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Dispersed spore assemblages from the Middle-Upper Devonian (mid Givetian to earliest Frasnian) Candás Formation of Northern Spain

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ABSTRACT

The Devonian sequence of the Cantabrian Zone of Northern Spain was deposited around an isolated group of islands (Armorican Terrane Assemblage - ATA) between the Laurussia and Gondwana supercontinents. The Candás Formation (Asturias) and equivalent Portilla Formation (Léon) represent one of the main episodes of reefal development within this sequence. Herein we report, for the first time, palynomorph assemblages recovered from these formations. Palynomorphs recovered from the Portilla Formation are poorly preserved and of high thermal maturity. They are dominated by dispersed spores but also contain

abundant and diverse marine elements (acritarchs, chitinozoans and scolecodonts). Due to the challenging preservation, it is not possible to undertake an in-depth study of these assemblages. Palynomorphs recovered from the Candás Formation (members B and D) are exceptionally well preserved and of low thermal maturity. They are dominated by dispersed land plant spores, but also contain rarer marine elements (acritarchs, chitinozoans and scolecodonts). Member B spore assemblages belong with the *triangulatus-catillus* Assemblage Zone (*catillus* Subzone) of mid Givetian age. Member D spore assemblages belong with the *langii-concinna* Assemblage Zone of late Givetian to earliest Frasnian age. This is concordant with independent age dating based on conodonts and invertebrates. The spore assemblages are of North Gondwana aspect but exhibit evidence for distinct endemism. They are dominated by progymnosperm spores indicating a vegetation dominated by arborescent archaeopteridaleans and aneurophytaleans.

Key words: spores, progymnosperms, palynofacies, Armorican Terrane Assemblage

1. Introduction

In Northern Spain, important Devonian rock outcrops are preserved in the so-called Cantabrian Zone, a Palaeozoic unit in the Alpine Cantabrian Mountains (Fig. 1). Here, the Candás Fm (Asturias) and stratigraphic equivalent Portilla Fm (Léon) span the mid Givetian to earliest Frasnian and record one of the main reef building episodes in the Devonian sequence (García-López, 2002) (Fig. 2). The lithostratigraphy and rich palaeontology are thoroughly documented with the palaeoenvironments well understood based on numerous sedimentological and palaeontological studies (Fernández et al., 1997; García-López and Sanz-López, 2002a, b; García-Alcalde, 2022). This enables tight biostratigraphical control based primarily on conodont and brachiopod faunas (Fig. 3). We have recovered, for the first time, rich palynomorph assemblages from these formations. These contain mixed terrestrial (land plant spores) and marine (acritarchs, chitinozoans and scolecodonts) palynomorphs. Herein we document these palynomorphs and use them to provide additional biostratigraphical, palaeoenvironmental and palaeobiogeographical evidence and to reconstruct the flora of the Armorican Terrane Assemblage (ATA), an archipelago situated

between the supercontinents of Laurussia, to the north, and Gondwana to the south. We also consider their bearing on the Taghanic Crisis and Genesee Crisis (considered to initiate and conclude the wider Taghanic Event) that occurred worldwide during the deposition of these rock units.

2. Geological Setting

The Candás Fm was defined by Barrois (1882) at the locality of Perán (Carreño city council, coast of Asturias, Fig. 1). It represents a return to carbonate sedimentation from the underlying siliciclastic Naranco Fm and was succeeded by a new interval of siliciclastic sediment supply of the Piñeres Fm (Adaro and Junquera, 1914; Radig, 1962) (Fig. 3). The Candás Fm corresponds to one of the most important reef-building episodes in the Devonian of the Cantabrian Mountains (so-called VII by Fernández-Martínez et al., 2006). The thickness of the Candás Fm is variable (57-240 m thick according to Rupke, 1965; Mohanti, 1972). Comte (1936) named an equivalent limestone (Portilla Fm) in the southern side of the Cantabrian Mountains (León Province), but the name from the north side of the cordillera has priority in the stratigraphic nomenclature. Below the Portilla Fm is the Huergas Fm, a shaley unit replacing the Naranco Fm deposited in the north side of the Cantabrian Mountains. Above the Portilla Fm are sandstones and shales of the Nocedo Fm (Comte, 1936) that correspond to the lower part of the Piñeres Fm on the north side of the Cantabrian Mountains (Fig. 2).

The Candás Fm accumulated on a shallow marine platform in sublittoral conditions although peritidal facies are also observed (Reijers, 1972). Two models have been proposed: reef-rimmed platform geometry (Reijers, 1972) and a gentle slope carbonate ramp with common biostromal development and local small isolated bioherms (Fernandez-Martínez et al., 1994; Méndez-Bedia et al., 1994; Fernández et al., 1997). The formation is locally subdivided into four informal members with locally established boundaries, although other terms and formal members have been used occasionally (Table I).

Member A of the Candás Fm consists of bioclastic limestones with marls with increasing proportions of stromatoporoid and thamnoporid tabulate corals upwards (García-Alcalde et al., 1979). It may be dominated by crinoidal, bryozoan and marly brachiopod packstones to

grainstones, with one to two oolite levels close to the base and the top (Raven, 1983). Member B is predominantly composed of frame-building organisms and contains stringocephalid brachiopods. Member C comprises shales, marls, sandy limestones and local sandstones. Low-angle cross-stratification, an oolite bed and a basal erosive surface have been described (Bereskin, 1978; van Loevezijn and Raven, 1984). Member D is biostromal, although it is absent from several sections of the southern Cantabrian Mountains, among them the Huergas de Gordón section studied here.

Biostratigraphy of the Candás Fm is based on invertebrates, mostly brachiopods, grouped into informal association zones or faunal interval (FIs) as defined by García-Alcalde (1996). In addition, García-Alcalde (2022) defined several interval zones based on brachiopods in the upper part of the Candás Fm. Conodont faunas have been reported by Adrichem Boogaert (1967), García-López (1972, 1976, 1987), García-Alcalde et al., (1979), Raven (1983) and García-López and Sanz-López (2002a, b). Conodonts are dominated by nearshore *Icriodus* species, whereas *Polygnathus* and other genera were restricted to deepening pulses.

The upper part of the underlying Huergas Fm and the lower part of the member A in the south side of the Cantabrian Mountains were assigned to the *Polygnathus timorensis* conodont Zone (Raven, 1983; García-López, 1987) (Fig. 3). The *P. timorensis* Zone of Bultynck (1987) is equivalent to the Lower *P. varcus* Subzone of the standard zonation (Ziegler et al., 1976) that is early Givetian in age. Brachiopods from the lower beds are included in FI 20 (Fig. 4). The basal beds of the Candás Fm are probably younger in age in several sections to the north and east of the Cantabrian Zone (middle Givetian *Polygnathus rhenanus*/*P. varcus* Zone), such as in the Vozmediano, Coallajú and Perán sections (Raven, 1983; García-López and Sanz-López, 2002a). Brachiopods in those locations are assigned to FI 21 (García-Alcalde, 1996, 2010, 2014, 2022).

The *Polygnathus ansatus* Zone of Bultynck (1987) or Middle *P. varcus* Subzone of Ziegler et al., (1976) is recognised at 8.5 m above the base of the formation in the Perán section and in member A of several sections (Adrichem Boogaert, 1967; Reijers, 1972; Raven, 1983; García-López, 1987; García-López and Sanz-López, 2002a) (Figs. 3, 4).

The lower part of member B includes typical reefal brachiopods, such as *Stringocephalus* and *Parastringocephalus* sp., in the upper part of FI 21 in the Perán section (García-Alcalde, 2022). An erosive transgressive surface on reefal sequences was buried by echinoderm calcarenites with cross-lamination in member B (Fernández et al., 1997; Fernández-Martínez

et al., 2008). It yielded an impoverished ostracod association and the first occurrence of brachiopods and corals of FI 22 (García-Alcalde et al., 1979; García-Alcalde, 2012, 2022; Maillet et al., 2016). Above, a deepening event at the base of member C is recorded in the alternation of skeletal limestone and shale that was correlated with the basal Taghanic Event / Biocrisis of House (1985), based on ostracod faunas (Maillet et al., 2016). Unfortunately, the conodont marker species for this event (*Polygnathus alveoliposticus*) is unknown in the Cantabrian Mountains. The early Taghanic onlap may be correlated with a deepening of sedimentation recognised by the occurrence of argillaceous limestone with alveolitid colonies, *Phyllisastrea*, and thamnoporids in the Huergas de Gordón section (unit B of García-Alcalde et al., 1979 in Fig. 4). The overlying crinoidal beds yielded *Polygnathus ovatinodosus* that can be correlated with the upper part of the *P. ansatus* Zone (Fig. 4). The correlation of the Taghanic Bio-crisis was supported by the correlation with the Gv26a zone in the magnetic susceptibility record (MS SRZ) associated with a transgressive pulse in the Huergas de Gordón section (García-Alcalde et al., 2012). This MS SRZ was correlated with the *Schmidtognathus latifossatus* / “*Ozarkodina*” *semialternans* Zone of Bultynck (1987) and the “*O.*” *semialternans* after Aboussalam (2003) in other basins. “*O.*” *semialternans* occurs close the top of Faunal Interval 22 in the Huergas de Gordón section and with *P. ovatinodosus* in the Perán section (García-López and Sanz-López, 2002a, b). A turnover on the fauna occurred at the boundary between FI 22 and FI 23 (García-Alcalde, 1996).

Cosmopolitan invertebrate genera of FI 23 radiated and dispersed during the Geneseo transgression, with the identification of the latter supported by magnetic susceptibility stratigraphy (García-Alcalde et al., 2012). The Geneseo Crisis, associated with this transgression, is seen as the culmination of the wider Taghanic Event (e.g. García-Alcalde et al., 2012). The brachiopod assemblage was correlated with Gosselet’s “Niveau des monstres” of Western Europe (García-Alcalde et al., 1979, 1986; García-Alcalde, 2022). The occurrence of the conodont *Schmidtognathus hermanni* in the Geneseo deepening of the studied sections coincides with siliciclastic dark shale with siltstone and sandy carbonates in member C.

The *Klapperina disparilis* conodont Zone correlates with the uppermost beds of the Candás Fm in the Huergas de Gordón section based on magnetic susceptibility (GV28 MS SRZ in García-Alcalde et al., 2012). Just above, the siliciclastic supply prevented coral development in the southernmost stratigraphic sections and caused the lateral replacement of the Candás Fm. by the Nocado Fm (Fig. 3). At the Perán section, sedimentation occurred in a

back-reef, lagoon setting area including interbedded crinoidal tempestites, siliciclastic beds and biostromes of *Disphyllum* and thamnoporid tabulate corals (Radig, 1962; García-Alcalde et al., 1986; Fernandez et al., 1997). The lowermost Frasnian conodont *Ancyrodella pristina* occurs 4 m below the top of the Candás Fm in this section (García-López and Sanz-López, 2002a). Above, the shallow-water siliciclastic Nocado/Piñeres fms extend along the Cantabrian Mountains (Fig. 3).

3. Materials and Methods

We sampled two sections: the section of the type Candás Fm at Perán on the north Asturian coast (García-López et al., 2002a) (11 samples) and the section of the Portilla Fm in the hillside south of Huergas de Gordón in the Cantabrian Mountains (García-López and Sanz-López, 2002b) (13 samples). Details of the samples are provided in the Appendix. The location of the sections is illustrated in Fig. 1 with the distribution of samples within these sections illustrated in Fig. 4.

Samples were processed at the University of Sheffield using standard HCl-HF-HCl palynological acid maceration techniques. Samples were sieved using a 20µm mesh, subjected to a heavy liquid separation using ZnCl₂, and further sieved using a 20µm mesh. The residues were then oxidised using fresh Schultz solution for varying periods of time before being strewn mounting onto glass coverslips and then glued to glass slides using epoxy resin. Slides were examined using standard light microscopy techniques and images captured using a Q Imaging MicroPublisher 3.3 RTV camera.

The samples from the Candás Fm section generally yielded abundant palynomorphs that were well preserved and of moderate thermal maturity (TAI 3- to 3+ based on the colour scheme in Traverse, 2007). Conodont Colour Alteration Index is low, although variable (1.5–2–2.5) according to García-López et al. (1997). Samples oxidised successfully producing well preserved, translucent palynomorphs. The samples from the Portilla Fm section generally yielded abundant palynomorphs that were poorly preserved and of high thermal maturity (TAI 3 to 4- based on the colour scheme in Traverse, 2007). Conodont Colour Alteration Index is 3.5 to 4 indicating deep diagenetic conditions (Aller et al., 2005). They did not oxidise successfully.

The Candás Fm slides were logged and a spore taxonomy erected with presence/absence data collected. The Portilla Fm slides were logged but only the presence of distinctive spore taxa could be ascertained due to their poor preservation and high thermal maturity, although spores, acritarchs, chitinozoans and scolecodonts could be differentiated. A basic palynofacies count of 200 palynomorphs (spores: acritarch: chitinozoans: scolecodonts) was undertaken on selected samples (22CAN02P, 22CAN04P, 22HdG15P).

All materials (rock, residues, slides) are housed in the collections of the Centre for Palynology of the School of Biosciences, University of Sheffield, UK. Figured specimens are located using England Finder Co-ordinates.

4. Results

All the productive samples from the Candás Fm section are dominated by spores. Scolecodonts are present in all samples and are relatively diverse. Acritarchs are present in all samples but are rare and constitute a few simple forms. Chitinozoans are only present in sample 22CAN02P and 22CAN07P where they are rare and constitute only a few taxa. All of the samples from the Portilla Fm section are dominated by spores. However, acritarchs and scolecodonts are abundant and diverse. Chitinozoans are present in most samples but are rare and constitute only a few taxa. It was not possible to consider the samples from the Portilla Fm section further as they are too poorly preserved.

The samples from the Candás Fm section include a single productive sample from the uppermost part of member B (22CAN02P) and numerous productive samples from the middle and upper part of member D. Table 1 provides a list of dispersed spore taxa encountered and their distribution among the samples. Plates I – V provide photographs of these taxa.

Breuer and Steemans (2013) proposed a number of ‘spore morphons’ of which seven are represented in the mid Givetian-earliest Frasnian of northwestern Gondwana (Saudi Arabia and North Africa). We have representatives of five of these in our spore assemblages: *Apiculiretusispora brandtii* morphon (*A. brandtii* and *R. minutus* but not *C. asymmetricus*), *Cymbosporites catillus* morphon (*C. cyathus* but not *C. catillus*), *Grandispora incognita* morphon (*G. incognita* but not *G. naumovae*), *Samarisporites eximius* morphon (*S. praetervisus* but not *S. angulatus* or *S. eximius*), *Verrucosisporites scurrus* morphon (*V.*

premnus and *V. scurrus* and less common representatives of *Dibolisporites farraginis* and *D. uncatus*). Notably representatives of the *Archaeozonotriletes variabilis* morphon and *Cristatisporites reticulatus* morphon are absent.

5. Discussion

5.1. Biostratigraphy

It is clear based on key absences/presences that the dispersed spore assemblages from the Candás Fm section have much more in common with those described from Gondwana compared to those from Laurussia (as discussed below). Thus, the spore biostratigraphy scheme developed by Breuer and Steemans (2013) for northwestern Gondwana is most appropriate. The Candás Fm section (member D) assemblage is herein equated with the *langii-concinna* Assemblage Zone of latest Givetian-earliest Frasnian age. This is concordant with the late Givetian earliest Frasnian age suggested by previous biostratigraphical studies based on conodonts and brachiopods as discussed in Section 2 (Figs. 3-4). Both nominal species of the zone are present as are several other taxa that are reported as characteristic of it (*Acinosporites lindlarensis*, *Chelinospora timanica*, *Cymbosporites catillus* Morphon, *C. variegatus*, *Dibolisporites farraginis*, *D. uncatus*, *Emphanisporites laticostatus*, *Geminospora lemurata*, *Grandispora incognita*?, *G. stolidata*, *Rhabdosporites langii*, *Samarisporites triangulatus*, *Verrucosisporites premnus*).

The assemblage from near the Candás Fm section (top of member B) is less species rich and the specimens less well preserved than those from member D. Nonetheless it is clearly very similar to the assemblages from member D. However, the absence of *Ancyrospora langii* and *Chelinospora concinna* exclude it from the *langii-concinna* Assemblage Zone. The presence of *Samarisporites triangulatus* indicates that it belongs with the *triangulatus-catillus* Assemblage Zone with the presence of the *Cymbosporites catillus* Morphon suggesting that it belongs with the *catillus* Subzone. This subzone extends from the mid to late (but not latest) Givetian age. Again, this is in agreement with previous biostratigraphical studies that suggest that member B has a late mid Givetian age correlated with the *P. ansatus* conodont Zone and pre-Taghanic Biocrisis episode as discussed in Section 2 (Figs. 3-4).

Regarding spore zonation schemes developed for Laurussia, the *langii-concinna* Assemblage Zone is equivalent to the *optivus-triangularatus* Spore Assemblage Biozone (OT SAB) in the scheme of Richardson and McGregor (1986) and TCo Oppel Zone in the scheme of Streel et al. (1987) (Fig. 5). In terms of the former, only one of the nominal species is present in the assemblages from the Candás Fm (member D) section, with *Samarisporites triangularatus* reported but not *Contagisporites optivus* var. *optivus*. Only a few of the named characteristic species are present, with the absence of the distinctive monolete spore *Archaeoperisaccus* being notable. In terms of the latter, both nominal species are present, although *Cirratriradites jekhowskyi*, which is characteristic of the zone, is not reported.

The *triangularatus-catillus* Assemblage Zone (*catillus* Subzone) is equivalent to the upper part of the *lemurata-magnificus* Spore Assemblage Biozone (LM SAB) in the scheme of Richardson and McGregor (1986) and upper part of the TA Oppel Zone in the scheme of Streel et al. (1987) (Fig. 5). Due to the depauperate nature of the solitary Spanish sample of this age from member B it is difficult to make meaningful comparisons. However, regarding the scheme of Richardson & McGregor (1986), only one of the nominal species is present in the assemblage from the Candás Fm (member B) section, with *Geminospora lemurata* reported but not *Cymbosporites magnificus*, and only a very few of the named characteristic species are present. Interestingly *C. magnificus* is associated with lycopsid forests from the late Givetian-early Frasnian equatorial regions (Berry and Marshall, 2015). Regarding the scheme of Streel et al. (1987), both nominal species are present.

The differences outlined above, for both member B and member D spore assemblages most likely reflect clear palaeophytogeographical differentiation between the floras of Gondwana and Laurussia as discussed below.

5.2. Palaeophytogeography

Previous palynological studies of the Silurian-Devonian sequence of the Cantabrian Zone of Northern Spain have addressed the affinities of these ATA assemblages with respect to Laurussia to the north and Gondwana to the south and discussed the degree of endemism. It is evident from the work of Rodríguez (1983) and Richardson et al. (2001) that the Ludlow-Lochkovian spore assemblages from the Furada/San Pedro fms are endemic. They are very different from coeval spore assemblages from Laurussia. They have more in

common with those from Gondwana, but there are significant differences, to the extent that the authors developed an independent zonation scheme. Richardson et al. (2001) noted that differences were most marked in the Pridoli before becoming less pronounced in the Lochkovian.

Emsian spore assemblage described from the upper part of the Rañeces/La Vid groups by Wellman et al. (2023) again have more in common with spore assemblages from Gondwana compared to those from Laurussia and are reported to still exhibit significant endemism. The same applies to Emsian/Eifelian boundary spore assemblages from the uppermost Moniello/lowermost Naranco fms reported by Lopes et al. (2024) and late Eifelian to early Givetian spore assemblages from the Naranco/Huergas fms most recently described by Askew and Wellman (2018). Marine elements (both acritarchs and chitinozoans) from the latter are also reported to exhibit significant endemism (Askew, 2019; Askew and Russell, 2019; Askew and Wellman, 2020).

When compared to *langii-concinna* AZ spore assemblages from northwestern Gondwana described by Breuer and Steemans (2013) the late Givetian-earliest Frasnian assemblages reported herein are slightly less diverse with only 40-or-so distinct common species compared to 55 (Table 2). Of these 20 species are common to both assemblages with the remaining 20-or-so present only in the Spanish assemblages (Table 2). Thus the Spanish assemblages can be said to have Gondwanan affinities in the sense that the *langii-concinna* AZ can clearly be recognised, but they still show evidence for endemism in that: (i) many taxa (and morphons) characteristic of the northern Gondwanan assemblages are missing (for example representatives of the *Archaeozonotriletes variabilis* morphon and *Cristatisporites reticulatus* morphon are not reported); (ii) approximately half of the taxa present are not reported from northern Gondwana. The latter includes taxa, such as *Emphanisporites annulatus*, that are present in northern Gondwana but only in older assemblages.

When compared to *triangulatus-catillus* AZ spore assemblages from northwestern Gondwana described by Breuer and Steemans (2013) the solitary late Givetian sample reported herein is depauperate containing only 18 taxa compared to a total of 55 from northwestern Gondwana (Table 3). Of these 13 species are common to both assemblages with the remaining 5 present only in the Spanish assemblages (Table 3). Overall, the Spanish assemblages can be said to have Gondwanan affinities, in the sense that the *triangulatus-*

catillus AZ can clearly be recognised, but little can be said regarding endemism due to the depauperate nature of the solitary sample.

Palaeo-continental reconstructions vary in the degree of rotation of Gondwana over the course of the Mid to Late Devonian. In some reconstructions, such as Torsvik and Cocks (2017) (Fig. 6), the extent of rotation is such that the ATA ends up closer to South America (western Gondwana) than North Africa (northwestern Gondwana). Numerous dispersed spore assemblages have been described from South America that are of similar age to the Spanish assemblages described herein (e.g. Argentina: Ottone, 1996, Amenabar, 2009, Noetinger and Di Pasquo, 2011, García-Muro et al., 2025; Bolivia: Di Pasquo, 2007, Troth et al., 2011; Brazil: Melo and Loboziak, 2003). The Spanish assemblages described herein have many common elements with those of southern South America but differ in overall composition. The South American assemblages are generally dominated by relatively simple spores including a significant abundance of the *Verrucosisporites premnus* morphon. Both *Geminospora lemurata* and *Cymbosporites* are present but never more than minor elements of the assemblage. Interestingly, *Cristatisporites triangulatus* is present together with elements absent from the ATA terrane such as *Archaeozonotriletes variabilis* and *Chelinospora concinna*. *Ancyrospora* and other bifurcate tipped spores are present but are similarly rare.

5.3. Palaeobotanical implications

One of the most striking aspects of the dispersed spore assemblages described herein is the high abundance of *Geminospora lemurata* and its high degree of morphological variation (illustrated in Plate IV). This range of variation is completely intergradational and consequently all the specimens can be accommodated within the taxon *G. lemurata*. However, in future it may be useful to consider this taxon with respect to the morphon concept as end members may well be assigned to other species of *Geminospora* if studied in isolation. It is noteworthy that *G. lemurata* often occurs with unusual haptotypic features. There is a monolete form (Plate IV fig. 25) and a form with a X-shaped haptotypic mark (Plate IV figs. 23-24). Similar forms are often documented in the literature and Breuer and Steemans (2013, p. 152) noted that in their *langii-concinna* Assemblage Zone “The monolete spores are above all present with the monolete form of *Geminospora lemurata*.”.

The abundance of *G. lemurata* and associated spores at similar stratigraphical levels has long been known. For example, Richardson and McGregor (1986, p.17) noted that their *optivus-triangulatus* SAB showed “Diversification of small-sculptured camerate spores with a thick exoexine (*Geminospora*) and their dominance in some nearshore marine and external continental facies.”.

The spores of archaeopteridalean progymnosperms are widely reported as *Geminospora* (microspore) and *Contagisporites* (megaspore) (Marshall et al., 2022). Thus, we can assume that the large populations of *G. lemurata* derives from extensive forests of *Archaeopteris* trees. The megaspore *Contagisporites* has yet to be reported from the Spanish Devonian sequence, although it is noteworthy that large megaspores are relatively rare in the Candás Fm assemblages. This megaspore has previously been reported from Gondwana (e.g. Troth et al., 2011). Aneurophytalean progymnosperms were also present as evidenced by the presence of *Rhabdosporites langii* that is known in situ from such plants as *Rellimia* (Marshall, 1996; Wellman, 2009).

The presence of lycopsids among the flora is evidenced by the occurrence of *Ancyrospora* that was produced by this group of plants (Wellman, 2002). Interestingly Askew and Wellman (2018) noted that spores with bifurcate or multifurcate-tipped spines are absent (or very rare) in pre-mid Givetian spore assemblages from the Spanish succession, suggesting their late arrival on the ATA compared to Laurussia. This seemingly mirrors the situation in northwestern Gondwana reported by Breuer and Steemans (2013).

The inception and migration of progymnosperms and lycopsids around the Devonian globe, with respect to homosporous and heterosporous forms, has recently been discussed based on new evidence from the isolated islands, including Mariana-type volcanic arcs, of North China and South China (Xu et al., 2014; Marshall et al., 2017). They suggested that lycopsids were the most mobile elements of the contemporary flora with spores such as *Acinosporites lindlarensis* ubiquitous. On the other hand, progymnosperms, particularly heterosporous forms, appear to have been less suited for long-distance dispersal. Thus, the isolated islands of South China and North China, located off North Gondwana, have spore assemblages of northern Gondwana affinity but also contain species with younger age ranges. This suggests the flora was somewhat relictual in nature. This is probably a very similar situation to that seen in the isolated ATA islands that also lay offshore from North Gondwana.

5.4. Palynofacies

There are clear differences in the abundance and diversity of non-marine versus marine palynomorphs present in the assemblages from the Candás Fm. Member B assemblage 22CAN02 is dominated by spores (97.0%) with rare acritarchs (0.5%), chitinozoans (0.5%) and scolecodonts (2.0%). Member D assemblage 22CAN04 is similarly dominated by spores (96.5%) with rare acritarchs (1.5%) and scolecodonts (2.0%). Whilst chitinozoans feature in the count of the former, with a few specimens per slide, they do not feature in counts of the latter, with only a few putative chitinozoans present in all of the slides examined. The succession of the Candás Fm at Perán was deposited in the inner part of the reefal bioconstructions (member B) and the backreef setting (member D), which may explain the paucity of marine elements other than scolecodonts. The succession of the Portilla Fm at Huergas de Gordón accumulated on the open side of the outer ramp of the reefal belt. This provides a clear explanation for the increased abundance and diversity of all marine elements. Sample 22HdG15 is still dominated by spores (65.0%) but with abundant marine palynomorphs in the form of acritarchs (33.0%), chitinozoans (0.5%) and scolecodonts (1.5%). The dominance of land-derived land plant spores in both environments suggests easy access and a steady supply from the land via inflow from rivers and offshore winds into proximal marine settings.

5.5. The Taghanic and Geneseo crises

The Taghanic Crisis (House, 1985) is a second order global biocrisis initially recognised as a series of time-transgressive events correlated with the Taghanic onlap in the Lower Tully Limestone of the New York sequence in Depophase IIa of the Johnson et al. (1985) sea level curve. The crisis was particularly severe for corals and other reef dwellers such as stromatoporoids, and this has been ascribed to thermal stress (warming) and locally, the expansion of anoxia into shallow waters (Aboussalam and Becker, 2011). Aboussalam and Becker (2011) placed the Taghanic Crisis interval in the *P. ansatus* Zone. This is below the level of the younger Geneseo Crisis which is placed in the basal *S. hermanni* Zone (Aboussalam and Becker, 2011). This latter event was first recognized as a further transgression that occurred at the top of the Tully Limestone in New York, where it manifested in the Geneseo Formation, an anoxic black shale. Aboussalam (2003) considers the interval between these two major transgressive events to represent the wider Taghanic

Event Interval, which therefore initiated with the Taghanic Crisis and culminated in the Geneseo Crisis. Marshall et al. (2011) recognised the Taghanic and Geneseo events within terrestrial sediments in Scotland. Here is has the motif of two warm and very wet intervals with subtle marine transgressions separated by an interval of sustained aridity. The overlying Geneseo Event marked a return to an active fluvial system. Palynologically the events are marked by a drop in spore diversity with the survivors being largely *Geminospora* spp. that comes from the progymnosperm *Archaeopteris*.

García-Alcalde et al. (2012) recognized the Taghanic Event in the Spanish sequences based on magnetic susceptibility stratigraphy and its coincidence with changes in invertebrate and conodont biotas. Productive palynological sample 22CAN02P is from directly below the top of member B and close to the onset of the Taghanic onlap (Fig. 4). Unfortunately, it is the only productive sample from this level and is of low diversity with the palynomorphs of moderate preservation. Nonetheless, it is the only sample in which chitinozoans are present in any appreciable quantity (albeit in relatively low numbers with low taxonomic diversity) and potentially the increase in marine influence may mark the onset of the Taghanic Event. In terms of flora, all of the assemblages from both members B and D, with the latter post Taghanic Crisis-Geneseo Crisis, are dominated by progymnosperm spores.

6. Conclusions

- Rich dispersed spore assemblages are reported from the Candás Fm (members B and D) that have been age constrained using conodonts and invertebrates as mid Givetian (member B) and late Givetian-earliest Frasnian (member D).
- Based on the spore zonation scheme developed by Breuer and Steemans (2013) for northwestern Gondwana the spore assemblages from member B are equated with the *triangulatus-catillus* Assemblage Zone and those from member D with the *langii-concinna* Assemblage Zone.
- The dispersed spore assemblages share greater similarity with those previously described from Gondwana than those from Laurussia. However, they exhibit significant endemism.
- The dominance of progymnosperm spores in the assemblages suggests a flora dominated by archaeopteridalean trees along with aneurophytaleans and also lycopsids.

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.

Data availability

Data will be made available on request.

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FIGURE, PLATE & TABLE CAPTIONS

Fig. 1. Outline map of Northern Spain showing the outcrop of Devonian deposits with the location of sampled sections. 1 = Perán section (type section of the Candás Fm); 2 = Huergas de Gordón section (Portilla Fm).

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

Fig. 3. Lithostratigraphy and biostratigraphy of the Candás Fm in the Cantabrian Mountains. Numerical ages, stages, proposed sub-stages and conodont zones according to Becker et al. (2020). *Polygnathus dengleri* should be subdivided in two zones. See the text for references concerning FI, faunal intervals, MS SRZ magnetic susceptibility zones and lithostratigraphy.

Fig. 4. Stratigraphical logs of the Portilla/Candás fms in the Huergas de Gordón and Perán sections with both sections illustrating the position of collected palynology samples. Note the different subdivision of formation informal units and members. Conodont zones, faunal intervals and MS SRZ zones located according to the description in the text. Proposed diachronic boundaries of the Candás Fm and the dashed lines show the correlation between

the two sections. The position of the Taghanic and Genesee events are indicated as outlined in the text.

Fig. 5. Devonian spore biostratigraphical schemes and correlation of the Candás Fm with the position of the dispersed spore assemblages highlighted in red (member B = *triangulatus-catillus* Assemblage Zone, *catillus* Subzone; member D = *langii-concina* Assemblage Zone).

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

Plate descriptions

Plate I. Dispersed spores from the Candás Fm of Northern Spain. Scale bar = 45 µm.

1. *Laevolancis divellomedium* (Slide 22CAN07P.1; E.F.no. M38/2).
2. *Latosporites* sp. 1 (Slide 22CAN04P.1; E.F.no. E36).
3. *Retusotriletes* sp. (Slide 22CAN03P.1; E.F.no. F48/4).
4. *Apiculiretusispora* sp. (Slide 22CAN07P.1; E.F.no. H36/3). Note the prominent lips.
5. *Dibolisporites* sp. A (Slide 22CAN04P.1; E.F.no. T42).
6. *Apiculiretusispora brandtii* (Slide 22CAN06P.1; E.F.no. L31/4).
7. *Apiculiretusispora brandtii* Slide (22CAN02P.1; E.F.no. R38/3). Specimen verging on *Rhabdosporites minutus*.
8. *Apiculiretusispora arabiensis* (Slide 22CAN07P.1; F.no. N34).
9. *Dibolisporites* sp. A (Slide 22CAN06P.1; E.F.no. H40/4).
10. *Dibolisporites* sp. A (Slide 22CAN06P.1; E.F.no. D36/2).
11. *Apiculatasporites adavalensis* (Slide 22CAN02P.1; E.F.no. P36/3).
12. *Dibolisporites* sp. (Slide 22CAN02P.1; E.F.no. L45/1).
13. *Ambitisporites* sp. (Slide 22CAN07P.1; E.F.no. E43/1/2).
14. *Ambitisporites* sp. (Slide 22CAN04P.1; E.F.no. E45).
15. *Apiculatasporites adavalensis* (Slide 22CAN08P.1; E.F.no. O38).
16. *Dictyotriletes* sp. A (Slide 22CAN06P.1; E.F.no. D33).
17. *Dictyotriletes* sp. A (Slide 22CAN07P.1; E.F.no. C39/1).
18. *Dictyotriletes* sp. A (Slide 22CAN04P.1; E.F.no. R38/3).
19. Crassitate spore with distal circular thickening (Slide 22CAN07P.1; E.F.no. V34/3).
20. Crassitate spore with distal circular thickening (Slide 22CAN07P.1; E.F.no. F39).
21. *Aneurospora* sp. A (Slide 22CAN06P.1; E.F.no. O46/2). Note the distinctive concentric distal folding.
22. *Aneurospora* sp. A (Slide 22CAN08P.1; E.F.no. E33/2). Note the distinctive concentric distal folding.
23. *Aneurospora* sp. A Slide (22CAN06P.1; E.F.no. M38/2). Note the distinctive concentric distal folding.
24. *Emphanisporites annulatus* (Slide 22CAN07P.1; E.F.no. R36/2).
25. *Emphanisporites rotatus* (Slide 22CAN04P.1; E.F.no. J51/3).
26. *Emphanisporites rotatus* (Slide 22CAN03P.1; E.F.no. Q47/2).
27. *Emphanisporites rotatus* (Slide 22CAN07P.1; E.F.no. L32).
28. *Emphanisporites rotatus* (Slide 22CAN03P.1; E.F.no. D36/2).

Plate II. Dispersed spores from the Candás Fm of Northern Spain. Scale bar = 45 µm.

1. *Brochotriletes foveolatus* (Slide 22CAN07P.1; E.F.no. F44/3).
2. *Brochotriletes foveolatus* (Slide 22CAN06P.1; E.F.no. F41/1).
3. *Chelinospora timanica* (Slide 22CAN06P.1; E.F.no. G48/3).
4. *Chelinospora timanica* (Slide 22CAN03P.1; E.F.no. J43).
5. *Convolutispora* sp. A (Slide 22CAN06P.1; E.F.no. L41/1).
6. *Emphanisporites laticostatus* (Slide 22CAN06P.1; E.F.no. C33/2).
7. *Brochotriletes foveolatus* (Slide 22CAN03P.1; E.F.no. F41/2).
8. *Chelinospora timanica* (Slide 22CAN03P.1; E.F.no. C34).
9. *Chelinospora timanica* (Slide 22CAN07P.1; E.F.no. D51).
10. *Convolutispora* sp. A (Slide 22CAN03P.1; E.F.no. P48/3).
11. *Verrucosisporites premnus* (Slide 22CAN06P.1; E.F.no. H41).
12. *Verrucosisporites premnus* (Slide 22CAN06P.1; E.F.no. R37).
13. *Verrucosisporites premnus* (Slide 22CAN02P.1; E.F.no. O44/1).
14. *Verrucosisporites* cf. *onostus* (Slide 22CAN03P.1; E.F.no. R40/3).
15. *Verrucosisporites* cf. *onostus* (Slide 22CAN06P.1; E.F.no. K34).
16. *Chelinospora concinna* (Slide 22CAN07P.1; E.F.no. W36/2).
17. Murornate spore with very distinctive double spiked ‘Viking helmet’ ornament (Slide 22CAN03P.1; E.F.no. M44).
18. Murornate spore with very distinctive double spiked ‘Viking helmet’ ornament (Slide 22CAN05P.1; E.F.no. Y45/4).
19. *Chelinospora ligurata* (Slide 22CAN07P.1; E.F.no. M35/3).
20. *Chelinospora ligurata* (Slide 22CAN07P.1; E.F.no. D33).
21. *Cymbosporites variegatus* (Slide 22CAN02P.1; E.F.no. X48/2).
22. *Cymbosporites variegatus* (Slide 22CAN06P.1; E.F.no. L40/1).
23. *Cymbosporites cyathus* (*Cymbosporites catillus* morphon) (Slide 22CAN06P.1; E.F.no. J44/4).
24. *Cymbosporites cyathus* (*Cymbosporites catillus* morphon) (Slide 22CAN06P.1; E.F.no. H44/3).
25. *Cymbosporites cyathus* (*Cymbosporites catillus* morphon) (Slide 22CAN03P.1; E.F.no. S37).
26. *Cymbosporites* sp. A (Slide 22CAN04P.1; E.F.no. L33). Note the prominent crassitude and prominent, raised labra.
27. *Cymbosporites* sp. A (Slide 22CAN04P.1; E.F.no. U42/2). Note the prominent crassitude and prominent, raised labra.

28. *Cymbosporites* sp. A (Slide 22CAN07P.1; E.F.no. C29/2). Note the prominent crassitude and prominent, raised labra.
29. Verrucate spore (Slide 22CAN02P.1; E.F.no. X48/2).
30. *Dibolisporites uncatus* (Slide 22CAN07P.1; E.F.no. C36/4).
31. *Dibolisporites farraginis* McGregor & Camfield 1982 (Slide 22CAN08P.1; E.F.no. T36/4).
32. *Dibolisporites farraginis* McGregor & Camfield 1982 (Slide 22CAN07P.1; E.F.no. H34).

Plate III. Dispersed spores from the Candás Fm of Northern Spain. Scale bar = 45 µm except for 9 = 60 µm and 10 = 90 µm.

1. *Ancyrospora langii* (Slide 22CAN03P.1; E.F.no. N39/1).
2. *Ancyrospora langii* (Slide 22CAN03P.1; E.F.no. F46/4).
3. *Corystisporites collaris* (LARGE) (Slide 22CAN06P.1; E.F.no. H44/3). Only half of the specimen is shown. Note the inner body with a ornamented inner body.
4. *Corystisporites collaris* (SMALL) (Slide 22CAN04P.1; E.F.no. J44/2).
5. *Corystisporites collaris* (SMALL) (Slide 22CAN07P.1; E.F.no. Q43/1).
6. *Corystisporites collaris* (SMALL) (Slide 22CAN05P.1; E.F.no. H41). Lateral view.
7. *Corystisporites collaris* (LARGE) (Slide 22CAN03P.1; E.F.no. P44).
8. *Corystisporites collaris* (LARGE) (Slide 22CAN08P.1; E.F.no. H47).
9. *Corystisporites collaris* (LARGE) (Slide 22CAN06P.1; E.F.no. Q32/3). Lateral view.
10. *Corystisporites* megaspore (Slide 22CAN05P.1; E.F.no. X41).
11. *Corystisporites* megaspore (Slide 22CAN04P.1; E.F.no. V33/4).
12. Verrucate megaspore (Slide 22CAN03P.1; E.F.no. Q43).

Plate IV. Dispersed spores from the Candás Fm of Northern Spain. Scale bar = 45 µm except for 2 = 60 µm.

1. *Acinosporites lindlarensis* (Slide 22CAN06P.1; E.F.no. N44/1).
2. *Acinosporites lindlarensis* (Slide 22CAN09P.1; E.F.no. J37/3).
3. *Acinosporites lindlarensis* (Slide 22CAN09P.1; E.F.no. U40/3).
4. *Acinosporites lindlarensis* (Slide 22CAN09P.1; E.F.no. W41).
5. *Acinosporites lindlarensis* (Slide 22CAN08P.1; E.F.no. R44).
6. *Geminospora lemurata* (Slide 22CAN03P.1; E.F.no. J31/4). Fine ornament; moderately robust interior body.
7. *Geminospora lemurata* (Slide 22CAN06P.1; E.F.no. L39/1). Fine ornament; subtle interior body.
8. *Geminospora lemurata* (Slide 22CAN07P.1; E.F.no. G50/3). Fine ornament; moderately robust interior body.
9. *Geminospora lemurata* (Slide 22CAN06P.1; E.F.no. U35/2). Medium ornament; subtle interior body.
10. *Geminospora lemurata* (Slide 22CAN05P.1; E.F.no. U46/3). Medium ornament; moderately robust interior body.
11. *Geminospora lemurata* (Slide 22CAN04P.1; E.F.no. W41). Fine ornament; moderately robust interior body.
12. *Geminospora lemurata* (Slide 22CAN04P.1; E.F.no. J49/2). Fine ornament; moderately robust interior body.
13. *Geminospora lemurata* (Slide 22CAN0&P.1; E.F.no.G48/3). Fine ornament; subtle interior body.
14. *Geminospora lemurata* (Slide 22CAN03P.1; E.F.no. F46). Medium ornament; subtle interior body.
15. *Geminospora lemurata* (Slide 22CAN04P.1; E.F.no. D39/2). Medium ornament; subtle interior body.
16. *Geminospora lemurata* (Slide 22CAN05P.1; E.F.no. O32). Medium ornament; subtle interior body.
17. *Geminospora lemurata* (Slide 22CAN04P.1; E.F.no. C47/2). Medium ornament; subtle interior body.
18. *Geminospora lemurata* (Slide 22CAN05P.1; E.F.no. E34/1). Medium ornament; subtle interior body.
19. *Geminospora lemurata* (Slide 22CAN03P.1; E.F.no. D32/3). Medium ornament; moderately robust interior body.
20. *Geminospora lemurata* (Slide 22CAN6P.1; E.F.no. F43/3). Coarse ornament; subtle interior body.
21. *Geminospora lemurata* (Slide 22CAN03P.1; E.F.no. O32/3). Coarse ornament; subtle interior body.

22. *Geminospora lemurata* (Slide 22CAN03P.1; E.F.no. F48). Coarse ornament; robust interior body.
23. *Geminospora lemurata* (Slide 22CAN09P.1; E.F.no. W32). Specimen with an X-shaped 'trilete mark'.
24. *Geminospora lemurata* (Slide 22CAN03P.1; E.F.no. U34/4). Specimen with an X-shaped 'trilete mark'.
25. *Geminospora lemurata* (Slide 22CAN06P.1; E.F.no. K35/3). Specimen with monolete mark.
26. *Rhabdosporites langii* (Slide 22CAN07P.1; E.F.no. F32/1).
27. *Rhabdosporites/Geminospora* with three wall layers (Slide 22CAN06P.1; E.F.no. N42/1).
28. *Rhabdosporites/Geminospora* with three wall layers (Slide 22CAN03P.1; E.F.no. K41).
29. *Rhabdosporites/Geminospora* with three wall layers (Slide 22CAN08P.1; E.F.no. T38).

Plate V. Dispersed spores from the Candás Fm of Northern Spain. Scale bar = 45 µm.

1. *Grandispora inculta* (Slide 22CAN04P.1; E.F.no. H33).
2. *Grandispora stolidata* (Slide 22CAN06P.1; E.F.no. Y42/4).
3. Type 3. *Grandispora* sp. (Slide 22CAN06P.1; E.F.no. D34/2). Note the folding over the inner body and spines over the entire distal surface.
4. *Samarisporites triangulatus* (Slide 22CAN08P.1; E.F.no. F42/3).
5. *Samarisporites triangulatus* (Slide 22CAN03P.1; E.F.no. Q41/4).
6. *Samarisporites triangulatus* (Slide 22CAN02P.1; E.F.no. L34).
7. *Samarisporites triangulatus* (Slide 22CAN06P.1; E.F.no. F40).
8. *Samarisporites triangulatus* (Slide 22CAN03P.1; E.F.no. R32/4).
9. *Grandispora incognita?* (Slide 22CAN06P.1; E.F.no. G38/2).
10. *Grandispora pseudoreticulata* (Slide 22CAN04P.1; E.F.no. S49/4).
11. *Grandispora pseudoreticulata* (Slide 22CAN06P.1; E.F.no. H48/2).
12. Type 9. *Samarisporites* cf. *triangulatus* (Slide 22CAN03P.1; E.F.no. J49/3). More spinose form.
13. Type 9. *Samarisporites* cf. *triangulatus* (Slide 22CAN06P.1; E.F.no. W46/2). More spinose form.
14. Type 6. Unornamented zonate spore that is thin-walled and folded. (Slide 22CAN06P.1; E.F.no. H48).
15. *Samarisporites praetervisus* (Slide 22CAN06P.1; E.F.no. K44/1).
16. Type 11. *Samarisporites?* cf. *triangulatus*. (Slide 22CAN09P.1; E.F.no. E43/3). Ornamented with a spinose reticulum.
17. Type 12. Very distinctive murornate form. (Slide 22CAN04P.1; E.F.no. W44).
18. Type 10. *Camptozonotriletes*-type (Slide 22CAN06P.1; E.F.no. Q48/4). Note the radial muri over the zona and inner body with muri.
19. *Samarisporites praetervisus* (Slide 22CAN07P.1; E.F.no. P49).
20. Type 11. *Samarisporites?* cf. *triangulatus*. (Slide 22CAN06P.1; E.F.no. Q50/4). Ornamented with a spinose reticulum.
21. Type 12. Very distinctive murornate form. (Slide 22CAN04P.1; E.F.no. K36).
22. Type 13. Zonate spore with long spines over the inner body. (Slide 22CAN06P.1; E.F.no. Y32/3).

Table 1: List of spore taxa reported and their distribution in the studied samples. Occ = Occurrence with respect to general relative abundances with R = rare, M = moderate abundance, C = common. Sample refers to sample number (see Appendix) with 0 = absent and X = present.

Appendix. List of palynological samples collected (those marked with an asterisk were sufficiently well preserved to be logged)

SAMPLE	LOCALITY FORMATION	GRID REFERENCE	PALYNOLOGY
22CAN01CHW (22CW103)	Type Candás Section Candás Fm (A Member Stromatoporoid Bed)	30T-UTM-0277411/4029447 (±15)	Assemblage of poorly preserved palynomorphs of moderate thermal maturity
22CAN02CHW* (22CW104)	Type Candás Section Candás Fm (uppermost B Member)	30T-UTM-0277512/4029361 (±6)	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN03CHW* (22CW105)	Type Candás Section Candás Fm (uppermost D Member)	30T-UTM-0277645/4829236 (±10)	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN03P* (22CW106)	Type Candás Section Candás Fm (uppermost D Member)	WP 1204 7639 9238	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN04P* (22CW107)	Type Candás Section Candás Fm (middle D Member)	WP 1205 7636 9243	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN05P* (22CW108)	Type Candás Section Candás Fm (middle D Member)	WP 1205 7636 9243	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN06P* (22CW109)	Type Candás Section Candás Fm (lower D Member)	WP1206 7617 9253	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN07P* (22CW110)	Type Candás Section Candás Fm (lower D Member)	WP1206 7617 9253	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN08P* (22CW111)	Type Candás Section Candás Fm (lowermost D Member)	WP 1207 7609 9261	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN09P* (22CW112)	Type Candás Section Candás Fm (lowermost D Member)	WP 1207 7609 9261	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22CAN10P (22CW113)	Type Candás Section Candás Fm (C Member Unit L)		Assemblage of poorly preserved palynomorphs of low-moderate thermal maturity
19SPAIN43 (19CW076)	Type Candás Section Candás Fm (uppermost D Member)	N43°34'58.8''/W005°45'15.2''(±14)	Assemblage of well preserved palynomorphs of low thermal maturity
19SPAIN44 (19CW077)	Type Candás Section Candás Fm (D Member)	N43°34'59.5''/W005°45'16.4''(±8)	Assemblage of well preserved palynomorphs of low thermal maturity
22HdG03P (22CW040)	Huergas de Gordón Portilla Fm (Bed 6)	WP 1004 3055 6527	Assemblage of poorly preserved palynomorphs of moderate thermal maturity
22HdG04P (22CW041)	Huergas de Gordón Portilla Fm	WP 1005 3056 6521	Assemblage of moderately preserved palynomorphs of moderate thermal maturity
22HdG07PA (22CW042)	Huergas de Gordón Portilla Fm (Bed 13)	WP 1006 3004 6512	Assemblage of well preserved palynomorphs of moderate thermal maturity
22HdG07PB (22CW043)	Huergas de Gordón Portilla Fm (Bed 13)	WP 1006 3004 6512	Assemblage of moderate-well preserved palynomorphs of moderate thermal maturity
22HdG07PC (22CW044)	Huergas de Gordón Portilla Fm (Bed 13)	WP 1006 3004 6512	Assemblage of well preserved palynomorphs of low-moderate thermal maturity
22HdG13PA (22CW045)	Huergas de Gordón Portilla Fm (Bed 18)	WP 1007 3051 6501	Assemblage of moderately preserved palynomorphs of high thermal maturity
22HdG13PB (22CW046)	Huergas de Gordón Portilla Fm (Bed 18)	WP 1007 3051 6501	Assemblage of moderately preserved palynomorphs of high thermal maturity
22HdG15P (22CW047)	Huergas de Gordón Portilla Fm (Bed 22)	WP 1008 3049 6484	Assemblage of moderately preserved palynomorphs of high thermal maturity
22HdG19P	Huergas de Gordón	WP 1009 3069 6478	Assemblage of moderately preserved palynomorphs of high thermal maturity

(22CW048)	Portilla Fm (Bed 25-26 boundary)		
22HdG25P (22CW049)	Huergas de Gordón Portilla Fm (Bed 34)	WP 1010 3077 6474	Assemblage of moderate-well preserved palynomorphs of moderate thermal maturity
22HdG26P (22CW050)	Huergas de Gordón Portilla Fm (+70 cm))	WP 1010 3077 6474	Assemblage of moderate-well preserved palynomorphs of moderate thermal maturity
22HdG27P (22CW051)	Huergas de Gordón Portilla Fm (+140 cm)	WP 1011 3081 6470	Assemblage of moderate-well preserved palynomorphs of low-moderate thermal maturity
22HdG28P (22CW052)	Huergas de Gordón Portilla Fm (+70 cm)	WP 1011 3081 6470	Assemblage of moderate-well preserved palynomorphs of low-moderate thermal maturity

SUPPLEMENTARY DATA

Supplementary Table 1: Spore taxa reported from the *langii-concinna* Assemblage Zone in northern Gondwana by Breuer and Steemans (2013) and the Candás Fm (member B).
TC AZ (TIZ) = *triangulatus-catillus* Assemblage Zone (*triangulatus* Interval Zone), TC AZ (CIZ) = *triangulatus-catillus* Assemblage Zone (catillus Interval Zone), X = present, O = absent, M = present as Spore Morphon. Taxa reported in this study but not reported by Breuer and Steemans (2013) are highlighted in red.

Supplementary Table 2: Spore taxa reported from the *langii-concinna* Assemblage Zone in northern Gondwana by Breuer and Steemans (2013) and the Candás Fm (member D).
LC AZ = *langii-concinna* Assemblage Zone, X = present, O = absent, M = present as Spore Morphon. Taxa reported in this study but not reported by Breuer and Steemans (2013) are highlighted in red.