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An endemic microphytoplankton assemblage from Middle Devonian Iberia and its paleogeographical significance

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ABSTRACT

Diverse microphytoplankton assemblages, including 72 taxa belonging to 27 genera of acritarchs and prasinophyte phycomata, have been recovered from Middle Devonian rocks in northern Spain, revealing an endemic flora dissimilar to coeval assemblages. These deposits are of early Givetian age and consist of the laterally equivalent Naranco, Huergas and Gustalapiedra formations of Asturias, León and Palencia provinces. At the time, Iberia was part of the Armorican Terrane Assemblage, a comparatively isolated island chain positioned between Laurussia and Gondwana. The studied formations represent a marine transect across a nearshore–offshore gradient and consist of a large clastic unit sandwiched between extensive carbonate deposits. This clastic unit incorporates the Kačák Event, an important global extinction event associated with marine anoxia. Herein, the suite of generally well-preserved microphytoplankton assemblages is described and their stratigraphical and biogeographical importance are considered. The microphytoplankton represents a single assemblage deposited in a short interval and is interpreted as being endemic. The assemblage is only moderately similar to contemporary assemblages from Laurussia and Gondwana and, although certain characteristic Middle Devonian taxa are present, other common species such as *Arkonites bilixus* and *Tyligmasoma alargada* are absent. While no unique taxa are found here, the taxa which are present represent a particular combination of species not seen elsewhere. Certain taxa appear which may have discordant temporal ranges, though no major inferences can be made from them as only two taxa both occur in significant numbers and have a confident identification. This assemblage adds to our knowledge of phytoplankton palaeobiogeography, representing a significantly endemic assemblage within the generally cosmopolitan microphytoplankton flora of the Middle Devonian.

1. Introduction

Prasinophyte phycomata and acritarchs (hereafter collectively termed microphytoplankton) from the Middle Devonian deposits of northern Spain have received very limited study, having only brief mentions in two papers predominantly focused on land–plant spores (Cramer, 1969; Fombella Blanco, 1988). This is in spite of the rock formations themselves being otherwise well studied and presenting a number of interesting features. They comprise a clastic unit positioned between thick carbonate deposits, representing a completely marine onshore–offshore transect, well age-constrained by conodonts and dispersed land–plant spores, and well characterized sedimentologically. The sequence merits particular attention owing to: (1) its location around a group of relatively small islands isolated from the large supercontinents of Laurussia and Gondwana (Torsvik and Cocks, 2013, 2016) and (2) the clastic unit incorporating the Kačák Event (García-Alcalde, 1998; Askew and Wellman, 2018), a major global extinction event of uncertain cause. This study comprehensively describes the composition of the microphytoplankton assemblage from this sequence for the first time, identifies differences between this community and contemporary assemblages from Laurussia and Gondwana and discusses the palaeobiogeographical implications of this assemblage within the Middle Devonian world.

2. Geological setting

This study utilizes the same samples as Askew and Wellman (2018) and their geological setting is described in detail therein. Briefly, the studied Naranco, Huergas and Gustalapiedra formations are lateral equivalents, found in Asturias, León and Palencia provinces, respectively. They are bounded by limestone formations, the older Moniello, Santa Lucía and Polentinos formations below, and the younger Candás, Portilla and Cardaño formations above, all similarly laterally equivalent (Fig. 1). The boundaries between the formations are described as conformable (IGME, 2015). The Naranco, Huergas and Gustalapiedra formations represent a clastic interruption in carbonate deposition and consist of a coarse, sandstone lower unit and a more mixed upper unit containing alternating sandstones and siltstones (with occasional limestone beds), indicating somewhat reduced clastic input compared with

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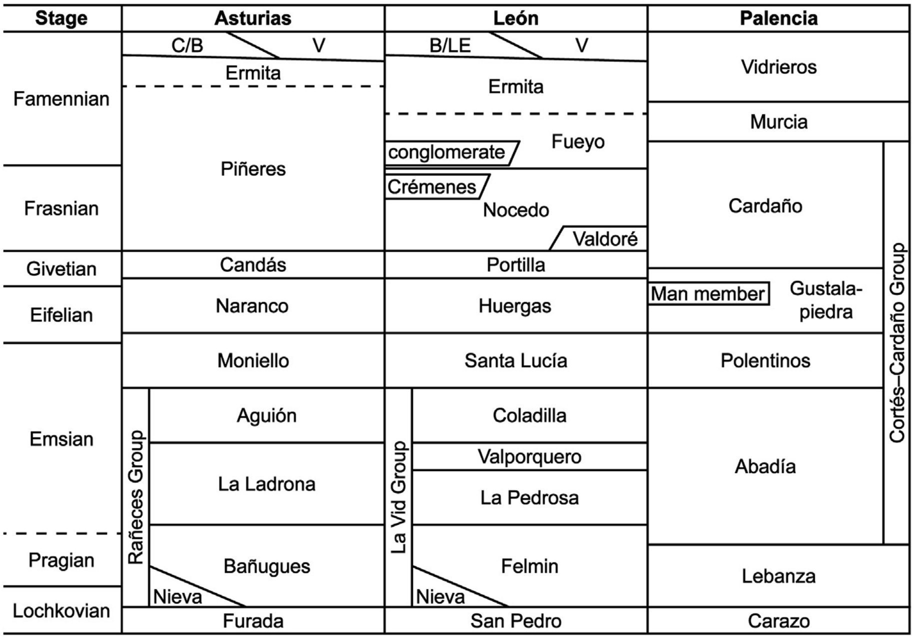

Fig. 1. Correlation and age of Devonian deposits in several Iberian areas. Dashed boundary lines indicate uncertainty. Diagram not to scale. Abbreviations for uppermost Famennian units: B, Baleas; C, Candamo; LE, Las Ermitas; V, Vegamián. Redrawn from García-Alcalde et al. (2002).

the lower unit. Detailed descriptions of the various facies present and their environmental interpretations can be found in García-Ramos (1978).

The marine macrofauna from the Naranco, Huergas and Gustalapiedra formations indicate an Eifelian–Givetian age (García-López et al., 2002), refined by conodont faunas found in the surrounding limestones. These give an age range from the *Polygnathus costatus costatus* zone (middle Eifelian; ca. 391–392 Ma (Becker et al., 2012)) to the lower *Polygnathus varcus* zone (early, but not earliest, Givetian; ca. 386–387 Ma (Becker et al., 2012)) (García-López et al., 2002; García-López and Sanz-López, 2002). The dispersed spore assemblage described in Askew and Wellman (2018) supports this, though suggests a short period of deposition for the palynomorph-bearing deposits of slightly more than 1.5 million years (ca. 386–387.7 Ma), entirely within the early Givetian *lemurata–langii* Assemblage Zone (*Geminospora lemurata* Interval Zone) (Breuer and Steemans, 2013). This places the assemblage outside the stratigraphic range of the Kačák Event as traditionally defined, though see Askew and Wellman (2018) for a fuller explanation.

Fig. 2 depicts the locations of this study's sample sites within northern Spain. Details of the 30 localities used and samples taken are given in Askew and Wellman (2018).

3. Previous palynological studies

The two previous studies on the Middle Devonian palynomorph assemblages from Spain focused primarily on the dispersed spore assemblages rather than the marine palynomorphs.

Cramer (1969) reported *Baltisphaeridium* spp., *Eisenackidium* sp., *Micrhystridium stellatum* Deflandre, 1945 and *Veryhachium trispinosum*

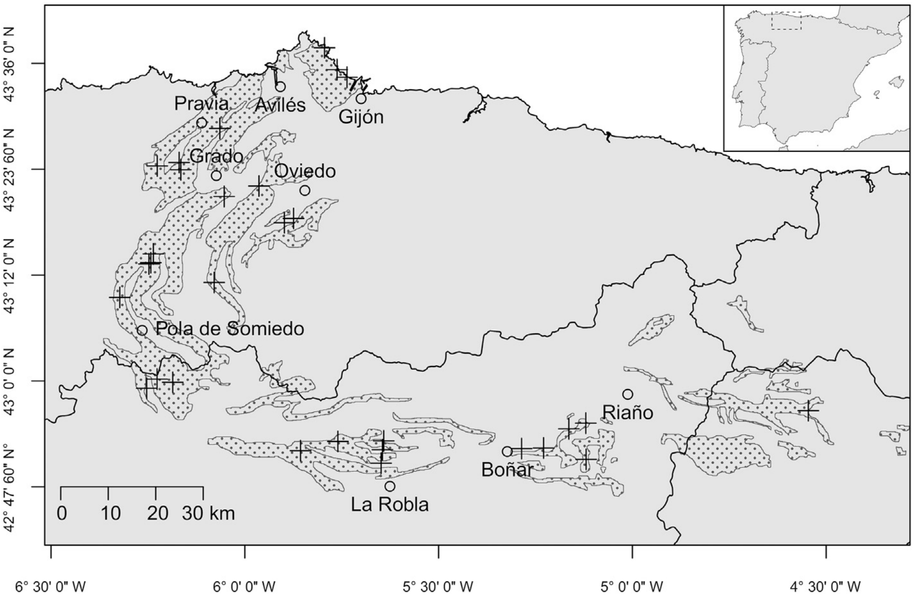

Fig. 2. Map of northern Spain. Crosses indicate sites surveyed in this study. Outlined, dotted areas indicate the Devonian sediments' outcrop area.

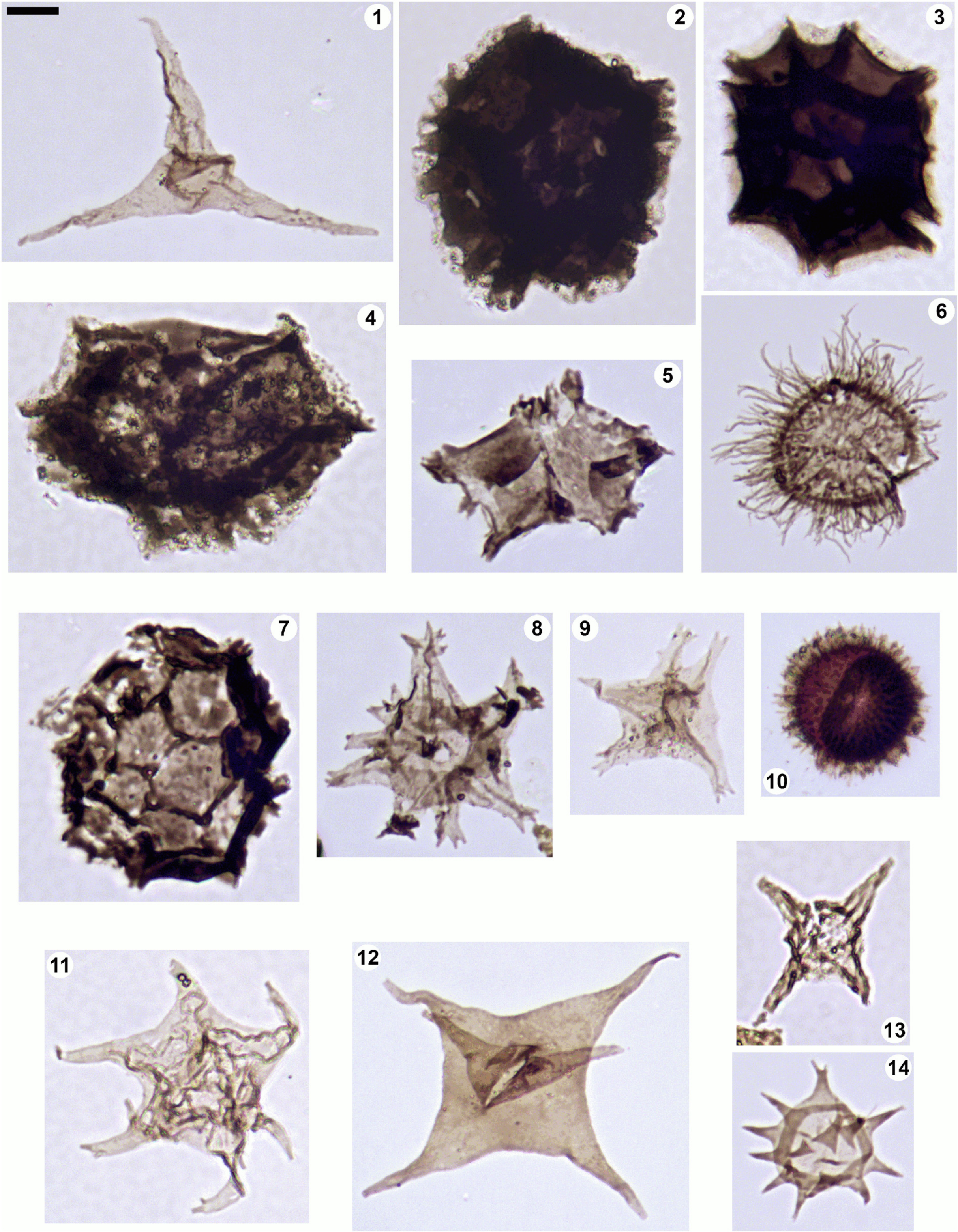

Plate I. Scale bar in 1 = 10 μm and is the same for all images. (1) *Palacanthus tripus*; AJA2-GD-O1; X49. (2) *Polyedryxium primarium*?; AJA2-GT-O2; U31. (3) *P.* sp. A; AJA2-GB-O1; H45. (4) *P.* sp. B; AJA2-GP-O2; F31/2. (5) *P.* sp. C; AJA2-GZ-O1; R32/3. (6) *Comasphaeridium silesiense*?; AJA2-20B-2-O2; L50/4. (7) *Polyedryxium* sp. D; AJA2-GZ-O1; M48/4. (8) *Stellinium* sp. B; AJA2-GW-O1; R38. (9) *S.* sp. A; AJA2-GD-O1; D36. (10) *Comasphaeridium hirsutum*?; AJA4B-O2; O33/2. (11) *Dateriocradus* sp. A; AJA2-GI-O1; C48. (12) *Estiastra* cf. *culcita*; AJA2-GH-O1; P38/2. (13) cf. *E.* sp. A; AJA2-7O-O1; O43/3. (14) *Micrhystridium cortracumense*?; AJA2-20A-O1; H29.

(Eisenack, 1938) Deunff, 1954a (an invalid combination (Fensome et al., 1990)) from five sampled sites in the Naranco Formation. These taxa are figured, but with no other information given. Additionally, the spore species *Acanthotriletes espinositus* Cramer and *A. tenuispinosus* Naumova are reported, though the figured specimens more closely resemble acritarchs, possibly species of *Gorgonisphaeridium*, with no description provided to confirm their spore affinity.

Fombella Blanco (1988) reported *Cymatiosphaera magnata* Pichler, 1971 (since reassigned to *Orygmahapsis* (Colbath, 1987); the figured specimen here is considered to be *Dictyotriletes* cf. *hemeri* Breuer and

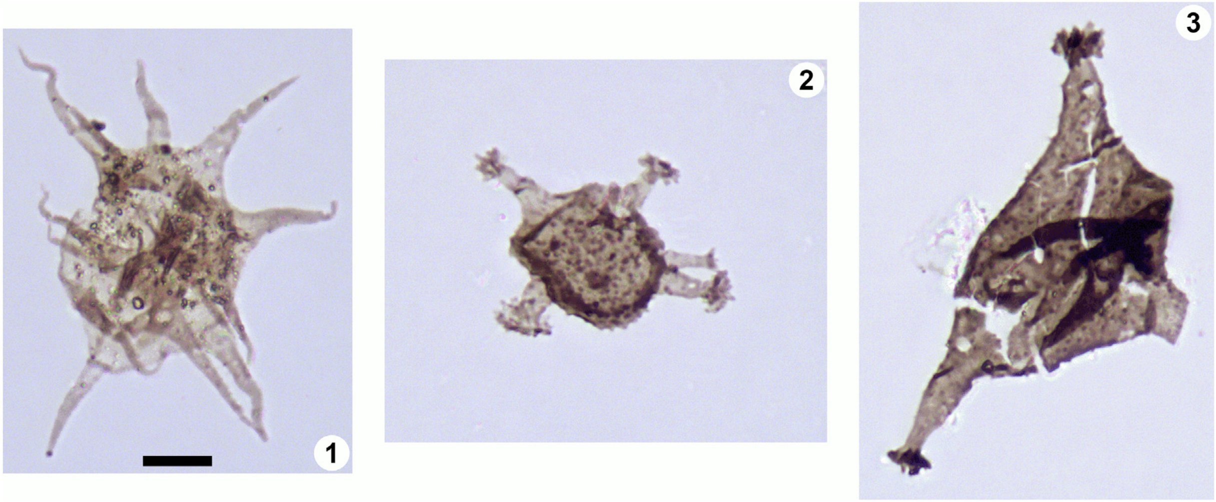

Plate II. Scale bar in 1 = 10 μm and is the same for all images. (1) *Micrhystridium* sp. A; AJA2-GY-O1; X35. (2) *Tylotopalla* sp. A; AJA2-GZ-O1; J39/4. (3) *Villosacapsula cazurra*?; AJA2-PD-O1; R46/4.

Steemans, 2013 (Askew and Wellman, 2018)) and *V. downiei* Stockmans and Willière, 1962 from one site in the Huergas Formation, although the specimens are only figured, with no description or other information given.

4. Material and methods

One hundred and thirty rock samples were collected, covering the outcrop area of the Naranco, Huergas and Gustalapiedra formations. Samples were taken from dark, fine-grained beds of siltstone and mudstone interspersed within the layers of sandstone that dominate the formations. Sample sites were mostly either single exposures or short sections, along with three relatively long sections sampled at intervals. Sample details are given in Askew and Wellman (2018). Samples were processed using standard acid maceration techniques; dissolution in HCl, followed by removal of HCl and replacement by HF and, finally, the addition of HCl to the samples after a short time. The resulting mixture was left until sample break-down was complete, at which point some fine mineral residues were removed using a 15 μm sieve. Heavy liquid centrifugation using $ZnCl_2$ removed remaining mineral matter. Subsequent assessment of the resulting kerogen samples determined three barren samples and one with very poor preservation; these were not processed further.

The palynomorphs are generally well preserved but thermal maturity is variable, with a Thermal Alteration Index (TAI) score between 2- and 4 (Traverse, 2008). Schulze's solution was used to oxidize all the samples for between 5 and 60 min, except for four very thermally mature samples that were oxidized for around 19 h. The samples were spiked with tablets containing modern *Lycopodium* spores at a ratio of one tablet per millilitre of solid residue, to facilitate quantitative assessment of the palynomorph assemblage using an equation derived from that given by Stockmarr (1971). Two to four strew mounts were made for each sample, with 113 samples counted. Two hundred palynomorphs were counted on each slide with additional species noted as rare. In the rare cases where a slide did not contain 200 palynomorphs, every palynomorph on the slide was counted. Such slides are evident in the count data given in Askew (2019). Slides were examined using a light microscope and specimens photographed using a Meiji Techno Infinity 1-5C camera attached to a Meiji Techno MT5300H transmitted light microscope.

5. Description of the microphytoplankton assemblage

Full systematic descriptions for the taxa found in this phytoplankton assemblage are given in the supplementary text and a list of taxa recorded is given in Appendix A. Plates I and II depict taxa that are either not assignable to existing species or have not been recorded from the Middle Devonian before (see Section 7).

The microphytoplankton assemblage consists of 72 taxa (59 identified species belonging to 27 genera) of which 10 taxa are assigned only to genera, having no previous representation in the literature at species level. Full charts of the sampled sections are presented as supplementary information, while charts of the quantitative abundances of selected taxa are given as Figs. 3–5. Count data are available as supplementary table S1 in Askew (2019). The proportions of different palynomorph types making up the quantitative data for each sample are presented in supplementary table S2 in Askew (2019). Phytoplankton make up a wide range of proportions of the different samples, from near dominance (96%) to being totally absent. Even within the sampled sections their proportions can be extremely variable, presumably representing short-term fluctuations in environmental conditions.

The taxonomic composition of the assemblages recovered from the different localities does not differ significantly and they are considered a single microphytoplankton assemblage. The composition of the assemblage is not particularly variable temporally, possibly related to the short space of time in which the sediments were deposited (see Section 2). The sampled sections contain almost all species seen in the wider assemblage, with the only exceptions being *Comasphaeridium hirsutum*?, *C. silesiense*?, *Cymatiosphaera octoplana*?, *Dictyotidium variatum*, *Ozotobrachion* cf. *furcillatus* and *Villosacapsula cazurra*?. Of these, *D. variatum* and *O. furcillatus* are known to occur across the stratigraphic range of the formation, while the remaining species are previously known only from much older deposits but are mostly rare here (discussed in Section 7). It is difficult to separate any of the small outcrop sites from the rest of the assemblage based on these data, given the close similarity of the assemblages as a whole. The sampled sections show few taxon inceptions during their duration, with no consistency in which taxa occur later and none becoming significant components of the assemblage.

Gorgonisphaeridium cumulatum is extremely common in this assemblage. When assessed quantitatively, this species alone constitutes ca. 70% of the assemblage. Of the other groups, multiplicisphaerids are the most common, making up 9% of the assemblage (30% excluding

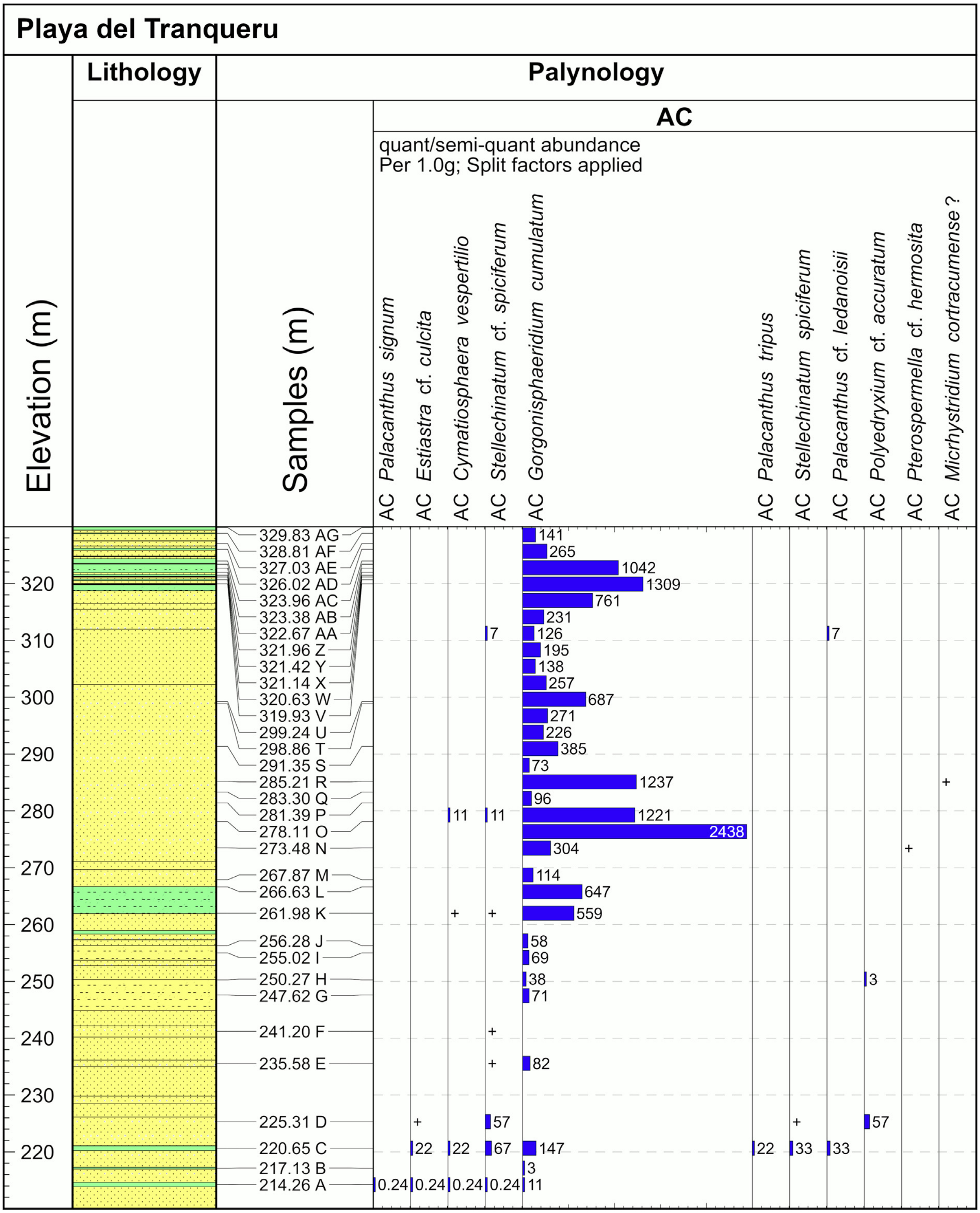

Fig. 3. Quantitative abundances of selected palynomorphs at the Playa del Tranqueru site. Abundances expressed in numbers per gram of rock. Each horizontal tick represents 100 specimens per gram. The section's lithology is also shown.

G. cumulatum), followed by *Cymatiosphaera* (6% of the assemblage; 20% excluding *G. cumulatum*), *Palacanthus* (5%; 15%), *Polyedryxium* (3%; 9%), *Micrhystridium* and *Solisphaeridium* (2%; 7%) and *Veryhachium* and *Villosacapsula* (2%; 6%). The remaining species of *Gorgonisphaeridium* constitute the same percentage (2%; 6%) of the assemblage.

Reworking is considered unlikely in this material. It is not evident in the dispersed spore assemblage as discussed by Askew and Wellman (2018). The phytoplankton show no apparent differences in preservation and thermal maturity and there is no obvious systematic reworking of older forms (e.g. those known from the underlying La Vid Group) into the assemblage.

6. Comparison with other microphytoplankton assemblages

Middle Devonian microphytoplankton assemblages are better known than, for example, Early Devonian ones, however the stratigraphic and geographic distribution of well-described assemblages is still uneven (Le Hérissé et al., 2000; Molyneux et al., 2013; Wicander and Playford, 2017a). Many are clustered in particular areas, particularly North America, yet many of these are not sufficiently stratigraphically constrained for valid comparisons to be made. These assemblages, as well as those of better stratigraphic constraint, are well-reviewed by Wicander and Playford (2017a, 2017b) for North America and Molyneux et al. (2013) globally. Differing taxonomic opinions also confuse the issue, with species concepts used differently by different authors. However, numerous papers, such as those cited in Table 1, can be used for comparative purposes, allowing comparisons to be made between this assemblage in northern Spain and contemporary assemblages in Laurussia, Gondwana and China (considered separately here).

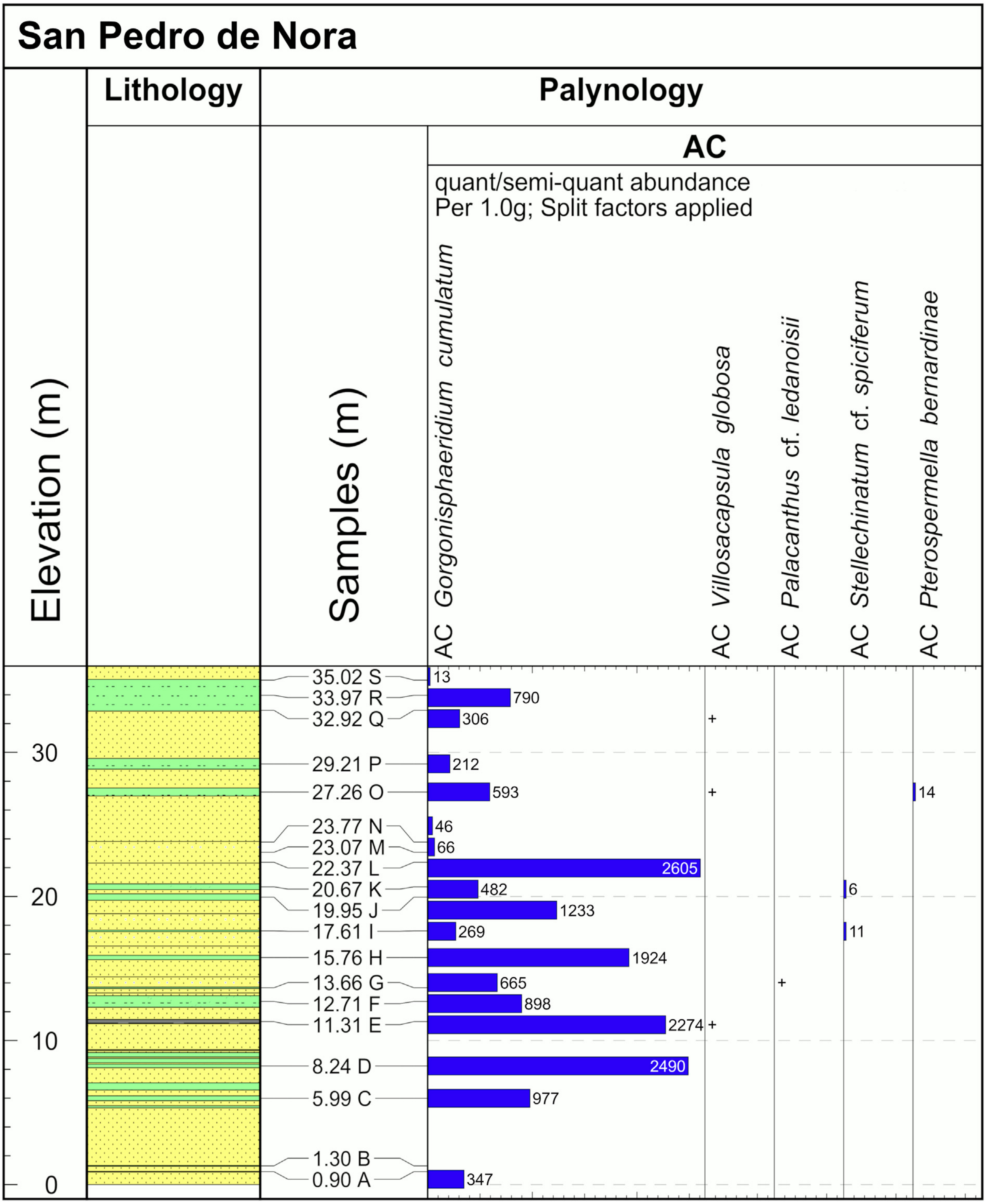

Fig. 4. Quantitative abundances of selected palynomorphs at the San Pedro de Nora site. Abundances expressed in numbers per gram of rock. Each horizontal tick represents 100 specimens per gram. The section's lithology is also shown.

Three measures of similarity are used here. (1) Percentage similarity (sensu Wicander and Playford (2017a, 2017b)) is simply the percentage of co-occurring species between this assemblage and another. (2) The coefficient of similarity (CS) (sensu Clark and Hatleberg (1983)) can be expressed as $CS = 2|x|/(|a+b|)$ where a and b are the total number of species in assemblages a and b, respectively, and x is the number of species they share. Results below 0.2 are considered to indicate low similarity with results between 0.2 and 0.55 considered moderate to high (Clark and Hatleberg, 1983). (3) The Jaccard Index (JI) can be expressed as $JI = |x|/(|a| + |b| - |x|)$ where a and b are the total number of species in assemblages a and b, respectively, and x is the number of species they share. This gives a value between 0, for completely dissimilar assemblages, and 1 for identical assemblages. These latter two measures have been used previously in Palaeozoic palynological applications (e.g. Le Hérissé et al., 1997; Wellman, 2018; Wellman et al., 2013). In all cases, taxa assigned only to genera and those designated "?" have been excluded from the calculation, while those designated "cf." have been treated as valid identifications where appropriate.

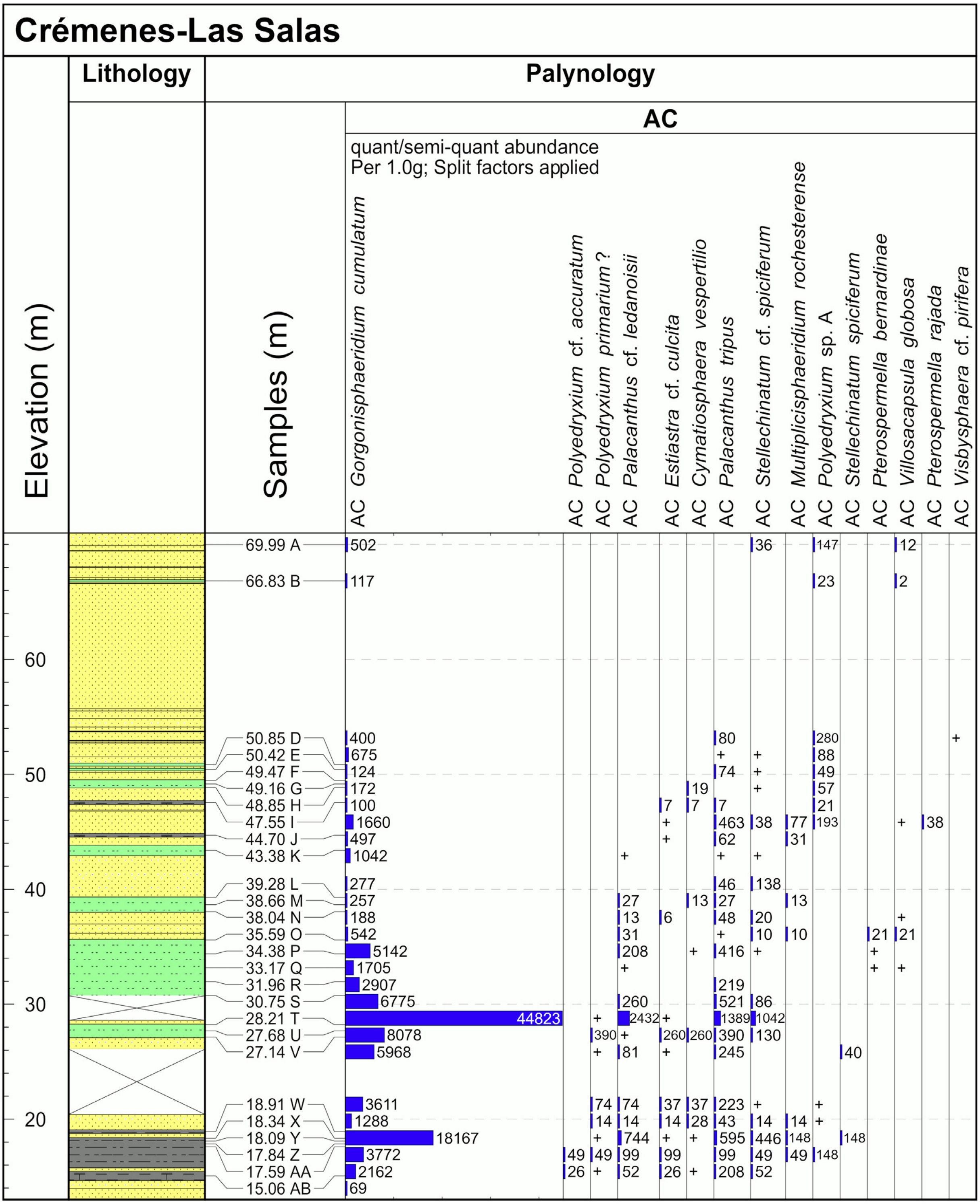

Fig. 5. Quantitative abundances of selected palynomorphs at the Crémenes-Las Salas site. Abundances expressed in numbers per gram of rock. Each horizontal tick represents 10,000 specimens per gram. The section's lithology is also shown.

Table 1
Measures of similarity calculated for various Middle Devonian assemblages compared with the Spanish one described here. The results given for Laurussia and Gondwana are calculated using a composite assemblage based on the individual studies listed.

Assemblage	Percentage similarity	Coefficient of similarity	Jaccard index
Laurussia	*28.57%*	*0.366*	*0.224*
Legault (1973) (Canada)	33.33%	0.100	0.053
Playford (1977) (Canada)	51.72%	0.375	0.231
Wicander and Playford (2017a) (Canada)	36.59%	0.326	0.195
Turnau and Racki (1999) (Poland)	45.83%	0.293	0.172
Wicander and Wood (1981) (USA)	36.17%	0.347	0.210
Wicander and Wright (1983) (USA)	32.43%	0.276	0.160
Wood and Clendening (1985) (USA)	52.17%	0.324	0.194
Wicander and Wood (1997) (USA)	33.33%	0.262	0.151
Wicander and Playford (2017b) (USA)	40.00%	0.296	0.174
Gondwana	*15.53%*	*0.236*	*0.134*
Jardiné and Yapaudjan (1968) (Algeria)	30.30%	0.238	0.135
Barreda (1986) (Argentina)	42.42%	0.333	0.200
Ottone (1996) (Argentina)	34.15%	0.304	0.179
Rubinstein (1999, 2000) (Argentina)	30.00%	0.100	0.053
Amenábar et al. (2006) (Argentina)	38.46%	0.260	0.149
Colbath (1990) (Australia)	8.96%	0.102	0.054
Anan-Yorke (1974) (Ghana)	47.62%	0.278	0.161
Moreau-Benoit (1984) (Libya)	44.00%	0.289	0.169
China (Zhu et al., 2008)	*38.46%*	*0.156*	*0.085*

Values for these metrics applied to 18 Middle Devonian microphytoplankton assemblages are given in Table 1. The locations of the assemblages are shown on a paleogeographical map in Fig. 6. Values for percentage similarity do not seem to scale well with the other metrics; the present author prefers to make the below conclusions based on CS and JI. The present assemblage is seen to not be particularly similar to any other Middle Devonian assemblage with good stratigraphic and taxonomic control. It is most similar to the assemblages of Playford (1977) (CS:0.375; JI:0.231) and Wicander and Wood (1981) (CS:0.347; JI:0.210) from Canada and the USA, but even this is no more than a moderate degree of similarity. A comparable degree of similarity is seen with the Argentinian assemblage of Barreda (1986) (CS:0.333; JI:0.200), showing similarity is not only with Laurussian assemblages.

On a continental scale, the Spanish material is more similar to Laurussia (CS:0.366; JI:0.224) than Gondwana (CS:0.236; JI:0.134), but not to a large degree and the similarity is still only moderate. The assemblage has a low similarity with one reported from China (CS:0.156; JI:0.085).

The species shared between this assemblage and others tend to be wide-ranging. Many of the most-often reported species in contemporary assemblages occur here, including *Duvernaysphaera angelae*, *Dictyotidium variatum*, *Navifusa bacilla*, *Polyedryxium pharaone* and *Stellinium micropolygonale*. However, various other widespread and well-defined species are absent here. Most notable are *Arkonites bilixus* and *Tyligmasoma alargada*, reported from the majority of the studies analysed, particularly in Laurussia, but not seen in Spain.

On a global scale, Middle Devonian microphytoplankton assemblages are broadly cosmopolitan in mid- to high palaeolatitudes, with many species in common between the two main supercontinents of Laurussia and Gondwana (Molyneux et al., 2013). Western China also shows a marked similarity to these supercontinental assemblages (Zhu et al., 2008). Some endemic species do, however, exist within this general cosmopolitanism, primarily in the high palaeolatitudes of Gondwana (Molyneux et al., 2013). Phytoplankton provincialism in the Late Devonian has been suggested to be a result of temperature differences and ocean currents (Shen et al., 2018), and there is no reason to believe similar factors are not at play in the Middle Devonian, restricting some species to high-latitude Gondwana.

The Spanish assemblage analysed here is shown to be endemic to a relatively large degree, being dissimilar to some extent to all the studies analyzed. It is important to note this is not due to new, endemic species found in Spain. Any potential new species in this study were not found in great enough numbers to justify erecting new species; they were left in open nomenclature and, hence, were excluded from the similarity analysis. Instead, it is the particular combination of species seen here, including both predominantly Laurussian and predominantly Gondwanan species while also lacking forms common elsewhere, that renders this assemblage distinct.

This assemblage contributes to our knowledge of Middle Devonian phytoplankton biogeography by describing an endemic assemblage outside the high latitudes of Gondwana, characterized by a specific combination of co-occurring species. Spain was an isolated island during the Middle Devonian (see Section 1 and Fig. 6), therefore its endemism could be due to this geographic isolation, possibly aided by ocean currents.

7. Biostratigraphical implications

Biostratigraphic schemes for Middle Devonian phytoplankton are lacking owing to a paucity of comprehensive study (Le Hérissé et al.,

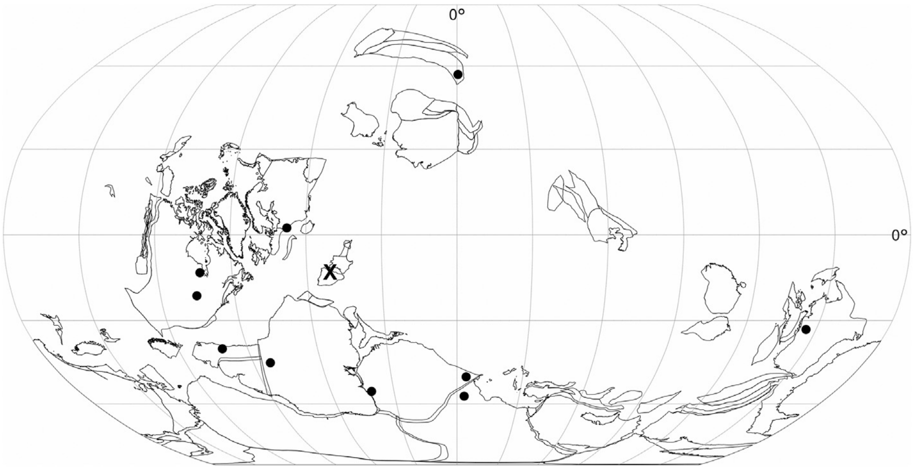

Fig. 6. Palaeocontinental reconstruction of the Middle Devonian world, with modern continents indicated. The location of the Spanish assemblage studied here is marked with a cross. Circles indicate the locations of phytoplankton assemblages mentioned in Table 1. Some circles indicate multiple assemblages positioned in a small area. Base map after Torsvik and Cocks (2016).

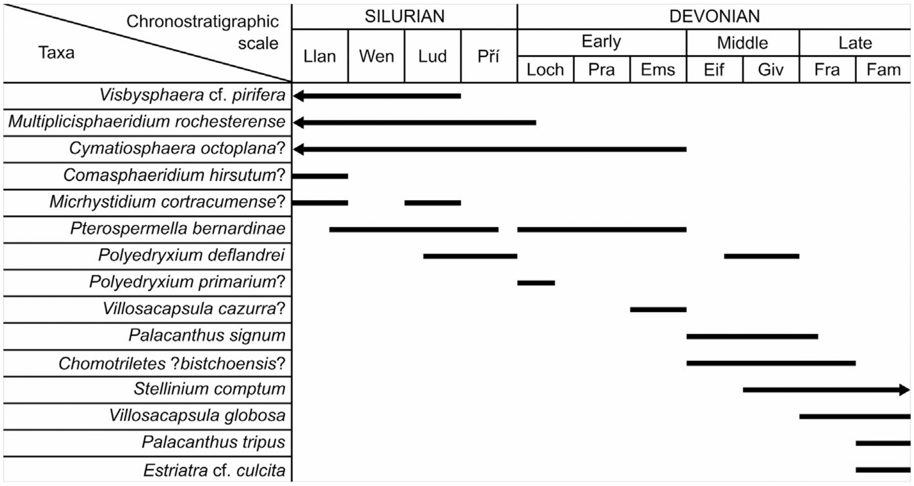

Fig. 7. Chronostratigraphic ranges of selected microphytoplankton species recorded in this study during the Silurian and Devonian periods. Taxa depicted are either not previously recorded from the Middle Devonian or have their extinctions or inceptions close to this study's early Givetian timeframe. See the supplementary text for full details, including some occurrences outside the Silurian and Devonian that are not depicted. Silurian epochs and Devonian ages have been subdivided into early, middle and late divisions in equal thirds.

2000). Simple range charts are more common, however they are not particularly useful here. For example, the only Spanish species that are used in the chart of Wicander and Wood (1997) range throughout the Middle Devonian. The same is almost true of the chart given by Le Hérissé et al. (2000); all but two species found here are shown to be long-ranging. The two exceptions are *Palacanthus tripus* and *Villosacapsula globosa* that are both indicated as Frasnian–Famennian species.

As mentioned in Section 2, the formation in which this assemblage was found is well age-constrained by conodonts and dispersed spores (Middle Devonian: early Givetian). In terms of acritarchs, the zonation scheme of Jardiné et al. (1974) has the Middle Devonian corresponding to zones L1–L3. Zones L1 and L2 are not differentiated, being characterized by (using modern taxonomy) *Duvernaysphaera angelae*, *D. kraeuselii*, *Eisenackidium valentina*, *Multiplicisphaeridium exasperatum*, *Navifusa bacilla*, *Polyedryxium decorum*, *P. fragosulum*, *P. pharaone*, *Stellinium micropolygonale* and *Veryhachium libratum*. Zone L3 is characterized by *Daillydium pentaster*, *Duvernaysphaera angelae*, *D. kraeuselii*, *D. radiata*, "*Polyedryxium* cf. *decorum* Deunff, 1955," "*P.* cf. *talus* Deunff, 1966" and *Veryhachium stelligerum*. The underlying K and overlying L4 zones do not include any species found in the present assemblage. Interestingly, this scheme depicts *V. valiente* as going extinct in the Ludlow, in stark contrast to other reports of its existence in the Devonian, many of them cited in Table 1.

This suite includes various taxa recorded in the Spanish assemblage, namely *D. angelae*, *N. bacilla*, *P. decorum*, *P. fragosulum*, *P. pharaone* and *S. micropolygonale* from the L1–L2 zones. Also found here are two representatives of the later L3 zone. *P.* "*talum*" has a complicated taxonomic history, ultimately being invalid as it was named in an unpublished thesis (Fensome et al., 1990). As the description for "*P.* cf. *talus* Deunff, 1966," cited by Jardiné et al. (1974), is in that thesis and unavailable to the present author, no stratigraphic conclusions have been drawn from it. This leaves only *V. stelligerum* representing the L3 zone, found here only in various samples taken from the section at the Crémenes-Las Salas site and potentially indicating a slightly later date. This would fit with the site's south eastern location, interpreted as further offshore; the clastic sediment may have taken longer to arrive here and produced a degree of diachronism in the Naranco, Huergas and Gustalapiedra formations. It should be noted, however, that *V. stelligerum* has been reported elsewhere across a much wider time range (see supplementary text). The lack of precise ages for these biozones is unfortunate; they simply indicate an Eifelian–Givetian age, agreeing with previous interpretations.

Certain taxa reported here have not been previously recorded in the Middle Devonian. *Comasphaeridium hirsutum*, *C. silesiense*, *Cymatiosphaera octoplana*, *Micrhystridium cortracumense*, *Multiplicisphaeridium rochesterense*, *Polyedryxium primarium*, *Pterospermella bernardinae*, *Villosacapsula cazurra* and *Visbysphaera pirifera* have all only been previously reported from before the Middle Devonian, though *P. bernardinae* and *V. cazurra* are both known from as late as the Emsian in Spain. The aforementioned *Palacanthus tripus* and *Villosacapsula globosa*, as well as *Estiastra culcita*, are all only previously known from after the Middle Devonian. The chronostratigraphic ranges of these taxa, as well as selected other species, are depicted in Fig. 7. Of these taxa not recorded from the Middle Devonian before, only *P. tripus*, *P. bernardinae* and *V. globosa* are identified confidently here, the rest are all in some form of open nomenclature. Then, out of these confident assignments, only *P. tripus* occurs in any numbers, known previously only from the Famennian.

The potentially discordant ranges of these taxa could be explained by reworking, though this is considered unlikely. There is no suggestion of reworking in the dispersed spore assemblage and the clear majority of the microphytoplankton community is typically Middle Devonian. The uncertain identification and rarity of most of the apparently temporally aberrant taxa mean they are probably not of great biostratigraphic importance.

8. Conclusions

- A rich assemblage of generally well-preserved microphytoplankton has been recovered from Middle Devonian deposits in northern Spain.
- The assemblage shows a marked endemism, having a low similarity to assemblages from both Laurussia and Gondwana, reflecting the isolated position of Iberia during the Middle Devonian. Certain taxa also have potentially discordant ranges.
- The microphytoplankton assemblage supports the Middle Devonian age of the formation, agreeing with conodont and dispersed spore data.
- This new assemblage adds to our knowledge of endemic assemblages existing within the broadly cosmopolitan microphytoplankton assemblages of the Middle Devonian.

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Appendix A. Alphabetic list of all microphytoplankton taxa recovered in this study

A.1. Prasinophytes

Cymatiosphaera cuba Deunff, 1954b ex Deunff, 1961
Cymatiosphaera octoplana? Downie, 1959
Cymatiosphaera pavimenta (Deflandre, 1945) Deflandre, 1954
Cymatiosphaera perimembrana Staplin, 1961
Cymatiosphaera vespertilio Deunff, 1976
Dictyotidium variatum Playford, 1977
Duvernaysphaera angelae Deunff, 1964a
Duvernaysphaera tenuicingulata? Staplin, 1961
Palacanthus cf. *ledanoisii* (Deunff, 1957) emend. Playford, 1977
Palacanthus signum (Deunff, 1964b) Wicander, 1974
Palacanthus tripus Martin, 1984
Polyedryxium cf. *accuratum* Deunff, 1971
Polyedryxium cf. *decorum* Deunff, 1955
Polyedryxium deflandrei Deunff, 1954b ex Deunff, 1961
Polyedryxium cf. *fragosulum* Playford, 1977
Polyedryxium mirum Deunff, 1957
Polyedryxium pharaone Deunff, 1954b ex Deunff, 1961
Polyedryxium primarium? Deunff, 1980
Polyedryxium robustum Deunff, 1971
Polyedryxium "*talum*" Deunff, 1971
Polyedryxium sp. A
Polyedryxium sp. B
Polyedryxium sp. C
Polyedryxium sp. D
Pterospermella bernardinae (Cramer, 1964) Eisenack et al., 1973
Pterospermella cf. *hermosita* (Cramer, 1964) Fensome et al., 1990
Pterospermella rajada (Cramer, 1964) Eisenack et al., 1973
Stellinium comptum Wicander and Loeblich Jr., 1977
Stellinium micropolygonale (Stockmans and Willière, 1960) Playford, 1977
Stellinium? *tetrahedroide* (Cramer, 1964) Eisenack et al., 1976
Stellinium sp. A
Stellinium sp. B

A.2. Acritarchs

Ammonidium microfurcatum (Deunff, 1957) Fensome et al., 1990
Chomotriletes? *bistchoensis*? Staplin, 1961
Comasphaeridium hirsutum? Johnson, 1985
Comasphaeridium silesiense? Moczydłowska, 1998
Crameria duplex (Cramer, 1964) Lister, 1970
Dateriocradus sp. A
Diexallophasis remota (Deunff, 1955) emend. Playford, 1977
Estiastra cf. *culcita* Wicander, 1974
cf. *Estiastra* sp. A
Exochoderma arca Wicander and Wood, 1981
Exochoderma triangulata Wicander and Wood, 1981
Gorgonisphaeridium cf. *absitum* Wicander, 1974
Gorgonisphaeridium cumulatum Playford, 1977
Gorgonisphaeridium disparatum? Playford, 1977
Gorgonisphaeridium evexispinosum Wicander, 1974
Micrhystridium cf. *adductum* Wicander, 1974
Micrhystridium cortracumense? Stockmans and Willière, 1963
Micrhystridium stellatum Deflandre, 1945
Micrhystridium sp. A
Multiplicisphaeridium ramispinosum Staplin, 1961 emend. Sarjeant and Vavrdová, 1997
Multiplicisphaeridium rochesterense (Cramer and Díez de Cramer, 1972) Eisenack et al., 1973
Navifusa bacilla (Deunff, 1955) Playford, 1977
Ozotobrachion cf. *furcillatus* (Deunff, 1955) Playford, 1977
Solisphaeridium inaffectum Playford *in* Playford and Dring, 1981
Stellechinatum spiciferum (Deunff, 1955) Sarjeant and Vavrdová, 1997
Stellechinatum cf. *spiciferum* (Deunff, 1955) Sarjeant and Vavrdová, 1997
Tunisphaeridium caudatum Deunff and Evitt, 1968
Tylotopalla sp. A
Veryhachium arcarium Wicander and Loeblich Jr., 1977
Veryhachium downiei Stockmans and Willière, 1962
Veryhachium europaeum Stockmans and Willière, 1960
Veryhachium polyaster Staplin, 1961
Veryhachium polyaster var. *hexaster* Staplin, 1961
Veryhachium polyaster cf. var. *hexaster* Staplin, 1961
Veryhachium stelligerum Deunff, 1957
Veryhachium cf. *trispininflatum* Cramer, 1964
Veryhachium valiente Cramer, 1964
Villosacapsula cazurra? (Cramer, 1964) Sarjeant and Vavrdová, 1997
Villosacapsula globosa Vanguestaine et al., 1983
Visbysphaera cf. *pirifera* (Eisenack, 1954) Kiryanov, 1978

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2019.04.001.

References

Amenábar, C.R., Di Pasquo, M., Carrizo, H.A., Azcuy, C.L., 2006. Palynology of the Chigua (Devonian) and Malimán (Carboniferous) formations in the Volcán Range, San Juan Province, Argentina. Part I. Paleomicroplankton and acavate smooth and ornamented spores. Ameghiniana 43, 339–375.
Anan-Yorke, R., 1974. Devonian chitinozoa and acritarcha from exploratory oil wells on the shelf and coastal region of Ghana, West Africa. Ghana Geol. Surv. Bull. 37, 1–217.
[dataset]Askew, A.J., 2019. Data for: An Endemic Microphytoplankton Assemblage from Middle Devonian Iberia and its Palaeogeographic Significance (Mendeley Data).
Askew, A.J., Wellman, C.H., 2018. An endemic flora of dispersed spores from the Middle Devonian of Iberia. Pap. Palaeontol. https://doi.org/10.1002/spp2.1245.
Barreda, V.D., 1986. Acritarcos Givetiano-Frasnianos de la cuenca del Noroeste, Provincia de Salta, Argentina. Rev. Española Micropaleontol. 18, 229–245.
Becker, R.T., Gradstein, F.M., Hammer, O., 2012. The Devonian Period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), The Geologic Time Scale 2012. Elsevier, Amsterdam, pp. 559–602.
Breuer, P., Steemans, P., 2013. Devonian spore assemblages from northwestern Gondwana: Taxonomy and biostratigraphy. Spec. Pap. Palaeontol. 89, 1–163.
Clark, D.L., Hatleberg, E.W., 1983. Paleoenvironmental factors and the distribution of conodonts in the Lower Triassic of Svalbard and Nepal. Foss. Strat. 15, 171–175.
Colbath, G.K., 1987. *Orygmahapsis*, a new genus of prasinophyte phycoma from the Siluro-Devonian. Neues Jahrb. für Geol. und Paläontologie, Monatshefte 1987, 65–68.
Colbath, G.K., 1990. Devonian (Givetian-Frasnian) organic-walled phytoplankton from the Limestone Billy Hills reef complex, Canning Basin, Western Australia. Palaeontogr. Abteilung B 217, 87–145.
Cramer, F.H., 1964. Microplankton from three Palaeozoic Formations in the Province of León, NW-Spain. Leidse Geol. Meded. 30, 253–361.
Cramer, F.H., 1969. Plant spores from the Eifelian to Givetian Gosseletia Sandstone Formation near Candas, Asturias, Spain. Pollen Spores 11, 425–447.
Cramer, F.H., Díez de Cramer, M.del C.R., 1972. North American Silurian palynofacies and their spatial arrangement: Acritarchs. Palaeontogr. Abteilung B Paläophytologie 138, 107–180.
Deflandre, G., 1945. Microfossiles des calcaires Siluriens de la Montagne Noire. Ann. Paléontol. 31, 41–75.
Deflandre, G., 1954. Systématique des Hystrichosphaerides: sur l'acception du genre *Cymatiosphaera* O. Wetzel. Compte rendu Somm. des séances la Société Géologique Fr. 12, 257–258.
Deunff, J., 1954a. *Veryhachium*, genre nouveau d'hystrichosphères du Primaire. Compte rendu Somm. des séances la Société Géologique Fr. 13, 305–306.
Deunff, J., 1954b. Sur un microplancton du Dévonien du Canada recélant des types nouveaux d'Hystrichosphaeridés. Comptes rendus des séances l'Académie des Sci. 239, 1064–1066.

Deunff, J., 1955. Un microplancton fossile Dévonien à hystrichosphères du Continent Nord-Américain. Bull. Micr. Appl. 2, 138–149.

Deunff, J., 1957. Microorganismes nouveaux (Hystrichosphères) du Dévonien de l'Amérique du Nord. Bull. la Société Géologique Minéralogique Bretagne, Nouv. série 2, 5–14.

Deunff, J., 1961. Quelques précisions concernant les Hystrichosphaeridées de Dévonien du Canada. Compte rendu Somm. des séances la Société Géologique Fr. 8, 216–218.

Deunff, J., 1964a. Le genre *Duvernaysphaera* Staplin. Grana Palynol. 5, 210–215.

Deunff, J., 1964b. Sur une série à acritarches dans la Dévonien noyen du Finistère. Colloque Français de Stratigraphie Sur Le Dévonien Inférieur En France et Dans Les Régions Voisines. Rennes.

Deunff, J., 1966. Recherches sur les microplanctons du Dévonien (Acritarches et Dinophyceae). Bull. la Société Géologique Minéralogique Bretagne, Nouv. série 1, 17–25.

Deunff, J., 1971. Le genre *Polyedryxium* Deunff. Revision et observations. Microfossiles Org. du Paleozoique 3, 7–49.

Deunff, J., 1976. Les Acritarches. Mémoires la Société géologique minéralogique Bretagne 19, 59–77.

Deunff, J., 1980. Le paléoplancton des Grès de Landévennec (Gedinnien de la rade de Brest - Finistère) étude biostratigraphique. Geobios 13, 483–539.

Deunff, J., Evitt, W.R., 1968. *Tunisphaeridium*, a new acritarch genus from the Silurian and Devonian. Stanford Univ. Publ. Geol. Sci. 12, 1–13.

Downie, C., 1959. Hystrichospheres from the Silurian Wenlock Shale of England. Palaeontology 2, 56–71.

Eisenack, A., 1938. Hystrichosphaerideen und verwandte Formen im baltischen Silur. Zeitschrift für Geschiebeforsch. und Flachlandsgeologie 14, 1–30.

Eisenack, A., 1954. Hystrichosphären aus dem baltischen Gotlandium. Senckenb. Lethaea 34, 205–211.

Eisenack, A., Cramer, F.H., Díez Rodríguez, M. del C.R., 1973. Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien Band III Acritarcha 1. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Eisenack, A., Cramer, F.H., Díez, M. del C.R., 1976. Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien Band IV Acritarcha 2. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Fensome, R.A., Williams, G.L., Barss, M.S., Freeman, J.L., Hill, J.M., 1990. Acritarchs and fossil prasinophytes: an index to genera, species and infraspecific taxa. AASP Contrib. Ser. 1–771.

Fombella Blanco, M.A., 1988. Miosporas de la formación Huergas, edad Devónico medio, Provincia de León, NO. de España. Acta Salmant. Bibl. las ciências 65, 299–305.

García-Alcalde, J.L., 1998. Devonian events in northern Spain. Newslett. Stratigr. 36, 157–175.

García-Alcalde, J.L., Carls, P., Alonso, M.V.P., López, J.S., Soto, F., Truyóls-Massoni, M., Valenzuela-Ríos, J.I., 2002. Devonian. In: Gibbons, W., Moreno, T. (Eds.), The Geology of Spain. The Geological Society of London, London, pp. 67–91.

García-López, S., Sanz-López, J., 2002. Devonian to Lower Carboniferous conodont biostratigraphy of the Bernesga Valley section (Cantabrian Zone, NW Spain). In: García-López, S., Bastida, F. (Eds.), Palaeozoic Conodonts from Northern Spain: Eighth International Conodont Symposium Held in Europe. Cuadernos Del Museo Geominero. Publicaciones del Instituto Geológico y Minero de España, Madrid, pp. 163–205.

García-López, S., Sanz-López, J., Sarmiento, G.N., 2002. The Palaeozoic succession and conodont biostratigraphy of the section between Cape Peñas and Cape Torres (Cantabrian coast, NW Spain). In: García-López, S., Bastida, F. (Eds.), Palaeozoic Conodonts from Northern Spain: Eighth International Conodont Symposium Held in Europe. Cuadernos Del Museo Geominero. Publicaciones del Instituto Geológico y Minero de España, Madrid, pp. 125–161.

García-Ramos, J.C., 1978. Estudio e interpretación de las principales facies sedimentarias comprendidas en las Formaciones Naranco y Huergas (Devónico medio) en la Cordillera Cantábrica. Trab. Geol. 195–266.

IGME, 2015. GEODE. Mapa Geológico Continuo de España.[Online]. Available from. http://mapas.igme.es/gis/rest/services/Cartografia_Geologica/IGME_Geode_50/MapServer [Accessed 09-02-18].

Jardiné, S., Yapaudjan, L., 1968. Lithostratigraphie et palynologie du Dévonien-Gothlandien gréseux du bassin de Polignac (Sahara). Rev. l'Institut Français Pétrole Ann. des Combust. Liq. 13, 439–469.

Jardiné, S., Combaz, A., Magloire, L., Peniguel, G., Vachey, G., 1974. Distribution stratigraphique des Acritarches dans le Paléozoïque du Sahara Algérien. Rev. Palaeobot. Palynol. 18, 99–129.

Johnson, N.G., 1985. Early Silurian palynomorphs from the Tuscarora formation in Central Pennsylvania and their paleobotanical and geological significance. Rev. Palaeobot. Palynol. 45, 307–359.

Kiryanov, V.V., 1978. Akritarkhi silura Volyno-Podolii. Akad. Nauk Ukr. SSR, Inst. Geol. Nauk. Kiev, Nauk. Dumka 1–116.

Le Hérissé, A., Gourvennec, R., Wicander, R., 1997. Biogeography of Late Silurian and Devonian acritarchs and prasinophytes. Rev. Palaeobot. Palynol. 98, 105–124.

Le Hérissé, A., Servais, T., Wicander, R., 2000. Devonian acritarchs and related forms. In: Bultynck, P. (Ed.), Subcommission on Devonian Stratigraphy. Fossil groups Important for Boundary Definition. Courier Forschungsinstitut Senckenberg, pp. 195–205.

Legault, J.A., 1973. Chitinozoa and Acritarcha of the Hamilton Formation (Middle Devonian), southwestern Ontario. Geol. Surv. Canada, Bull. 221, 1–103.

Lister, T.R., 1970. The Acritarchs and Chitinozoa from the Wenlock and Ludlow Series of the Ludlow and Millichope areas, Shropshire. Palaeontogr. Soc. Monogr. 124, 1–100.

Martin, F., 1984. Acritarches du Frasnien supérieur et du Famennien inférieur du bord méridional du bassin de Dinant (Ardenne belge). Inst. R. des Sci. Nat. Belgique, Sci. la terre, Bull. 55, 1–57.

Moczydłowska, M., 1998. Cambrian acritarchs from Upper Silesia, Poland - biochronology and tectonic implications. Foss. Strat. 46, 1–121.

Molyneux, S.G., Delabroye, A., Wicander, R., Servais, T., 2013. Biogeography of early to mid Palaeozoic (Cambrian-Devonian) marine phytoplankton. Geol. Soc. London, Mem. 38, 365–397.

Moreau-Benoit, A., 1984. Acritarches et chitinozoaires du Devonien Moyen et Superieur de Libye Occidentale. Rev. Palaeobot. Palynol. 43, 187–216.

Ottone, G.E., 1996. Devonian palynomorphs from the Los Monos formation, Tarija Basin, Argentina. Palynology 20, 105–155.

Pichler, R., 1971. Mikrofossilien aus dem Devon der südlichen Eifeler Kalkmulder. Senckenb. Lethaea 52, 315–357.

Playford, G., 1977. Lower to Middle Devonian acritarchs of the Moose River Basin, Ontario. Geol. Surv. Canada, Bull. 279, 1–87.

Playford, G., Dring, R.S., 1981. Late Devonian acritarchs from the Carnarvon Basin, Western Australia. Spec. Pap. Palaeontol. 27, 1–78.

Rubinstein, C., 1999. Primer registro palinológico de la Formación Punta Negra (Devónico Medio-Superior), de la Precordillera de San Juan, Argentina. 10o Simp. Argentino Paleobotánica y Palinol. 6, pp. 13–18 (Buenos Aires), Publicación Espec.

Rubinstein, C., 2000. Middle Devonian palynomorphs from the San Juan Precordillera, Argentina: biostratigraphy and paleobiogeography. Int. Congr. Ibérico Paleontol. Jornadas la Soc. Española Paleontol. VIII Int. Meet. IGCP. 421, pp. 274–275.

Sarjeant, W.A.S., Vavrdová, M., 1997. Taxonomic reconsideration of *Multiplicisphaeridium* Staplin, 1961 and other acritarch genera with branching processes. GeoLines 5, 1–52.

Shen, Z., Song, J., Servais, T., Gong, Y., 2018. Late Devonian palaeobiogeography of marine organic-walled phytoplankton. Palaeogeogr. Palaeoclimatol. Palaeoecol. https://doi.org/10.1016/j.palaeo.2018.03.018.

Staplin, F.L., 1961. Reef-controlled distribution of Devonian microplankton in Alberta. Palaeontology 4, 392–424.

Stockmans, F., Willière, Y., 1960. Hystricosphères du Dévonien belge (Sondage de l'Asile d'aliénés à Tournai). Senckenb. Lethaea 41, 1–11.

Stockmans, F., Willière, Y., 1962. Hystricosphères du Dévonien belge (Sondage de l'Asile d'aliénés à Tournai). Bull. la Société Belge Géologie Paléontologie d'Hydrologie 71, 41–77.

Stockmans, F., Willière, Y., 1963. Les Hystrichosphères ou mieux les acritarches du Silurien Belge, Sondage de la Brasserie Lust à Courtrai (Kortrijk). Bull. la Société Belge Géologie Paléontologie d'Hydrologie 71, 450–481.

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 615–621.

Torsvik, T.H., Cocks, L.R.M., 2013. Gondwana from top to base in space and time. Gondwana Res. 24, 999–1030.

Torsvik, T.H., Cocks, L.R.M., 2016. Earth History and Palaeogeography. Cambridge University Press, Cambridge.

Traverse, A., 2008. Paleopalynology. Topics in Geobiology, 2nd ed Springer, Dordrecht.

Turnau, E., Racki, G., 1999. Givetian palynostratigraphy and palynofacies: new data from the Bodzentyn Syncline (Holy Cross Mountains, Central Poland). Rev. Palaeobot. Palynol. 106, 237–271.

Vanguestaine, M., Declairfayt, T., Rouhart, A., Smeesters, A., 1983. Zonation par Acritarches du Frasnien Supérieur - Famennien Inférieur dans les bassins de Dinant, Namur, Herve et Campine (Dévonien Supérieur de Belgique). Ann. la Société Géologique Belgique 106, 121–171.

Wellman, C.H., 2018. Palaeoecology and palaeophytogeography of the Rhynie chert plants: further evidence from integrated analysis of in situ and dispersed spores. Philos. Trans. R. Soc. B Biol. Sci. 373, 20160491.

Wellman, C.H., Steemans, P., Vecoli, M., 2013. Palaeophytogeography of Ordovician-Silurian land plants. Geol. Soc. London, Mem. 38, 461–476.

Wicander, R., 1974. Upper Devonian–Lower Mississippian Acritarchs and Prasinophycean Algae from Ohio, USA. Palaeontogr. Abteilung B Paläophytologie 148, 9–43.

Wicander, R., Loeblich Jr., A.R., 1977. Organic-walled microphytoplankton and its stratigraphic significance from the Upper Devonian Antrim Shale, Indiana, USA. Palaeontogr. Abteilung B Paläophytologie 160, 129–165.

Wicander, R., Playford, G., 2017a. Organic-walled microphytoplankton assemblage of the Middle Devonian (Givetian) Arkona, Hungry Hollow and Widder formations, Ontario, Canada: biostratigraphic and palaeogeographic significance. Bol. Geológico y Min. 128, 839–883.

Wicander, R., Playford, G., 2017b. Organic-walled microphytoplankton from the Middle Devonian (Givetian) Gravel Point Formation, Michigan, USA. Palynology 41, 158–177.

Wicander, R., Wood, G.D., 1981. Systematics and biostratigraphy of the organic-walled microphytoplankton from the Middle Devonian (Givetian) Silica Formation, Ohio, USA. AASP Contrib. Ser. 8, 1–137.

Wicander, R., Wood, G.D., 1997. The use of microphytoplankton and chitinozoans for interpreting transgressive/regressive cycles in the Rapid Member of the Cedar Valley Formation (Middle Devonian), Iowa. Rev. Palaeobot. Palynol. 98, 125–152.

Wicander, R., Wright, R.P., 1983. Organic-walled microphytoplankton abundance and stratigraphic distribution from the Middle Devonian Columbus and Delaware Limestones of the Hamilton Quarry, Marion County, Ohio. Ohio J. Sci. 83, 2–13.

Wood, G.D., Clendening, J.A., 1985. Organic-Walled Microphytoplankton and Chitinozoans from the Middle Devonian (Givetian) Boyle Dolomite of Kentucky, U.S.A. Palynology 9, 133–145.

Zhu, H., Wicander, R., Marshall, J.E.A., 2008. Biostratigraphic and paleogeographic significance of a palynological assemblage from the Middle Devonian Ulusubasite Formation, eastern Junggar Basin, Xinjiang, China. Rev. Palaeobot. Palynol. 152, 141–157.