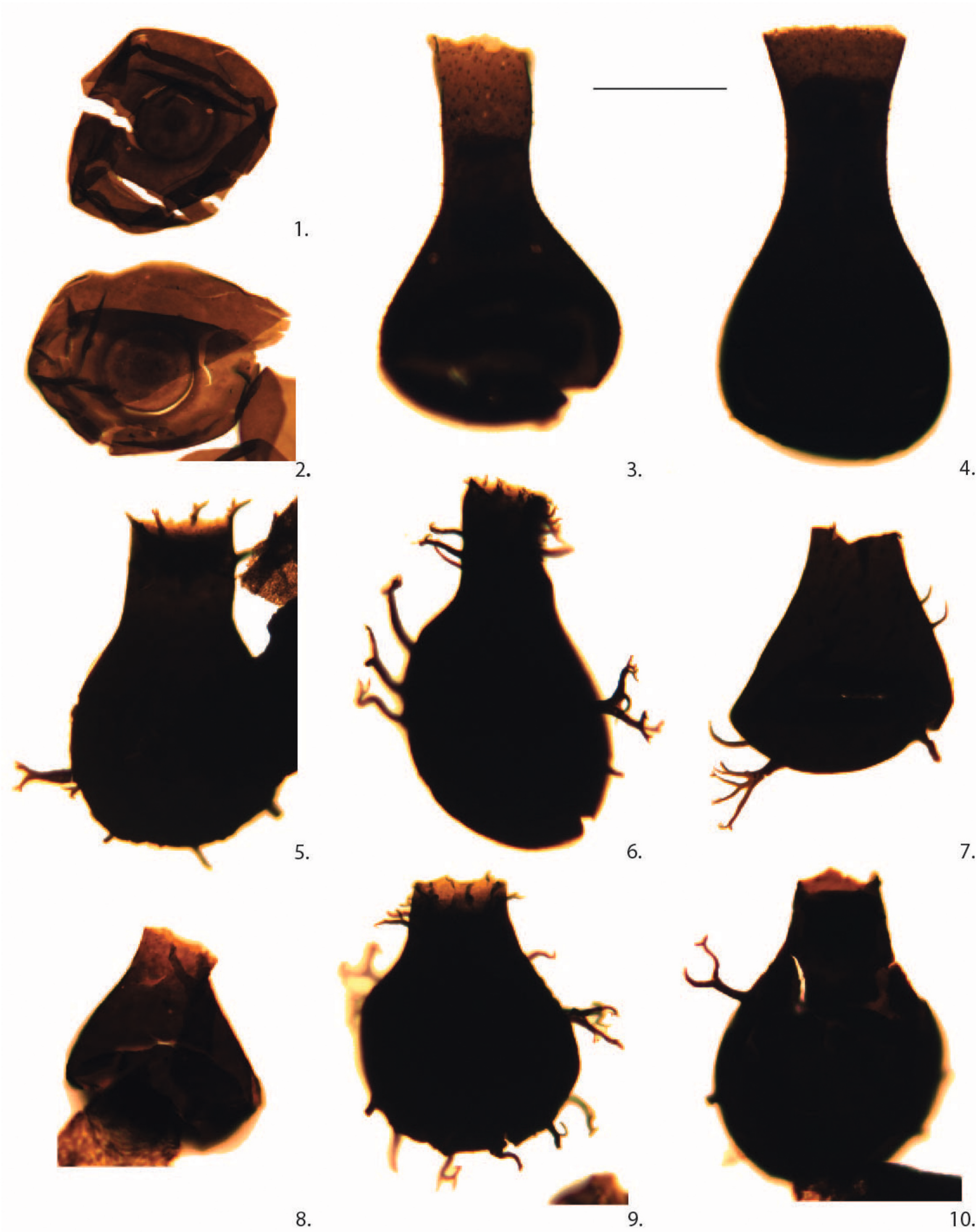

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Plate VII. Chitinozoans from the Santa Lucía and Naranco fms of Northern Spain. Scale bar = 50 μm.
1. *Hoegisphaera* cf. *H. glabra* (Sample 22ALE10P; Slide 1; E.F.no. Q32).
2. *Hoegisphaera* cf. *H. glabra* (Sample 22ALE11P; Slide 1; E.F.no. U30/4).
3. *Fungochitina pilosa* (Sample 22ALE10P; Slide 1; E.F.no. F45/3).
4. *Angochitina* cf. *A. daemoni* (Sample 22ALE10P; Slide 1; E.F.no. S48).
5. *Angochitina devonica* (Sample ETP01P; Slide 1; E.F.no. U44/2).
6. *Ramochitina* cf. *R. magnifica* (Sample ETP01P; Slide 1; E.F.no. J30/3).
7. *Ancyrochitina* cf. *A. ancyrea* (Sample ETP01P; Slide 1; E.F.no. K39/3).
8. *Saharochitina* sp. 1 (Sample 22CAB16P + 0.25 m; Slide 1; E.F.no. T28/4).
9. *Ramochitina* cf. *R. magnifica* (Sample ETP01P; Slide 1; E.F.no. S41/1).
10. *Angochitina devonica* (Sample 22SL13P; Slide 1; E.F.no. O45).

information on Lower Devonian forms making it challenging to discuss their age and distribution (Molyneux et al., 2014). However, there is slightly more information available for the Middle Devonian, as mentioned by Askew (2019). Given the limitations and considering the section's age as indicated by the conodonts and spore assemblages (late Emsian-early Eifelian), our analysis of taxon ranges relies primarilly on the works of Le Hérissé et al. (2000) and Molyneux et al. (2014).

Member III of the Santa Lucía Fm has a less diverse and less well-preserved assemblage compared to Member IV, the Cabornera Bed and the Cebolledo Mb. The assemblage mainly consists of long-ranging taxa in open nomenclature such as: *Cymatiosphaera* spp., *Leiosphaeridia* spp., *Multiplicisphaeridium ramusculosum*, and the *Veryhachium trispinosum* Group specimens (Le Hérissé et al., 2000; Molyneux et al., 2014). This does not provide sufficient evidence to confirm a late Emsian age.

Member IV and the Naranco/Huergas fms yielded a diverse and moderately to well-preserved assemblage, except for four samples from the Cabornera road section (18SPAIN29, 18SPAIN24, 22CAB22P + 0.1, 18SPAIN25A), which are almost barren of acritarchs. The assemblage includes long-ranging Early and Mid Devonian taxa (e.g. *Eisenackidium duplex, Diexallophasis remota, Polyedryxium pharaonis, Stellinium micropolygonale, Tyligmasoma alargada*) (Le Hérissé et al., 2000; Molyneux et al., 2014). However, the presence of *Muraticavea munifica*, whose range starts at the base of the Eifelian (Wicander and Playford, 2017), is concordant with the age provided by the conodonts and spores from Member IV. Nevertheless, other taxa extend their ranges above or below the Emsian/Eifelian Boundary, making it difficult to confirm the age based solely on acritarchs and prasinophytes. The acritarch *Exochoderma triangulata*, which according to Molyneux et al. (2014) has its range starting at the base of the Eifelian, is observed already from the top of Santa Lucía Fm (late Emsian age). *Florisphaeridium toyetae, Multiplicisphaeridium lindum,* and *Veryhachium trispininflatum* are taxa whose last occurrence is observed at the top of the Emsian, according to Molyneux et al. (2014). However, these taxa are also present in samples from the Member IV (this study), indicating that their range may be slightly extended into the lower Eifelian in this area. The prasinophyte *Cymatiosphaera carminae*, which is characteristic of the Emsian (La Vid Group) in this region (Cramer, 1964), appears to extend its range until the early Eifelian in Member IV. It was not reported from the middle and upper part of this formation by Askew (2019). The ranges of *Duvernaysphaera angelae, Eisenackidium appendiculum* and *Stellinium comptum* are recognised from the base of the Givetian onwards (Molyneux et al., 2014). However, they seem to have an extended older range in this region, occurring since the early Eifelian, with *D. angelae* and *S. comptum* also being present in the younger levels of the Huergas Fm (Askew, 2019). Another peculiarity relates to the presence of *Tyligmassoma alargada*, a long-ranging Middle Devonian acritarch, which is observed in Member IV and the Cabornera Bed. However, it is not present in the upper part of the Huergas Fm within the Givetian (Askew, 2019).

5.2. Palaeophytographical implications

The Armorican Terrane Assemblage (ATA) was situated at approximately 30°S during the Early to Mid Devonian transition (Fig. 6). It is clear that by this time terrestrial vegetation was diverse on landmasses at all latitudes, including islands (Xu et al., 2014) and by now the equator (Wellman et al., 2022). However, previous work has reported that Devonian land plant spore assemblages from Northern Spain exhibit a degree of endemism, although they clearly have closer affinities with Northern Gondwana than Laurussia in both the Early Devonian (Wellman et al., 2023) and the Mid Devonian (Askew and Wellman, 2020). The spore assemblages described herein do indeed seem to have more in common with the northwestern Gondwanan material described by Breuer and Steemans (2013).

In terms of composition of the dispersed spore assemblages the presence of the highly distinctive, but rarely reported spores *Lophotriletes devonicus* and *Diatomozonotriletes franklinii* is interesting. These have previously been reported from Laurussia (McGregor and Camfield, 1982) and Gondwana (Breuer and Steemans, 2013). Also a number of spore taxa of similar morphology were described from the Emsian Eastwood Fm of the Adavale Basin in Australia by Hashemi and Playford

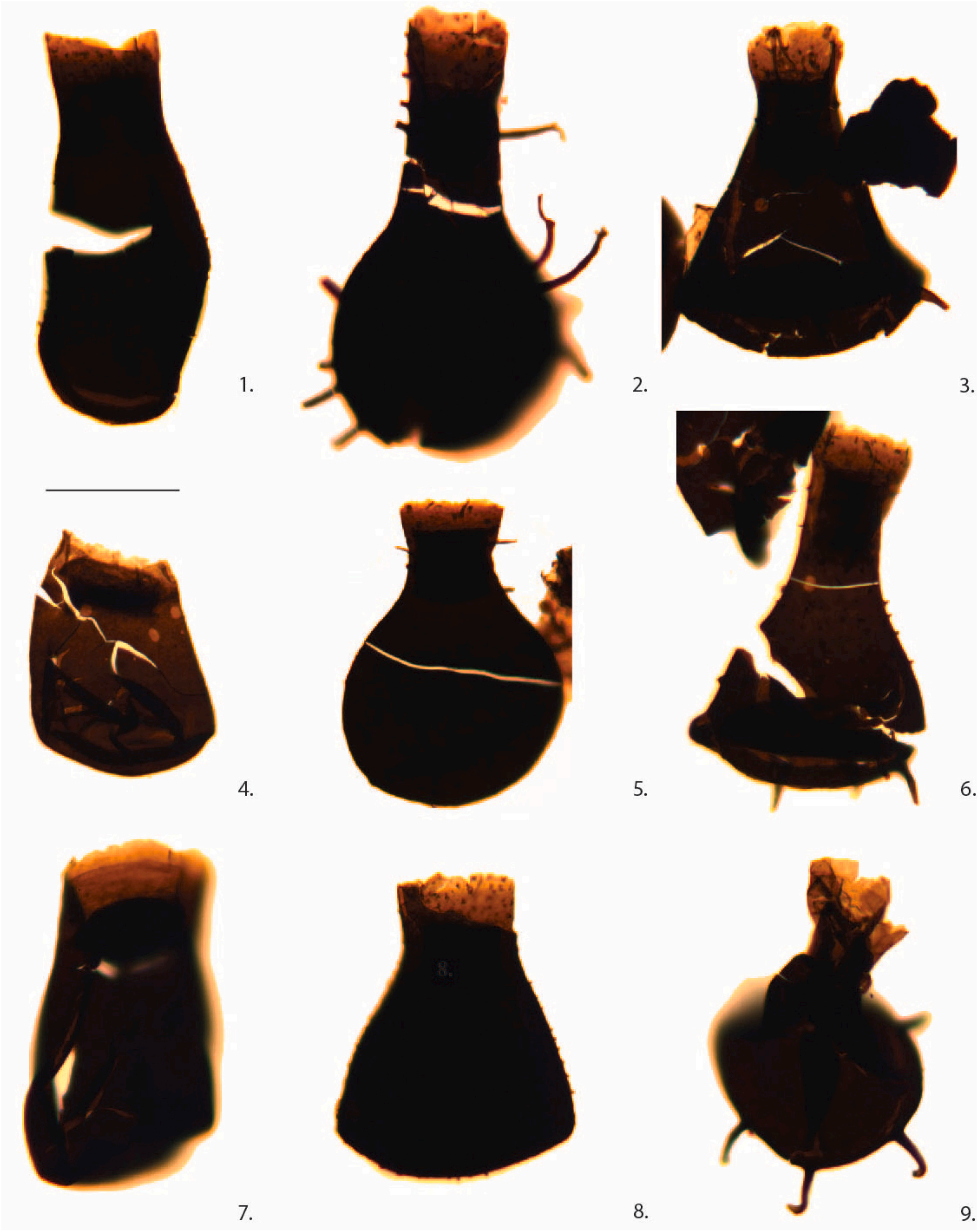

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Plate VIII. Chitinozoans from the Santa Lucía, Naranco and Huergas fms of Northern Spain. Scale bar = 50 μm.
1.?*Belochitina* sp. (Sample 22ALE10P; Slide 1; E.F.no. C31/2).
2. *Angochitina devonica* (Sample 18SPAIN27; Slide B; E.F.no. R29/4).
3. *Ancyrochitina* cf. *A. taouratinensis* (Sample 22ALE10P; Slide 1; E.F.no. P34/3).
4.?*Bulbochitina* sp. (Sample 22ALE10P; Slide 1; E.F.no. W39/4).
5. *Angochitina* cf. *A. capillata* (Sample ETP01P; Slide 1; E.F.no. K35).
6. *Ancyrochitina* cf. *A. taouratinensis* (Sample 22ALE10P; Slide 1; E.F.no. P34/2).
7. *Angochitina* cf. *A. calcarata* (Sample 22ALE11P; Slide 1; E.F.no. M35/1).
8. *Fungochitina* sp. 2 (Sample 22ALE10P; Slide 1; E.F.no. R32/2).
9. *Ancyrochitina fragilis* (Sample 22ALE10P; Slide 1; E.F.no. W36).

(2005).

Regarding the chitinozoans, the poorly diversified and preserved assemblage provides limited insight regarding palaeophytogeography. *Ancyrochitina capillata, Fungochitina pilosa*, and *Hoegisphaera* cf., *H. glabra*, are recognised as cosmopolitan species (e.g. Askew, 2018). However, based on the presence of *Ancyrochitina* cf. *A. taouratinensis*, *Angochitina daemoni* and *Ramochitina* cf. *R. magnifica*, we can see a correlation with Western Gondwana chitinozoan assemblages (Paris et al., 2000; Grahn, 2005).

According to Molyneux et al. (2014), there was a reasonably high degree of cosmopolitanism within the acritarch and prasinophyte assemblages of mid to high palaeolatitudes during the Mid Devonian, with many species in common between Laurussia and Gondwana. These similarities were related to the closing of the Rheic Ocean that brought both continental masses into closer proximity (e.g. Molyneux et al., 2014). This idea seems to be corroborated by several of the taxa present in our assemblages (Huergas Fm), which are observed in the margins of Laurussia (North America) and Gondwana (South America and Ghana): *Polyedryxium pharaonis, Pyloferites escobaides, Stellinium micropolygonale* and *Tyligmassoma alargada* (e.g. Molyneux et al., 2014; García-Muro and Rubinstein, 2022). These taxa appear together with other known cosmopolitan species (*Diexallophasis remota, Veryhachium europaeum* and the *V. lairdii* and *V. trispinosum* groups) (e.g. Molyneux et al., 2014), with the only endemic species observed in these assemblages being *Cymatiosphaera carminae*. Increased endemism among acritarchs and prasinophytes was reported from younger beds in the Naranco/Huergas fms by Askew (2019).

5.3. *Palaeoenvironments, biotic change and implications for the Choteč Event*

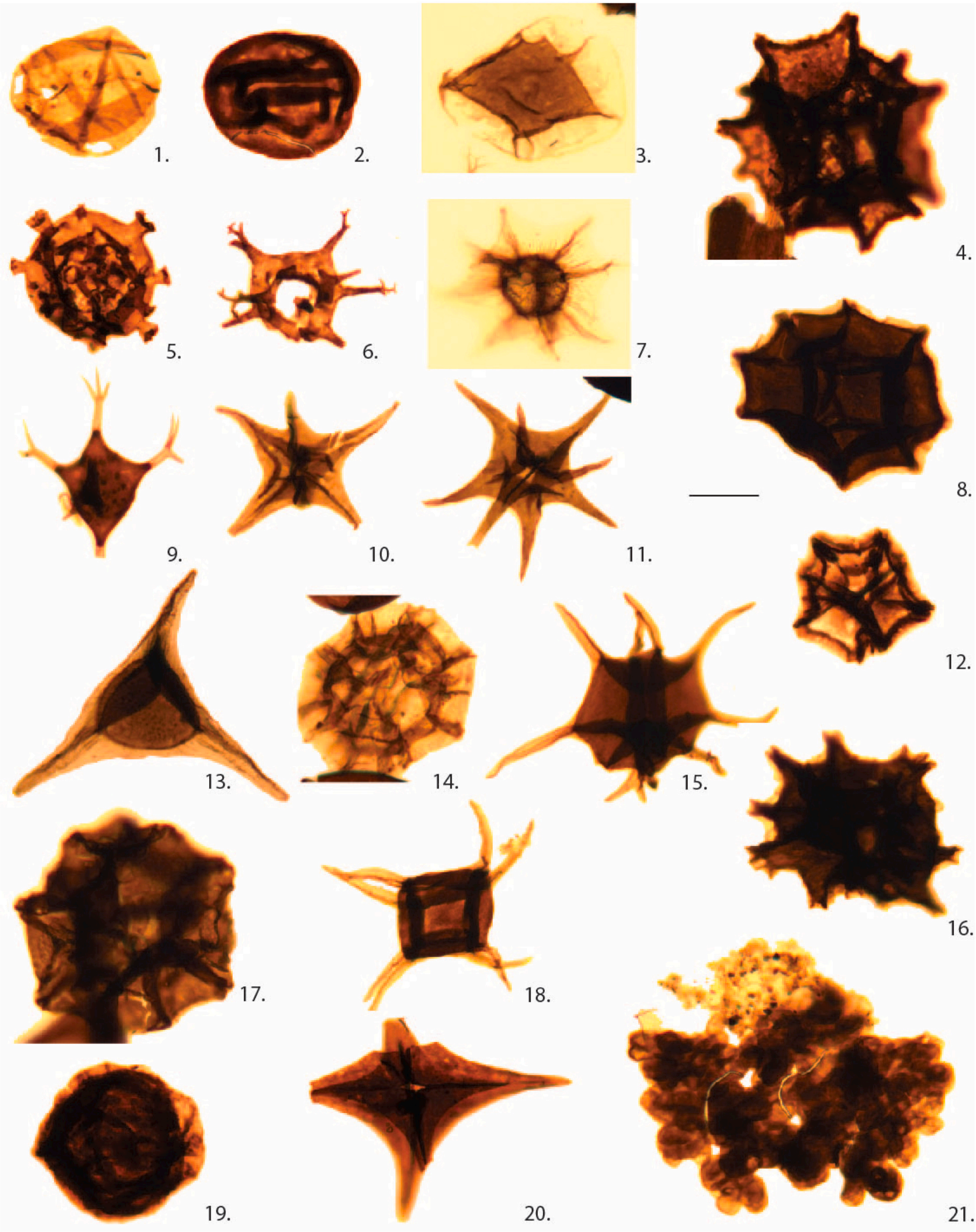
The transition from the limestones of the Moniello/Santa Lucía fms into the siliciclastics of the Naranco/Huergas fms varies in the different sections studied. The change from the Moniello to Naranco fms is abrupt at the base of the Cebolledo Mb (traditional lower part of the Naranco Fm) where limestones are replaced by thick sandstones. However, it may be transitional as at the Aleje section (limestone/shale intercalations of Member IV). In both settings, marine elements (acritarchs, prasinophytes and chitinozoans) show a diversity increase in the *Polygnathus partitus* Zone. However, this change may be artificially inflated because the assemblages from Member III are from carbonate facies unsuitable for palynomorph preservation and the palynological preparations are of low organic content and the palynomorphs only moderately preserved.

At the Cabornera Bed the diversity of both chitinozoans and acritarchs/prasinophytes decreases moderately. However, dispersed spore diversity increases slightly. On entering the classic shales of the basal Huergas Fm the diversity of marine palynomorphs falls away dramatically. However, land plant spore diversity remains relatively stable.

The Choteč Event (392.5–393.1 Ma) occurs near the end of the *Polygnathus partitus* Conodont Zone (392.5–394.1 Ma) in the earliest Eifelian according to Becker et al. (2020), although it seems the episode extends into beds of the *Polygnathus costatus* Zone in the Bohemian Basin (Vodrážková et al., 2013). There is no obvious change in palynomorph biota related to the Choteč Event in Northern Spain. However, the increase in abundance and diversity of continental amd marine palynomorphs is coeval with the loss of the reefal ecosystem in the lowermost beds of the *P. partitus* Zone and its replacement by an open marine community with brachiopod and echinoderms of the Faunal Interval 17 (‘OCA’ fauna in García-Alcalde, 2017).

The increase in the diversity of marine palynomorphs during the *P. partitus* Zone is associated with sea-level increase and the arrival of siliclastic supply (and presumably nutrients) near coastal areas (Naranco Fm) that destroyed the carbonate reefal system. The Cabornera Bed is interpreted as a maximum transgressive horizon in the *P. costatus* Zone (van Loevezijn and Raven, 2017). Note that a pelagic component (dacryoconarids and cephalopods) occurs in the Huergas Fm. Perhaps a change to a warmer and wetter climate promoted weathering/erosion and terrigenous runoff from the Armorican Terrane Assemblage land mass, causing diversity increases of phytoplankton (acritarchs and prasinophytes) and zooplankton (chitinozoans).

The oxygen-depleted episode described in the basal part of the Cabornera Bed (Van Loevezijn and Raven, 2017) appears to have been of insufficient magnitude to record any change of diversity of the biota, either terrestrial or marine, related to the Choteč Event in Northern Spain. Nevertheless, in the basal beds of the Huergas Fm there is a strong decrease in acritarch and prasinophyte diversity (with scarce occurrences of long ranging-taxa). The decline in marine plankton may indicate a loss of nutrient supply to the ocean. However, terrestrial spores show a similar diversity to the pre-Choteč Event indicating little change in the terrestrial vegetation.



(caption on next page)

Plate IX. Acritarchs and prasinophytes from the Santa Lucía and Naranco fms of Northern Spain. Scale bar = 20 μm.
1. *Leiosphaeridia* sp. (Sample ETP01P; Slide 1; E.F.no. U30/1).
2. *Tasmanites* sp. (Sample 18SPAIN24; Slide 1; E.F.no. V30/2).
3. *Duvernaysphaera angelae* sp. (Sample 22ALE10P; Slide 1; E.F.no. H37/2).
4. *Polyedryxium* cf. *P. robustum* (Sample 22CAB16P + 0.25 m; Slide 1; E.F.no. F29).
5. *Visbysphaera dilatispinosa* (Sample 22CAB16P + 0.25 m; Slide 2; E.F.no. F42/2).
6. *Pyloferites escobaides* (Sample 22CAB16P + 0.40 m; Slide 1; E.F.no. M44/1).
7. *Cymatiosphaera carminae* (Sample 22ALE10P; Slide 1; E.F.no. N35).
8. *Polyedryxium decorum* (Sample 22ALE11P; Slide 1; E.F.no. H30/3).
9. *Ozotobrachion* cf. *O. furcillatus* (Sample 22SL13/1P; Slide 1; E.F.no. U30).
10. *Stellinium comptum* (Sample 22ALE10P; Slide 1; E.F.no. M36/4).
11. *Stellinium micropolygonale* (Sample 22ALE10P; Slide 1; E.F.no. P34).
12. *Stellinium?rabians* (Sample 22CAB16P + 0.40 m; Slide 1; E.F.no. P36/4).
13. *Polyedryxium fragosolum* (Sample 22ALE10P; Slide 1; E.F.no. D32/4).
14. *Cymatiosphaera pavimenta* (Sample 22ALE11P; Slide 1; E.F.no. R36/3).
15. *Eisenackidium duplex* (Sample ETP01P; Slide 1; E.F.no. N29/4).
16. *Polyedryxium helenaster* (Sample ETP01P; Slide 1; E.F.no. E45/2).
17. *Muraticavea munifica* (Sample 22ALE11P; Slide 1; E.F.no. K33/2).
18. *Eisenackidium pharaone* (Sample ETP01P; Slide 1; E.F.no. P29).
19. *Divietipellis ventricosa* (Sample 22CAB16P + 0.25 m; Slide 1; E.F.no. L27).
20. *Stellinium pseudopharaonis* (Sample 22CAB16P + 0.25 m; Slide 1; E.F.no. R25/2).
21. *Botryococcus* sp. (Sample ETP01P; Slide 1; E.F.no. Q34/1).

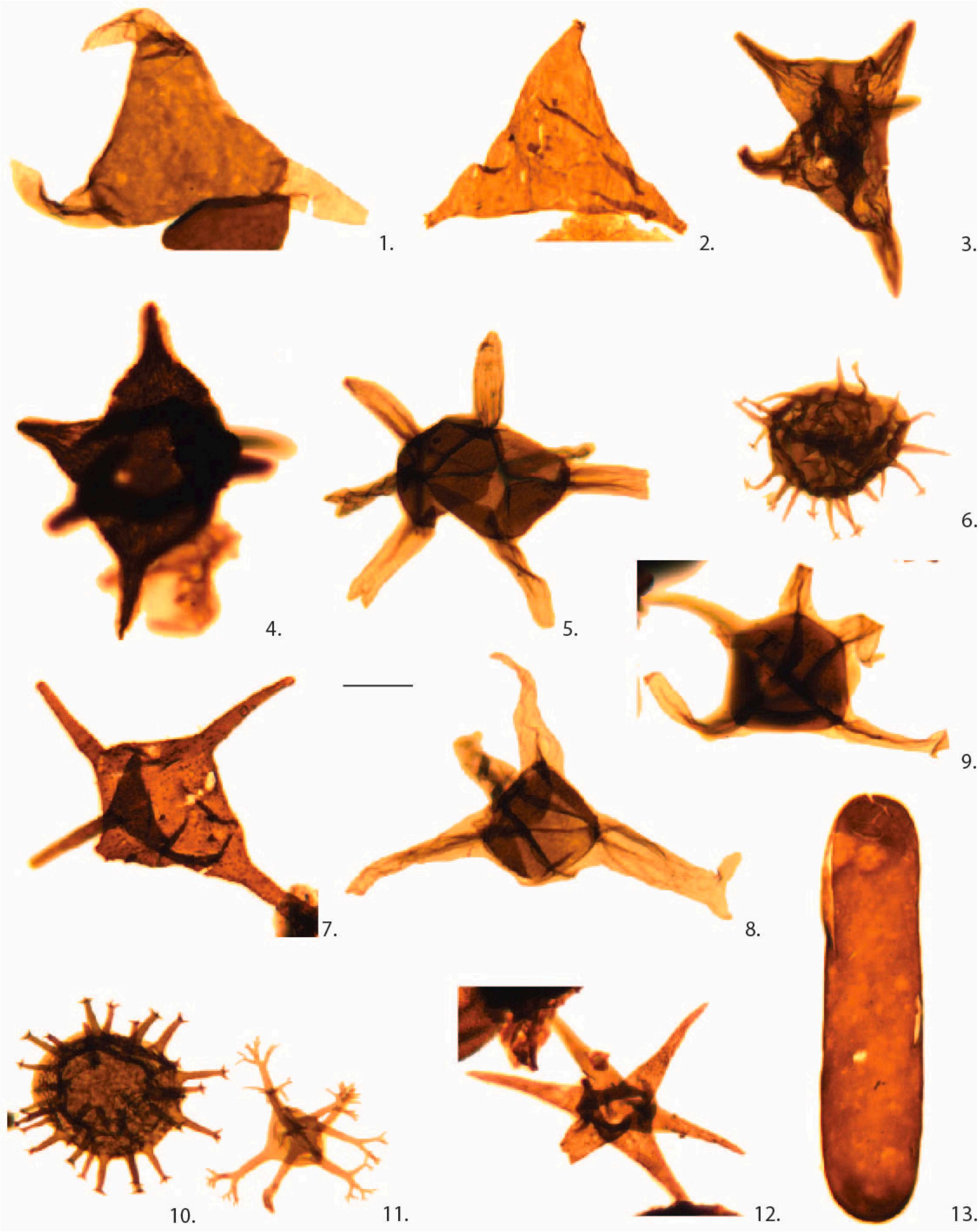
The increase of diversity, particularly of the marine plankton, from the Cantabrian Mountains in the earliest Eifelian (*P. partitus* Zone) seems to be concordant with the Choteč Event as described by Brocke et al. (2016) in the Nedrow Mb (Appalachian Basin, USA). Here it is characterised by abundant prasinophyceans with the acritarch *Hoegisphaera* cf. *H. glabra*, possibly fungi, and an immigration of dacryoconarid species. It ended in two anoxic horizons, located near the culmination of a transgression in the basal *P. costatus Zone*. This is probably equivalent to the Cabornera Bed in Spain. This sea-level maximum was equated with the Basal Choteč Event, where an ecological epibole of prasinophycean algae occurs in the Bohemian Basin (Brocke et al., 2016). Above, the planktonic biota shows a lower diversity in both basins as is observed in the Spanish Huergas Fm.

6. Conclusions

- Biostratigraphical evidence (including conodonts) suggests the Emsian-Eifelian boundary occurs in the uppermost part of the Santa Lucía Fm (close to the boundary of Members III/IV). Below this boundary dispersed spore assemblages belong to the *annulatus-protea* Spore Zone and above the boundary they belong to the *svalbardiae-eximius* Spore Zone.
- The early Eifelian seems to correspond in the Cantabrian Mountains to increased rainfall leading to an influx of terrigenous sediments to the ocean that shut down limestone deposition and reef communities. The increased nutrient input to the ocean at this warmer and wetter time may have led to marine plankton biodiversity increase (possibly associated with algal blooms) during the *P. partitus* Zone. On land, vegetation biodiversity increased with the wetter climate.
- The Cabornera Bed, which has been equated with the Choteč Event, occurs at the maximum transgressive surface. It shows a slight increase in terrestrial spore diversity, but a small decrease in marine phytoplankton and zooplankton diversity. However, biodiversity changes are not noticeable in associated low-oxygen horizons of the Cabornera Bed.
- Marine palynomorphs (acritarchs, prasinophycean cysts and chitinozoans) decreased dramatically in diversity in the basal beds of the Huergas Fm, possibly in relation to the early Eifelian warming trend or global changes on ocean circulation. However, land plant spore diversity remains relatively stable.

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.



(caption on next page)

Plate X. Acritarchs and prasinophytes from the Santa Lucía and Naranco fms of Northern Spain. Scale bar = 20 μm.
1. *Tyligmassoma alargada* (Sample 22ALE10P; Slide 1; E.F.no. F36).
2.?*Florisphaeridium toyetae* (Sample ETP01P; Slide 1; E.F.no. R38/1).
3. cf. *Estiastra* sp. (Sample 22ALE11P; Slide 1; E.F.no. O45/3).
4.?*Costatilobus aremoricanus* (Sample 22CAB16P + 0.25 m; Slide 1; E.F.no. O34).
5. *Eisenackidium appendiculum* (Sample 22ALE11P; Slide 1; E.F.no. O31).
6. *Ammonidium cornuatum* (Sample 22ALE11P; Slide 1; E.F.no. U29).
7. *Exochoderma arca* (Sample 22SL13/1P; Slide 1; E.F.no. L29).
8. *Eisenackidium colle* (Sample 22ALE10P; Slide 1; E.F.no. G32).
9. *Eisenackidium colle* (Sample 22ALE11P; Slide 1; E.F.no. Q37/4).
10. *Acriora* cf. *A. petala* (Sample 22ALE10P; Slide 1; E.F.no. H35/1).
11. *Multiplicisphaeridium ramusculosum* (Sample 22ALE10P; Slide 1; E.F.no. H35/1).
12. *Goniosphaeridium*?*raczii* (Sample 22CAB16P + 0.40 m; Slide 1; E.F.no. P28/2).
13. *Navifusa bacilla* (Sample 22CAB16P + 0.40 m; Slide 1; E.F.no. C35/4).

Table 1
List of all palynormorphs recovered in this study.

Spores
Acinosporites acanthomammillatus Richardson, 1965 [I, 13; III, 1]
Acinosporites lindlarensis Riegel, 1968 [I, 12; IV, 11]
Ambitisporites spp. [II, 7; IV, 9]
Ancyrospora nettersheimensis Riegel 1973 [I, 17; III, 11; VI, 10–11]
Apiculatasporites perpusillus (Naumova) McGregor, 1973 [IV, 4]
Apiculatisporis elegans McGregor, 1960 [IV, 5]
Apiculiretusispora arabiensis Al-Ghazi, 2009 [II, 5; IV, 7; V, 11]
Apiculiretusispora brandtii Streel, 1964 [I, 1; V, 10]
Apiculiretusispora plicata (Allen) Streel, 1967 [I, 2; II, 2; IV, 3; IV, 8]
Apiculiretusispora spp. [IV, 6]
Archaeozonotriletes chulus (Cramer) Richardson and Lister, 1969
Brochotriletes hudsonii McGregor and Camfield, 1976 [IV, 12]
Camarozonotriletes sextantii McGregor and Camfield, 1976 [II, 14]
Cymbosporites senex McGregor and Camfield, 1976 [II, 10]
Cymbosporites spp. [IV, 10]
Devonomonoletes sp. [IV, 17]
Diatomozonotriletes franklinii McGregor and Camfield, 1982 [II, 16]
Dibolisporites echinaceus (Eisenack) Richardson, 1965 [I, 3; II, 4; V, 12]
Dibolisporites eifeliensis (Lanninger) McGregor, 1973 [II, 3]
Dibolisporites tuberculatus Breuer and Steemans, 2013 [I, 4; VI, 2]
Dictyotriletes hemeri Breuer and Steemans, 2013 [II, 6]
Emphanisporites annulatus McGregor, 1961 [I, 9]
Emphanisporites mcgregorii Cramer, 1966 [II, 9]
Emphanisporites rotatus McGregor emend. McGregor, 1973 [I, 8; II, 8; IV, 13; VI, 1]
Geminospora convoluta Breuer and Steemans, 2013 [I, 15; V, 1]
Geminospora svalbardiae (Vigran) Allen, 1965 [I, 14; III, 2; III, 3; V, 2–4; VI, 4]
Grandispora douglastownensis McGregor, 1973 [III, 9; V, 8; VI, 8]
Grandispora protea (Naumova) Moreau-Benoit, 1980 [I, 11]
Grandispora velata (Richardson) McGregor [V, 7; VI, 6]
Grandispora sp. 1 [I, 16]
Granulatisporites spp.
Latosporites sp. [IV, 18]
Lophotriletes devonicus (Naumova ex Chibrikova) McGregor and Camfield, 1982 [II, 12–13,15; IV, 15–16]
Retusotriletes triangulatus (Streel) Streel, 1967 [II, 1; IV, 2]
Retusotriletes spp. [I, 10; IV, 1]
Rhabdosporites minutus Tiwari and Schaarschmidt, 1975 [VI, 3,5]
Samarisporites praetervisus (Naumova) Allen, 1965 [I, 18; III, 4–6; V, 5–6,9]
Verrucosisporites spp. [II, 11; IV, 14]
Zonotriletes armillatus Breuer et al., 2007 [III, 7–8]

ACRITARCHS
Acriora cf. *A. petala* Wicander, 1974 [X, 10]
Ammonidium cornuatum Loeblich and Wicander, 1976 [X, 6]
Ammonidium sp. A sensu Wicander and Playford, 2017b
?*Ammonidium* sp.

(*continued on next page*)

Table 1 (*continued*)

Comasphaeridium?hirsutum Johnson, 1985
?*Costatilobus aremoricanus* Deunff, 1980 [X, 4]
Cymbosphaeridium cf. *C. pilar* (Cramer) Lister, 1970
Diexallophasis cf. *D. denticulata* (Stockmans & Willière) Loeblich, 1970
Diexallophasis remota (Deunff) Playford, 1977
Diexallophasis sp. 1
Diexallophasis spp.
Divietipellis ventricosa Wicander, 1974 IX, 19]
Eisenackidium appendiculum Wicander and Wood, 1981 [X, 5]
Eisenackidium colle Cramer and Diez, 1976 [X, 8,9]
Eisenackidium duplex (Cramer) Eisenack et al., 1973 [IX, 15]
Eisenackidium spp.
Ephelopalla cf. *E. elongata* Wicander, 1974
cf. *Estiastra* sp.[X, 3]
Exochoderma arca Wicander and Wood, 1981 [X, 7]
Exochoderma triangulata Wicander and Wood, 1981
cf. *Exochoderma* sp.
Exochoderma spp.
?*Florisphaeridium toyetae* (Cramer) Cramer and Diez, 1976 [X, 2]
Goniosphaeridium?raczii (Cramer) Eisenack et al., 1973 [X, 12]
Goniosphaeridium sp. 1
Goniosphaeridium sp. 2
Gorgonisphaeridium cf. *G. granatum* Playford, 1977
Gorgonisphaeridium sp. 1
Gorgonisphaeridium spp.
cf. *Hapsidopalla* sp.
Micrhystridium stellatum (Deflandre) Deflandre, 1945
Micrhystridium spp.
Multiplicisphaeridium lindum Cramer and Diez, 1976
Multiplicisphaeridium paraguaferum (Cramer) Lister, 1970
Multiplicisphaeridium?paraguaferum (Cramer) Lister, 1970
Multiplicisphaeridium ramusculosum (Deflandre) Lister, 1970 [X, 11]
Multiplicisphaeridium sp. 1
Multiplicisphaeridium spp.
Navifusa bacilla (Deunff) Playford, 1977 [X, 13]
Navifusa multistriata (Brito) Eisenack et al., 1979
?*Oppilatala* sp.
Ozotobrachion cf. *O. furcillatus* (Deunff) Playford, 1977 [IX, 9]
?*Ozotobrachion* sp.
Pyloferites escobaides (Cramer) Daners et al. emend. García-Muro and Rubinstein, 2022 [IX, 6]
Solisphaeridium sp. 1
Tyligmasoma alargada (Cramer) Playford, 1977 [X, 1]
Veryhachium europaeum Stockmans and Williere, 1960
Veryhachium lairdii Group Deflandre ex Loeblich, 1970
Veryhachium trispininflatum Cramer, 1964
Veryhachium trispinosum Group (Eisenack) Stockmans and Williere, 1962
Veryhachium spp.
cf. *Villosacapsula tetraedron* (Deunff ex Deunff) Deunff, 1980
Visbysphaera dilatispinosa (Downie) emend. Lister, 1970 [IX, 5]

PRASINOPHYTES
Botryococcus sp. [IX, 21]
Cymatiosphaera carminae Cramer, 1964 [IX, 7]
Cymatiosphaera cornifera Deunff, 1955

(*continued on next page*)

Table 1 (*continued*)

Cymatiosphaera cuba Deunff ex Deunff, 1961
Cymatiosphaera pavimenta (Deflandre) Deflandre, 1954 [IX, 14]
Cymatiosphaera perimembrana Staplin, 1961
Cymatiosphaera winderi (Deunff) Playford, 1977
Cymatiosphaera sp. 1
Cymatiosphaera spp.
Dictiotydium cohora Wicander and Wood, 1981
Dictyotidium sp.
Dictiotydium spp.
Duvernaysphaera angelae Deunff, 1964 [IX, 3]
Leiosphaeridia sp. 1
Leiosphaeridia spp. [IX,1]
Lophosphaeridium spp.
Muraticavea munifica Wicander and Wood, 1981 [IX, 17]
Polyedryxium cf. *P. accuratum* sensu Askew, 2018
Polyedryxium bathyaster Deunff, 1961
Polyedryxium carnatum Playford, 1977
Polyedryxium decorum Deunff, 1955 [IX, 8]
Polyedryxium cf. *P. decorum* Deunff, 1955
Polyedryxium embudum Cramer, 1964
Polyedryxium fragosolum Playford, 1977 [IX, 13]
Polyedryxium helenaster Cramer, 1964 [IX, 16]
Polyedryxium pharaone Deunff ex Deunff, 1961 [IX, 18]
Polyedryxium cf. *P. robustum* sensu Askew, 2018 [IX,4]
Polyedryxium *'talum'* Deunff, 1971
Polyedryxium sp. A, sensu Askew, 2018
Polyedryxium sp. C sensu Askew, 2018
Polyedryxium spp.
Pterospermella sp. 1
Pterospermella sp. 2
Pterospermella spp.
Stellinium comptum Wicander and Loeblich Jr., 1977 [IX, 10]
Stellinium micropolygonale (Stockmans & Willière) Playford, 1977 [IX, 11]
Stellinium cf. *S. micropolygonale* (Stockmans and Willière) Playford, 1977
Stellinium pseudopharaone (Stockmans & Willière) Eisenack et al., 1976 [IX, 20]
Stellinium?rabians (Cramer) Eisenack et al., 1976 [IX, 12]

(*continued on next page*)

Table 1 (*continued*)

Stellinium spp.
Tasmanites spp. [IX, 2]
CHITINOZOANS
Ancyrochitina cf. *A. ancyrea* (Eisenack) Eisenack, 1955 [VII, 7]
Ancyrochitina fragilis Eisenack, 1955 [VIII, 9]
Ancyrochitina cf. *A. taouratinensis* Boumendjel, 1985 [VIII, 3,6]
Ancyrochitina sp. 1
?*Ancyrochitina* sp. 1
?*Ancyrochitina* sp. 2
?*Ancyrochitina* sp. 3
Angochitina cf. *A. calcarata* Legault, 1973 [VIII, 7]
Angochitina cf. *A. capillata* Eisenack, 1937 [VIII, 5]
Angochitina daemoni Grahn, 2000 [VII, 4]
Angochitina cf. *A. daemoni* Grahn, 2000 [VII, 4]
Angochitina devonica Eisenack, 1955 [VII, 5,10]
Angochitina cf. *A. devonica* Eisenack, 1955 [VIII, 2]
Angochitina capillata Eisenack, 1937
?*Angochitina* sp.
Angochitina spp.
?*Belonechitina* sp. [VIII, 1]
?*Bulbochitina* sp. [VIII, 4]
?*Bursachitina* sp.
Fungochitina pilosa Collinson and Scott, 1958 [VII, 3]
Fungochitina sp. 1
Fungochitina sp. 2 [VIII, 8]
?*Fungochitina* sp.
Hoegisphaera cf. *H. glabra* Staplin, 1961 [VII, 1,2]
Lagenochitinidae
Ramochitina cf. *R. magnifica* Lange, 1967 [VII, 6,9]
?*Ramochitina* sp.
Saharochitina sp. 1 [VII, 8]

Table 2

Distribution of terrestrial spores in the logged samples. The taxon counts include raw counts and in parentheses those including range through taxa.

Locality	(3) Santa Lucía		(4) Cabornera	(5) Aleje	(1) El Tranquero	(4) Cabornera					
Sample	22SL13/1	22SL13–1/1	18SPAIN27A	22ALE01 & 02	ETP01/1	22CAB16P + 0.25	22CAB16P + 0.40	18SPAIN29	18SPAIN24	22CAB22 + 0.10	18SPAIN25A
Formation	Santa Lucía Fm				Naranco Fm	Santa Lucía Fm		Huergas Fm			
Member/Bed	Mb III	Mb III	Mb III	Mb IV		Cabornera Bed	Cabornera Bed				
TAXA											
Ambitisporites spp.	X	X	X	X	X	X	X	X	X	X	X
Apiculiretusispora brandtii	X	X	X	X	X	O	X	O	O	X	X
Apiculiretusispora plicata	X	X	X	X	X	X	X	X	X	X	X
Apiculiretusispora spp.	X	X	X	X	X	X	X	X	X	X	X
Dibolisporites echinaceus	X	X	X	X	X	O	X	X	X	O	X
Grandispora protea	X	X	X								
Grandispora sp. 1	X										
Retusotriletes spp.	X	X	X	X	X	X	X	X	X	X	X
Samarisporites praetervisus	X	O	O	O	O	X	X	O	O	X	X
Acinosporites lindlarensis		X	X	X	O	X	X	O	X		
Archaeozonotriletes chulus		X									
Emphanisporites annulatus		X	X	X	O	O	X				
Emphanisporites rotatus		X	X	X	X	X	X	X	X	X	X
Ancyrospora nettersheimenesis			?	X	X	X	X	O	O	X	X
Acinosporites acanthomamillatus			X	O	O	X					
Dibolisporites tuburculatus			X	X	X	O	X	O	O	X	
Geminospora convoluta			X	O	O	X	X				
Brochotriletes hudsonii				X	X	O	O	O	O	X	
Diatomozonotriletes franklinii				X	O	O	X				
Geminospora svalbardiae				X	X	X	X	X		X	X
Grandispora douglastownensis				X	X	X	X	O	O	X	
Grandispora velata				X	X	O	O	O	O	X	
Rhabdosporites minutus				X	X	O	X				
Apiculiretusispora arabiensis					X	X	O	X			
Dibolisporites eifeliensis					X	X	O	O	O	X	
Camarozonotriletes sextantii						X					
Cymbosporites senex						X					
Dictyotriletes hemeri						X					
Emphanisporites mcgregorii						X	X	O	O	X	
Lophotriletes devonicus						X	X	O	X		
Zonotriletes armillatus						X					
Apiculatasporites perpusillus							X				
Granulatisporites spp.							X	X	X	O	X
Apiculatisporis elegans										X	
Devonomonoletes sp.										X	
Latosporites sp.								X	O	X	
Number of taxa (36 Total)	9	11 (12)	14 (15)	17 (20)	16 (22)	20 (28)	21 (25)	10 (21)	9 (19)	18 (20)	11

Table 3

Distribution of marine acritarchs, prasinophytes and chitinozoans in the logged samples. The taxon counts include raw counts and in parentheses those including range through taxa.

Section	(4) Santa Lucía		(3) Cabornera	(5) Aleje		(1) El Tranquero	(3) Cabornera					
Sample ref.	22SL13/1	22SL13–1/1	18SPAIN27A	22ALE10P	22ALE11P	ETP01/1	22CAB16P + 0.25	22CAB16P + 0.40	18SPAIN29	18SPAIN24	22CAB22P + 0.10	18SPAIN25A
Lithostratigraphy	Santa Lucía Fm. Member III		Member III	Member IV	Member IV	Naranco Fm.	Santa Lucía Fm. Cabornera Bed	Cabornera Bed	Huergas Fm.			
TAXA												
Prasinophytes												
Botryococcus sp.						X						
Cymatiosphaera carminae Cramer, 1964		X		X								
Cymatiosphaera cornifera Deunff, 1955						X						
Cymatiosphaera cuba Deunff ex Deunff, 1961						X						
Cymatiosphaera pavimenta (Deflandre) Deflandre, 1954				X								
Cymatiosphaera perimembrana Staplin, 1961					X							
Cymatiosphaera winderi (Deunff) Playford, 1977				X								
Cymatiosphaera sp. 1					X							
Cymatiosphaera spp.		X	X		X		X				X	
Dictiotydium cohora Wicander and Wood, 1981				X								
Dictyotidium sp.				X								
Dictiotydium spp.							X					
Duvernaysphaera angelae Deunff, 1964				X		X						
Leiosphaeridia sp. 1						X						
Leiosphaeridia spp.	X	X	X	X	X	X	X	X		X	X	
Lophosphaeridium spp.	X		X		X	X		X			X	
Muraticavea munifica Wicander and Wood, 1981					X							
Polyedryxium cf. *P. accuratum* sensu Askew, 2018			X	X			X	X				
Polyedryxium bathyaster Deunff, 1961				X	X	X	X	X				
Polyedryxium carnatum Playford, 1977				X				X				
Polyedryxium decorum Deunff, 1955				X	X	X		X				
Polyedryxium cf. *P. decorum* Deunff, 1955	X		X				X					
Polyedryxium embudum Cramer, 1964				X	X							
Polyedryxium fragosolum Playford, 1977				X	X							
Polyedryxium helenaster Cramer, 1964						X	X					
Polyedryxium pharaone Deunff ex Deunff, 1961				X	X	X						
Polyedryxium cf. *P. robustum* sensu Askew, 2018				X	X		X			X		
Polyedryxium '*talum*' Deunff, 1971					X							
Polyedryxium sp. A, sensu Askew, 2018				X	X	X		X		X		
Polyedryxium sp. C sensu Askew, 2018				X			X					
Polyedryxium spp.				X	X		X	X		X	X	
Pterospermella sp. 1				X								
Pterospermella sp. 2					X							
Pterospermella spp.				X								
Stellinium comptum Wicander and Loeblich Jr., 1977				X	X		X					

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Table 3 (*continued*)

Section	(4) Santa Lucía		(3) Cabornera	(5) Aleje		(1) El Tranquero	(3) Cabornera					
Sample ref.	22SL13/1	22SL13–1/1	18SPAIN27A	22ALE10P	22ALE11P	ETP01/1	22CAB16P + 0.25	22CAB16P + 0.40	18SPAIN29	18SPAIN24	22CAB22P + 0.10	18SPAIN25A
Stellinium micropolygonale (Stockmans & Willière) Playford, 1977			X	X			X					
Stellinium cf. *S. micropolygonale* (Stockmans and Willière) Playford, 1977			X									
Stellinium pseudopharaone (Stockmans & Willière) Eisenack et al., 1976						X	X	X				
Stellinium?rabians (Cramer) Eisenack et al., 1976								X				
Stellinium spp.			X	X	X							
Tasmanites spp.			X	X	X	X	X	X		X		
Algae cluster				X		X						
	3	**3 (5)**	**9 (10)**	**25 (28)**	**19 (25)**	**15 (23)**	**14 (17)**	**11 (13)**	**0 (7)**	**5 (7)**	**4 (4)**	**0**
Acritarchs												
Acriora cf. *A. petala* Wicander, 1974				X	X							
Ammonidium cornuatum Loeblich and Wicander, 1976				X	X		X					
Ammonidium sp. A sensu Wicander and Playford, 2017				X								
?*Ammonidium* sp.						X						
Comasphaeridium?hirsutum Johnson, 1985	X											
?*Costatilobus aremoricanus* Deunff, 1980			X		X							
Cymbosphaeridium cf. *C. pilar* (Cramer) Lister, 1970		X		X			X	X				
Diexallophasis cf. *D. denticulata* (Stockmans & Willière) Loeblich, 1970								X				
Diexallophasis remota (Deunff) Playford, 1977				X	X		X	X				
Diexallophasis sp. 1		X	X									
Diexallophasis spp.		X		X			X	X		X		
Divietipellis ventricosa Wicander, 1974				X		X	X	X				
Eisenackidium appendiculum Wicander and Wood, 1981				X	X							
Eisenackidium colle Cramer and Diez, 1976				X	X							
Eisenackidium duplex (Cramer) Eisenack et al., 1973						X						
Eisenackidium spp.				X		X						
Ephelopalla cf. *E. elongata* Wicander, 1974						X						
cf. *Estiastra* sp.				X	X	X						
Exochoderma arca Wicander and Wood, 1981		X		X				X				
Exochoderma triangulata Wicander and Wood, 1981		X		X	X	X	X	X				
cf. *Exochoderma* sp.	X			X	X	X	X	X				
Exochoderma spp.						X		X				
?*Florisphaeridium toyetae* (Cramer) Cramer and Diez, 1976						X						

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Table 3 (*continued*)

Section	(4) Santa Lucía		(3) Cabornera	(5) Aleje		(1) El Tranquero	(3) Cabornera					
Sample ref.	22SL13/1	22SL13–1/1	18SPAIN27A	22ALE10P	22ALE11P	ETP01/1	22CAB16P + 0.25	22CAB16P + 0.40	18SPAIN29	18SPAIN24	22CAB22P + 0.10	18SPAIN25A
Goniosphaeridium?raczii (Cramer) Eisenack et al., 1973					X			X				
Goniosphaeridium sp. 2				X	X							
Goniosphaeridium sp. 1						X						
Gorgonisphaeridium cf. *G. granatum* Playford, 1977			X									
Gorgonisphaeridium sp. 1				X		X	X	X				
Gorgonisphaeridium spp.		X		X				X				
cf. *Hapsidopalla* sp.				X								
Micrhystridium stellatum (Deflandre) Deflandre, 1945						X	X	X				
Micrhystridium spp.				X	X	X		X				
Multiplicisphaeridium lindum Cramer and Diez, 1976					X							
Multiplicisphaeridium paraguaferum (Cramer) Lister, 1970				X		X	X	X				
Multiplicisphaeridium?paraguaferum (Cramer) Lister, 1970					X							
Multiplicisphaeridium ramusculosum (Deflandre) Lister, 1970		X		X		X						
Multiplicisphaeridium sp. 1				X		X						
Multiplicisphaeridium spp.				X	X	X						
Navifusa bacilla (Deunff) Playford, 1977				X	X		X	X		X		
Navifusa multistriata (Brito) Eisenack et al., 1979							X					
?*Oppilatala* sp.		X										
Ozotobrachion cf. *O. furcillatus* (Deunff) Playford, 1977		X										
?*Ozotobrachion* sp.						X						
Pyloferites escobaides (Cramer) Daners et al. emend. García-Muro and Rubinstein, 2022								X				
Solisphaeridium sp. 1				X				X				
Tyligmasoma alargada (Cramer) Playford, 1977				X	X		X	X				
Veryhachium europaeum Stockmans and Williere, 1960					X			X				
Veryhachium lairdii Group Deflandre ex Loeblich, 1970			X		X	X						
Veryhachium trispininflatum Cramer, 1964				X	X							
Veryhachium trispinosum Group (Eisenack) Stockmans and Williere, 1962				X			X					
Veryhachium spp.	X		X		X							
cf. *Villosacapsula tetraedron* (Deunff ex Deunff) Deunff, 1980				X								
Visbysphaera dilatispinosa (Downie) emend. Lister, 1970						X	X					
	3	**9 (11)**	**5 (11)**	**29 (32)**	**21 (32)**	**21 (32)**	**15 (19)**	**20 (20)**	0 (2)	**2 (2)**	**0 (0)**	**0**

(*continued on next page*)

Table 3 (*continued*)

Section	(4) Santa Lucía		(3) Cabornera	(5) Aleje		(1) El Tranquero	(3) Cabornera					
Sample ref.	22SL13/1	22SL13–1/1	18SPAIN27A	22ALE10P	22ALE11P	ETP01/1	22CAB16P + 0.25	22CAB16P + 0.40	18SPAIN29	18SPAIN24	22CAB22P + 0.10	18SPAIN25A
Chitinozoans												
Ancyrochitina cf. *A. ancyrea* (Eisenack) Eisenack, 1955						X						
Ancyrochitina fragilis Eisenack, 1955				X								
Ancyrochitina cf. *A. taouratinensis* Boumendjel, 1985					X							
Ancyrochitina sp. 1				X								
?*Ancyrochitina* sp. 1			X									
?*Ancyrochitina* sp. 2			X									
?*Ancyrochitina* sp. 3								X				
Angochitina cf. *A. calcarata* Legault, 1973					X							
Angochitina capillata Eisenack, 1937					X	X						
Angochitina cf. *A. capillata* Eisenack, 1937						X						
Angochitina daemoni Grahn, 2000				X				X				
Angochitina cf. *A. daemoni* Grahn, 2000		X	X	X		X		X				
Angochitina devonica Eisenack, 1955	X		X	X		X						
?*Angochitina* sp.						X						
Angochitina spp.				X								
?*Belonechitina* sp.				X								
?*Bulbochitina* sp.							X					
?*Bursachitina* sp.				X	X		X					
Fungochitina pilosa Collinson and Scott, 1958					X							
Fungochitina sp. 1				X				X				
Fungochitina sp. 2				X								
?*Fungochitina* sp.				X								
Hoegisphaera cf. *H. glabra* Staplin, 1961				X	X							
Lagenochitinidae				X	X		X	X		X		X
Ramochitina cf. *R. magnifica* Lange, 1967						X						
?*Ramochitina* sp.						X						
Saharochitina sp. 1				X			X					
	1	**1 (2)**	**4 (4)**	**14 (14)**	**7 (12)**	**8 (13)**	**4 (7)**	**5 (5)**	**0 (1)**	**1 (1)**	**0 (1)**	**1**
Lithostratigraphy	**Santa Lucía Fm.**					**Naranco Fm.**	**Santa Lucía Fm.**		**Huergas Fm.**			
	Member III		**Member III**	**Member IV**	**Member IV**		**Cabornera Bed**	**Cabornera Bed**				
Sample ref.	**22SL13/1**	**22SL13–1/1**	**18SPAIN27A**	**22ALE10P**	**22ALE11P**	**ETP01/1**	**22CAB16P + 0.25**	**22CAB16P + 0.40**	**18SPAIN29**	**18SPAIN24**	**22CAB22P + 0.10**	**18SPAIN25A**
Section	**(4) Santa Lucía**		**(3) Cabornera**	**(5) Aleje**		**(1) El Tranquero**	**(3) Cabornera**					

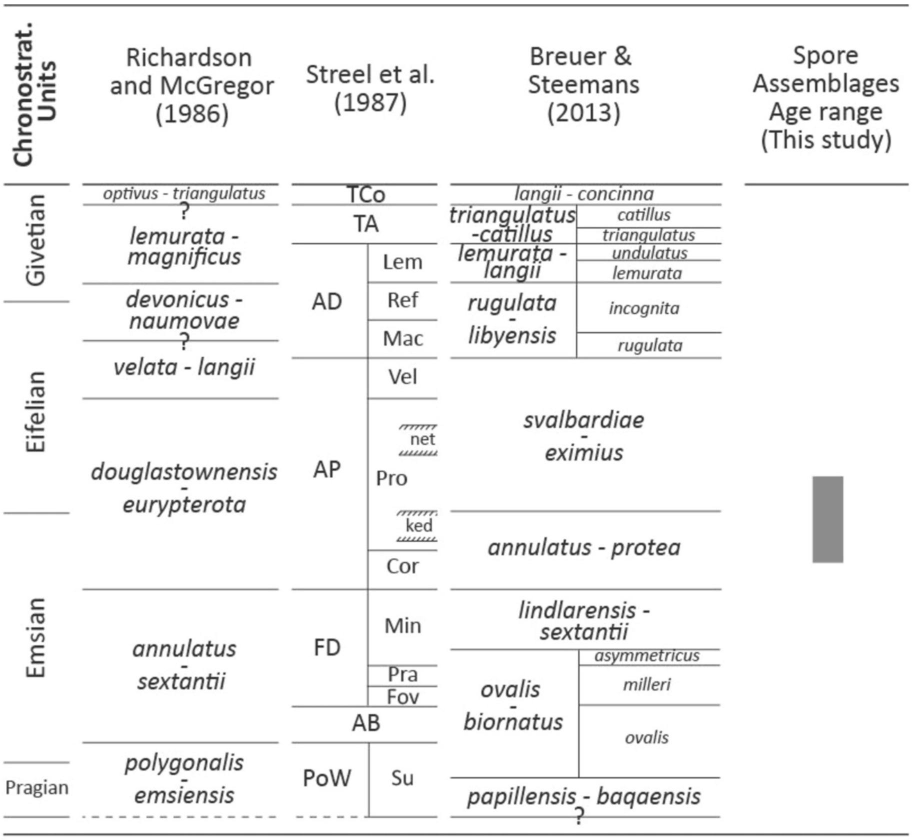

Fig. 5. Early-Middle Devonian spore biostratigraphical schemes and correlation of the dispersed spore assemblages from Northern Spain.

Fig. 6. Palaeocontinental reconstruction of the Early Devonian with the position of the Armorican Terrane Assemblage indicated. Palaeocontinental reconstruction from Torsvik and Cocks (2017) with permission.

Data availability

Data will be made available on request.

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Appendix A

Palynological samples collected from the Moniello – Santa Lucía fms and basal Naranco – Huergas fms. Sample in bold with asterisks are productive samples with well preserved palynomorphs of low-moderate thermal maturity that were suitable for palynological investigation and logged.

Sample	Locality	Lithology	GR	Palynology
ETP01*	1) El Tranquero Naranco Fm	Thin shale parting in massive sandstone unit	0279294/4828025	Assemblage of well preserved palynomorphs of low thermal maturity
19SPAIN06	2) Type Section Moniello Fm	Dark muddy limestone	N43°38′08.6” W005°47′39.1”	Barren
19SPAIN07	2) Type Section Moniello Fm	Dark muddy limestone	N43°37′48.5” W005°47′38.9”	Assemblage of moderately preserved palynomorphs of high thermal maturity
19SPAIN08	2) Type Section Moniello Fm	Dark muddy limestone	N43°37′51.1” W005°47′41.1”	Barren
22SL-51	3) Type Section Santa Lucía Fm Mb II	Thin intercalation of calcareous mudstone		Dominated by inertinite, AOM and phytodebris with very rare poorly preserved palynomorphs
22SL-50	3) Type Section Santa Lucía Fm Mb II	Thin intercalation of calcareous mudstone		Dominated by inertinite, AOM and phytodebris with very rare poorly preserved palynomorphs
22SL-26	3) Type Section Santa Lucía Fm Mb III	Thin intercalation of calcareous mudstone		Dominated by inertinite, AOM and phytodebris with rare poorly preserved palynomorphs
22SL-19 + 1	3) Type Section Santa Lucía Fm Mb III	Thin intercalation of calcareous mudstone		Dominated by AOM and phytodebris with a moderate number of poorly preserved palynomorphs
22SL-18 + 3.5	3) Type Section Santa Lucía Fm Mb III	Thin intercalation of calcareous mudstone		Dominated by inertinite and AOM with a moderate number of poorly preserved palynomorphs
22SL-14 + 2B	3) Type Section Santa Lucía Fm Mb III	Thin intercalation of calcareous mudstone		Dominated by inertinite and AOM with a moderate number of poorly preserved palynomorphs
22SL14 + 2	3) Type Section Santa Lucía Fm Mb III	Thin intercalation of calcareous mudstone		Dominated by inertinite and AOM with rare very poorly preserved palynomorphs
22SL-13*	3) Type Section Santa Lucía Fm Mb III	Thin intercalation of calcareous mudstone		Abundant moderate-well preserved palynomorphs of low thermal maturity.
22SL13–1*	3) Type Section Santa Lucía Fm Mb III	Thin intercalation of calcareous mudstone		Abundant moderate-well preserved palynomorphs of low thermal maturity
22SL-9.5	3) Type Section Santa Lucía Fm Mb IV	Thin intercalation of calcareous mudstone		Barren-dominated by inertinite
18SPAIN27*	4) Roadcut Cabornera to Buiza (E of road) Santa Lucía Fm	Thin shale in Santa Lucia Fm 50 m below contact with Huergas Fm	0280562/4749985	Assemblage of moderately preserved palynomorphs of moderate thermal maturity
18SPAIN26	4) Roadcut Cabornera to Buiza (E of road) Santa Lucía Fm	Thin shale in Santa Lucia Fm 48 m below contact with Huergas Fm	0280562/4749985	Barren
22CAB16P (+0.25 m)*	4) Roadcut Cabornera to Buiza (E of road) Cabornera Bed	Dark grey shale	0280562/4749985	Assemblage of moderately preserved palynomorphs of moderate thermal maturity
22CAB16P (+0.40 m)*	4) Roadcut Cabornera to Buiza (E of road) Cabornera Bed	Dark grey shale	0280562/4749985	Assemblage of well preserved palynomorphs of moderate thermal maturity
18SPAIN23	4) Roadcut Cabornera to Buiza (W of road) Cabornera Bed	Dark grey shale	N42°52′14.9” W005°41′17.0”	Poorly preserved assemblages (rare spores) that did not oxidise well
18SPAIN28	4) LE473 roadcut S of Cabornera-Buiza road Cabornera Bed	Lowermost shale of Cabornera Bed	N42°52′17.2” W005°41′38.1”	Poorly preserved palynomorph assemblage
22CAB22P (+0.10 m)*	4) Roadcut Cabornera to Buiza (E of road) Basal Huergas Fm	Dark grey silty shale	0280562/4749985	Assemblage of well preserved palynomorphs of moderate thermal maturity
18SPAIN24*	4) Roadcut Cabornera to Buiza (W of road) Basal Huergas Fm	Dark grey shale	N42°52′15.3” W005°41′11.3”	Assemblage of moderately preserved palynomorphs of low thermal maturity
18SPAIN29*	4) LE473 roadcut S of Cabornera-Buiza road Basal Huergas Fm	Huergas Formation shale directly above Cabornera Bed	N42°52′17.2” W005°41′38.1”	Assemblage of moderately preserved palynomorphs of low thermal maturity
18SPAIN25*	4) Roadcut Cabornera to Buiza (E of road) Basal Huergas Fm	Dark grey shale	N42°52′15.3” W005°41′11.3”	Assemblage of moderately preserved palynomorphs of low thermal maturity

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Sample	Locality	Lithology	GR	Palynology
22CAB25P (+0.60 m)	4) Roadcut Cabornera to Buiza Basal Huergas Fm	Dark grey silty shale	0280562/4749985	Barren
22ALE10P*	5) Aleje Santa Lucía Fm Mb IV (upper half)	First mudstone in sequence wrapped around limestone	0326651/4746597	Assemblage of well preserved palynomorphs of low thermal maturity
22ALE11P*	5) Aleje Santa Lucía Fm Mb IV (upper half)	Mudstone 1 m above 22ALE10P	0326651/4746597	Assemblage of well preserved palynomorphs of low thermal maturity
C623/11 – C623/15 (5 samples)	6) CL-626 roadcut at Los Barrios de Luna Santa Lucia Fm	Thin, muddy limestone intercalations in massive limestone	4227/9214–4218/9215	Limited organic residue with very rare and highly coalified palynomorphs

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