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Reconstructing the terrestrial flora and marine plankton of the Middle Devonian of Spain: implications for biotic interchange and palaeogeography

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Abstract: A rich and well-preserved palynomorph assemblage from the Middle Devonian of northern Spain is analysed with regard to palaeobiogeography and palaeocontinental reconstruction. The communities of terrestrial plants (dispersed spores), marine zooplankton (chitinozoans) and marine phytoplankton (acritarchs and prasinophytes) all show significant endemism. They are depauperate in some respects, missing common species found elsewhere, but also containing many endemic taxa. Measures of similarity and cluster analysis reveal little relatedness to other contemporary assemblages, with both the spore and phytoplankton communities being sister groups to all other communities except one. Attempted correlation with local, regional and global sea-level and transgression–regression schemes is complicated by the absence of key index palynomorphs in this unusual assemblage. The distinctive sedimentary sequence of northern Spain may reflect an increased clastic input to the marine shelf resulting from an increasingly monsoonal climate, possibly connected to the Kačák extinction event. The assemblage's unusual, endemic character requires restrictions on dispersal. The terrestrial spore assemblage suggests that large tracts of ocean existed, without appreciable land bridges, between the Armorican Terrane Assemblage and Laurussia to the north and Gondwana to the south. The phytoplankton communities support existing evidence for significant east to west ocean currents through the Rheic Ocean.

Supplementary material: Supplementary Tables 1–3 contain presence–absence data for spores, chitinozoans and phytoplankton respectively, in various assemblages, used to construct the dendrograms in Figures 4–6. The tables are available at <https://doi.org/10.6084/m9.figshare.c.4726862>

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A detailed palynological analysis of the Middle Devonian Naranco, Huergas and Gustalapedra formations has shed light on the nature of the Armorican Terrane Assemblage flora (through analysis of dispersed spores) and nearshore marine plankton (through analysis of the acritarch and prasinophyte phytoplankton and chitinozoan zooplankton) (Askew & Wellman 2018; Askew 2019; Askew & Russell 2019). The aim of this study is to assess the palaeobiogeographical affinities of both the terrestrial vegetation and marine plankton. Our findings are utilized to comment on reconstructions of palaeogeography and continental configuration, the nature of oceanic currents and the effects of contemporary Devonian sea-level changes and extinction events.

Palaeogeography and geological setting

Palaeogeographical reconstructions of the Iberian Peninsula during the Middle Devonian vary significantly. It should be noted that Iberia is made up of at least five terranes (García-Alcalde *et al.* 2002) that were not necessarily close to one another during the Devonian. The ambiguity surrounding their exact position means that for convenience most reconstructions consider Iberia as a single entity without attempting to place its terranes (Torsvik & Cocks 2016).

Iberia separated from Gondwana some time from the Cambrian onwards, depending on the reconstruction (Torsvik & Cocks 2007), together with other parts of Europe as part of the Armorican Terrane Assemblage. By the Middle Devonian, the focus of the present study, the Armorican Terrane Assemblage was a series of relatively

small landmasses separated by tracts of ocean from Laurussia to the north and Gondwana to the south, although reconstructions differ significantly in the size of these oceans (e.g. Stampfli *et al.* 2002; Cocks & Torsvik 2006; Torsvik & Cocks 2016). In addition, the rotational orientation of Gondwana differs significantly between reconstructions. Torsvik & Cocks (2016) depicted Iberia as being off the coast of South America, whereas Scotese (2008, 2016) rotated Gondwana so as to place North Africa closest to the Armorican Terrane Assemblage. This latter reconstruction also depicts a land bridge across the Rheic Ocean between Laurussia and Gondwana, in contrast to Torsvik & Cocks (2016), who depicted an open seaway.

The area of the present study is in the Cantabrian Zone in northern Spain. Here, Devonian rocks crop out in a large arc from the northern coast near Gijón, south through Asturias, then in an east–west orientation across León and Palencia provinces (García-Alcalde *et al.* 2002) (see Fig. 1). This structure is interpreted as representing a transect across a marine shelf from nearshore (Asturias) to offshore (Palencia) (García-Alcalde *et al.* 2002). Details of the stratigraphic sequence are given in Figure 2. The sedimentary sequence alternates between calcareous and clastic deposition. This paper concerns a Middle Devonian clastic unit identified as the Naranco, Huergas and Gustalapedra formations located in Asturias, León and Palencia, respectively. These formations are recognized as lateral equivalents, with differences in thickness, gradational sedimentary differences and possibly a limited degree of diachronism reflecting their proximity to the palaeoshoreline (García-Alcalde *et al.* 2002), with Asturias (over

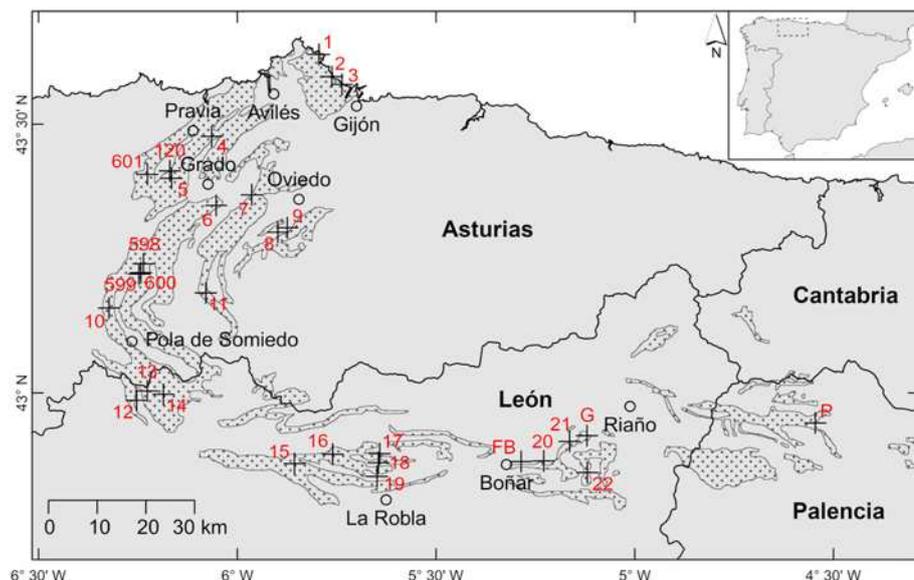


Fig. 1. Map of northern Spain. Outlined areas with dotted fill indicate the Devonian sediments' outcrop area. Crosses indicate sites surveyed in this study: 1, Moniello–Punta la Vaca; 2, Candás–Perán; 3, Playa del Tranqueru; 4, Veneros–Santoseso; 5, Sobrerriba–Santa Eufemia; 6, La Gábara–Coalla; 7, San Pedro de Nora; 8, Los Alfilorios; 9, Soto de Ribera–Tellego; 10, Aguasmestas–Pigüña; 11, Las Ventas–Entrago; 12, Lumajo; 13, Puerto de Somiedo; 14, Quejo; 15, Mirantes de Luna; 16, Geras; 17, Ciñera; 18, Vega de Gordon; 19, Huergas de Gordon; 20, Vozmediano; 21, Comiero; 22, Aleje; FB, Fombella Blanco; G, Crémenes–Las Salas; P, Man member.

500 m thick) being nearshore and Palencia (50 m thick) being further offshore. They are bounded by thick, laterally equivalent limestone sequences both below (the Moniello, Santa Lucía and Polentinos formations) and above (the Candás, Portilla and Cardaño formations). The Naranco, Huergas and Gustalapedra formations are characterized by distinct lower and upper units. The lower unit is coarser in character, dominated by thick sandstone layers representing a more abundant terrigenous clastic input. The upper unit is more mixed, with alternating sandstone and siltstone beds (with occasional limestones), representing a combination of coarse terrigenous and finer basinal deposits. (See [García-Ramos \(1978\)](#) for a more thorough description.)

The Naranco, Huergas and Gustalapedra formations have been determined to be Eifelian–Givetian in age based on biostratigraphical analysis of various marine macrofaunal groups ([García-López et al. 2002](#)). Conodonts are very rare in the clastic deposits, but those from the bounding limestone formations provide a more refined age constraint. Those from the underlying Santa Lucía Formation (and possibly lowermost Huergas and Naranco formations) belong to the *Polygnathus costatus costatus* zone of

mid-Eifelian age (c. 391–392 Ma based on [Becker et al. \(2012\)](#)). Those from the overlying Portilla and Candás formations belong to the lower *Polygnathus varcus* zone of early, but not earliest, Givetian age (c. 386–387 Ma based on [Becker et al. \(2012\)](#)) ([García-López & Sanz-López 2002](#); [García-López et al. 2002](#)). [García-López et al. \(2002\)](#) also reported on some conodonts recovered from within the upper part of the Naranco Formation in the El Tranqueru section. They suggested correlation with the *P. c. costatus* zone, which would indicate that the Eifelian–Givetian boundary occurs within the topmost 86 m of the Naranco Formation. This is slightly higher than where we place it based on spore biostratigraphy. Analysis of the terrestrial spore record of these rocks has refined the age of the upper, palynomorph-bearing part of the Naranco, Huergas and Gustalapedra formations to the *lemurata-langii* Assemblage Zone (*lem* Interval Zone) of [Breuer & Steemans \(2013\)](#), entirely within the early Givetian ([Askew & Wellman 2018](#)).

The alternating pattern of these sedimentary rocks between calcareous and clastic deposition represents repeated changes in depositional environment, caused by marine transgressions, clastic influxes or other major environmental changes. This pattern could

Stage	Asturias	León	Palencia
Famennian	C/B / V	B/LE / V	Vidrieros
	Ermita	Ermita	
Frasnian	Piñeres	conglomerate / Fueyo	Murcia
		Crémenes / Nocedo	
Givetian	Candás	Portilla	Cardaño
Eifelian	Naranco	Huergas	
Emsian	Moniello	Santa Lucía	Polentinos
	Aguión	Coladilla	
Pragian	La Ladrona	Valporquero	Abadía
	Bañugues	La Pedrosa	
Lochkovian	Nieva	Felmin	Lebanza
	Furada	San Pedro	
			Man member / Gustalapedra

Fig. 2. Age and correlation of Devonian rock units in several Iberian areas. Dashed boundary lines indicate uncertainty. Diagram not to scale. Abbreviations for uppermost Famennian units: B, Balears; C, Candamo; LE, Las Ermitas; V, Vegamián. Redrawn from [García-Alcalde et al. \(2002\)](#).

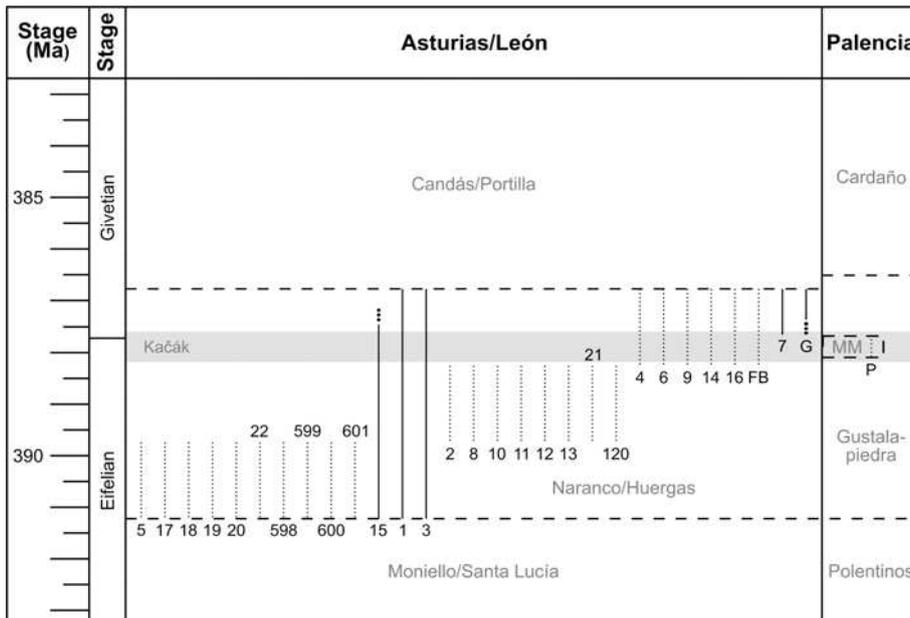


Fig. 3. Age and stratigraphic interval of the sites used in this study, numbered according to Figure 1, with formations marked. Formation boundaries were dated using conodont biostratigraphy from García-López & Sanz-López (2002) and García-López *et al.* (2002) and the absolute age determination from Becker *et al.* (2012). Formation diachronism is not depicted here owing to its variable and uncertain extent. Dotted site intervals indicate the stratigraphic range in which the site is located based on mapping. Solid site intervals indicate sections whose stratigraphic interval is known with certainty, although not all were sampled and the dotted ends on sections 15 and G indicate uncertainty as to their precise extent. Grey shaded area indicates the extent of the Kačák Event, assuming its depiction by Becker *et al.* (2016) as a long, polyphase event extending into the Givetian is correct. MM, Man Member.

be linked to the numerous climatic events recognized in the Devonian Period (House 2002). Of particular interest is the Kačák Event, as it is known to occur within the age range of the Naranco, Huergas and Gustalapedra formations in the late Eifelian. The Kačák Event is a period of sedimentary change representing benthic anoxia, possibly caused by sea-level change and associated with extinctions in the benthic fauna, often represented by black shale deposits (House 1996, 2002). The temporal extent of this event is uncertain (Dowding & Ebach 2018); it has variously been described as of short duration (Truyóls-Massoni *et al.* 1990; House 1996, 2002) or as a longer, possibly polyphase event reaching into the earliest Givetian (Walliser & Bultynck 2011; Becker *et al.* 2016; Grahn *et al.* 2016) (see Fig. 3). This could potentially place the event as contemporary with the palynomorph assemblage analysed here and with the marked depositional changes taking place across the Cantabrian Zone.

Material and methods

The palynomorph assemblage analysed here was recovered from 130 samples collected from 30 localities; 26 single outcrops yielding one or a few samples and four extended sections through the formation. These sections ranged from around 30 m long at San Pedro de Nora to around 300 m long at the Playa del Tranqueru. The approximate or known intervals in which the samples occur are shown in Figure 3. Further details, along with a thorough documentation of this palynomorph assemblage, can be found in three papers covering marine zooplankton (Askew & Russell 2019), marine phytoplankton (Askew 2019) and land-derived spores (Askew & Wellman 2018). These publications include the taxonomy of the assemblage, detailed descriptions of selected species, associated count data and biostratigraphical interpretations. The cluster analysis presented here was calculated according to the UPGMA method using Euclidean distances between communities, calculated using the R program (R Core Team 2018). Dendrogram figures (Figs 4–6; see also supplementary material Tables 1–3) were produced using the ‘dendextend’ package for R (Galili 2015). The other assemblages used in this analysis were selected based on their taxonomy and stratigraphic position. The studies used have confident taxonomic assignments, in line with or adapted to modern usage of taxa, and well-constrained late Eifelian–early Givetian ages, coeval with the present assemblage. Efforts were also made

to achieve a widespread palaeogeographical coverage by using palynomorph assemblages reported from many palaeocontinents.

Terrestrial vegetation

The community of land-derived spores comprises a depauperate and endemic flora, missing key taxa commonly found elsewhere but also containing unique taxa, not seen elsewhere (Askew & Wellman 2018). For example, characteristic spores with grapnel-tipped processes (*Ancyrospora* and other genera) are notable by their absence, despite their wide distribution across both Laurussia and Gondwana in contemporaneous strata (Wellman 2002). Also of interest is the absence of *Rhabdosporites langii*, an important component of most other Middle Devonian assemblages, and recognized as belonging to the aneurophyte lineage that was important in the rise to prominence of progymnosperm plants (Marshall 1996a; Wellman 2009).

When the Spanish community is compared with contemporary ones from around the world it is found to be a sister group to all other assemblages except that of McGregor & Camfield (1982) from Canada (see Fig. 4). There is undoubtedly an ‘authorship effect’ in this analysis (whereby some authors’ work appears to cluster independently of their locality, presumably because of the taxonomic concepts they embrace (Marshall 1996b)). However, overall the impression is clear. The Spanish community is not particularly similar to any other Middle Devonian spore assemblage. It is most closely related to the composite assemblage of Breuer & Steemans (2013) from Saudi Arabia and North Africa, followed by two other Gondwanan floras from Australia and Argentina, so a slight bias towards a Gondwanan affinity is indicated.

This analysis raises various questions around how such an unusual, to some degree endemic flora could arise in this area. *Geminospora lemurata* is represented here in all three sampled sections and, importantly, throughout almost the entire sampled thickness of the Playa del Tranqueru section, which includes the whole thickness of the Naranco Formation (Askew & Wellman 2018). It is fairly rare, making up between 0.5 and 2% of the spore community when assessed quantitatively, but its presence is definite. *G. lemurata* is considered to have originated from *R. langii* by heterochrony and to have been produced by the archaeopteridalean progymnosperms (Marshall 1996a). The presence of *G. lemurata*,

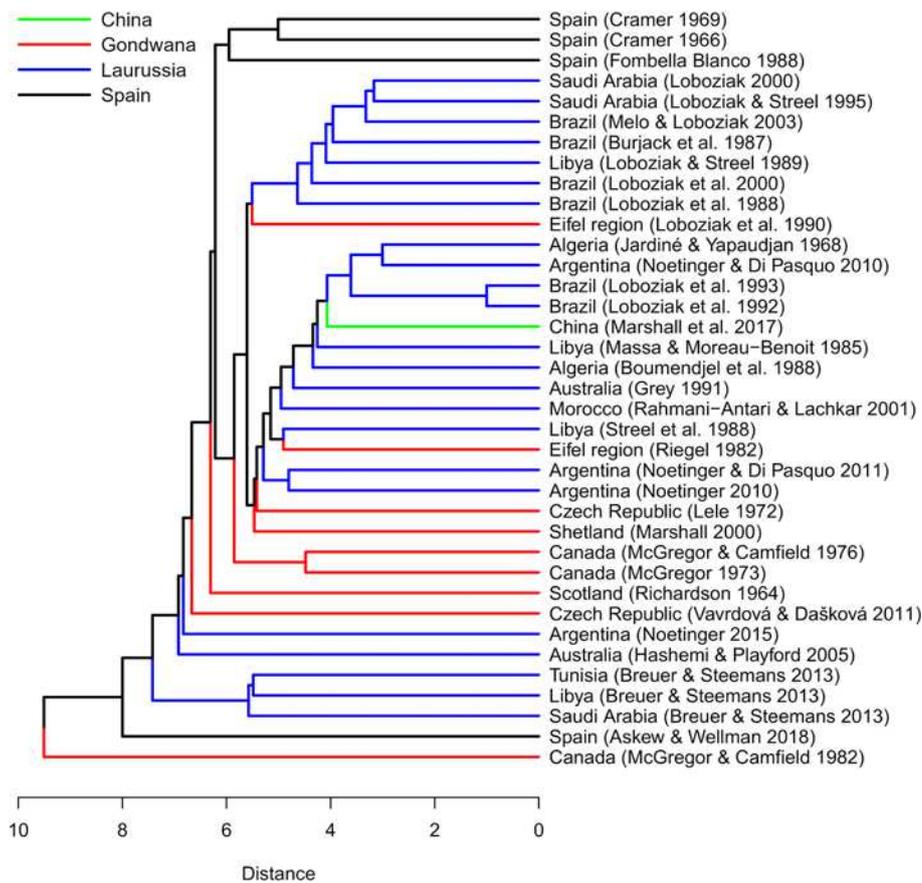


Fig. 4. Dendrogram of a cluster analysis of Middle Devonian spore assemblages, with locations indicated. Distances were calculated using Euclidean distance. Hierarchical clustering used the UPGMA method. Branch colours indicate the assemblages' palaeocontinent of origin.

in the absence of its 'ancestor' *R. langii*, which remained contemporaneous with it, and its associated megaspore, *Contagisporites optivus*, suggests a restriction on dispersal. *R. langii* and *C. optivus* are significantly larger than *G. lemurata*,

therefore the latter should be better able to disperse to more remote areas. There are several possible explanations for this pattern. Early *G. lemurata* existed before true heterospory evolved (Marshall 1996a); megaspores would, naturally, be absent if this form is the

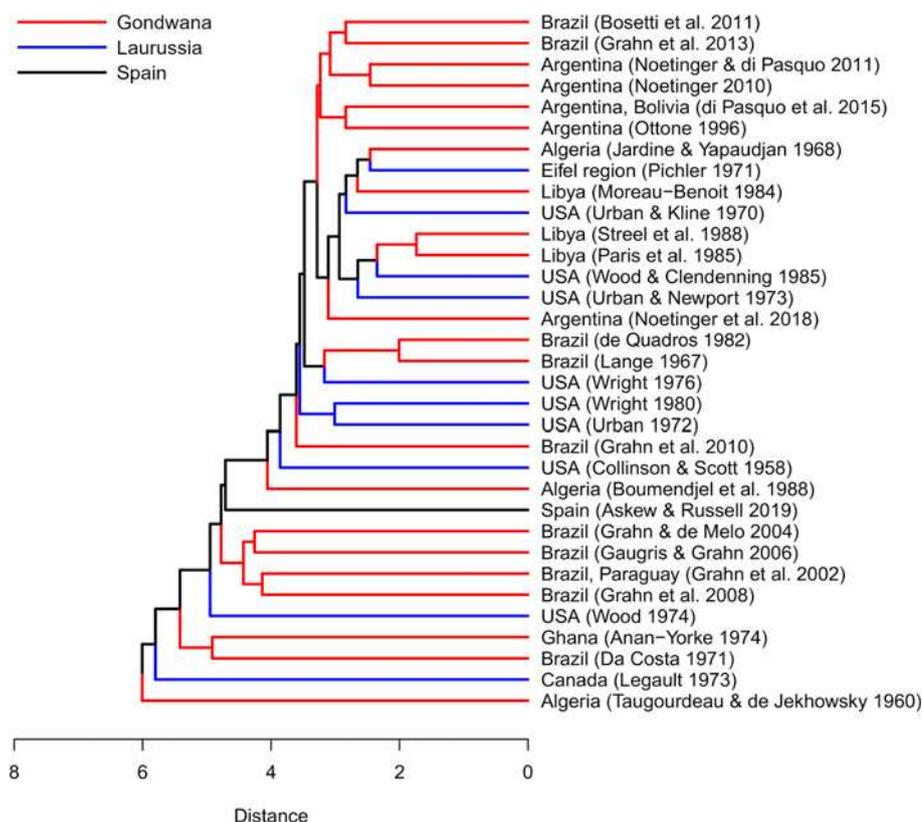


Fig. 5. Dendrogram of a cluster analysis of Middle Devonian chitinozoan assemblages, with locations indicated. Distances were calculated using Euclidean distance. Hierarchical clustering used the UPGMA method. Branch colours indicate the assemblages' palaeocontinent of origin.

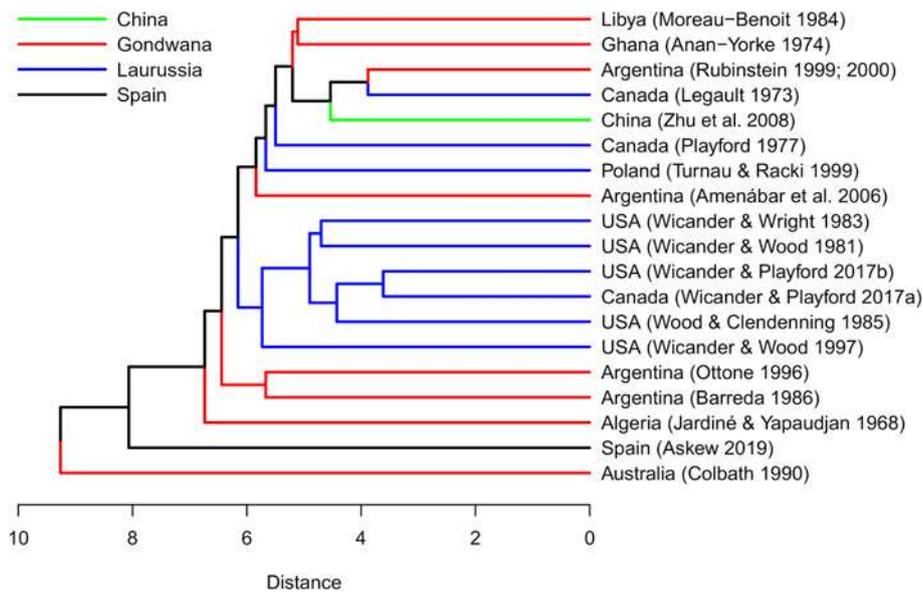


Fig. 6. Dendrogram of a cluster analysis of Middle Devonian phytoplankton assemblages, with locations indicated. Distances were calculated using Euclidean distance. Hierarchical clustering used the UPGMA method. Branch colours indicate the assemblages' palaeocontinent of origin.

one represented here. Alternatively, the truly heterosporous form has evolved and either has not yet dispersed to the Cantabrian Zone or it is present but we do not find the megaspores in this assemblage. This could be because they are too rare (*G. lemurata* accounts for only 0.5–2% of the assemblage, and the megaspores should be even rarer), or because the sediments studied here were deposited too far offshore and the megaspores never reached here. There is, in fact, a near-total lack of megaspores in this flora, with only two specimens of megaspore size, both left in open nomenclature, being found in the whole assemblage. This lack of large spores supports the idea of the Cantabrian Zone sediments being deposited in a geographically isolated area.

Marine plankton

Marine zooplankton

The chitinozoan community of the Naranco, Huergas and Gustalapedra formations has been described by Askew & Russell (2019). It is not particularly similar to contemporary assemblages from elsewhere when they are compared by their coefficient of similarity (CS) (*sensu* Clark & Hatleberg 1983) and Jaccard Index, with a slightly closer similarity to Gondwana observed (Askew & Russell 2019). When the interrelatedness between all these assemblages is assessed by cluster analysis the present community is seen to nest within them, most closely related to a group of Brazilian–Paraguayan assemblages and one from Algeria (see Fig. 5), all of which are Gondwanan localities. The assemblages as a whole, however, show no clear groupings of Laurussian or Gondwanan groups. This is potentially a taxonomic or authorship artefact or may indicate a lack of provinciality in chitinozoan faunas in the Devonian.

Despite this rather inconclusive result the Spanish community still presents various unusual compositional features that suggest a degree of endemism. Various common species including *Ancyrochitina cornigera* and *Ramochitina ramosi* are absent, and it is also unusual for a Middle Devonian assemblage to lack representatives of the genera *Eisenackitina* and *Urochitina*. Indeed, the only desmochitimid recorded here is *Hoegisphaera* cf. *glabra*, a long-ranging form possibly including numerous homeomorphs.

Marine phytoplankton

The community of acritarchs and prasinophyte phycmata from the Naranco, Huergas and Gustalapedra formations has been described by Askew (2019). Like the chitinozoan community, it is not similar

to contemporary assemblages from elsewhere, although with a slight bias towards Laurussia in this case (Askew 2019), and it lacks various species that are common elsewhere, notably *Arkonites bilixus* and *Tyligmasoma alargada*.

A cluster analysis of these phytoplankton assemblages (see Fig. 6) shows the present community to be a sister group to all others except the Australian assemblage of Colbath (1990). Further Gondwanan assemblages are close to the present one, with most of the Laurussian ones forming a distinct group within the dendrogram, although this could be related to authorship and similar use of taxonomy. The association of this community with those from Gondwana is in discord with CS and Jaccard Index methods, although this cluster analysis corroborates this community's distinctiveness compared with other contemporary groupings from around the world.

Evidence for ocean currents

The distribution of plankton raises a similar question to the one posed by the terrestrial flora: how did such an endemic assemblage arise in the oceans around the isolated landmasses of Iberia? Although the seas were continuous, isolation may have arisen because of ocean currents. Evidence for such currents may come in the form of contourites, sedimentary features produced by currents in deep water. Contourites are known to occur in the Middle Devonian, with evidence for them being found in Germany, Morocco, Australia, Canada and the Carnic Alps (Hüneke 2006, 2013; Du *et al.* 2008; Knapp *et al.* 2017). Reconstructions of ocean currents based on these indicate a northeasterly current flowing past Iberia into the narrowing Rheic Ocean to the west (Hüneke 2006). This would place Iberia upstream of the locations of the other microphytoplankton assemblages it is compared with here (see Fig. 7). This would have been a serious barrier to the dispersal of all but the most widespread taxa, those found on both major continents. Species more limited in their distribution would have been unable to disperse to Iberia across these currents.

It should be noted that, as discussed in the section 'Palaeogeography and geological setting', palaeocontinental reconstructions disagree on the position of Gondwana and the extent and continuity of the Rheic Ocean in the Middle Devonian. Scotese (2008, 2016) depicted a land bridge across the Rheic Ocean in the Givetian, possibly impeding the flow of ocean currents, whereas Torsvik & Cocks (2016) reconstructed an open seaway. The ocean current reconstruction of Hüneke (2006) includes an open Rheic

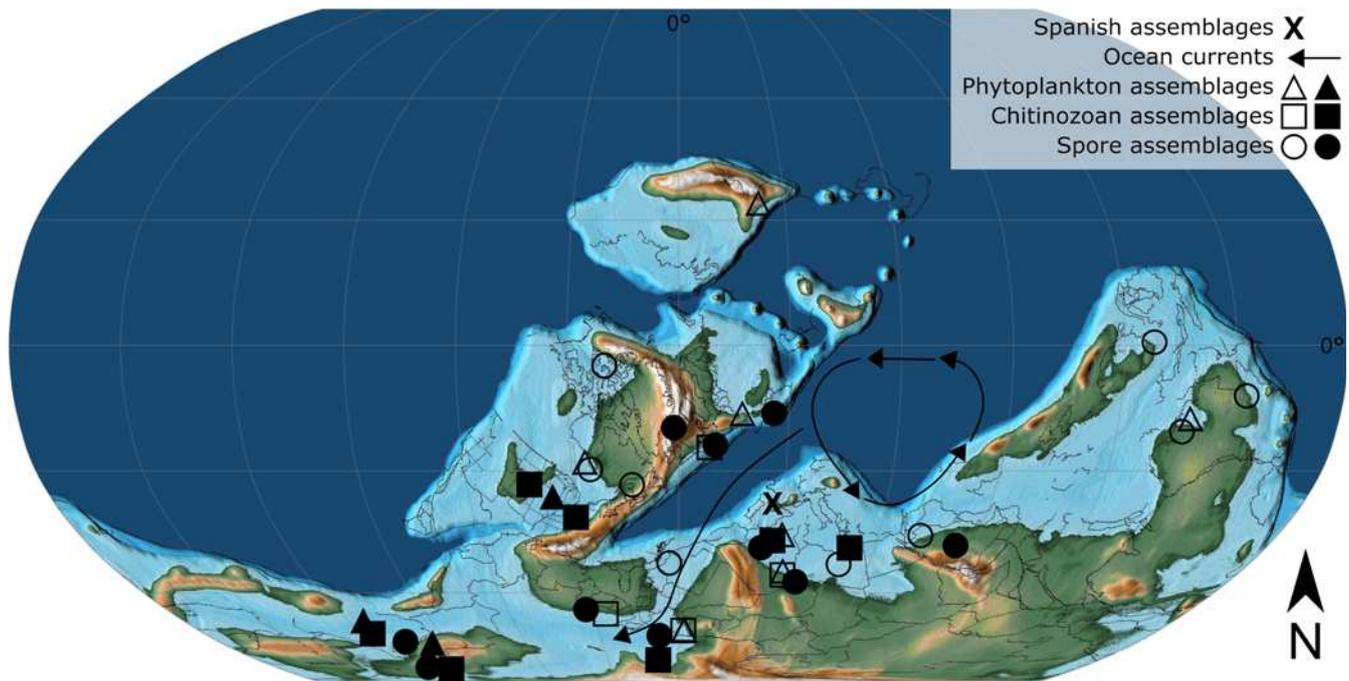


Fig. 7. Palaeocontinental reconstruction of the Middle Devonian world, with modern continents indicated. The location of Spain is marked and some palaeocurrents are indicated. Symbols indicate the locations of assemblages mentioned in Figures 4–6. Filled symbols represent locations with multiple assemblages very close to one another. Base map was modified from Scotese (2016). Palaeocurrent reconstruction is after Hüneke (2006).

Ocean but with Gondwana in a similar rotational position to that depicted by Scotese (2008, 2016). The biogeographical findings here support the existence of strong ocean currents in an open Rheic Ocean unimpeded by land bridges. This suggests that the narrow land bridge between Laurussia and Gondwana depicted by Scotese (2008, 2016) was not fully formed in the early Givetian.

Devonian sea-level and global events

Sea-level change

The pattern of sedimentary change observed in the Cantabrian Zone may be related to Devonian sea-level changes. The Euramerican transgression–regression curve of Johnson *et al.* (1985) places the conodont-defined interval in which the Naranco, Huergas and Gustalapedra formations were deposited (see section ‘Palaeogeography and geological setting’) in the Ic to If zones, with each zone representing a transgression–regression cycle. The present authors deem it unlikely that all these cycles are represented (or can be identified) in the sedimentary sequence of the Cantabrian Zone. The most complete and best described Spanish section is at the Playa del Tranqueru (Askew & Wellman 2018; Askew 2019; Askew & Russell 2019), which includes the entire thickness of the Naranco Formation, the Asturian representative of the three laterally equivalent formations studied here. The lower half of the formation is entirely composed of a thick, undifferentiated, sandy unit, as described by Garcia-Ramos (1978). The upper part of the formation shows interbedding with finer clay- and siltstones. Based on spore biostratigraphy detailed by Askew & Wellman (2018) we suggest that the upper part falls entirely within the If zone of Johnson *et al.* (1985). It is possible that the formation represents the regression of the Ie zone (the lower sandstone unit) and the transgression of the If zone (the interbedded upper unit), with a possible disconformity at the base of the formation representing the Ic and Id zones.

The finer scale sea-level reconstructions of Brett *et al.* (2007, 2011) for eastern North America resolve three or four transgression–regression cycles within the time period represented by the upper

part of the Naranco, Huergas and Gustalapedra formations. Four relatively thick units, with a higher than average proportion of fine sedimentary rock layers and possibly representing periods of higher sea-level, can be seen at the Playa del Tranqueru section. However, beds of clay- and siltstone are distributed throughout the upper part of the formations fairly evenly, rendering any correlation with the North American curve speculative at best.

High-resolution studies of marine transgressions linked to palynological markers have also been carried out in Brazilian basins. The age of the rocks studied here corresponds to the top of sequence C and sequences D and E of the third-order depositional sequence scheme of Grahn *et al.* (2013), defined using facies association patterns, biostratigraphic markers, gamma-ray logs and total organic carbon data. Sequence E is defined as having a more transgressive character than the two lower sequences, represented by a distinct change from sandy to shaly deposits, and it is tempting to align this change with the boundary between the lower and upper parts of the Naranco, Huergas and Gustalapedra formations. Unfortunately, few of the palynomorphs used to calibrate this Brazilian sequence stratigraphic scheme are found in Spain, and the specific early Givetian markers are absent.

A further Brazilian scheme describes regressions at an even finer scale of fourth–fifth order, described as ‘minor forced regression unconformities’ (Young 2006; Young & Borghi 2006). This sequence stratigraphic analysis has been applied in late Eifelian–early Givetian rocks in the Parnaíba Basin that contain abundant palynomorphs, allowing potential marker species to be identified (Grahn *et al.* 2008). Again, the rocks studied here can be likened on purely lithological grounds to the sandy sequence B followed by the much finer grained sequences C and D above. In the Parnaíba Basin the chitinozoan *Alpenachitina eisenacki* is found in both sequences C and D, whereas *Ancyrochitina flexuosa* is restricted to sequence C and *Fungochitina pilosa* is found only in sequence D. These species occur in the Playa del Tranqueru section in this same sequential order, with *F. pilosa* first appearing about 27 m above *A. flexuosa* (Askew & Russell 2019). Grahn *et al.* (2008) indicated the Eifelian–Givetian boundary as being at the boundary between sequences C

and D; however, in Spain *G. lemurata* occurs at the same level as *A. flexuosa*, suggesting a Givetian age. If sequence C is represented in these rocks it must be much thinner than in Brazil.

The paucity of useful palynomorphs, particularly chitinozoans, prevents any serious attempt to correlate these Spanish strata with Brazil. Many studies report a transgressive episode in the earliest Givetian (e.g. Grahn & de Melo 2004; Grahn *et al.* 2010), but without key palynomorph marker species any link between the Cantabrian Zone and Brazilian sequences, or any of these regional schemes, must remain speculative. Another possible confounding factor is the short time in which the studied material was deposited; there was insufficient time for many transgression–regression cycles to take place before carbonate deposition resumed following a fall in clastic input, which we suggest resulted from climatic changes.

The Kačák Event

The Kačák Event is the subject of some debate as regards its markers and duration. The event is difficult to characterize (García-Alcalde 1998) and, although numerous studies and reviews have attempted to further define the event (e.g. García-Alcalde 1998; Troth *et al.* 2011; Becker *et al.* 2016; Königshof *et al.* 2016; Marshall 2016), a universal global marker for the event is difficult to identify. Its duration is also the subject of conflicting indicators. It is generally considered to have begun shortly before the Eifelian–Givetian boundary and ended at the boundary or just after, possibly extending into the early Givetian. Some authors have suggested a relatively short time interval with a single marine anoxic event, whereas others have preferred a more extended time interval possibly with numerous marine anoxic events (see section ‘Palaeogeography and geological setting’ for a fuller explanation). In either case, the event takes place during the time interval in which the Naranco, Huergas and Gustalapedra formations were deposited.

The Kačák Event has previously been identified in northern Spain (House 1996; García-Alcalde 1998; García-Alcalde *et al.* 2002) as a thin (1 m) black siltstone unit in the Asturian Naranco Formation (House 1996), a thick unit of euxinic black shales in the Leónese Huergas Formation (House 1996; García-Alcalde *et al.* 2002) and a thin (5–7 m) dark sandstone unit (the Man Member) in the Palencian Gustalapedra Formation (García-Alcalde 1998; García-Alcalde *et al.* 2002). García-Alcalde *et al.* (2002) suggested that it demarcates the start of the upper sedimentary cycle of the Naranco and Huergas formations.

Palynomorph assemblages are reported from strata above and below units identified as the Kačák Event in the Naranco and Huergas formations (Askew & Wellman 2018; Askew 2019; Askew & Russell 2019). These all belong with the *lemurata*–*langii* Assemblage Zone (*lem* Interval Zone) indicating an early (but not earliest) Givetian age. This would suggest that they are younger than the Eifelian–Givetian boundary and therefore post-date the onset of the Kačák Event. Of course, these observations may simply reflect incorrect biozonal interpretation, inaccuracies or coarseness of the spore biozonation scheme, or misplacement of the Kačák Event in the sequences from the Cantabrian Zone. Alternatively, the Kačák Event may have occurred over a more extended period rather than representing a discrete event of short duration.

Considered together, the deposits of the Naranco, Huergas and Gustalapedra formations clearly represent a relatively long period of clastic sedimentation, interrupting background carbonate deposition. Presumably, this was the result of increased terrigenous input of clastic sediment. Either the Kačák Event is a rapid, discrete event that lies somewhere within this sequence, or it can be considered a more prolonged, possibly polyphase, event representing an extended period of environmental perturbation, manifested in increased terrigenous input from the land. A potential cause for the Kačák Event, outlined by Marshall *et al.* (2007) based on work

in the terrestrial sequences of the Orcadian Basin of Scotland, was an increasingly monsoonal climate, brought about by increased insolation. This would have increased freshwater runoff from the land, resulting in ocean stratification and the spread of hypoxia, but also causing an increase in the amount of clastic sediment reaching the sea. The Cantabrian Zone sequences clearly point to a significant period of increased terrigenous runoff that may indeed have been a consequence of the onset of a monsoonal climate. The Kačák Event possibly represents a prolonged climatic crisis, with the black shales reported from some areas simply representing discrete horizons when oceanic anoxia occurred in certain places, with the event manifesting differently in other areas, such as with large terrigenous deposits in nearshore locations.

Implications for palaeogeographical reconstruction

The results presented here indicate that the Cantabrian Zone was sufficiently isolated during the Middle Devonian for a significantly endemic assemblage of dispersed spores and marine plankton to arise. Ocean currents provide a plausible mechanism for functional isolation to arise in the marine realm, preventing the dispersal of many planktonic species to the area. This does not, of course, account for the presumably wind-based dispersal of land plant spores to this region. This must, instead, be accounted for by geographical distance from the spores’ point of origin.

Different palaeogeographical reconstructions differ on the distance between the Armorican Terrane Assemblage and both Gondwana and Laurussia. Some favour a larger distance, particularly from Laurussia (Scotese 2001, 2008, 2016), some depict a position close to Laurussia and far from Gondwana (e.g. Stampfli *et al.* 2002) and others favour less separation from both continents (e.g. Cocks & Torsvik 2006; Torsvik & Cocks 2013). The presence of *Geminospora lemurata* in this assemblage, in the absence of the related *Rhabdosporites langii* and *Contagisporites optivus* as discussed in the section ‘Terrestrial vegetation’, suggests some restriction on megaspore dispersal. The rest of the dispersed spore community, which exhibits some degree of endemism, also implies separation from nearby continents.

The endemic palynomorph assemblage of the Cantabrian Zone supports early Givetian reconstructions with a large separation between the Armorican Terrane Assemblage and both Laurussia and Gondwana, along with a probably open Rheic Ocean through which strong currents could flow. The final closing of this ocean and the collision between the Armorican Terrane Assemblage and Laurussia (featured in all published palaeogeographical reconstructions) cannot have occurred until later.

Conclusions

Cluster analysis of the Middle Devonian dispersed spore and marine plankton assemblage of northern Spain has confirmed its unusual, endemic character, demonstrating a distinct lack of relatedness to contemporary assemblages from elsewhere. The unique characteristics of the terrestrial spore community suggest that the Cantabrian Zone, within the Armorican Terrane Assemblage, was a significant distance offshore by the Middle Devonian, sufficient to prevent subaerial dispersal of many widespread species. Similarly, the marine plankton community suggests a functional separation from other assemblages, perhaps by ocean currents preventing the dispersal of many planktonic species to the Armorican Terrane Assemblage. The Middle Devonian palynomorph assemblage and sedimentary record of the Cantabrian Zone support a large separation between the Armorican Terrane Assemblage and the supercontinents of Laurussia and Gondwana, with an open Rheic Ocean containing strong ocean currents.

The endemic nature of this palynomorph assemblage, and hence the lack of species used as stratigraphic markers elsewhere, makes it difficult to correlate this sequence with sea-level curves or transgression–regression schemes defined in other regions. Biostratigraphy shows that the sedimentary sequence of the Cantabrian Zone contains the Kačák Event, which may represent periods of anoxia during a generally wetter time when a monsoonal climate increased terrigenous sedimentation, reflected in the particular pattern of sedimentary deposits seen in northern Spain.

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