Algal diversity during the onset of the Late Palaeozoic Ice Age in low-latitude basins of the Western Palaeotethys

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ABSTRACT

A study of calcareous algae from the late Viséan to Serpukhovian interval in basins from the western margin of Palaeotethys (basins located currently in Western Europe and Northern Africa) shows varied responses in terms of palaeoecological diversity, specimen abundance, genus richness and taxonomic distinctness for the low-latitude basins. Algal associations are more similar in cratonic areas, although many local diversity peaks correspond to ecological/environmental factors. Terranes with Laurussian affinities contain the most unusual abundances and seem to be the most affected by palaeogeographic reorganization and local tectonics. Algae from the palaeo-equatorial zone show more dramatic changes than those in the southerly tropics. The varied results suggest that it is not suitable to extrapolate a particular diversity result from a single region to global conditions, since many factors have influenced the regional assemblages.

The main taxonomic turnover of most fossil groups occurred from the uppermost Serpukhovian, linked to a severe cooling phase inferred by $\delta^{18}O$ data from brachiopods. It coincides with the post-glacial phase C1 defined in eastern Australian basins. Most ecological changes occurred from the early Serpukhovian, predating the glacial phase C1 and coinciding with the Main Eustatic Signal. Far-field proxies used to define the onset of icehouse intervals in the LPIA are inconsistent and are located several million years before the main biota changes. This questions the definition of the onset of sustained icehouse glaciation at different levels of the low palaeolatitude Viséan, without the resulting modifications in the warm-water biota.

Keywords: calcareous algae; diversity; icehouse; LPIA; Mississippian; Palaeotethys

1. Introduction

The Late Palaeozoic Ice Age (LPIA) is the longest-lived glaciation recorded in the entire Phanerozoic, and its duration at approx. 70 Myr, is commonly considered to extend from the Famennian (Late Devonian) to the Sakmarian (Early Permian) (e.g., Montañez, 2021). Ice accumulation becomes more significant from the middle Viséan onwards, a period where sustained glacial conditions have been inferred (Montañez, 2021). However, some authors consider the onset of sustained cooling conditions began later, in the Serpukhovian (Fielding et al., 2008a, 2008b, 2023; Ahern and Fielding, 2021a). Most glaciogenic signatures are recorded in high-latitude basins (e.g., Fielding et al., 2008a, 2008b, 2023; Limarino et al., 2014; Isbell et al., 2021; López-Gamundi et al., 2021), whereas in low-latitude areas, the effects of glaciation are archived in stratigraphic architectures and stratal stacking patterns, which are recognized from the Asbian onwards (e.g., Rygel et al., 2008).

LPIA-focused studies have generally analysed either the long-term evolution during the Phanerozoic of invertebrate and microfossil groups, such as the brachiopods, rugose corals, conodonts, foraminifers and crinoids (e.g., Sepkoski, 1996; Stanley and Powell, 2003; Alroy et al., 2008; Fan et al., 2020), or alternatively, analysed macroevolutionary processes for shorter periods of time (e.g., Saunders and Ramsbottom, 1986; Raymond et al., 1990; Shen et al., 2006; Wang et al., 2006; Groves and Lee, 2008; Powell, 2008; Groves and Wang, 2009; Segessenman and Kramer, 2018). However, in these studies, a key uncertainty is the chronostratigraphic control on the stratigraphic record, which is not always as precise as would be desirable, leading to differing inferred synchroneity of faunal evolution (Yao et al., 2020; Shi et al., 2021).

A second important confounding factor is that biota sensitivity also changes between organisms. Nektonic faunas (such as ammonoids and conodonts) are typically widespread in open-marine conditions in the Carboniferous, but are less sensitive to rapid environmental changes, and consequently were less affected, because they were less impacted by the areal reduction in the continental shelves due to sea-level falls (Brenchley and Newall, 1984). Benthic organisms (such as brachiopods and crinoids) are rather tolerant organisms, and so are widespread from warm-tropical to temperate platforms, as shown for example by modern brachiopods (Giles, 2012). Similarly, Mississippian foraminifers occur in variable types of platforms and conditions, mostly as endobenthic organisms living in the sediment or seawater/sediment interface, and in contrast with other foraminifers, widely accepted as not being associated with endosymbiotic algae (Vachard et al., 2010). Modern calcareous algae and corals, on the other hand, are the most sensitive organisms to stressed conditions in platform environments (e.g., Graham and Wilcox, 2000; Hoegh-Guldberg et al., 2017). Global studies on the taxonomic biodiversity of marine invertebrates (as well as others focused on rugose corals), that include this latter clade have rather divergent results (for example compare Wang et al., 2006, Yao et al., 2020 and Shi et al., 2021).

1.1. Mississippian calcareous algae

Studies dedicated to Mississippian calcareous algae are scarce compared to the above-mentioned invertebrate and microfossil groups, with studies mostly focused on algal taxonomy, biostratigraphy and stratigraphic evolution, with less on their palaeoecology and habitat preference. Studies establishing the relationship between ecology and environments during the Mississippian, are generally focused on regions (e.g., Horbury and Adams, 1996; Pille, 2008) or particular environments (e.g., Adams,

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1984; Cózar et al., 2019). However, only a few Late Palaeozoic taxa extend into the Mesozoic and Cenozoic, and hence, comparisons with modern life styles and environmental conditions is not plausible in extinct taxa without modern equivalents (e.g., Algospongia). Mississippian taxa also seem to have survived in distinctly different environments to their modern counterparts (e.g., Cózar et al., 2018b). Also in modern carbonate platforms, living bryopsidales contribute three times more fine-grained carbonate <mark>sediment</mark> than living dasycladales, whereas in sand- and gravel-sized deposits, remains of bryopsidales can reach up to 50% in carbonates (Granier, 2012). The genera-balance during the Mississippian is distinctly different, with only some ancestral rhodophytes, scarce bryopsidales and common dasycladales and problematic algae.

This scarcity of Mississippian algal studies is a clear gap in knowledge, compared with their importance as ecological indicators in Modern oceans and ancient environments, where they are commonly used to determine important parameters, such as water temperature, bathymetry, salinity and acidification (e.g., Johnson et al., 2014; Leaf et al., 2020). Considering this good potential as <mark>ecological indicators</mark>, surprisingly little is known about the biodiversity of calcareous algae in relation to the onset of the LPIA, which this study aims to address. The aims are to: (i) characterise the diversity of calcareous algae in low-latitude basins in the Western Palaeotethys during the late Viséan to Serpukhovian interval. Our dataset includes Carboniferous basins in Western Europe and Northern Africa (including data from northern England, Ireland, Sierra Morena (SW Spain), Cantabrian Zone (N Spain), Moroccan Meseta and Tindouf (S Morocco-W Algeria). These basins were located in the western end of the Palaeotethys, between the equator and southern tropical zones (Fig. 1) and preceded the Gondwana-Laurussia collision, which lead to emergent land for most of the Pennsylvanian in the region (e.g., Nance et al., 2010); (ii) assess critical regional and global factors

controlling their diversity; and (iii) contrast the changes in diversity of calcareous algae with those described for other faunas during the LPIA interval.

2. Methodology

In this work, bryopsidales, dasycladales, blue-green algae (also known as cyanobacteria) and problematic algae Algospongia are hereafter considered as calcareous algae (Wray, 1977; Pille, 2008; Leaf et al., 2020). The overall taxonomic classifications followed here are those summarised in Pille (2008), and Vachard and Cózar (2010) for the problematic algae Algospongia, which in other cases have been interpreted as red algae, dasycladales, bryopsidales or even, foraminifers. Details of the considered algae, as well as their suprageneric classification are included in the Supplementary Information. Data for some calcareous algae used here have not been previously published, such as those of the Tindouf Basin and most of the succession from northern England sections (see Supplementary Information and Appendix A). Data is based on analysis of material from 1977 stratigraphic levels sampled in carbonates and examination of more than 5100 thin sections. Shaley intervals are omitted for the diversity analysis due to their minor influence on the total diversity recorded for each interval.

Genus richness (GR), based on the occurrence of genera compiled from the literature (including originations and extinctions), has the handicap that there are many endemic algal genera (Cózar and Somerville, 2021c), which have a wide geographic distribution, but not sufficiently widespread to be considered cosmopolitan for the large oceans (Appendix C in the Supplementary Information). A second handicap is the preferred suprageneric classification, which, depending on the authors, can be

considered as valid or not for the same taxa. Hence, to consider only originations/extinctions for substages, is not the best or only approach to determine the actual algal contribution to the geological record for this interval. Furthermore, due to the scarcity of studies of algae, the first appearance and distribution of many algal genera remains questionable (e.g., Mamet, 1991; Pille, 2008; Vachard and Cózar, 2010). Any analysis at species or genus levels assessing the diversity of most taxa is questionable, due to data scarcity. Consequently, genera have been grouped into tribes or orders, depending on the overall palaeoecological conditions and only two rather abundant genera (*Koninckopora* and *Ungdarella*) have been studied separately. In total, ten groups have been utilised: blue-greens, bryopsidales, dasycladales, rhodophyta, aoujgaliales, calcifoliids, donezellids, moravamminids, as well as the genera *Koninckopora* and *Ungdarella* (see Supplementary Information, Figs. S1–S5). The diversity of these groups has been analysed independently, as well as the total diversity, abundance and volume, as well as evaluation of various statistical metrics outlined in Table 1.

Analysis of the abundance of species and genera was undertaken using sub-division into four classes, rather than actual counts. This emphasises the role of the "rare" species/genera and minimises the importance of the "common" species/genera. For the more unusual algae, the counts for each class are: 1 = 1-2 specimens, 2 = 3-5 specimens, 3 = 6-10 specimens, and 4 = >10 specimens. For the more common genera (i.e., *Koninckopora*, donezellids and *Ungdarella*), these counts are modified, where 3 = 6-20 specimens and 4 = >20 specimens.

3. Stratigraphic successions investigated

All the analysed basins are located in the far western part of the Palaeotethys region during the late Viséan to Serpukhovian (and the earliest Bashkirian in some sections where limestones are recorded). These basins occur in stable cratonic areas and mobile terranes involved in tectonics of the Variscan Orogeny and closure of the Rheic-Palaeotethys gateway (RPG) (e.g., Nance et al., 2010) (Fig. 1).

Sections selected include those from northern England and platforms of the Dublin Basin (Ireland) for the Laurussia Platform. As an example of a Gondwana platform succession, that from the northwestern Tindouf Basin in southern Morocco, is included (Fig. 2).

In between these two regions, are basins located in the Western Palaeotethys and in western positions closer to the RPG - the Laurussian Palaeotethyan terranes (abbreviated as LPT). These show a higher palaeobiogeographical affinity with Laurussia. In contrast, those in the more eastern positions of the Palaeotethys - Gondwana Palaeotethyan terranes (GPT) are palaeobiogeographically closer to Gondwana, and are located in more open water conditions in the Palaeotethys (Cózar et al., 2018a; Cózar and Somerville, 2021c). Successions located in the LPT include those from Adarouch (Western Moroccan Meseta) and the Guadiato-Guadalmellato valleys (Sierra Morena in SW Spain). Successions located in the GPT are exemplified by sections in the Montagne Noire (southern France) and the Valdediezma Platform of the Cantabrian Mountains (NW Spain). Sampling in each basin, including the stratigraphic sections, location and biostratigraphic details are included in the Supplementary Information and Appendix A. In addition, the complete succession from Britain and Ireland for the Viséan to Serpukhovian has also been studied, as detailed in Appendix B.

Following palaeogeographic reconstructions, such as Blakey (2008), northern England and Ireland were located in equatorial positions at 10°S, with the LPT and the GPT at about 20-25°S. The LPT were in more western locations than the GPT, along the closing Rheic-Palaeotethys corridor, and the Tindouf Basin was at about 30°S, within more tropical and subtropical latitudes (Fig. 1).

The timescale used here for the correlation between sections, involves the Viséan Series for the British substages, up to and including the early Brigantian, whereas above this level, the substages of the East European Platform of Russia (EEP) (within the Serpukhovian Series) are used (see shaded parts in Fig. 3). Significantly, in the scale used here, there is no late Brigantian, because, as demonstrated by Cózar and Somerville (2014, 2016), it is virtually equivalent to the early Serpukhovian. The precision of the correlation between the Russian and British substages has been subsequently discussed in Cózar and Somerville (2021a, 2021b).

4. Palaeoecological diversity (PD)

4.1. Laurussia (northern England and Ireland)

As is well known (e.g., Walkden, 1987; Wright and Vanstone, 2001), the late Asbian platform successions in northern England shows marked cyclicity punctuated by emergent surfaces in largely carbonate successions. From the early Brigantian, a second style of cyclicity ('Yoredale- type') is developed, composed of thick siliciclastic deposits above carbonates which occur lower in the cycles, usually with coal in the upper part (Fig. 2). These limestone-clastic cycles have been interpreted as the typical stratigraphic pattern of glaciogenic periods, as recognised in the USA and Russia.

In general, in northern England, the algal group diversity (D_{group}) decreases into the Serpukhovian, although some taxa represent the most abundant algae during the Asbian (Table 2; see Supplementary Information Fig. S1A). Nevertheless, the diversity of each particular group allows recognition of four main algal associations (1-4; Supplementary Information Fig. S2). Furthermore, Association-1 can be also subdivided into 1A, 1B and 1C due to differences in abundances, thus making a total of six algal associations, which are variably recognized in time in the different basins (Figs. 4–5). The paucity of algae in the uppermost early Serpukhovian and late Serpukhovian does not permit the recognition of the predominance of any taxa or group.

In northern England, Association-1 is commonly recorded in dark grey bioclastic limestones (mostly packstone), which are non-cyclic during the early Asbian but cyclic for the late Asbian (Fig. 2). The three sub-associations (1A, 1B and 1C), show a progressive increase in *Ungdarella* and progressive reduction in donezellids, whilst the abundance in *Koninckopora* remains rather constant (Figs. 4A, 6A–6D).

Close to the Asbian/Brigantian boundary, there are frequent dark grey to black limestones, composed of dominantly mudstone and wackestone (Fig. 2), commonly interrupted by palaeokarsts (of short duration), with common quiet-water lagoonal facies. Most of the abundant algae in the underlying Asbian become rare or have disappeared, and a bloom of the dasycladales is observed, forming Association-2 (or the dasycladales association; Figs. 4A, 6E).

In the middle part of the early Brigantian, there was a dominance of pale grey limestones, and the presence of *Falsocalcifolium* allows recognition of Association-3 (the *Falsocalcifolium* association; Figs. 4A, 6F). This interval is also characterised by a reduction in the number of dasycladales. Association-3 is dominant up to the middle part of the early Serpukhovian, whereas, above this level, the occurrence of *Calcifolium*

distinguishes Association-4 (the *Calcifolium* association; Figs. 4A, 6G). The accompanying algae are similar to those in Association-3.

Although the highest D_{group} are observed in the Asbian, the highest peaks of total diversity (D_{total}) are observed in the early Brigantian (Fig. 4A). The total diversity in the late Serpukhovian is the lowest throughout the Asbian-Serpukhovian interval, since the calcareous algae are rather scarce (Fig. 4A).

The specimen abundance (SA) shows the highest values in intermediate levels of the late Asbian, early Brigantian and early Serpukhovian, but with an overall upwards-decreasing trend into younger intervals (Fig. 5A).

In Ireland, although there are no upper Serpukhovian carbonates recorded in the succession, the total diversity (Fig. 4A) and the group diversity (Table 2; Supplementary Information Fig. S1B) follow similar changes to those observed in northern England. The stratigraphical style during the Asbian is rather similar to that in northern England, with rhythmic limestones capped by emergent surfaces, whereas in Ireland a more continuous limestone succession is recorded for the early Brigantian and Serpukhovian (Fig. 2). Subtle differences are observed, such as lower dasycladal and calcifoliid D_{group} values in the early Serpukhovian, which could be interpreted as local environmental differences (Fig. 4A).

In Ireland, most of the algal associations recognised in northern England are also present, with the associations-1A, 1B, 1C and 2 also occurring in the same stratigraphic order and nearly covering the same stratigraphic intervals (Fig. 4A). In Ireland the dasycladales association only occurs above the base of the Brigantian, although the presence of emergent surfaces at this level in Ireland implies a sedimentary gap, with the probable absence of the uppermost Asbian strata (Cózar et al., 2022c).

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The specimen abundance shows a decreasing trend from the early Brigantian, similar to that seen in the northern England data (Fig. 5A). Peaks in SA recognized in the late Asbian and base of the early Brigantian are synchronous between Ireland and northern England, whereas trends in both these regions differ during the Serpukhovian.

4.2. LPT (Sierra Morena and Adarouch)

The successions in Sierra Morena and Adarouch are both mainly non-cyclic in character, with that of Sierra Morena representing a continuous carbonate accumulation in the lower part of the succession (predominantly with microbially-mediated carbonates), whereas thick shale intervals are recorded between limestone intervals in Adarouch (suggesting four major deepening sequences and a final fifth shallowing sequence, Se1 to Se5 in Fig. 2).

The late Asbian, mostly recorded in Sierra Morena, shows rather consistent values in total diversity (Fig. 4B), with the same algal components as observed in Laurussia, although with larger D_{group} values for blue-green algae (Table 2; Supplementary Information Fig. S3A). The larger contribution from blue-green algal is a consequence of the common microbial facies in the inner platform (Fig. 2), a facies not present in the British/Irish inner platforms.

The early Brigantian shows higher D_{total} values (Fig. 4b) than in the late Asbian, and in contrast with Laurussia, the dominant groups of the late Asbian also extend into the early Brigantian (Supplementary Information Fig. S3A). The overall changes in D_{group} in the Adarouch region are similar to those in Sierra Morena (Table 2; Supplementary Information Fig. S3B). Small differences are interpreted to be local characters, influenced by ecological or environmental conditions. In contrast with Laurussia, marked lows (D_{total} <0.5) in the total diversity are scarcer (Fig. 4B), and

generally D_{total} values exceed 2 during the early Brigantian. The absence of these lows, as well as the absence of associations-2 and 3 during the early Brigantian, might be related to the absence of typical Yoredale-type cycles in the LPT, and thus the differing environmental and ecological conditions.

The early Serpukhovian contains marked changes in D_{total} (Fig. 4B), like those in Laurussia. These D_{total} changes are more marked in Sierra Morena than in Adarouch, with slightly lower D_{total} values in the upper part of this substage. The late Serpukhovian seems to show a recovery in the total diversity, reaching similarly high values (D_{total} >1.5) to those during the early Brigantian, an effect mostly due to the dasycladales (Fig. 4B). During the Serpukhovian, basins analysed herein were tectonically active (e.g., Cózar et al., 2006, 2023b).

The recognition of associations in the LPT is rather similar to that in Britain, and the association-1A is recognised in the late Asbian of Adarouch (but is not observed in Sierra Morena), but the stratigraphic interval covered by each association differs from the Laurussia sections (Fig. 4).

In term of abundances, in Sierra Morena, the late Asbian has consistently larger values (SA >10), whereas larger SA at Adarouch is more consistently located in the early Brigantian (Fig. 5B). In both cases, abundances generally decrease into the early Serpukhovian. The late Serpukhovian in Sierra Morena also contains large abundance values (Fig. 5B). Thus, the uppermost part of the succession in the LPT is different from the Laurussia Platform, with the peaks in Laurussian SA data during the late Asbian-Brigantian which are not observed in the LPT. This is perhaps the result of differing cyclic sedimentation patterns (Fig. 2).

Both successions show a transition into deltaic facies in the upper part, at the top of the Protvian in Sierra Morena, and also at Adarouch, dated to the Voznesenkian (Fig.

2), where carbonates commonly contain quartz grains, representing more hostile facies for algae. Nevertheless, during the Bashkirian, representatives of the groups dasycladales, blue-greens, donezellids and rare aougaliids are recorded in these beds, belonging to the same genera/species seen in older Serpukhovian levels in the LPT.

4.3. GPT (Montagne Noire and Valdediezma)

This region contains the thickest carbonate accumulation of all those in the study area (Fig. 2). Late Asbian strata in the Montagne Noire are poorly represented, with the lower parts of the substage commonly represented by siliciclastic turbidites (Cózar et al., 2017), or absent because of faulting in the Valdediezma Platform. This latter succession from northern Spain displays the oldest carbonates, dated to the upper part of the Mikhailovian Substage (= early Brigantian; Fig. 3) (Blanco-Ferrera et al., 2021).

The short late Asbian interval in Montagne Noire contains smaller D_{total} values than the Brigantian (Fig. 4C), as also observed in the LPT platforms. The negligible contributions of *Koninckopora* to the diversity are a remarkable and unique feature, which characterises the GPT (Table 2; Supplementary information Fig. S4).

The early Brigantian shows a similar scale of fluctuations in total diversity as in other regions (Fig. 4), and the most important groups are similar to those in the Asbian elsewhere in Laurussia and LPT (Table 2).

D_{total} values greater than 1.5 in the early Serpukhovian in the GPT are in marked contrast with the LPT, because these values exceed those during the early Brigantian (Fig. 4B, 4C). This represents a somewhat similar relationship to that observed in northern England. The incoming of dasycladales is the main group contributing to the higher D_{group} values in the GPT (Supplementary Information Fig. S4).

The late Serpukhovian contains high D_{total} values for the lower part (equivalent to the Protvian), and a marked decrease for the upper part (equivalent to the Zapaltyubian) at Valdediezma (Fig. 4C). Similar variation in D_{total} in the upper part of the Montagne Noire succession is not observed, because the interval corresponding to the Zapaltyubian is composed of siliciclastic deltaic deposits and algae were not recorded (Cózar et al., 2019).

The GPT contains the most unusual algal associations, and only associations 1B, 3 and 4 are found (Fig. 4C), with no similarities between sections, or with the other regions.

In terms of algal abundance, smaller values occur during the Brigantian, increasing towards the top of the early Serpukhovian, then generally decreasing to the top of the GPT successions (Fig. 5C).

The succession in the Valdediezma Platform contains well-developed early Bashkirian carbonates (Fig. 2), interrupted by an overlying unconformity, onlapped by Moscovian carbonates. In the early Bashkirian units, total diversity is <1.0, with mostly calcifoliids and donezellids occurring. These are noteworthy for the occurrence of *Donezella* (Fig. 6H), a typical Pennsylvanian taxon, which is the only renovation within the GPT assemblages.

4.4. Gondwana (Tindouf)

The succession in the Tindouf Basin is distinctly cyclic from the early Brigantian onwards (Fig. 2), although complete cyclothems veneered by coal were not developed (Cózar et al., 2014).

This platform shows large total diversity (generally D_{total} >1.5) during the late Asbian and early Brigantian (Fig. 4D). The early Serpukhovian has more D_{total} values,

largely > 2, with often total diversity < 1 for the late Serpukhovian (Fig. 4D). The overall changes in D_{total} are similar to those observed in Laurussia, with both regions showing an overall decreasing trend into the late Serpukhovian.

In terms of group diversity, *Koninckopora* largely makes a major contribution throughout the succession, much like that shown by aoujgaliales (Table 2; Supplementary Information Fig. S5). Negligible contributions are from blue-green algae, whereas the dasycladales form a smaller contribution to the diversity, which is particularly important during the early Serpukhovian. These features are also observed in the Laurussian platforms.

The succession in Tindouf contains five of the six algal associations, with only the association-1C not recognised (Fig. 4D). The timings of the appearance of associations shows a marked delay compared to the British/Irish data (Fig. 4).

The interval equivalent to the Zapaltyubian and Voznesenkian in the Tindouf succession are composed of sandy supratidal sabkhas (Fig. 2), with rare occurrence of algae. However, in the upper part of the carbonate succession (assigned to the Krasnopolyanian Substage), there is a recovery in the total diversity and abundance of algae (Figs. 4D, 5D). The main components in the Krasnopolyanian age beds are aoujgaliids (mostly *Aoujgalia*), *Ungdarella*, calcifoliids (*Calcifolium* and *Falsocalcifolium*) and donezellids (*Praedonezella*). These genera are the same as those from the Serpukhovian in Tindouf, and thus there are no new typically Pennsylvanian taxa.

5. Volumetric contribution (%V) of calcareous algae to the carbonate factory

The late Asbian is the interval with the largest contribution made by calcareous algae, forming 40% to 70% of the total content in beds (including allochems, matrix and cement) (Fig. 7). The fluctuations in %V values in the Laurussia Platform successions seem to be controlled by glacioeustatic cycles (Fig. 7A), which are rather similar to the foraminiferal trends defined between emergent surfaces in Britain and Ireland (Cózar et al., 2022c). Surprisingly, at Sierra Morena, virtually free of emergent surfaces for this interval and with no recognisable cyclicity, similarly-timed peaks of similar algal composition and cycles are also observed (Fig. 7A, 7B). However, other lithologically non-cyclic successions, such as that in the Brigantian of Adarouch and Montagne Noire, express high-frequency cyclicity, recognised by detailed statistical analysis of components and matrix (e.g., Cózar et al., 2019, 2022a). This suggests that cryptic ordering of the late Viséan allochem components at Sierra Morena probably also occurs. Thus, the modulation in %V could be a result of glacioeustasy, or perhaps Milankovitch-forced cyclicity. The distribution and abundance of algae in these cycles is controlled by the transgressive, highstand and regressive phases defined in each cycle, and thus, environmental changes modulate between favourable and unfavourable conditions during the cycles. Nevertheless, an important problem to recognise in those more consistent patterns in algal distribution and abundance in each cycle, are "missing beats" in the stratigraphical record.

In Laurussia and the GPT the early Brigantian shows a large reduction in the role of the calcareous algae in forming limestone allochems, with contributions then ranging between 5% and 20% (Fig. 7A, 7C), and common intervals of absence. In contrast, the early Brigantian of the LPT, commonly has intervals where algae reach 40-50% by volume (Fig. 7B).

The early Serpukhovian represents a recovery in the algal abundance (except for Ireland), an effect which is progressively more pronounced in the south-eastern higher palaeolatitudes, with increasing abundances ordered from Laurussia – LPT – GPT to Gondwana (Fig. 7), although values from the GPT and Gondwana are rather similar.

In general, the late Serpukhovian shows the same (but more pronounced) increases in V% towards southern-eastern higher palaeolatitudes, as also observed for the early Serpukhovian.

In the Laurussia and LPT successions, a progressive decrease in the volumetric importance of algae from the late Asbian to late Serpukhovian can be recognised. Whereas, the inverse pattern is recognised for the GPT successions, with increasing %V values. These increasing values in GPT could be interpreted as due to the massive occurrence of limestones (Fig. 2). However, other successions in Adarouch and Sierra Morena, such as in the late Serpukhovian, only show similar inner platform limestones, and the trends are clearly decreasing. In Gondwana, there is a weakly-defined inverse change in %V from the late Asbian to the Early Serpukhovian, and although some large %V are shown in parts of the late Serpukhovian, this inverse pattern is not sustained, but contrasts with the similar stratigraphical successions from northern England.

6. Genus richness (GR)

Genus richness shows the largest values during the late Viséan (Fig. 8A), decreasing progressively into the Bashkirian. This peak is conditioned by the high number of originations during the late Viséan, although the number of originations decrease notably for the early Serpukhovian. In contrast, the number of extinctions is low, but increases from the early Viséan to the late Serpukhovian, decreasing again in

the early Bashkirian (Fig. 8A). The large and increasing genus richness during the Viséan coincides with the high genus diversity in dasycladales (Appendix C), which also coincides with the largest species diversity for the Viséan described by Bucur (1999) and Aguirre and Riding (2005).

The transition between the Viséan and Serpukhovian is the main point of inflexion in the GR curves, where extinctions become more important than originations (Fig. 8A). The data controlling these are mostly changes in the diversity and originations/extinctions in the Western Palaeotethys sections (Fig. 8B). This is similar to that from the Eastern Palaeotethys, which is however less pronounced. The diversity in both the North American and Uralian realms is lower, but weakly increases through this same time interval (Fig. 8B).

Overall, the transition between the Viséan and Serpukhovian is the most significant interval for change in the genus richness, although with regional differences.

7. Taxonomic distinctness (Δ^+)

Despite the marked differences in the overall genus richness (GR), specimen abundance (SA) and palaeoecological diversity (PD) between the different regions and realms (Figs. 4, 5, 8B), there are no large differences in their taxonomic distinctness (Fig. 9A). Taxonomic distinctness (Δ^+) decreases from the Tournaisian to the Viséan and shows a near-plateau (with a minor increase) for the Viséan and Serpukhovian, in spite of the numerous new genera appearing in the late Viséan. The transition into the Bashkirian shows a strong overall decrease (Fig. 9A). However, Δ^+ for the studied regions display very different responses (Fig. 9B), as was previously outlined for

palaeoecological diversity, suggesting local factors controlled the regional distribution of algae.

Nevertheless, the agglomeration of the data from the seven regions in the Western Palaeotethys, gives a small increase in Δ^+, from the late Asbian to the Zapaltyubian (Fig. 9C), which is approximately the same behaviour as that in the global curve (Fig. 9A). In the Western Palaeotethys the lower Δ^+ values are from the late Asbian (Fig. 9C). The Δ^+ data from Britain and Ireland, also show low values in the Chadian, 'lower' values in the Holkerian, late Asbian and early Serpukhovian, and high values in the "lower" Arundian, "upper" Holkerian-early Asbian, and early Brigantian (Fig. 9D). These decreases and increases in some regional successions (Fig. 9B, 9D) are possibly related to local factors, whereas the most marked change in Δ^+ for global associations is located in the uppermost Serpukhovian-early Bashkirian transition (Fig. 9A), which is interpreted to be conditioned by global factors.

8. Comparison of the algal palaeoecological diversity (PD), specimen abundance (SA), volumetric abundance (%V), genus richness (GR) and taxonomic distinctness (Δ^+)

The timing of important changes in algal populations is not uniform, with differing trends in the algal diversity, richness and abundance. However, when comparing datasets with smaller between-section distances, the results are more consistent, with basins in Laurussia, LPT and GPT showing a good deal of similarity (Figs. 4, 5, 7).

In general, there are declining abundances (%V and SA) in younger levels in the more palaeoequatorial regions, whereas the opposite trend occurs in regions closer to the palaeotropics. The specimen abundance usually mimics the curve of volumetric

abundance in most regions, but in the Serpukhovian differing relationships are observed (Figs. 5, 7). Both SA and %V are likely mostly controlled by ecological and environmental factors, and to a lesser extent by local tectonics (controlling changing accommodation space, water depth, clastic inputs, etc.). The interplay of these factors likely produced differing results in the mobile terranes (LPT and GPT), which also impacted the contrasting trends in SA and %V between Laurussia and Gondwana (Figs. 5, 7).

The palaeoecological total diversity shows more consistent patterns, largely starting from the base of the Brigantian. From this level, the total diversity decreases in the Brigantian, has a maximum value during the early Serpukhovian, and then declines in younger intervals in the late Serpukhovian (Fig. 4). On the other hand, during the late Asbian, total diversity can display increasing values in some LPT and GPT sections. The maximum observed in the early Serpukhovian in most regions is, however, recorded as lower values in the LPT. Consequently, total diversity in the LPT is more influenced by regional factors compared to global factors- possibly the stronger basin-tectonics acting in the LPT for this period had an impact (e.g., Cózar et al., 2006, 2023b).

The genus richness (GR) follows a consistent decreasing trend from the late Viséan onwards (Fig. 8A) as that of abundance in Laurussia and Sierra Morena (Fig. 5A, 5B), whereas the taxonomic distinctness follows increasing patterns as that observed for %V in the GPT (Fig. 7C).

Owing to the different palaeogeographic position of the basins, differing oceanic current influences and different environmental settings, the differences during the Serpukhovian, particularly the late Serpukhovian, are most likely conditioned by the Rheic Gateway closure (due to active tectonics during the Laurussia-Gondwana

collision), and the subsequent reorganization of the emergent land. This factor surely also conditioned the variable diversity (in terms of D_{total}) observed in the late Serpukhovian of some regions (Fig. 4). In contrast, the decreasing diversity patterns (D_{total}) starting from the Brigantian, in turn, coincides with the period when the sea-level falls have been claimed as more pronounced (e.g., Smith and Read, 2000; Rygel et al., 2008), and thus, as a result of more global changes. This similarity in D_{total} patterns might correspond to global cooling conditions of sea water.

The pattern observed in taxonomic diversity in the algae, of a progressive decrease during the early Bashkirian (Fig. 9A), is coincident with those observed in foraminifers, conodonts, ammonoids, and is related to the major cooling phase recorded during the early Bashkirian, as showed by markedly positive oxygen isotopes (e.g., Grossman and Joachimski, 2020).

9. Comparison with other fossil groups

One of the most important studies on Carboniferous calcareous algae is that of Mamet (1991), who inferred that the Serpukhovian-Bashkirian transition was the main turnover within the algae, mostly because consideration was only given to 26 last occurrences and 15 first occurrences of algal genera at this boundary. This transition using dasycladales also marks an overall decline in genus richness (Aguirre and Riding, 2005). This same overall trend is recognised in our study, but the number of included genera is greatly increased, since knowledge of the algae (and distributions) in the late 1980's was much less. Thus, (i) many of the taxa formally considered by Mamet (1991) as extinct at the top of the Serpukhovian are now known to extend into the early Bashkirian; (ii) other genera became extinct in the mid-late Viséan to basal late

Serpukhovian interval. In contrast, some genera considered by Mamet (1991) as having first occurrences at the base of the Bashkirian, (i) are now known to first occur from the late Viséan; whereas others, (ii) first occur in later stages of the Bashkirian. Only 6 out of the 26 last occurrences mentioned by Mamet (1991) at the top of the Serpukhovian can be confidentially considered as valid, as well as only 6 out of the 15 first occurrences. Positioning the major algal turnover at the Serpukhovian/Bashkirian boundary (as suggested by Mamet, 1991) is questioned here, and our improved knowledge about algal ranges no longer supports the conclusion of that study. We agree though, that during the early Bashkirian, there is a change in the algal associations and ecosystems. However, this renovation of the algal ecosystems is progressive from the Serpukhovian. We infer the marked decrease in taxonomic distinctness at the Serpukhovian-Bashkirian transition to be the main ecosystem turnover (Fig. 9A), although it is not a rapid or dramatic change, since diversity also increased progressively during the early Bashkirian.

For a comparison to be made with algae, it is inappropriate to use a mixture of benthic and planktonic organisms to characterise the Mid-Late Mississippian, since ecological conditions will differ distinctly. Data on genus or species diversity have been compiled for the Phanerozoic based on extinctions/originations of marine invertebrates (Sepkoski, 2002; Alroy et al., 2008; Zaffos et al. 2017; Fan et al. 2020). However, as mentioned previously, firstly, the genus/species occurrence is not the most appropriate method to analyse the biota diversity, and secondly, biostratigraphic calibration of some published studies is questionable, and thus the potential for comparison is limited. In some cases, the biostratigraphy of some publications could be revised due to extant published data (see Supplementary information), but in other cases, biostratigraphic

data were scarce as to recalibrate the successions, and their use has to be taken with caution.

During the LPIA, there is a pronounced decrease in the species richness of conodonts from the Famennian to the Sakmarian (Shi et al., 2021), although by the late Viséan to early Bashkirian, the species richness had plateaued. The main turnover in conodonts occurred during the Bashkirian, at slightly different times for each basin (Sanz-López et al., 2013), with this turnover coinciding with the downturn in taxonomic distinctness seen in the algae (Fig. 9A).

Ammonoids had a similar response to the conodonts, with major extinctions from the latest Serpukhovian, with radiation of survivors and originations of new taxa in the early Bashkirian (Saunders and Ramsbottom, 1986).

Foraminiferal diversity changes are presented differently by Groves and Lee (2008) and Groves and Wang (2009), but they do show increasing diversity from the base of the late Viséan in Eurasia and North America. However, although Groves and Lee (2008) showed higher richness persisting during the early Serpukhovian, and a decrease for the late Serpukhovian, Groves and Wang (2009), demonstrated an alternative pattern, with decrease in the early Serpukhovian and an increase in the late Serpukhovian (compare lines C3 and C4 in Fig. 10C). These foraminiferal diversity changes differ distinctly from those observed in China, where it had plateaued from the late Tournaisian-latest Viséan, followed by a sustained increase during the early Serpukhovian (line C5 in Fig. 10C), and a less pronounced increase to a 'middle' Bashkirian bloom (Shi et al., 2021). In contrast, Aretz et al. (2014) claimed that the foraminiferal richness trend decreases from the top part of the Tournaisian, slightly increasing in the early Serpukhovian part of the MFZ15 foraminiferal zone (see Fig. 3),

and again decreasing for the interval higher up in the Serpukhovian (line C6 in Fig. 10C).

Since these previous studies include different realms (North America, Western Palaeotethys and Eastern Palaeotethys), the similar changes in conodonts, ammonoids and foraminifers are interpreted to be a reaction to the main cooling phase of oceanic waters. The same can be also inferred for the calcareous algae, highlighted by the drop in taxonomic distinctness from the uppermost Serpukhovian to early Bashkirian (Fig. 9A).

For benthic macrofauna, such as rugose corals, differing responses were inferred by Wang et al. (2006) and Shi et al. (2021) from China, with an increase in taxonomic diversity during the Viséan, but largely focused in the Serpukhovian (line C2 in Fig. 10C). This contrasts with the results in Yao et al. (2020), where the maximum worldwide coral diversity and reefs is located in the late Viséan (which, according to them, includes the upper late Asbian and early Brigantian), with a marked decrease from the uppermost late Viséan. Biostratigraphic calibration in the latter study has been questionable (Liu et al., 2023), and the maximum diversity instead likely corresponds to the latest Viséan (similar to the algal maximum recorded here), possibly including up to the early Serpukhovian. Their diversity maximum allows Yao et al. (2020) to define the "marine ecosystem resurgence (MER)", which is considered as a period of warm climate, and is compared with the "high point of Carboniferous global warming" (HPCW) of Giles (2012) (Fig. 10). Coral data from the Western Palaeotethys, suggests that the largest diversity occurred in the latest Viséan to earliest Serpukhovian, followed by a progressive decline (Rodríguez et al., 2012; Denayer et al., 2016). This decline in coral species diversity is observed in China from the late Bashkirian (Shi et al., 2021, fig. 6A). Currently, there is no detailed coral diversity analysis from Western Europe,

but apparently, from published data, the overall genus richness is similar to that observed in the calcareous algae (C7 in Fig. 10C), but not with the other parameters measured here, and might coincide with those data in Yao et al. (2020). The coincident peaks in the late Viséan for both corals and calcareous algae are possibly the result of stable and favourable ecosystems on the carbonate platforms. It would be interesting to better test if the acme in coral diversity in both Western and Eastern Palaeotethys is really differently timed, a fact that is not observed in the calcareous algae. In such a scenario, the maxima in coral diversity would be a response to extremely favourable ecological conditions, unrelated to glaciogenic influence.

Brachiopods show differing responses, depending on palaeolatitude, with low rates of originations up to the early Bashkirian in equatorial forms. In contrast, non-equatorial forms show higher rates of originations at the base of the late Viséan (Powell, 2008), with major extinctions within the clade during the early Serpukhovian. Raymond et al. (1990) also infer some origination/extinctions with a maximum of diversity in the lower part of the late Viséan and a progressive decrease during the Serpukhovian. In contrast, Shi et al. (2021) showed a minor increasing richness from the middle Tournaisian to basal Moscovian interval. The timing of brachiopod extinctions for the early Serpukhovian are similar to the declines seen in the calcareous algae in the PD and GR metrics (and more rarely in %V and SA).

None of the above-described timing of diversity changes are precisely similar to that observed in the calcareous algae, but other similarities occur. The main similarity is the diversity decline during the early Serpukhovian (in term of species/genus richness), with decreasing diversity in foraminifers, algae and corals, or even major extinctions in some brachiopod groups, all of which are benthic biota widespread in the shallow-water platforms. The second main similarity is observed in the uppermost Serpukhovian,

which is an interval of turnover in many fossil groups, benthonic and nektonic (McGhee et al., 2012), leading to a progressive diversity increase during the Bashkirian.

The most similar group to the algae seems to be the foraminifers described by Groves and Lee (2008) and Groves and Wang (2009). To display this similarity, the palaeoecological diversity of algae and foraminifers from Britain/Ireland are shown in Figure 10A–10B. Only the interval between the mid Viséan and the lower half of the late Asbian contains some differently-timed peaks in diversity. Major peaks (inflexions) in diversity can be defined in the algal curve: close to the base of the Chadian; at the base of the Holkerian; in the early-late Asbian boundary; and close to the base of the early Serpukhovian (Fig. 10A). The early Serpukhovian algal inflexion is coincident with that for the foraminifers. The inflexions near the base of the Chadian, Holkerian and early-late Asbian are recorded also in the foraminifers, but in slightly younger levels than for the algae. In contrast, the foraminifers show a marked peak in the upper Holkerian with very low values during the early Asbian, with no equivalence in the calcareous algae dataset (Fig. 10A–10B). We suggest that coincident or nearly coincident inflexion points reflect global factors such as glacioeustasy and tectonics (or any of its possible implications on the platforms), whereas the other non-coincident inflexions might correspond to more intrinsic controls on ecological factors. In the case of the early-mid Viséan boundary, the inflexion point can be related to a major sea-level fall produced by tectonic activity in the Palaeotethys, showing a major unconformity, commonly with development of fluviatile sediments in Belgium, Holland, Germany, Russia, Ukraine, China, and Turkey (Cózar et al., 2023a). The inflexion point during the early Serpukhovian can be related to the high-latitude cooling coincident with the "Main Eustatic Signal" (MES in Fig. 10) of Fielding and Frank (2015) and predating the phase C1 of Fielding et al. (2008b). The coincident point at the base of the Viséan does not

have an apparent direct cause, but similar marked changes are also observed in global marine genus/species diversity (Shi et al., 2021, fig. 1). Nevertheless, this level coincides with a major hiatus in SW Britain caused by a high amplitude and rapid sea-level fall (Wright and Vanstone, 2001), although this so-called Avonian unconformity is not recognized in NW Britain.

10. Discussion: Onset of the sustained LPIA or icehouse conditions

The Famennian is the first stage where the icehouse cooling phase commences, and thus, the onset of the LPIA sensu stricto. It was during the Tournaisian and early Viséan, that gradual cooling and short-lived glacial events are interpreted to occur (e.g., Buggisch et al., 2008; Liu et al., 2019), whereas the timing of sustained glaciation is still debated (e.g., Fielding et al., 2008a, 2008b, 2023; Bishop et al., 2009; Giles, 2012; Limarino et al., 2014; Montañez and Poulsen, 2013; Montañez, 2021). In addition, the timing of accumulation of ice centres or large ice caps is debated (e.g., Stephenson et al., 2010; Lowry et al., 2014; Chen et al., 2016; Isbell et al., 2021).

10.1 Seawater palaeotemperatures from $\delta^{18}O$

To precisely define the cooling effects of the LPIA, studies of $\delta^{18}O$ values on brachiopods, conodonts and whole rocks have been commonly used (e.g., Veizer et al., 1999; Joachimski et al., 2006; Prokoph et al., 2008; Grossman et al., 2008; Chen et al., 2016; Grossman and Joachimski, 2020). $\delta^{18}O$ data from conodonts show increasing values from the Tournaisian to the Bashkirian (changes of >5‰, are interpreted as a fall of ca. 20º in seawater temperature), with the most rapid $\delta^{18}O$ increases possibly in the late Serpukhovian and early Bashkirian (see Grossman and Joachimski, 2020, fig. 10.8).

Nevertheless, more rapid $\delta^{18}O$ increases have been described from some regions, such as in the Northwest Ireland Basin by Barham et al. (2012), with +2.4‰ rise over an interval of ca. 3 Myr, although such a marked shift is not observed in other global curves (Fig. 10E). Similar isotopic increases, more than 2‰ in ca. 1 Myr, are recorded by Yao et al. (2022) from China, around the Asbian-Brigantian boundary interval, unrecorded in other global curves. The Asbian-Brigantian boundary was suggested by Barham et al. (2012) as the "major LPIA onset", an interval that Yao et al. (2020) include as part of a period of warm climate, coinciding with beginning of the "marine ecosystem resurgence (MER)" (Fig. 10).

In contrast, the $\delta^{18}O$ curve for brachiopods shows a decline in the Viséan, which was used by Giles (2012) to define the 'high point of Carboniferous warming' in the late Asbian. Only the late Serpukhovian $\delta^{18}O$ data show an increase (Fig. 10D). The data from brachiopods have been commonly criticised due to the confounding problem of aridification (Grossman et al., 2008; Grossman and Joachimski, 2022), and also that brachiopods are mostly recorded from shallow-water platform facies. Hence, most of the Carboniferous brachiopod $\delta^{18}O$ data incorporate data from epeiric platforms, where shelfal or near-shore organisms are inferred to be impacted by changes in surface seawater temperature, evaporation, precipitation and freshwater influx (Shackleton, 1967; Miller et al., 2005, 2011; Brand et al., 2009; Chen et al., 2013).

Most of the currently available data on Carboniferous conodonts have similar problems as those for brachiopods, because they have been commonly sampled in the same epeiric platforms as the brachiopods, and rarely, do they belong to outer platform to slope environments, such as those described by Chen et al. (2016) from the Youjiang Basin in China. Certainly, contamination of $\delta^{18}O$ data is due to these shallower-water settings, although brachiopod and conodont $\delta^{18}O$ curves have contrasting increasing and

decreasing trends (compare Fig. 10D–10E). The Middle Mississippian-Lower Pennsylvanian interval is the period were these discrepancies between $\delta^{18}O$ values in brachiopods and conodonts are more marked (Grossman and Joachimski, 2022).

Therefore, there are no major inflexions in the $\delta^{18}O$ curves, which allow a definition of sustained icehouse cooling, evidenced in seawater proxies within the mid Viséan to the base of the Serpukhovian (Fig. 10D–10E). The exception is from brachiopods during the uppermost Serpukhovian, where there are some progressive changes, expressed as declines in the case of the brachiopods and increase in $\delta^{18}O$ for conodonts. Thus, there is an absence of consistency in defining the "onset" of seawater cooling.

10.2 Sea-level and biotic changes

In terms of macroevolutionary processes, the most sensitive biota suggest that there is a marked diversity decrease in the latest Viséan, shown by calcareous algae (Fig. 8A) and coral and skeletal reefs (Yao et al., 2020). However, this is not universally observed, with the peak diversity of corals occurring during the Serpukhovian or in the late Viséan, whereas other fossil groups (foraminifers and brachiopods) have increasing diversity in this interval. Nevertheless, there seem to be an ecological change in the diversity of some fossil groups in the early Serpukhovian and the onset of the main taxonomic turnover in these fossil groups is frequently associated with the latest Serpukhovian (i.e., in ammonoids, conodonts, foraminifers and calcareous algae). These features could be interpreted as a result of sustained glaciation conditions, with the coolest conditions possibly from the early Serpukhovian (coinciding with the Main Eustatic Signal of the LPIA of Fielding and Frank, 2015), but becoming cooler in the uppermost Serpukhovian-earliest Bashkirian (representing the final stages of the glacial

phase C1 up to phase C2 of Fielding et al., 2008b). Nevertheless, taxonomic turnover could be the result of changes in Palaeotethys water chemistry or circulation, since the late Serpukhovian coincides with the closure of the Rheic-Palaeotethys gateway (Davydov and Cózar, 2019), giving more intense hydrothermal and continental weathering, and consequent runoff to marine basins (Bruckschen et al., 1999; Steuber and Veizer, 2002). This led to continental reorganization and isolation of some basins, modification of north-south aligned platforms, and the possibility of enhanced migration of biota, a potentially important factor in extinctions (Saupe et al., 2020).

The local relationship between sea-level fluctuations and global ice accumulation is a complex response depending on orbitally-driven sea-level changes in eustasy, basin accommodation space, glacial isotopic adjustment, thermal expansion, aquifer eustasy (Isbell et al., 2021), as well as tectonic uplift (Dávila et al., 2023). In addition, the synchronicity and the importance of sea-level falls is variable from the early Asbian (Wright and Vanstone, 2001; Barnett et al., 2002), late Asbian (Giles, 2009; Cózar et al., 2022c), early Brigantian (Smith and Read, 2000), as well as for the early Serpukhovian (e.g., Ahern and Fielding, 2019, 2021a). These confounding factors question if the onset of typical cyclic successions can really be used to define the onset of icehouse conditions, since there are other controls to explain cyclicity, such as tectonics, autocyclicity, and regional wet-to-dry climate changes (e.g., Weller, 1930; Wanless, 1964; Horbury, 1989; Cecil, 1990). Hence, alternative explanations to glacioeustasy could control the onset of cyclicity (Rygel et al., 2008).

In the Palaeotethys, a major sea-level fall occurs in the early-middle Viséan boundary (or equivalent early-late Viséan boundary in the Russian Platform; Fig. 3). A sedimentary gap or deposition of non-marine sediments occurred during ca.1-2 Myr interval near the top of the early Viséan (Cf4δ and Cf5α foraminiferal zones; Fig. 3) and

the base of the middle Viséan (in some cases extending down into the entire early Viséan) in some regions of the Palaeotethys (Mid Viséan Unconformity, MVU in Fig. 10). In other regions, such as in England, this hiatus is almost negligible, but perhaps present (Cózar et al. 2023a). This major sea-level fall, although more-or-less global, is likely more related to tectonic events and continental readjustment, with common volcanic events represented by cinerites in these levels (Delcambre, 1989; Pointon et al., 2021). This mid Viséan boundary coincides with the onset of the diversity increase of many fossil groups (Fig. 10C), which does not seem to be the expected response to cooling events.

In Britain, as mentioned above, the hiatus is of lesser importance (recognisable in some basins; Waters et al., 2021), but some bentonitic layers are recognisable in sections (Hounslow et al., 2022), near the base of the revised Holkerian (sensu Cózar et al. 2022b, 2023a), which shows a notable peak in calcareous algal diversity (Fig. 10A).

10.3. The timing of possible glaciogenic onset

There are no unanimous features which allow a precise pin-pointing of the timing of the onset of sustained icehouse conditions. The base of the Asbian, if biostratigraphic calibration is correct, does not coincide with any faunal, sedimentological nor isotopic change, and thus, this possibility can be discarded. Some key events at several distinct times are possible candidates:

(Event 1): At a major sea-level fall at the base of the mid Viséan (Fig. 10A), coinciding with a widespread hiatus, but without clearly defined cyclic sequences. Following this event is an overall increase in taxonomic diversity of some fossil groups, and marked ecosystem changes in both foraminiferal and algal diversity. These changes and reduction of the diversity are recorded in Britain/Ireland in horizons in the

uppermost part of this interval (Fig. 10A, 10B). However, as discussed above, a tectonic control on this hiatus seems to be a better explanation.

(Event 2): At the onset of cyclic-rhythmic sequences at the base of the late Asbian, which also coincides with ecosystem changes (Fig. 10A). This event is not free of controversy, since in Britain at least, apart from possible cumulative autogenic sedimentation processes, local/regional tectonics and eustasy have all been suggested as originators of these rhythms/cycles (see revision in Horbury, 1987). The inference has been, that in the sections in NW England, the lower five of these rhythms were considered tectonically-driven cycles by Horbury (1987, 1989). There is certainly a larger influence of local tectonics in these older cycles which are not veneered by terrestrial deposits in some parts of Ireland and Wales (Cózar et al., 2022c). The consistent foraminiferal diversity changes attributed to glacioeustasy also confirm the influence of this factor from the base of the late Asbian. Assuming a tectonic control on the lower five cycles, the occurrence of the overlying cycles of entirely glacioeustatic-origin would then be situated in the Cf6γ2 British foraminiferal subzone (Fig. 3), a level which is difficult to identify and calibrate outside of Britain and Ireland and where no significant biota changes are observed.

(Event 3): At the base of rather fluctuating biotic-responses close to the base of the early Serpukhovian, which coincides with the Main Eustatic Signal (MES) of Fielding and Frank (2015), also recognized in some North American basins (Ahern and Fielding, 2019, 2021a); which post-dates the Marine Ecosystem Resurgence (MER) (Fig. 10A, 10B).

(Event 4): At the onset of the main taxonomic turnover of the biota in the latest Serpukhovian, which coincides with sustained changes in $\delta^{18}O$ values of brachiopods, and the ending of the C1 glacial phase of Fielding et al. (2008a, 2008b) (Fig. 10A, 10B).

Owing to its likely tectonic control, event 1 is not of the same worldwide significance (Cózar et al. 2023a). Event 2, the onset of the cyclic sedimentation as a result of glacioeustasy at the base of the late Asbian, needs to be further investigated to solve problems in biostratigraphy, and precisely constrain the synchronicity of the onset of glacioeustatic cycles, or onset of high-amplitude sea-level falls. The possible influence of regional tectonics in some basins needs to be better understood. Event 3 seems to be synchronous in terms of biota changes, and coincides with the MES, and its post-dating of the MER. Event 4 coincides with the end of glacial phase C1, but also with major changes in ocean water circulation due to the closure of the Rheic-Palaeotethys gateway. This stimulated stronger weathering of silicates leading to water chemistry changes, and narrower shallow-marine habitats (Sandberg, 1983; Hardie, 1996; Morse et al., 2007; Davydov and Cózar, 2019).

Therefore, it is questionable whether a 'sustained glaciation' can be applied in the interval of the LPIA until the Serpukhovian. This is because far-field proxies are inconsistent with each other (such as cyclicity), and isotopic signatures progressively change during the Mississippian, without clearly defined cooling events. In terms of biota, an important change occurred in ecosystems during the early Serpukhovian, whereas taxonomic turnovers started in the uppermost Serpukhovian. In consequence, to establish a point in the middle of a continuum of isotopic enrichment, or thresholding what is a significant sea level fall (i.e. >25 m) does not firmly establish the onset of sustained icehouse conditions.

The time when progressive cooling affected the biota in equatorial-tropical regions is a more pragmatic level for the definition of when global icehouse conditions were first sustained in the LPIA. In contrast, if commonly inferred times of icehouse initiation are used, such as the base of the middle Viséan (339 Ma approx.) and late

Asbian (334 Ma approx.), it is unclear why the main ecosystem change occurred during the early Serpukhovian (330.34 Ma to 327 Ma approx.), and taxonomic changes in the most sensitive biota occurred from the uppermost Serpukhovian to the early Bashkirian (around 323.4 Ma). This is some 4 to 17 Myr later (depending on the selected levels) than the assumed onset of icehouse conditions in the middle Viséan or late Asbian. If greenhouse to icehouse transitions typically occurred over durations of 1-1000 kyrs (Saupe et al., 2020), then either the duration of such brief transitions is incorrect for the Mississippian, or instead transitions were of much longer duration in low palaeolatitudes during the LPIA, or the onset of sustained icehouse conditions should be restricted to the Serpukhovian.

11. Conclusions

Study of the calcareous algae from the late Viséan to Serpukhovian interval in low-palaeolatitude basins from the western margin of the Palaeotethys show diverse responses in terms of palaeoecological diversity, richness, abundance, genus diversity and taxonomic distinctness. Conclusions inferred from these changes are:

- Algal associations are more similar in cratonic areas, although many diversity peaks correspond to local ecological/environmental factors.

- The Laurussian Palaeotethyan terranes contain the most unusual algal abundances and are the most affected by active tectonics and palaeogeographic reorganization.

- Algae in palaeo-equatorial regions show more dramatic changes than in the palaeo-tropical regions, which are possibly more rapidly affected by the reduction of continental shelves.

- Genus richness shows an inflexion in the curve of originations/extinctions in the late Viséan-early Serpukhovian interval.

- Taxonomic distinctness decreases significantly from the uppermost Serpukhovian.

- The variety of algal diversity responses suggests that it is not appropriate to extrapolate particular diversity responses from a single region to global conditions, and many factors likely influenced the regional assemblages.

- The main taxonomic turnover of most fossil groups started from the uppermost Serpukhovian, likely linked to a significant phase of cooling based on $\delta^{18}O$ from brachiopods. This coincides with final stages of the glacial phase C1 defined in Australian basins, but most palaeo-equatorial ecological changes occurred from the early Serpukhovian, coinciding with the Main Eustatic Signal seen in British and North American basins.

- Foraminifers and algae show rather similar ecological diversity for the Viséan and Serpukhovian in Britain, with a single coincident inflexion point in their trends in the early Serpukhovian.

Far-field proxies defining the onset of icehouse period in the LPIA are inconsistent in timing, and are located in distinct stratigraphical levels far from the main biota changes. This questions the usefulness of the previously inferred onset of sustained icehouse glaciation for the palaeo-equatorial Viséan, and a better level to define this major event was when low-palaeolatitude biota suffered the effects of water cooling during the Serpukhovian.

Data availability

All data used are presented in the Supplementary files.

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Supplementary Information. Supplementary data

Appendix A. Genera diversity and richness of algal groups. Supplementary data

Appendix B. Viséan-Serpukhovian algal and foraminiferal diversity in Britain and Ireland. Supplementary data

Appendix C. Stratigraphic distribution of calcareous algae during the Viséan to the early Bashkirian and suprageneric classification. Supplementary data

Supplementary data to this article can be found online at https://..........

References

Adams, A.E., 1984. Development of algal-foraminiferal-coral reefs in the Lower
Carboniferous of Furness, northwest England. Lethaia 17, 233–249.
https://doi.org/10.1111/j.1502-3931.1984.tb01623.x

Aguirre, J., Riding, R., 2005. Dasycladacean algal biodiversity compared with global
variations in temperature and sea level over the Past 350 Myr. Palaios 20, 581–588.
https://doi.org/10.2110/palo.2004.p04-33

Ahern, J.P., Fielding, C.R., 2019. Onset of the Late Paleozoic glacioeustatic signal: a
stratigraphic record from the paleotropical, oil-shale-bearing Big Snowy Trough of
Central Montana, U.S.A. J. Sed. Res. 89, 761–783.
http://dx.doi.org/10.2110/jsr.2019.44

Ahern, J.P., Fielding, C.R., 2021a. Carboniferous Manning Canyon Formation, northern
Utah, USA: A carbonate-mud-dominated cyclothem motif recording the main onset
of late Paleozoic Ice Age. Sed. Geol. 418, 105903.
https://doi.org/10.1016/j.sedgeo.2021.105903

Ahern, J.P., Fielding, C.R., 2021b. Paleotropical climate oscillations from upper
Mississippian and Pennsylvanian stratigraphic records of western Laurentia: A
convolution of plate migration and Gondwanan ice dynamics. Palaeogeogr.
Palaeoclimatol. Palaeoecol 561, 110019. https://doi.org/10.1016/j.palaeo.2020.110019

Alekseev, A.S., Nikolaeva, S.V., Goreva, N.V., Donova, N.B., Kossovaya, O.L.,
Kulagina, E.I., Kucheva, N.A., Kurilenko, A.V., Kutygin, R.V., Popeko, L.I.,
Stepanova, T.I., 2022. Russian regional Carboniferous stratigraphy in: Lucas, S.G.,
Schneider, J.W., Wang, X., Nikolaeva, S. (Eds.), The Carboniferous Timescale.
Geol. Soc., London, Sp. Publ. 512, 49–117. https://doi.org/10.1144/SP512-2021-134

Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fursich, F.T., Harries, P.J., Hendy, A.J.W., Holland, S.M., Ivany, L.C., Kiessling, W., 2008. Phanerozoic trends in the global diversity of marine invertebrates. Science 321 (5885), 97–100. https://doi.org/10.1126/science.1156963

Aretz, M., Nardin, E., Vachard, D., 2014. Diversity patterns and palaeobiogeographical relationships of latest Devonian–Lower Carboniferous foraminifers from South China: What is global, what is local? J. Palaeogeogr. 3(1), 35–59. https://doi.org/10.3724/SP.J.1261.2014.00002

Baccelle, L., Bosellini, A., 1965. Diagrammi per la stima visiva della composizione percentuale nelle rocce sedimentarie. Ann. Univ. Ferrara NS Sez. IX 1, 59–62.

Barham, M., Murray, J., Joachimski, M.M., Williams, D.M., 2012. The onset of the Permo-Carboniferous glaciation: reconciling global stratigraphic evidence with biogenic apatite $\delta^{18}O$ records in the late Viséan. J. Geol. Soc. London 169, 119–122. https://doi.org 10.1144/0016-76492011-102.

Barnett, A.J., Burgess, P.M., Wright, V.P. 2002. Icehouse world sea-level behaviour and resulting stratal patterns in late Visean (Mississippian) carbonate platforms: integration of numerical forward modelling and outcrop studies. Basin Res. 14, 417–438.

Bishop J.W., Montañez, I.P., Gulbranson, E.L., Brenckle P.L., 2009. The onset of mid-Carboniferous glacio-eustasy: sedimentologic and diagenetic constraints, Arrow Canyon, Nevada. Palaeogeogr. Palaeoclimatol. Palaeoecol. 276, 217–243. https://doi.org/10.1016/j.palaeo.2009.02.019

Blakey, R.C., 2008. Gondwana paleogeography from assembly to breakup—A 500 m.y. odyssey. Geol. Soc. Am. Spec. Pap. 441, 1–28. https://doi.org/10.1130/2008.2441(01)

Blanco-Ferrera, S., Cózar, P., Sanz-López, J., 2021. Development of a Mississippian–
Lower Pennsylvanian isolated carbonate platform within the basinal griotte facies of
the Cantabrian Mountains, NW Spain. Facies 67, 21. https://doi.org/10.1007/s10347-
021-00629-w

Brand, U., Tazawa, J.-I., Sano, H., Azmy, K., Lee, X., 2009. Is mid-late Paleozoic
Ocean-water chemistry coupled with epeiric seawater isotope records? Geology 37
(9), 823–826. https://doi.org/10.1130/G30038A.1

Brenchley, P.J., Newall, G., 1984. Late Ordovician environmental changes and their
effect on faunas, in: Bruton, D. L. (Ed.), Aspects of the Ordovician System.
Palaeontol. Contrib. Univ. Oslo, 295, 65–79

Bruckschen, P., Oesmann, S., Veizer, J., 1999. Isotope stratigraphy of the European
carboniferous. Proxy signals for ocean chemistry, climate and tectonics. Chem. Geol.
161, 127–163. https://doi.org/10.1016/S0009-2541(99)00084-4

Bucur, I., 1999, Stratigraphic significance of some skeletal algae (Dasycladales,
Caulerpales) of the Phanerozoic, in: Farinacci, A., Lord, A.R. (Eds.), Depositional
Episodes and Bioevents. Palaeopelagos Sp. Publ. 2, pp. 53–104.

Buggisch, W., Joachimski, M.M., Sevastopulo, G., Morrow, J.R., 2008. Mississippian
δ13Ccarb and conodont apatite δ18O records; their relation to the late Palaeozoic
glaciation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 268, 273–292.
https://doi.org/10.1016/j.palaeo.2008.03.043

Cecil, C.B., 1990. Paleoclimate controls on stratigraphic repetition of chemical and
siliciclastic rocks. Geology 18 (6), 533–536.

Chen, B., Joachimski, M.M., Shen, S.-Z., Lambert, L.L., Lai, X.-L., Wang, X.-D.,
Chen, J., Yuan, D.-X., 2013. Permian ice volume and paleoclimate history: Oxygen

isotope proxies revisited. Gondwana Res. 24, 77–89.

https://doi.org/10.1016/j.gr.2012.07.007

Chen, J., Joachimski, M.M., Wang, X.D., Shen, S.Z., Qi, Y.P., Qie, W.K., 2016. Ice

volume and paleoclimate history of the late Paleozoic ice age from conodont apatite

oxygen isotopes from Naqing (Guizhou, China). Palaeogeogr. Palaeoclimatol.

Palaeoecol. 448, 151–161. https://doi.org/10.1016/j.palaeo.2016.01.002

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness and its statistical

properties. J Appl. Ecol. 35, 523–531. https://doi.org/10.1046/j.1365-

2664.1998.3540523.x

Cózar, P., Somerville, I.D., 2014. Latest Viséan-Early Namurian (Carboniferous)

foraminifers from Britain: implications for biostratigraphic and glacioeustatic

correlations. Newsl. Stratigr. 47, 355–367. https://doi.org/10.1127/nos/2014/0052

Cózar, P., Somerville I.D., 2016. Problems correlating the late Brigantian-Arnsbergian

Western Europen substages within northern England. Geol. J. 51, 817–840.

https://doi.org/10.1002/gj.2700

Cózar, P., Somerville, I.D., 2021a. Serpukhovian in Britain: use of foraminiferal

assemblages for dating and correlating. J. Geol. Soc., London 178, jgs2020-170.

https://doi.org/10.1144/jgs2020-170

Cózar, P., Somerville, I.D., 2021b. Irish Serpukhovian revisited. Geol. J. 56, 1403–

1423. https://doi.org/10.1002/gj.3981

Cózar, P., Somerville, I.D., 2021c. Palaeotethyan faunal/floral evidence in the

Mississippian Maritimes Basin of Canada: an overview. J. Paleontol. 95, 653–672.

https://doi.org/10.1017/jpa.2021.20

Cózar, P., Somerville, I.D., Rodríguez, S., Mas, R., Medina-Varea, P., 2006.

Development of a late Viséan (Mississippian) mixed carbonate/siliciclastic platform

in the Guadalmellato Valley (southwestern Spain). Sed. Geol. 183, 269–295. https://doi.org/10.1016/j.sedgeo.2005.09.018

Cózar, P., Medina-Varea, P., Somerville, I.D., Vachard, D., Rodríguez, S., Said, I., 2014. Foraminifers and conodonts from the late Viséan to early Bashkirian succession in the Saharan Tindouf Basin (southern Morocco): biostratigraphic refinements and implications for correlations in the western Palaeotethys. Geol. J. 49, 271–302. https://doi.org/10.1002/gj.2519

Cózar, P., Izart, A., Vachard, D., Coronado, I., 2017. A mid-Tournaisian-late Viséan carbonate ramp reconstructed from nappes and olistolites in the southern Montagne Noire (France). Sed. Geol. 358, 148–175. https://doi.org/10.1016/j.sedgeo.2017.07.007

Cózar, P., Somerville, I. D., Blanco-Ferrera, S., Sanz-López, J., 2018a. Palaeobiogeographic context in the development of shallow-water late Viséan-early Bashkirian benthic foraminifers and calcareous algae in the Cantabrian Mountains (Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 511, 620–638. https://doi.org/10.1016/j.palaeo.2018.09.031

Cózar, P., Somerville, I.D., Coronado, I., Vachard, D., Izart, A., Aretz, M., 2018b. States of preservation and role of dascyladal algae in Mississippian carbonate mounds. Palaios 33, 419–430. https://doi.org/10.2110/palo.2018.009

Cózar, P., Izart, A., Somerville, I.D., Aretz, M., Coronado, I., Vachard, D., 2019 Environmental controls on the development of Mississippian microbial carbonate mounds and platform limestones in southern Montagne Noire (France). Sedimentology 66, 2392–2424. http://dx.doi.org/10.1111/sed.12594

Cózar, P., Coronado, I., García-Frank, A., Izart, A., Somerville, I.D., Vachard, D., 2022a. Alternating microbial mounds and ooidal shoals as a response to tectonic,

eustatic and ecological conditions (late Viséan, Morocco). Sed. Geol. 431, 106109. https://doi.org/10.1016/j.sedgeo.2022.106109

Cózar, P., Somerville, I.D., Hounslow, M.W., 2022b. Foraminifers in the Holkerian Stratotype, regional substage in Britain: key taxa for the Viséan subdivision. Newsl. Stratigr. 55, 159–172. https://doi.org/10.1127/nos/2021/0674

Cózar, P., Somerville, I.D., Hounslow, M.W., Coronado, I., 2022c. Far-field correlation of palaeokarstic surfaces in Mississippian successions using high-frequency foraminiferal diversity trends. Palaeogeogr. Palaeoclimatol. Palaeoecol. 601, 111088. https://doi.org/10.1016/j.palaeo.2022.111088

Cózar, P., Somerville, I.D., Hounslow, M.W., 2023a. A potential global chronostratigraphic boundary for the subdivision of the Viséan. Newsl. Stratigr. 56, 357–376. https://doi.org/10.1127/nos/2023/0746

Cózar, P., Somerville, I.D., Rodríguez, S., El Houicha, M., Vachard, D., García-Frank, A., Coronado, I., Izart, A., Said, I. 2023b. Contrasting reef patterns during the evolution of the Carboniferous Azrou-Khenifra Basin (Moroccan Meseta). Facies 69:1. https://doi.org/10.1007/s10347-022-00657-0

Dávila, F.M., Martina, F., Ávila, P., Ezpeleta, M., 2023. Mantle contribution to Late Paleozoic glaciations of SW Gondwana. Glob. Planet. Change 220, 104018. https://doi.org/10.1016/j.gloplacha.2022.104018

Davydov, V.I., Cózar, P., 2019. The formation of the Alleghenian Isthmus triggered the Bashkirian glaciation: Constraints from warm-water benthic foraminifera. Palaeogeogr. Palaeoclimatol. Palaeoecol. 531, 108403. https://doi.org/10.1016/j.palaeo.2017.08.012

Delcambre, B., 1989. Marqueurs tephrostratigraphiques au passage des calcaires de Neffe vers ceux de Lives. Bull. Soc. belge Géol. 98, 163–170.

Denayer, J., Aretz, M., Poty, E., Mottequin, B. 2016. Royseux: a palaeodiversity hotspot in the late Viséan (Carboniferous) of Belgium. Geol. Belg. 19, 7–20. http://dx.doi.org/10.20341/gb.2016.003

Fan, J.X., Shen, S.Z., Erwin, D.H., Sadler, P.M., MacLeod, N., Cheng, Q.M., Hou, X.D., Yang, J., Wang, X.D., Wang, Y., Zhang, H., Chen, X., Li, G.X., Zhang, Y.C., Shi, Y.K., Yuan, D.X., Chen, Q., Zhang, L.N., Li, C., Zhao, Y.Y., 2020. A high-resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity. Science 367 (6475), 272–277. https://doi.org/10.1126/science.aax4953

Fielding, C.R., Frank, T.D., 2015. Onset of the glacioeustatic signal recording late Palaeozoic Gondwanan ice growth: New data from palaeotropical East Fife, Scotland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 426, 121–138. https://doi.org/10.1016/j.palaeo.2015.03.002

Fielding, C.R., Frank, T.D., Birgenheier, L.P., Rygel, M., Jones, A.T., 2008a. Stratigraphic imprint of the Late Palaeozoic Ice Age in eastern Australia: a record of alternating glacial and nonglacial climate regime. J. Geol. Soc., London 165, 129–140. https://doi.org/10.1144/0016-76492007-036

Fielding, C.R., Frank, T.D., Isbell, J.L., 2008b. The late Paleozoic ice age- A review of current understanding and synthesis of global climate patterns, in: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geol. Soc. Am. Spec. Pap. 441, 343–354. https://doi.org/10.1130/2008.2441(24).

Fielding, C.R., Frank, T.D., Birgenheier, L.P., 2023. A revised, late Palaeozoic glacial time-space framework for eastern Australia, and comparisons with other regions and events. Earth-Sci. Rev. 236, 104263. https://doi.org/10.1016/j.earscirev.2022.104263

Giles, P.S., 2009. Orbital forcing and Mississippian sea level change: time series analysis of marine flooding events in the Viséan Windsor Group of eastern Canada and implications for Gondwana glaciation. Bull. Can. Petrol. Geol. 57, 449–572.

Giles, P.S., 2012. Low-latitude Ordovician to Triassic brachiopod habitat temperatures (BHTs) determined from $\delta^{18}O$ [brachiopod calcite]: a cold hard look at ice-house tropical oceans. Palaeogeogr. Palaeoclimatol. Palaeoecol. 317/318, 134–152. https://doi.org/10.1016/j.palaeo.2012.01.002

Graham, L.E., Wilcox L.W., 2000. Algae: Prentice Hall, Upper Saddle River, New Jersey.

Granier, B., 2012. The contribution of calcareous green algae to the production of limestones: a review: Geodiversitas 34, 35–60. https://doi.org/10.5252/g2012n1a3

Grossman, E.L., Joachimski, M.M., 2020. Oxygen isotope stratigraphy, in: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), Geologic Time Scale 2020. Elsevier, Amsterdam, pp. 279–307. https://doi.org/10.1016/B978-0-12-824360-2.00010-3

Grossman, E.L., Joachimski, M.M., 2022. Ocean temperatures through the Phanerozoic Reassessed. Sci. Rep. 12, 8938. https://doi.org/10.1038/s41598-022-11493-1

Grossman, E.L., Yancey, T.E., Jones, T.E, Bruckschen, P., Chuvashov, B., Mazzullo, S., Mii, H.-S., 2008. Glaciation, aridification, and carbon sequestration in the Permo-Carboniferous: the isotopic record for low latitudes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 268, 222–233. https://doi.org/10.1016/j.palaeo.2008.03.053

Groves, J.R., Lee, A., 2008. Accelerated rates of foraminiferal origination and extinction during the Late Paleozoic ice age. J. Foram. Res. 38, 74–84. https://doi.org/10.2113/gsjfr.38.1.74

Groves, J.R., Wang, Y., 2009. Foraminiferal diversification during the late Paleozoic ice age. Paleobiology 35, 367–392.

Hardie, L.A., 1996. Secular variation in seawater chemistry: An explanation for the coupled secular variation in the mineralogies of marine limestones and potash evaporites over the past 600 m.y. Geology 24, 279–283. https://doi.org/10.1130/0091-7613(1996)024<0279:SVISCA>2.3.CO;2

Hoegh-Guldberg, O., Poloczanska, E.S., Skirving, W., Dove, S., 2017. Coral reef ecosystems under climate change and ocean acidification. Frontiers in Marine Sciences, 29. https://doi.org/10.3389/fmars.2017.00158

Horbury, A.D., 1987. The sedimentology of the Urswick Limestone in south Cumbria and north Lancashire. Ph.D. thesis, University of Manchester.

Horbury, A.D., 1989. The relative roles of tectonism and eustacy in the deposition of the Urswick Limestone in south Cumbria and north Lancashire, in: Arthurton, R.S., Gutteridge, P., Nolan, S.C. (Eds.), The role of tectonics in Devonian and Carboniferous sedimentation in the British Isles. Yorkshire Geological Society Occasional Publication, 6, York, pp. 153–169.

Horbury, A.D., Adams A.E., 1996. Microfacies associations in Asbian carbonates: an example from the Urswick Limestone Formation of the southern Lake District, northern England, in: Strogen, P. Somerville, I.D., Jones, G.LL. (Eds.), Recent Advances in Lower Carboniferous Geology. Geological Society, London, Special Publications 107, Oxford, pp. 221–238.

Hounslow, M.W., Somerville, I.D., Cózar, P., Chew, D., Drakou, F., 2022. A reassessment of Arundian-Holkerian carbonates in South Cumbria, UK. Proc. Geol. Assoc. 133, 227–249. https://doi.org/10.1016/j.pgeola.2022.04.005

Isbell, J.L., Vesely, F.F., Rosa, E.L.M., Pauls, K.N., Fedorchuk, N.D., Ives, L.R.W.,

McNall, N.B., Litwin, S.A., Borucki, M.K., Malone, J.E., Kusick, A.R., 2021.

Evaluation of physical and chemical proxies used to interpret past glaciations with a

focus on the late Paleozoic Ice Age. Earth-Sci. Rev. 221, 103756.

https://doi.org/10.1016/j.earscirev.2021.103756

Joachimski, M.M., von Bitter, P.H., Buggisch, W., 2006. Constraints on Pennsylvanian

glacioeustatic sea-level changes using oxygen isotopes of conodont apatite. Geology

34, 277–280. https://doi.org/10.1130/G22198.1

Johnson, M.D., Price, N.N., Smith, J.E., 2014. Contrasting effects of ocean acidification

on tropical fleshy and calcareous algae. PeerJ, 2, e411.

https://doi.org/10.7717/peerj.411

Lane, H.R., Brenckle, P.L., 2005. Type Mississippian subdivisions and biostratigraphic

succession, in: Heckel, P.H. (ed.), Stratigraphy and Biostratigraphy of the

Mississippian Subsystem (Carboniferous System) in its Type Region, the Mississippi

Valley of Illinois, Missouri, and Iowa. Illinois State Geological Survey Guidebook,

34, pp. 76–105.

Leaf, M.C., Gay, J.S., Newbould, M.J., Hewitt, O.R., Rogers, S.L., 2020. Calcareous

algae and cyanobacteria. Geol. Today 36, 75-80. https://doi.org/10.1111/gto.12304

Limarino, C.O., Cesari, S.N., Spalletti, Taboada, A.C., Isbell, J.L., Geuna, S.,

Gulbranson, E.L., 2014. A paleoclimatic review of southern South America during

the late Paleozoic: a record from icehouse to extreme greenhouse conditions.

Gondwana Res. 25, 1396–1421. https://doi.org/10.1016/j.gr.2012.12.022

Liu, C., Vachard, D., Cózar, P., Coronado, I., 2023. Middle to Late Mississippian and

Early Pennsylvanian foraminiferal zonal scheme of South China — a case study

from the Youjiang Basin: biostratigraphic and palaeobiogeographic implication. Lethaia, 56(1), 1-23. https://doi.org/10.18261/let.56.1.6

Liu, J., Algeo, T.J., Qie, W., Saltzman, M.R., 2019. Intensified oceanic circulation during Early Carboniferous cooling events: evidence from carbon and nitrogen isotopes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 531, 108962. https://doi.org/10.1016/j.palaeo.2018.10.021

López-Gamundi, O., Limarino, C.O., Isbell, J.L., Pauls, K., Césari, S.N., Alonso-Muruaga, P.J., 2021. The late Paleozoic Ice Age along the southwestern margin of Gondwana: Facies models, age constraints, correlation and sequence stratigraphic framework. J. S. Am. Earth Sci., 107, 103056. https://doi.org/10.1016/j.jsames.2020.103056

Lowry, D.P., Poulsen, C.J., Horton, D.E., Torsvik, T.H., Pollard, D., 2014. Thresholds for Paleozoic ice sheet initiation. Geology 42, 627–630. https://doi.org/10.1130/G35615.1

Mamet, B.L., 1991. Carboniferous calcareous algae, in: Riding, R. (ed.), Calcareous algae and stromatolites. Springer-Verlag, Berlin-Heidelberg- New York, pp. 370–451.

McGhee, G.R. Jr., Sheehan, P.M., Bottjer, D.J., Droser, M.I., 2012. Ecological ranking of Phanerozoic biodiversity crises: The Serpukhovian (early Carboniferous) crisis had a greater impact than the end-Ordovician. Geology 40, 147–150. https://doi.org/10.1130/G32679.1

Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N., Peka, S.F., 2005. The Phanerozoic Record of Global Sea-Level Change. Science 310, 1293–1298. https://doi.org/10.1126/science.1116412

Miller, K.G., Mountain, G.S., Wright, J.D., Browning, J.V., 2011. A 180-million-year record of sea level and ice volume variations from continental margin and deep-sea isotopic records. Oceanography 24(2), 40–53. https://doi.org/10.5670/oceanog.2011.26

Montañez, I.P., 2021. Current synthesis of the penultimate icehouse and its imprint on the Upper Devonian through Permian stratigraphic record, in: Lucas, S.G., Schneider, J.W., Wang, X., Nikolaeva, S. (Eds.), The Carboniferous Timescale. Geological Society, London, Special Publications 512, pp. 213–245. https://doi.org/10.1144/SP512-2021-124

Montañez, I.P., Poulsen, Ch., 2013. The Late Paleozoic Ice Age: An evolving Paradigm. Annu. Rev. Earth Planet. Sci. 41, 629–56. https://doi.org/10.1146/annurev.earth.031208.100118

Morse, J.W., Wang, Q., Tsio, M.Y., 1997. Influences of temperature and Mg:Ca ratio on CaCO3 precipitates from seawater. Geology 25, 85–87. https://doi.org/10.1130/0091-7613(1997)025<0085:IOTAMC>2.3.CO;2

Nance, R.D., Gutiérrez-Alonso, G., Keppies, J.D., Linnemann, U., Murphy, J.B., Quesada, C., Strachan, R.A., Woodcock, N.H., 2010. Evolution of the Rheic Ocean. Gondwana Res. 17, 194–222. https://doi.org/10.1016/j.gr.2009.08.001

Nemirovska, T.I., 2017. Late Mississippian–Middle Pennsylvanian conodont zonation of Ukraine. Stratigraphy 14, 299–318. https://doi.org/10.29041/strat.14.1-4.299-318

Pille, L., 2008. Foraminifères et algues calcaires du Mississippien supérieur (Viséen supérieur-Serpukhovien): rôles biostratigraphique, paléoécologique et paléogéographique aux échelles locale, régionale et mondiale. Thèse Université de Lille 1.

Pointon, M.A., Chew, D.M., Ovtcharova, M., Delcambre, B., Sevastopulo, G.D., 2021.
Uranium-lead dates from Livian (middle Viséan) bentonites of the Namur-Dinant
Basin, Belgium. Newsl. Stratigr. 54, 317–334. https://doi.org/10.1127/nos/2021/0622

Poletaev, V.I., Vdovenko, M.V., Shulga, V.F., Nemyrovska, T.I., Shchegolev, A.K.,
Boyarina, N.I., 2013 Chapter 7. Carboniferous System, in: Gozhik P.F. (Ed.),
Stratigraphy of Upper Proterozoic, Paleozoic and Mesozoic of Ukraine. Volume 1.
Upper Paleozoic of Ukraine. IGS NAS, Logos, Kiev, pp. 247–356. IGS NAS (in
Ukrainian).

Poty, E., Devuyst, F., Hance, L. 2006. Upper Devonian and Mississippian foraminiferal
and rugose coral zonations of Belgium and northern France: a tool for Eurasian
correlations. Geol. Mag. 143, 829–857. https://doi.org/10.1017/S0016756806002457

Powell, M.G., 2008. Timing and selectivity of the Late Mississippian mass extinction of
brachiopod genera from the central Appalachian Basin. Palaios 23, 525–534.
https://doi.org/10.2110/palo.2007.p07-038r

Prokoph, A., Shields, G.A., Veizer, J., 2008. Compilation and time-series analysis of a
marine carbonate δ^{18}O, δ^{13}C, ^{87}Sr/^{86}Sr and δ^{34}S database through Earth history.
Earth-Sci. Rev. 87, 113–133. https://doi.org/10.1016/j.earscirev.2007.12.003

Raymond, A., Kelley, P.H., Lutken, C.B., 1990. Dead by degrees: Articulate
brachiopods, paleoclimate and the mid-Carboniferous extinction event. Palaios 5,
111–123. https://doi.org/10.2307/3514808

Rodríguez, S., Somerville, I.D., Said, I., Cózar, P., 2012. Late Viséan coral fringing reef
at Tiouinine (Morocco): implications for the role of rugose corals as building
organisms in the Mississippian. Geol. J. 47, 462–476. https://doi.org/10.1002/gj.2452

Rygel, M.C., Fielding, C.R., Frank, T.D., Birgenheier, L.P., 2008. The magnitude of late Paleozoic glacioeustatic fluctuations: a synthesis. J. Sediment. Res. 78, 500–511. https://doi.org/10.2110/jsr.2008.058

Sandberg, P.A., 1983. An Oscillating Trend in Phanerozoic Non-Skeletal Carbonate Mineralogy. Nature 305(5929), 19–22. https://doi.org/10.1038/305019a0

Sanz-López, J., Blanco-Ferrera, S., Sánchez de Posada, L.C., 2013. Conodont chronostratigraphical resolution and *Declinognathodus* evolution close to the Mid-Carboniferous Boundary in the Barcaliente Formation type section, NW Spain. Lethaia 46, 438–453. https://doi.org/10.1111/let.12021

Saunders, W.B., Ramsbottom,W.H.C., 1986. The mid-Carboniferous eustatic event. Geology 14, 208–212. https://doi.org/10.1130/0091-7613(1986)14<208:TMEE>2.0.CO;2

Saupe, E.E., Qiao, H., Donnadieu, Y., Farnsworth, A., Kennedy-Asser, A.T., Ladant, J.-B., Lunt, D.J., Pohl, A., Valdes, P., Finnegan, S., 2020. Extinction intensity during Ordovician and Cenozoic glaciations explained by cooling and palaeogeography. Nature Geosci. 13, 65–70. https://doi.org/10.1038/s41561-019-0504-6

Segessenman, D.C., Kammer, T.W., 2018. Testing reduced evolutionary rates during the Late Palaeozoic Ice Age using the crinoid fossil record. Lethaia 51, 330–343. https://doi.org/10.1111/let.12239

Sepkoski, J.J., 1996, Patterns of Phanerozoic extinction: A perspective from global data bases, in: Walliser, O.H. (ed.), Global events and event stratigraphy. Berlin, Springer-Verlag, pp. 35–51.

Sepkoski, J.J., 2002. A compendium of fossil marine animal genera. Bull. Am. Paleontol. 363, 1–560.

Shackleton, N., 1967. ==Oxygen Isotope Analyses and Pleistocene Temperatures Re-==
assessed. Nature 215, 15–17. https://doi.org/10.1038/215015a0

Shen, S.Z., Zhang, H., Li, W.Z.,Mu, L., Xie, J.F., 2006. Brachiopod diversity patterns
from Carboniferous to Triassic in South China. Geol. J. 41, 345–361.
https://doi.org/10.1002/gj.1047

Shi, Y., Wang, S., Fan, J., Huang, H., Xu, H., Zhao, Y., Shen, S., 2021. Carboniferous-
earliest Permian marine biodiversification event (CPBE) during the Late Paleozoic
Ice Age. Earth-Sc. Rev. 103699. https://doi.org/10.1016/j.earscirev.2021.103699.

Smith, L.B., Read, J.F., 2000. Rapid onset of late Paleozoic glaciation on Gondwana:
evidence from Upper Mississippian strata of the Midcontinent, United States.
Geology 28, 279–282. https://doi.org/10.1130/0091-
7613(2000)28<279:ROOLPG>2.0.CO;2

Stanley, S.M., Powell, M.G., 2003. Depressed rates of origination and extinction during
the late Paleozoic ice age: a new state for the global marine ecosystem. Geology 31,
877–880. https://doi.org/10.1130/G19654R.1

Stephenson, M.H., Angiolini, L., Cózar, P., Jadoul, F., Leng, M.J., Millward, D.,
Chenery, S., 2010. Northern England Serpukhovian (early Namurian) farfield
responses to southern hemisphere glaciation. J. Geol. Soc., London, 167, 1171–1184.
https://doi.org/10.1144/0016-76492010-048

Steuber, T., Veizer, J., 2002. Phanerozoic record of plate tectonic control of seawater
chemistry and carbonate sedimentation. Geology 30, 1123–1126.
https://doi.org/10.1130/0091-7613(2002)030<1123:PROPTC>2.0.CO;2

Vachard, D., Cózar, P., 2010. An Attempt of classification of the Palaeozoic incertae
sedis Algospongia. Rev. Esp. Micropaleont. 42, 129–141.

Vachard, D., Pille, L., Gaillot, J., 2010. Palaeozoic Foraminifera: Systematics, palaeoecology and responses to global changes. Rev. micropaléont. 53, 209–254. https://doi.org/10.1016/j.revmic.2010.10.001

Vachard, D., Cózar, P., Aretz, M., Izart, A., 2016. Late Viséan-early Serpukhovian cyanobacteria and algae from the Montagne Noire (France); taxonomy and biostratigraphy. Bull. Geosci. 91, 433–466. https://doi.org/10.3140/bull.geosci.1613

Veizer, J., Ala, D., Azmy, K., Bruckschen, P., Buhl, D., Bruhn, F., Carden, G.A.F., Diener, A., Ebneth, S., Godderis, Y., Jasper, T., Korte, C., Pawellek, F., Podlaha, O.G., Strauss, H., 1999. $^{87}Sr/^{86}Sr$, $\delta^{13}C$ and $\delta^{18}O$ evolution of Phanerozoic seawater. Chem. Geol. 161, 59–88. https://doi.org/10.1016/S0009-2541(99)00081-9

Walkden, 1987. Sedimentary and diagenetic styles in late Dinantian carbonates of Britain, in: Miller, J., Adams, A.E., Wright, V.P. (Eds.), European Dinantian Environments. John Wiley & Sons, Chichester, pp. 131–155.

Wang, X.D., Wang, X.J., Zhang, F., Zhang, H., 2006. Diversity patterns of Carboniferous and Permian rugose corals in South China. Geol. J. 41, 329–343. https://doi.org/10.1002/gj.1041

Wanless, H.R., 1964. Local and regional factors in Pennsylvanian cyclic sedimentation. Bull. Kansas Geol. Surv. 169, 593–605.

Waters, C.N. 2011. Chapter 2. Definitions of chronostratigraphic subdivisions: geochronology and event stratigraphy, in: Waters, C.N., Somerville, I.D., Jones, N.S., *et al.* (Eds,), A revised correlation of Carboniferous rocks in the British Isles. Geol. Soc., London, Sp. Rep. 26, 3–10. https://doi.org/10.1144/SR26.2

Waters, C.N., Burgess, I.C., Cózar, P., Holliday, D.W., Somerville, I.D., 2021. Reappraisal of Arundian–Asbian successions of the Great Scar Limestone Group

across northern England. Proc. York. Geol. Soc. 63, pygs2021-002.

https://doi.org/10.1144/pygs2021-002

Wray, J.L., 1977. Calcareous algae. Elsevier, New York.

Weller, J.M., 1930. Cyclical sedimentation of the Pennsylvanian period and its

significance. J. Geol. 38 (2), 97–135.

Wright, V.P., Vanstone, S.D., 2001. Onset of Late Palaeozoic glacio-eustasy and the

evolving climates of low latitude areas: a synthesis of current understanding. J. Geol.

Soc. London 158, 579–582. https://doi.org/10.1144/jgs.158.4.579

Yao, L., Aretz, M., Wignall, P. B., Chen, J., Vachard, D., Qi, Y., Shen, S., & Wang, X.

2020: The longest delay: re-emergence of coral reef ecosystems after the Late

Devonian extinctions. Earth-Sc. Rev. 203, 103060.

https://doi.org/10.1016/j.earscirev.2019.103060

Yao, L., Jiang, G., Mii, H.-S., Lin, Y., Aretz, M., Chen, J., Qi, Y., Lin, W., Wang, Q. &

Wang, X. 2022: Global cooling initiated the Middle-Late Mississippian biodiversity

crisis. Glob. Planet. Change 2015, 103852.

https://doi.org/10.1016/j.gloplacha.2022.103852

Zaffos, A., Finnegan, S., Peters, S.E., 2017. Plate tectonic regulation of global marine

animal diversity. Proc. Natl. Acad. Sci. 114, 5653–5658.

https://doi.org/10.1073/pnas.1702297114

Captions

Fig. 1. Palaeogeographic map of the studied sections during the Mississippian. 1, Tindouf (southern Morocco); 2, Western Moroccan Meseta; 3, Sierra Morena (SW Spain); 4, Cantabrian Mountains (northern Spain); 5, Montagne Noire (southern France); 6, northern England; 7, Ireland. RPG=Rheic-Palaeotethys gateway, LPT=Laurussian Palaeotethyan terranes, GPT= Gondwana Palaeotethyan terranes. Modified from Blakey (2008). (colour online)

Fig. 2. Schematic stratigraphic successions of the studied regions showing the predominant lithologies and environments. Coloured tie lines: green line, Asbian/Brigantian boundary; red line, base of early Serpukhovian; blue line, base of late Serpukhovian. Abbreviations: e Asb= early Asbian; e Brig= early Brigantian; Krasno.= Krasnopolyanian; L= Lissylisheen Member (Slievenaglasha Formation); P-Z = Protvian-Zapaltyubian; Prot. Protvian; St. Steshevian; Taru = Tarusian; Vo = Voznesenkian; (see details of the stratigraphic sections and precise biostratigraphic information of Formation/Member/samples in Supplementary information and Appendix A). (colour online)

Fig. 3. Chronostratigraphical correlation of some regional substages (modified from Liu et al., 2023). British scale based on Cózar and Somerville (2021a, 2021b) and Hounslow et al. (2022) for the Mississippian, and Waters (2011) for the Pennsylvanian. Note that the base of the Holkerian and Asbian are modified (dotted lines). Scale from Belgium is based on Poty et al., (2006); East European Platform (EEP) from Russia is based on Alekseev et al. (2022); Donetz substages in Ukraine are based on Poletaev et al. (2013)

and modification by Nemyrovska (2017) for the Serpukhovian; the Chinese scale is based on Wang et al. (2019); and the American scale is based on the type series in the Mississippi River Valley in Illinois by Lane and Brenckle (2005). The dark shaded parts in the Britain and EEP scales are the selected regional substages division used in this study. Abbreviations: Arn Arnsbergian, Cha. Chadian, up. Upper, (colour online)

Fig. 4. Margalef diversity index for total algal diversity (D_{total},). Abbreviation: e. early. Taru. Tarusian, Stesh. Steshevian, Prot. Provian, Zapalt. Zapaltyubian, Voz. Voznesenkian, Krasno. Krasnopolyanian. LPT= Laurussian Palaeotethys terranes, GPT= Gondwana Palaeotethys terranes. Y-scale= ordered stratigraphic position of samples. Database included in Appendix A (colour online)

Fig. 5. Specimen abundance (SA). Abbreviation: e. early. Taru. Tarusian, Stesh. Steshevian, Pro. Protvian, Zapalt. Zapaltyubian, Voz. Voznesenkian. See Fig. 3 for other details. (colour online)

Fig. 6. Algal associations (scale bar = 1 mm). A. *Kamaenella* (white arrows)-*Koninckopora* (*k*) association, sample 1274, early Asbian, Tankardstown Borehole, Ireland; *Kamaenella* has been arrowed in a small part of the picture, but the entire small rounded sections in the matrix correspond to this genus. B. *Kamaenella* (white arrows)-*Koninckopora* (*k*) association, sample TQ-205, late Asbian, Trowbarrow Quarry, northwest England; only a few *Kamaenella* have been arrowed. C. *Kamaenella* (white arrows)-*Ungdarella* (*u*)-*Koninckopora* (*k*) association, sample TQ-75, late Asbian, Trowbarrow Quarry, northwest England; only a few *Kamaenella* have been arrowed. D. *Ungdarella* (*u*)-*Kamaenella* (*k*) association, sample TQ-139, late Asbian, Trowbarrow

Quarry, northwest England. E. Dasycladales association (*w Windsoporella, c Coelosporella, n Nanopora*), sample PC918, early Brigantian, Clogrenan Quarry, Ireland. F. *Falsocalcifolium* association, late Serpukhovian, La Serre, Montagne Noire (France). G. *Calcifolium* association, late Serpukhovian, Jitu l'Escarandi, Cantabrian Mountains (Spain). H. Facies with *Donezella* (white arrows), early Bashkirian, Jitu l'Escarandi, Cantabrian Mountains (Spain); only a few *Donezella* have been arrowed, but most rounded forms correspond to this taxon, which is rather recrystallized. (colour online)

Fig. 7. Volumetric abundance (%V) of algae in percentage of total components in a sample (including allochems, matrix and cement). Ft0 to Ft13 are foraminiferal trends and rhythms in the left 2 columns as published in Cózar et al. (2022c). Database included in Appendix A. Abbreviation: Zapalt. Zapaltyubian (colour online)

Fig. 8. Genus richness (GR) of algae for the late Tournaisian to early Bashkirian. Scale (in axis-Y) is the number of genera. A. Overall diversity and originations/extinctions. B. As A, but split by the main palaeobiogeographic realms during the Mississippian. Database included in Appendix C. Abbreviation: Serpukhov. Serpukhovian, Tournais. Tournaisian. (colour online)

Fig. 9. Taxonomic distinctness (Δ^+) of the algae (values in axis Y). A. Overall Δ^+ subdivided by the main palaeobiogeographical realms. B. Individual Δ^+ in the seven studied regions. C. Average of the Δ^+ for the seven studied regions. D. Δ^+ for the Viséan-Serpukhovian in Britain (and using the data from Ireland for the early Asbian, see Supplementary Information). Database included in Appendix C. Abbreviations:

Serpukhov. Serpukhovian, Stesh. Steshevian, Taru. Tarusian, Tournais. Tournaisian, Zapal. Zapaltyubian. (colour online)

Fig. 10. Comparison of biota, sedimentological and $\delta^{18}O$ isotope data for the Viséan-Serpukhovian. Left column represents the main four events described in the text: 1. Mid-Viséan unconformity (MVU; the dark band represents the interval usually represented by a gap in many European basins); 2. onset of rhythmic sequences in NW-SW England and Wales sensu Cózar et al. (2022c); 3. Onset of sustained glaciation, Main Eustatic Signal (MES) of Fielding and Frank (2015); 4. Onset of main biota turnover. HPCW high point of Carboniferous warming of Giles (2012). MER marine ecosystem resurgence of Yao et al. (2020). Phase C1 of Fielding et al. (2008b). A. Algal total diversity (with 6-point running average) and overall trends in Britain and Ireland (see Supplementary Information for the construction of the log, database included in Appendix B). B. Foraminiferal total diversity (D_{total}) (with 6-point running average) and overall trends (database included in Appendix B). C. Species richness curves for brachiopods (dashed line C1 sensu Shi et al., 2021), corals (dashed line C2, sensu Shi et al., 2021) and foraminifers (dotted line C3 sensu Groves and Lee, 2008; dashed line C4 sensu Groves and Wang, 2009; line C5 sensu Shi et al., 2021; dashed line C6 sensu Aretz et al., 2014) compared to the genus richness of algae (thick green line C7); scale 0 to 80 is valid for the number of species of brachiopods, corals and foraminifers from China (lines C1, C2, C5 and C6), and algal genera, and 0 to 400 for foraminiferal species in lines C4 and C5. Scale for line C6 of 0 to 80 is valid for algal genera. D. Curve of $\delta^{18}O$ based on brachiopods (curves for the Serpukhovian are not readjusted); line D1 sensu Grossman et al., 2008 for Russia; dotted line D2 sensu Grossman et al.,

2008 for North America; dashed line D3 sensu Grossman and Joachimski, 2020. E.

Curve of $\delta^{18}O$ based on conodonts; line E1 curve of Barham et al., 2012 has been

biostratigraphically readjusted; dotted line E2 sensu Grossman and Joachimski, 2020;

dashed line E3 sensu Chen et al., 2016. (colour online)

Legend:
- cyclic limestones
- non-cyclic limestones
- microbial limestones with cryptic ciclicity
- microbial limestones
- sandstones
- shales-marlstones-mudstones

M.a.	BRITAIN					BELGIUM		EEP		DONETZ	CHINA	USA
315.15												
	WESTP.		Duckmantian			WESTP.	Duckmantian	BASHKIRIAN	Melekessian	Krasnodonsky	Dalun	Atokan (part)
										Maeevsky		
			Langsettian				Langsettian		Cheremshanian	Avdot'insky		
320			Yeadonian				Yeadonian		Prikamian	Blagodatnensky	Huashibanian	
			Marsdenian				Marsdenian		Severokeltmian	Manuilovky		Morrowan
			Kinderscoutian				Kinderscoutian		Krasnopolyanian	Feninsky		
			Alportian				Alportian		Voznesenkian	Voznesenkian	Luosuan	
323.4			Chokierian				Chokierian					
	NAMURIAN	Arn.	Pendleian		Cf7	14	NAMURIAN	Arn.	MFZ 16	SERPUKHOVIAN	upper	Zapaltyubian	Zapaltyubian		Grove Church / Kinkaid
325						13								Clore / Menard / Vienna
						12	Pendleian					Protvian	Novolyubovsky	Dewuan	
						11			MFZ 15						
						10					lower	Steshevian	Prokhorovsky		Tar Spring
				upper		9								
						8						Tarusian	Samarsky		Glen Dean
					Cf6δ	7								
330.34	VISEAN	Brigantian	lower		4-6		upper VISEAN	Warnantian			Venevian	Mezhevskoy	Shangsian	Fraileys Shale / Beech Creek / Renault
		late	up.	Cf6γ2	12-3				MFZ 14		Mikhailovian			Ste. Genevieve
			Cf6γ1											
335		Asbian	lower	Cf6α–β		MFZ 13		Aleksinian		Donetsky		St. Louis
		middle	Holkerian	upper	Cf5β2		MFZ 12	Livian	Tulian			Salem
			lower	Cf5β1				middle VISEAN			Styl'sky		
340			Cf5α									upper Warsaw
		early	Arundian	Cf4δ					Bobrikian	Sukhonsky	Jiusian	
			Cf4γ		Moliniacian	MFZ 11						
			Cf4β			MFZ 10		Glubokinsky		Osagean (part)
345			Cha.	Cf4α2		early VISEAN	MFZ 9	lower VISEAN	Radaevian			
346.73												

LAURUSSIA
northern England — Ireland

LPT
Sierra Morena — Adarouch

GPT
Montagne Noire — Valdediezma

GONDWANA
Tindouf

Legend:

- **4** — *Calcifolium* association
- **3** — *Falsocalcifolium* association
- **2** — dasycladales association
- **1C** — *Ungdarella-Koninckopora* association
- **1B** — *Kamaenella-Ungdarella-Koninckopora* association
- **1A** — *Kamaenella-Koninckopora* association

LAURUSSIA

northern England Ireland

LPT

Sierra Morena Adarouch

GPT

Montagne Noire Valdediezma

GONDWANA

Tindouf

4			*Calcifolium* association
3			*Falsocalcifolium* association
2			dasycladales association
1C			*Ungdarella-Koninckopora* association
1B			*Kamaenella-Ungdarella-Koninckopora* association
1A			*Kamaenella-Koninckopora* association

A LAURUSSIA

B LPT

C GPT

D GONDWANA
Tindouf
%V

Montagne Noire Valdediezma

northern
England

Ireland

Sierra Morena   Adarouch

%V
0 10 20 30 40 50 60 70 80 90

%V
0 10 20 30 40 50 60 70 80 90

%V
0 10 20 30 40 50 60 70 80 90

%V
0 10 20 30 40 50 60 70 80 90

%V
0 10 20 30 40 50 60 70 80 90

%V
0 10 20 30 40 50 60 70 80 90

%V
0 10 20 30 40 50 60 70 80 90

%V
0 10 20 30 40 50 60 70 80 90

Bashk
Zapalt.
late Serpukhovian
Protvian
Steshevian   early Serpukhovian
Tarussian
early Brigantian   upper Viséan
late Asbian
early Asbian

Brigantian

Main rhythms and foraminiferal trends in the late Asbian of UK

Ft13
Ft12
Ft11
Ft10
Ft9
Ft8
Ft7
Ft6
Ft5
Ft4
Ft3
Ft2
Ft1
Ft0

Early Asbian

Ft13
Ft12
Ft11
Ft10
Ft9
Ft8
Ft7
Ft6
Ft5
Ft4
Ft3
Ft2
Ft1
Ft0

323.4
(M.a.)

325

330.34

335

- blue-green
- bryopsidales
- dasycladales
- *Koninckopora*
- red algae
- aoujgaliids
- *Ungdarella*
- calcifoliids
- donezelliids
- moravamminids

A

late	early	middle	late	early	late	early
Tournais.	Viséan			Serpukhov.		Bashkirian

350 345 340 335 330 325 320

B

genus richness

- Global
- Western Palaeotethys
- Eastern Palaeotethys
- North America
- Uralian

originations

extinctions

late	early	middle	late	early	late	early
Tournais.	Viséan			Serpukhov.		Bashkirian

350 345 340 335 330 325 320

A — taxonomic distinctness Δ⁺

Legend:
- Global
- Western Palaeotethys
- Eastern Palaeotethys
- North America
- Uralian

Time scale (A):
late Tournais. | early, middle, late Viséan | early, late Serpukhov. | early Bashkirian

350 — 345 — 340 — 335 — 330 — 325 — 320

B — Regional taxonomic distinctness Δ⁺

Time scale (B):
early, late Asbian | early Brigantian | Taru., Stesh., Protvian, Zapal. Serpukhovian

335 — 330 — 325

Legend:
- northern England
- Ireland
- Sierra Morena
- Adarouch
- Montagne Noire
- Valdediezma
- Tindouf

C — Western Palaeotethys taxonomic distinctness Δ⁺

Time scale (C):
early, late Asbian | early Brigantian | Taru., Stesh., Protvian, Zapal. Serpukhovian

335 — 330 — 325

D — Bristish Viséan-Serpukhovian taxonomic distinctness Δ⁺

Categories (D):
latest Courceyan | Chadian | 'lower' Arundian | 'upper' Arundian | 'lower' Holkerian | 'upper' Holkerian | early Asbian | late Asbian | early Brigantian | early Serpukhovian | late Serpukhovian

350 — 345 — 340 — 335 — 330 — 325

inflexion points in the PD curve   gaps in the succession   strongly dolomitized intervals
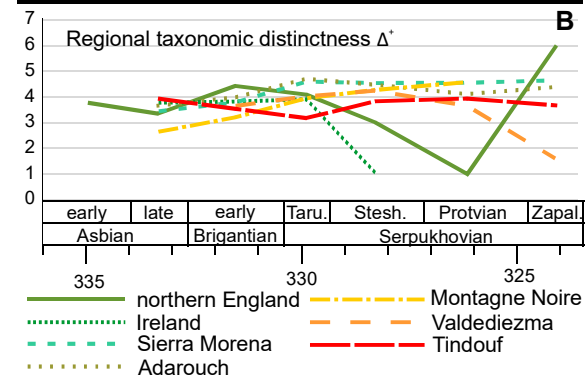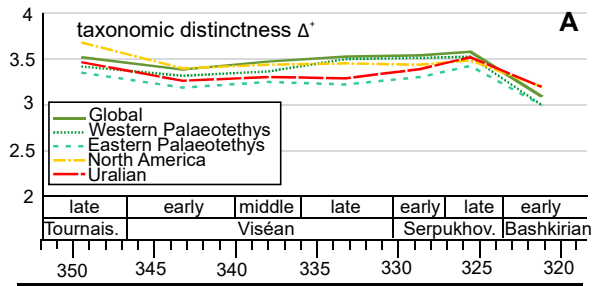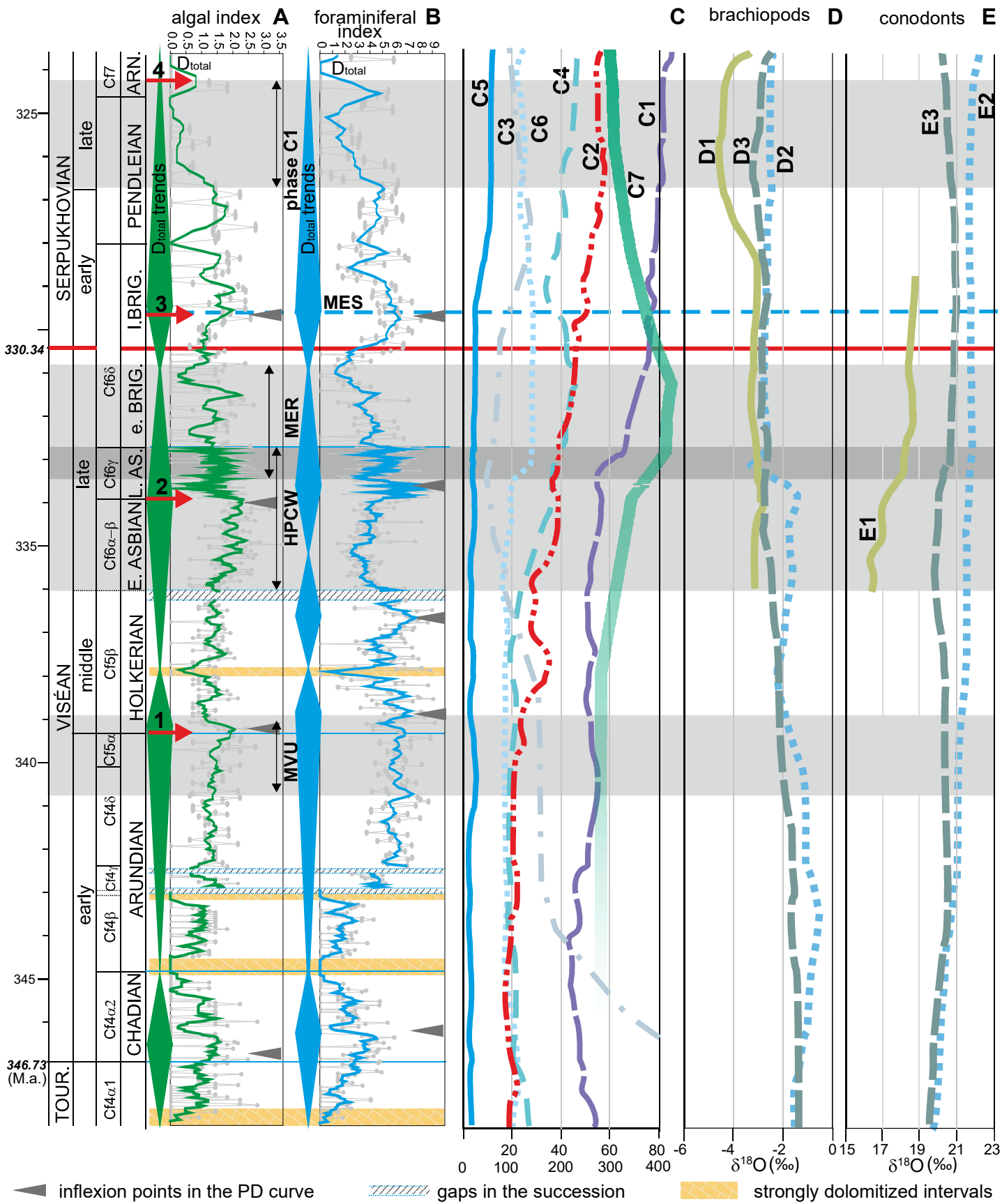
Algal diversity during the onset of the late Palaeozoic Ice Age in low latitude basins of the

Western Palaeotethys

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1. BIOSTRATIGRAPHY AND STRATIGRAPHIC SECTIONS

1.1. Northern England

The late Asbian-Serpukhovian interval includes a range of diverse sections to obtain complete stratigraphic coverage and comprises some of the best preserved outcrops. The Trowbarrow Quarry (proposed late Asbian stratotype) contains the topmost Park Limestone Formation, Urswick Limestone Formation up to the Gleaston Formation (= Alston Formation). This interval includes the top of the early Asbian and entire late Asbian, whereas the Gleaston Formation corresponds to the Brigantian. Biostratigraphy of the section has been recently revised (Cózar et al., 2022c). The lower part of the early Brigantian is selected in the Janny Wood section (Brigantian Stratotype), including the Peghorn Limestone and Smiddy Limestone members. Its biostratigraphy has been revised in Cózar and Somerville (2004) and McLean et al. (2018). The middle and upper part of the early Brigantian is selected in the interval between the Grain Beck Limestone to the Single Post Limestone from the Rookhope Borehole. Stratigraphy and biostratigraphy of this borehole were described in Johnson and Nudds (1996) and Cózar and Somerville (2004).

The late Brigantian (or upper Cf6δ subzone) is selected in some natural outcrops, which contain wider and more diverse assemblages than those recorded in boreholes. Therefore, the lower level, the Scar Limestone Member was sampled in Croglin (Scar Limestone Stratotype), Five Yard Limestone Member in Heathery Cleugh, Four Fathom Limestone Member in Smeltmill Beck, whereas no good natural outcrops of the Three Yard Limestone Member were recorded. Data from the Rookhope Borehole were also used for the Three Yard Limestone Member. Biostratigraphic details of the limestones were published in Cózar and Somerville (2014, 2016), which allow correlation of these limestones with the Tarusian and Steshevian Russian substages (early Serpukhovian).

The Great Limestone Member (base of the Pendleian Substage) and Little Limestone Member were also selected in natural outcrops at Killhope Sike Stream and Borrowdale Beck, with their biostratigraphy allowing correlation with the Steshevian Substage (published in Cózar and Somerville, 2014).

Thin limestone beds of the Pendleian have been selected in the Woodland Borehole, from the Shelly Band to the Rookhope Shell Band, although with varied stages of preservation for the limestones, which were not always desirable. The biostratigraphy of these beds was published in Stephenson et al. (2010) and Cózar and Somerville (2014), and foraminifers allow correlation to the Protvian Russian Substage (lower half of the late Serpukhovian), which occurs in the Crag Limestone.

Owing to the poor preservation in the Woodland Borehole of the Lower Felltop Limestone (base of the Arnsbergian) additional data is selected from the Rowlands Gill Borehole, studied

in Stephenson et al. (2010), whereas the younger Arnsbergian limestones have been selected from the Woodland Borehole.

The Holkerian-Asbian succession from the Great Scar Limestone Group (only present in northern England) have been recently revised by Waters et al. (2021). On the other hand, the entire Serpukhovian succession, from the Midland Valley of Scotland to the Southern Culm Basin has been revised by Cózar and Somerville (2021a). In this study, the base of the Zapaltyubian Russian Substage is not clearly defined enough, because there are questionable Zapaltyubian foraminifers from the Rookhope Shell Band, Lower Felltop Limestone, Coalcleugh and Upper Felltop Limestone beds. The Grindstone Limestone contain typical Zapaltyubian assemblages, nevertheless, further investigation is needed to clarify the possible equivalence of this substage in Britain.

The calcareous algae have been rarely published, and only those from Janny Wood and Rookhope Borehole were previously published (Cózar and Somerville, 2004), and a summary of the latest Asbian-early Brigantian algal record was published by Cózar and Somerville (2005a). Hence, most of the algae used in this study are from unpublished data (Appendix A).

late Viséan to Serpukhovian limestones in northern England

Limestone	locality	[British Grid] (geographic coordinates)
top Park Lst.	Trowbarrow Quarry	(N54°10'39''/ W2°47'49.15'')
Urswick Lst.	Trowbarrow Quarry	(N54°10'39''/ W2°47'49.15'')
Peghorn Lst.	Janny Wood	[NY 783038]
Smiddy Lst.	Janny Wood	[NY 783038]
Grain Beck	Rookhope Borehole	[NY 938 428]
Lower Little Lst.	Rookhope Borehole	[NY 938 428]
Jew Lst.	Rookhope Borehole	[NY 938 428]
Tynebottom Lst.	Rookhope Borehole	[NY 938 428]
Single Post	Rookhope Borehole	[NY 938 428]
Scar Lst.	Croglin	[NY581 484]
Five Yard Lst.	Heathery Cleugh	[NY8460 4198]
Four Fathom Lst.	Smeltmill Beck	[NY848 143]
Great Lst.	Killhope Sike Stream	[NY845 468]
Little Lst.	Borrowdale Beck	[NY837 164]
Shelly band	Woodland Borehole	[NZ0909 2769]
Faraday	Woodland Borehole	[NZ0909 2769]
Crag Lst.	Woodland Borehole	[NZ0909 2769]
Knucton Lst.	Woodland Borehole	[NZ0909 2769]
Unnamed Limestone	Woodland Borehole	[NZ0909 2769]
Rookhope Shell Band	Woodland Borehole	[NZ0909 2769]
Lower Felltop Lst.	Rowlands Gill Borehole	[NZ1664 5815]
Coalcleugh Lst.	Woodland Borehole	[NZ0909 2769]
Upper Felltop Lst.	Woodland Borehole	[NZ0909 2769]
Grindstone Lst.	Woodland Borehole	[NZ0909 2769]

1.2. Ireland

The succession in Ireland shows more continuous carbonates, even for the Brigantian, and the selection of only seven stratigraphic sections covers the studied interval.

The transition from the top of the early Asbian (non-cyclic) into the late Asbian (cyclic) is recorded in the Ballyadams Quarry (County Laois) which contains 5 out of the 6 major cycles described by Cózar and Somerville (2005b). The upper two cycles up to the base of the Brigantian are recorded in the Clogrenan B Borehole (County Carlow). All these units correspond to the upper part of the Ballyadams Formation, which takes into consideration thicknesses recorded in boreholes (e.g. 220 m in the Durrow-2 Borehole), a thickness between 300 m and 400 m is likely. Units 3 and 4 of the Brigantian (sensu Cózar and Somerville, 2005b) are recorded in the Clogrenan Quarry. It is noteworthy that foraminifers marking the base of the Serpukhovian are recorded from the middle part of unit 3 (Cózar and Somerville, 2021b). Units 5 and 6 are selected from the Dunamase Quarry, also in the County Laois. Units 3 to 6 belong to the Clogrenan Formation, which is assumed to cover an interval from the Peghorn Limestone to the Five Yard Limestone as at Janny Wood in England.

In Carlow, above the carbonate succession, there is a large hiatus, and the Leggacurren Shale Formation overlies the carbonates at an unconformity. These shales can possibly be correlated with the Zapaltyubian.

The Slievenaglasha Formation is the lateral equivalent in the Burren, where the upper part of the Ballyelly Member is present in the Lisdoonvarna Quarry, and represents slightly younger horizons than the top of the Clogrenan Formation. The top of this member as well as the succeeding Lissylisheen Member are better represented in the upper part of the Deer Park Formation in the Ardagh Platform, within the Poulmore Scarp Quarry.

The uppermost carbonates in Ireland, correspond to the Magowna Formation, which has been sampled in Kilnamona. The section (e.g., Skompski et al., 1995) contains the top of the Slievenaglasha Formation and also a transition which is not recorded in the Deer Park Formation (Cózar and Somerville, 2021b). The Magowna Formation is mostly composed of shales, with thin carbonate lenses and beds, and contains typical Pendleian ammonoids equivalent to the Great Scar Limestone in Northern England. Thus, foraminifers which could indicate a late Serpukhovian age do not occur in Ireland, and even, the upper part of the early Serpukhovian is represented only by shales.

The detailed biostratigraphy of these latter sections is only included in the revision of the Serpukhovian in Ireland by Cózar and Somerville (2021b), whereas the biostratigraphy of the lower formations is published in Cózar and Somerville (2005b) and Somerville and Cózar (2005).

Calcareous algae from the Ballyadams and Clogrenan formations were published by Cózar and Somerville (2005a, 2005c), whereas the algae from younger levels remained unpublished until now (Appendix A).

late Viséan to Serpukhovian limestones in Ireland

Limestone	locality	[Irish Grid]
upper Ballyadams Lst.	Ballyadams Quarry	[S 621916]

top Ballyadams Lst.	Clogrenan B Borehole	[S 688 720]
lower Clogrenan Lst.	Clogrenan Quarry	[S 688 720]
upper Clogrenan Lst.	Dunamase Quarry	[S 542 993]
Ballyelly Lst.	Lisdoonvarna Quarry	[R 1540 9950]
Deer Park Formation	Poulmore Scarp Quarry	[N 823 959]
Magowna Formation	Kilnamona	[R27821 80339]

1.3. Sierra Morena

In the Guadiato and Guadalmellato valleys, there is no formal lithostratigraphical subdivision due to the complex synsedimentary and postsedimentary tectonics, allowing only definition of large tectonostratigraphic units in the region (e.g., Cózar and Rodríguez, 1999a). In this region of SW Spain, there is no carbonate sedimentation older than the late Viséan, and even the inclusion of some outcrops in the early Asbian (e.g., Sierra Palacios; Cózar and Rodríguez, 1999b) is a questionable possibility. In addition, most sections are delimited at their bases by faults, and thus, for instance, in the Castillo Quarry section it is not possible to quantify the missing parts of the late Asbian. However, it is possible to measure more than 100 m of continuous limestones (with rare emergent surfaces in the upper part) of late Asbian rocks in the Castillo Quarry, whereas the early Brigantian contain about 100 m of limestones (non-cyclic but with some palaeokarsts) in the El Collado section. The succession is interrupted by 'Namurian' continental conglomerates. The precise biostratigraphy of the sections was published in Cózar (2004).

The transition into the Serpukhovian is only recorded in the parallel Guadalmellato Valley, a syncline, where, the northern flank of the syncline contains the uppermost early Brigantian up to the middle part of the early Serpukhovian in carbonates and shales, in sections such as at Casa de la Nava. It was not possible to determine the biostratigraphy of the complete succession in the syncline because it represents a rapidly deepening sequence (in younger units), with shaley slumps and black shales in the core of the syncline, within a tectonically active context (Cózar et al., 2006a).

Surprisingly, the younger part of the marine succession is recorded in the San Antonio Unit of the Guadiato Valley; thus, there is no representation of the early Serpukhovian in this valley. The upper Serpukhovian carbonates, developed within a strike-slip basin (Cózar and Rodríguez, 2004), such as those recorded in the La Cornuda Section. It is possible there is a gap in the algal succession between the Casa de la Nava and La Cornuda sections, but due to the scarce and sparsely distributed carbonates in the region, this gap is presumed, but not quantified. The transition into the Bashkirian continental conglomerates is observed in sections like Lavadero de la Mina, although the younger beds (assumed to be upper Zapaltyubian) are a rather hostile facies for foraminifers and algae, with restricted sandy beds representative of supratidal nearshore facies.

The calcareous algae from the Castillo Quarry and El Collado sections were published in Cózar (2005), and those from the La Cornuda section in Cózar (2005). Only the main algal groups of Casa de la Nava section were published (Cózar et al., 2006a), but are listed here in extended form (Appendix A).

late Viséan to Serpukhovian limestones in Sierra Morena (SW Spain)

Limestone	locality	(geographic coordinates)
Castillo Unit	Castillo Quarry	(N38º15'43''/W5º2'21'')
Castillo Unit	El Collado	(N38º10'1''/W5º1'36'')
Guadamellato Unit	Casa de la Nava	(N38º2'2''/W4º36'44'')
San Antonio Unit	La Cornuda	(N38º12'50''/W5º6'43'')

1.4. Adarouch

This region is the northern extreme of the Azrou-Khenifra Basin in the Western Meseta of Morocco, juxtaposed to the east by the Nappes Zone. The basin was tectonically active for most parts of the succession (Cózar et al., 2023a), a fact, which together with the multiple Ph.D. projects studying different parts of the basin, has resulted in a complex lithostratigraphical framework of formations from north to south, whose correlation is still in progress. The late Viséan in the northern outcrops is mostly represented by the Tizra Formation. Nevertheless, other formations attributed to the early and mid Viséan in the region are also of a late Viséan age, and usually, correspond to tectonic duplexes in the region as well as gliding nappes (Cózar et al., 2023a). The most complete succession is measured in the southern extremity of the Tizra Hills, where cycles are recognised in the lower part (Cózar et al., 2022a), in which the late Asbian is recorded in the Tizra 3 section (originally published in Cózar et al., 2008). The basal cycle 0, with transitional faunas between the Asbian and Brigantian is only recorded in the Tizra 3-3 section. Other cycles are better represented in the Tizra 3-2 section (Cózar et al., 2022a).

Above the lowermost early Brigantian, there are 85 m of shales up to the Tizra 4-2 section, and above, another 40 m of shales up to Tizra 2 section. Thus, there are two large deepening sequences with thick shales in their upper parts.

The base of the Serpukhovian is recognised in the middle part of the Tizra 2 section, representative of the Tarusian Substage. The early Serpukhovian parts can be completed by using the Tizra 9 section and Tizra 5 section data, although the Steshevian Substage is not clearly recognised, and it could be represented exclusively by shales. The late Serpukovian is identified in some sections (Cózar et al., 2011), of which, the best exposure, including the transition into the Bashkirian, is recorded in the Idmarrach 2 section. This section contains a few metres of Bashkirian marine carbonates succeeded by more widely distributed continental conglomerates and sandstones. However, the Tirhela section contains the longest Bashkirian succession, also in transitional continental facies, and the Bashkirian samples have been added to the top of the succession in this region.

The biostratigraphy of the sections was studied by Cózar et al. (2008, 2011), who have been updated by Cózar et al. (2023 b). Calcareous algae of some sections (Tizra 3, Tizra 2, Idmarrach 2) were published in Cózar et al. (2008, 2011), and more recent sections, such as

Tizra 3-2, Tizra 3-3, Tizra 4-2 and Tizra 9, are included in Cózar et al. (2023b). All the data are compiled herein (Appendix A).

late Viséan to Serpukhovian limestones in Adarouch (Moroccan Meseta)

Limestone	locality	(geographic coordinates)
base Tizra Formation	Tizra 3	(N33º33'15''/W5º24'49'')
lower cycle Tizra Formation	Tizra 3-3	(N33º33'22.45''/W5º24'42.68'')
lower Tizra Formation	Tizra 3-2	(N33º33'19.41''/W5º24'43.91'')
middle Tizra Formation	Tizra 4-2	(N33º33'24.94''/W5º24'28.62'')
upper Tizra Formation	Tizra 2	(N33º33'23.67''/W5º24'24.28'')
top Tizra Formation	Tizra 9	(N33º33'25.11''/W5º24'22.63'')
top Tizra Formation	Tizra 5	(N33º33'30.10''/W5º24'10.58'')
Idmarrach Formation	Idmarrach 2	(N33º32'05''/W5º23'26'')
Idmarrach Formation	Tirhela	(N33º32'50''/W5º23'20'')

1.5. Montagne Noire (southern France)

The Mississippian sedimentation of the Montagne Noire is included in large olistolites corresponding to a wild-flysch in the Cabrière Slice, the southern slice of the Palaeozoic complex of the Montagne Noire (Engel et al., 1981). There, the late Asbian is poorly represented, as small boulders or as calciturbidites with a poor algal representation in the La Serre section and in the Colonnes Formation in several sections (Cózar et al., 2017). The best intact succession is recognised in the 'calcaires stratiformes de Vailhan', such as in the Tour de Castellas section, although some faults are present. The Brigantian is complete in the Roque Redonde sections, as well as the Tarusian Substage, represented by the Roque Redonde Formation. For the Steshevian, the succession is followed by the Roc de Murviel Formation, which in its lower part is represented by the Roc de Murviel section. The transition between the Steshevian and Protvian is recorded in the La Serre Section, which is covered with sparse small outcrops in the Roc de Murviel section. The uppermost part of the Protvian is only recorded in the La Serre de Péret section, in which its upper part occur deltaic sandstones (Vachard et al., 2017; Cózar et al., 2019).

It is assumed that the flysch and wild-flysch started during the Zapaltyubian, and carbonates of this age are not recorded anywhere here. The biostratigraphy of most sections were published by Vachard et al. (2016b, 2017), whereas the algal content was published by Vachard et al. (2016a), and is duplicated herein (Appendix A).

late Viséan to Serpukhovian limestones in Montagne Noire (Southern France)

Limestone	locality	(geographic coordinates)
calcaires stratiformes de Vailhan	Tour de Castellas	(N43º33'00''/E3º18'13'')
Roque Redonde Formation	Roque Redonde Quarry	(N43º32'53''/E3º18'29'')
Roque Redonde and base of Roc de Murviel formations	Roc de Murviel	(N43º33'08''/E3º16'41'')
upper Roc de Murviel Formation	La Serre	(N43º31'18''/E3º21'22'')

Top Roc de Murviel Formation	La Serre de Péret	(N43°34'52''/E3°22'06'')

1.6. Valdediezma Platform (northwest Spain)

In the Cantabrian Mountains, the studied interval is usually represented by deep-water basinal carbonates of the Alba Formation and the lowermost part of the Barcaliente Formation (Sánz-López et al., 2018), and thus, devoid of calcareous algae. However, in the core of the Picos de Europe province, the Valdediezma Limestone contains the only shallow-water carbonates in NW Spain. Numerous sections have been measured to analyse the complete succession, which is commonly interrupted by faults (Blanco-Ferrera et al., 2021). The most complete and continuous section is that from the Valdediezma stream to the Jitu l'Escarandi col. In its upper part, more than 100 m of the Voznesenkian are recorded, and by way of a fault, possibly Krasnopolyanian age strata are recognised in the "cheese cave". The calcareous algae from the Valdediezma Limestone were published by Cózar et al. (2018), and the content of the additional samples acknowledged by Blanco-Ferrera et al. (2021) are included in this study (Appendix A).

late Viséan to Serpukhovian limestones in Valdediezma (Northwest Spain)

Limestone	locality	(geographic coordinates)
Valdediezma Limestone	Valdediezma to Jitu l'Escarandi	(N43°14'17''/W4°42'13'')
Valdediezma Limestone	Cheese cave at Tresviso	(N43°15'09''/W4°41'21'')

1.7. The Tindouf Basin (Morocco)

The western extremity of this basin is exposure in Morocco, whereas no access to the Algerian part of the basin was possible. Even in Morocco this area is a military zone of restricted access (Cózar et al., 2014a). Thus, sampling is not simple, and so not many stratigraphic sections could be measured.

The succession, possibly including from the base of the Asbian, is composed of shales of the Betaina Formation, which contains thin carbonate beds in its uppermost part. Above, this is a continuous cyclic succession of the Djebel Ouarkziz Formation (frequently abbreviated as Ouarkziz Formation) from the Brigantian up to the top of the Serpukhovian, well exposed in section 2 of Cózar et al. (2014b). The Bashkirian part of the succession (up to the Krasnopolyanian) is observed in section 3 (not included in this study). The biostratigraphy for the Serpukhovian in previous publications on these sections was wrongly applied, because the identification and mixture of British and international substages/stages, led to a confusing subdivision. This problem is related to the wrong Serpukhovian to Namurian correlation usually used before the publication of Cózar and Somerville (2016).

Thus, using the notation for the cyclic beds described in Cózar et al. (2014a, 2014b), the late Asbian carbonates includes beds 2, 1, A to D; the early Brigantian includes beds E to J; the early Serpukhovian is represented by beds K to N, of which, K-L correspond to the Tarusian and M-N to the Steshevian. The late Serpukhovian included beds O to S3, although owing to the faunal paucity in the upper beds, the Protvian and Zapaltyubian cannot be clearly distinguished, although the occurrence of *Plectostaffella* species from bed Q suggest a probable Zapaltyubian age for this part of the section. The top part, with a transition into the Bashkirian, and most of the Krasnopolyanian age beds are recorded from section 3.

For the calcareous algae, although some of the main genera were published in Cózar et al. (2014c), most of them remained unpublished until herein (Appendix A).

late Viséan to Serpukhovian limestones in the Tindouf Basin

Limestone	locality	(geographic coordinates)
Djebel Ouarkziz Formation	Section 2 in Tinguiz Remz	(N28°24'45''/W9°24'20'')
Djebel Ouarkziz Formation	Section 3 in Tinguiz Remz	(N28°22'08''/W9°29'04'')

1.8. Courceyan to early Asbian succession

In order to analyse the foraminiferal and algal diversity during the Viséan, some stratigraphic sections mostly from south Cumbria (northwest England) have been added to the previously analysed sections (Appendix B).

The uppermost Courceyan-Chadian transition is analysed in the Meathop Quarry (Cf4α1-Cf4α2 foraminiferal subzones), from the Martin Limestone Formation (Rose and Dunham, 1977; Johnson et al., 2001). The succeeding lower parts of the Red Hill Formation (Johnson et al., 2001), are mostly studied in the Sunnyside section, situated a few hundreds metres to the east of the Meathop Quarry, a section with complete coverage of the lower part of the Arundian (Cf4β foraminiferal subzone). The upper part of the Arundian, represented by the Dalton Formation (Cf4γ-Cf4δ subzones) is analysed with a composite section between the Cat Cragg, Coastguard Quarry and Blackstone Point sections (Hounslow et al., 2022). Nevertheless, a good continuous section representative of the Cf4γ subzone has not been studied yet, and it cannot be easy estimated (for the time being), the biostratigraphic gaps at the base and top of the Cat Cragg section.

The top part of the Arundian, the Cf5α subzone, and lower part of the Holkerian Cf5β subzone, up to the top of the Dalton Formation is selected in the Grubbins Wood section (Cózar et al. 2023b), which contains the best Arundian-Holkerian transition in the region.

Other foraminiferal zones assigned to the Holkerian are recorded in the Park Limestone at the Barker Scar (former Holkerian stratotype) (Cózar et al. 2022b). From the top of the section, there is of the order of half the thickness of the Park Limestone Formation remaining to the base of the Urswick Limestone Formation. As Cózar et al. (2022c) highlighted, the late Asbian

base is located near the top of the Park Limestone Formation, and in the Trowbarrow Quarry, ca. 20 m of early Asbian strata are recorded in the Park Limestone Formation, whereas the top of Barker Scar section is still Holkerian. Thus, the base of the early Asbian is in the non-studied upper half of the Park Limestone Formation. To avoid this problem, and owing to their faunal similarities, the early Asbian is well-constrained in County Laois, and the upper part of the Tankardstown Borehole (GSI 89-10) is selected, with the base of the early Asbian located at 138 m depth, and the base of the late Asbian at 26 m depth.

The biostratigraphy of the Dalton Formation and lower part of the Park Limestone have been already published (Hounslow et al., 2022; Cózar et al., 2022b, 2023b), whereas the other sections are unpublished. Calcareous algae of the sections are unpublished (Appendix C).

Courceyan to middle Viséan limestones in northern England

Limestone	locality	[British Grid] (geographic coordinates)
lower Martin Lst.	Meathops Quarry	[SD 433 792], (N54°12'21''/W2°52'21'')
upper Martin Lst.	Sunnyside	(N54°12'17''/W2°52'12'')
mid Red Hill Lst.	Cat Craig Quarry	[438824], (N54°14'4''/W2°51'51'')
top Red Hill Lst.	Coastguard Quarry	[452784], (N54°11'54''/W2°50'35'')
lower Dalton Lst.	Coastguard Quarry	[452784], (N54°11'54''/W2°50'35'')
middle Dalton Lst.	Blackstone Point	[436776] (N54°11'27''/W2°51'42'')
upper Dalton Lst.	Grubbins Wood	[445779], (N54°11'37''/W2°51'12'')
top Dalton Lst.	Barker Scar	[333783], (N54°11'50''/W3°1'28'')
lower and mid Park lst.	Barker Scar	[333783], (N54°11'50'/W3°1'28'')

early Asbian limestones in Ireland

lower Ballyadams Formation	Tankardstown Borehole (GSI-89-10)	Irish Grid 268703/186868

2. CALCAREOUS ALGAE AND CYANOBACTERIA

Taxonomic classifications of Mississippian calcareous algae are varied and not free of controversy, and usually, publications have focused on some orders and families, but comprehensive classifications are scarce (e.g., Wray, 1977; Chuvashov et al., 1987; Bogush et al., 1990; Mamet, 1991). There are classifications dedicated to the Dasycladales (e.g., Bassoulet et al., 1979; Deloffre 1988; Bucur 1999), to the Rhodophycophyta (e.g., Mamet and Roux, 1977; Shuysky, 1999), as well as Algospongia (Termier et al., 1977). However, as it can be observed, most advances in the knowledge of the Mississippian algae are from the 70's and 80's decades, and later, precision and details on some genera and descriptions of new genera/species have not been commonly published. In rare cases, in recent publications, there are some attempts to summarize suprageneric classifications, such as Ivanova (2013) and the unpublished Ph.D. by Pille (2008), as well as Vachard and Cózar (2010) for the Algospongia, and the revisions of cyanobacteria by Riding (1991, 2011).

Furthermore, it is highlighted that the solenoporaceans, classically considered as red algae, are mostly composed of genera currently considered as porifera (Riding, 2004). Nevertheless, most current publications only focused on some groups of families (Cózar and Vachard, 2006; Chuvashov and Anfimov, 2007; Cózar et al., 2009; Pille and Vachard, 2011; Granier, 2012). This scarcity in studies explains the complex scenario presented to us to approach the algal analysis used here, and the numerous unsolved or questionable issues within this phylum.

Within the cyanobacteria, still assigned to an indeterminate order, *Renalcis* Vologdin, 1932 is one of the most common genus's, exclusively present in microbially-mediated carbonates (microbial mounds), and some synonyms have been described for Mississippian strata, such as *Izhella* Antropov, 1955 and *Shuguria* Antropov, 1950. Like Mamet and Roux (1983) and Vachard (1993) proposed, there are no significant morphological differences between these genera to consider them independent genera. Even Luchinina (2009) considered *Renalcis* as an evolutive stage regrouping of several genera of cyanobacteria, although, the inclusion of *Epiphytum* Bonnerman, 1886 as another stage does not seem to confirm this single taxon because *Epiphyton* has never been recorded above the Tournasian (Mamet, 1991).

Widely distributed genera are those of the order Aphralysiales, particularly *Aphralysia* Garwood, 1914, which could be a synonym with *Polymorphocodium* Derville, 1931 and *Stylocodium* Derville, 1931 (see Pille, 2008). There are numerous species of the genus, described from the Silurian, and possibly, five to six Carboniferous species and commonly, many small specimens in open nomenclature. Thus, the number of species might be more. *Sparaphralysia* Vachard in Vachard and Beckary, 1991 is more unusual, and with a more restricted stratigraphic range. Apart from the type species *S. tacania* Vachard in Vachard and Beckary, 1991, there is only a second species, *Sparaphralysia* sp. 1 Cózar, 2005, of much smaller size.

Typical Mississippian Girvanellaceae are *Girvanella* Nicholson and Etheridge, 1878, *Mitcheldeania* Wethered, 1886 emend. Mamet and Roux, 1975b and *Malakhovella* Mamet and Roux, 1977, although only the two first genera have been recorded by us. There have been five published species of *Girvanella* during the Mississippian and only two species of *Mitcheldeania*. In the case of *Girvanella,* there are numerous synonyms (see Mamet, 1991), including *Subtifloria* Maslov, 1956b. More flexuous and dichotomous tubes allow distinction of both genera. Questionably, differences between species are commonly based on tube size, a weak feature which could question the validity of some of them. In this study, the Garwoodiaceae has been included within the Cyanobacteria, *Garwoodia* Wood, 1941, *Hedstroemia* Rothpletz, 1913, *Nansanella* Mamet and Roux, 1977, *Ortonella* Garwood, 1914, *Ortonellopsis* Vachard and Cózar in Vachard et al., 2016a, and *Pseudohedstroemia* Mamet and Roux, 1978, although some authors (e.g., Mamet and Roux, 1975b; Mamet, 1986, 2002) considered them as nodular Codiaceae (green algae). Environmental conditions suggest these genera are more similar to other cyanobacteria than to the typical Codiaceae (e.g., Cózar et al., 2019).

Pille (2008) interpreted *Bacinella* Radoicic, 1959 as a cyanobacterial biofilm, similar to *Aranea* Hance, 1983, although these structures have been considered as microbial biofilms

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produced in rhizoconcretions (Cózar and Vachard, 2005), and thus, excluded from this study. Ivanova (2013) interpreted as incertae sedis cyanobacteria *Stipulella* Maslov, 1956b and *Rectangulina* Antropov, 1950. This latter taxon in particularly abundant in microbial mounds, although the cyanobacterial affinity of both genera is questioned here, and thus, excluded from the analysis.

Within the Clorophycophyta, of the class Bryopsidaceae, the most common representatives belong to the Caulerpales. Although these are rare, five genera have been identified, with three of them only recognised in the Montagne Noire and in very scarce levels, *Orthosiphon* Johnson and Konishi, 1956, *Poncetellina* Mamet and Roux, 1984, and *Mellporella* Racz, 1965 (Pille, 2008; Vachard et al., 2016a). *Pseudokulikia* Mamet, 1997 is recorded only in Morocco, SW Spain and Ireland (NBT and Laurussia). Some of the genera have not been recorded in the analysed sections due to their scarcity. Only *Saccamminopsis* Sollas, 1921 emend Vachard and Cózar, 2003 is common in most basins, although it is restricted to the Western Palaeotethys. There are populations with a varied average-size, although due to the simple morphology of the genus is difficult to decide if they belong to a single species or might be two or three species. Nevertheless, the size of the specimens increases, and specimens of the late Asbian are much smaller than those of the Brigantian, which in turn are smaller than those in the early Serpukhovian. Bryopsidales Ulotrichales are also *Anatolipora* Konishi, 1956 (= *Loomisella* Mamet and Bergeron in Bergeron and Mamet, 1992) and *Richella* Mamet and Roux in Mamet et al., 1987 sensu Pille and Vachard, 2011.

The Dasycladales are the most common Clorophycophyta, and mostly belong to the family Diploporaceae (e.g., Pille and Vachard, 2011), whereas the Seletonellaceae are the second group, although this latter taxa diversifies notably in the Pennsylvanian and younger strata (e.g., Granier and Grgrasovic, 2001). Within the Diploporaceae, there are some genera supposedly endemic to the American Realm, mostly occurring in the Tournasian, such as *Albertaporella* Johnson, 1966, *Pekiskopora* Mamet, 1974, *Queenslandella* Mamet and Roux, 1983, *Columbiapora* Mamet 1974 emend Mamet and Roux, 1981 and *Yukonella* Mamet and Rudloff, 1972. Nevertheless, *Albertaporella* is recorded in the early Viséan of the Palaeotethys (Cózar and Somerville, 2005d) and other genera have been considered as junior synonyms of *Windsoporella* (Cózar et al., 2009). This latter genus was considered as endemic to the Maritime Provinces of Canada by Mamet (1991), but this region is usually considered as part of the Palaeotethys (e.g., von Bitter et al., 2007) and in fact, there are more than eight Mississippian species described from the Western Palaeotethys (see Cózar et al., 2009; Pille and Vachard, 2011). In the present study, only *Windsoporella* and *Albertaporella* have been recorded.

Another unusual Diploporaceae is *Clavaporella* Kochansky-Devidé and Herak, 1960 recorded from the Serpukhovian in SW Spain. Since the genus is typically distributed in the Moscovian-Permian, the Mississippian species might belong to a different and new genus.

Other more usual Diploporaceae, widely distributed in the Palaeotethys are *Borladella* Cózar Somerville, Rodríguez and Medina-Varea, 2007, *Guadiatella* Somerville, Rodríguez and Medina-Varea, 2007, *Cabrieropora* Mamet and Roux, 1975a, *Cabrieroporellopsis* Pille and Vachard, 2011, *Murvielopora* Pille and Vachard, 2011, *Kulikia* Golubtsov, 1961 (= *Sphinctoporella* Mamet and Rudloff, 1972) and *Eovelebitella* Vachard, 1974. *Frosterleyella*

Elliot 1988 is rather similar to *Kulikia*, and its validity as an independent genus is questionable. *Japhetella* Mamet and Roux 1983 is considered as a junior synonym of *Eovelebitella*.

The Seletonellaceae are represented by *Atractyliopsis* Acordi, 1956, *Coelosporella* Wood, 1940, *Borisovella* Ivanova, 1988, *Epimastoporella* Roux, 1979, *Paraepimastopora* Roux, 1979 and *Palaepimastoporella* Cózar and Vachard, 2004. Except for *Coelosporella* (with two Mississippian species), all of them are rare. It is emphasised that the typical Mississippian genera are *Coelosporella* and *Palaepimastoporella*, whereas the other genera are more typically distributed in the Pennsylvanian and Permian. In some cases, some authors considered that the four species of Mississippian *Atractyliopsis* should be described as a new genus because they believe that they are not related to the typical Permian *Atractyliopsis*.

Another common genus is *Nanopora* Wood, 1964 possibly the only representative of the family Dasycladaceae during the Mississippian (Vachard and Aretz, 2004), although Pille also considered it as independent and included it in the family *Dutroella* Mamet and Roux, 1978, which was considered as a Diploporaceae endemic to Tennessee. Its validity is questioned herein, even more when the taxon is endemic to a small part of the American Realm. Other dasycladales are very rare in the Mississippian, and of questionable suprageneric affiliation, such as *Masloviporella* Kulik, 1973, *Arengaepora* Pille 2008 nomen nodum, *Neoradiosphaeroporella* Cózar and Vachard in Vachard et al., 2016a. The scarcity of those algae is a handicap to achieve clearer classifications. Other questionable green algae are *Vermiporella* Stolley 1893 emend. Pia, 1927 (typical in the Silurian and Ordovician), whose Mississippian specimens possibly belong to another genus; *Sandoella* Mamet and Roux, 1978 and *Bolivianella* Mamet, 1996, which are indeterminate perforate and microsparised remains; *Eouraloporella* Berchenko, 1981, but it became extinct at the Devonian-Carboniferous boundary.

In contrast, *Koninckopora* Lee, 1912 is the most abundant genus of green algae, questionably assigned to the dasycladales in older publications (e.g., Mamet, 1991) due to its microgranular wall, unusual for the fossil dasycladales (except for *Yukonella*), but recently, less questioned as such (e.g., Granier, 2012). Surely, there are other undescribed genera of Mississippian dasycladales, that owing to their scarcity are assigned to other genera or are in open nomenclature. Without the finding of well-oriented material, the description of new species and genera is rather complicated. For instance, a few of them have been included in Appendix C, such as *Clavaporella* and *Mellporella*, because they have been illustrated, although their definite classification is still pending. In addition, two specimens similar to *Cabrieropora*, but bifurcated, were recorded in the Serpukhovian of Adarouch. The occurrence of a bifurcated diploraceae is against the main suprageneric criteria defined by Bassoulet et al. (1979) and Deloffre (1988), a fact that questions the validity of the family used in their classifications. Nevertheless, those specimens were never illustrated in Cózar et al. (2008, 2011), although included as '*Paracabrieropora*' nomen nodum in Pille (2008).

The Rhodophycophyta are in an incipient stage during the Mississippian (Cózar and Vachard, 2005), and only a few genera occur, such as *Principia* Brenckle in Brenckle et al., 1982, *Hortonella* Cózar and Vachard, 2005, *Neoprincipia* Cózar and Vachard, 2003 and *Archaeolithophyllum* Johnson, 1956. Most of them disappeared in the Mississippian, *Hortonella* in the Bashkirian, and in contrast, *Archaeolithophyllum* diversified in the

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Pennsylvanian and Permian. It is noteworthy that Vachard et al. (2001) considered the 'phylloid' algae as derived from *Archaeolithophyllum*, and thus, as rhodophycophyta, whereas a most widely accepted interpretation for the phylloids is as Codiacean green algae (e.g., Wray, 1977; Baars and Torres, 1991), as typically bioconstructors of late Pennsylvanian-Permian mounds. The often poor preservation of phylloid's could contribute to this suprageneric classification, although rarely cathodoluminescence has allowed recognition of internal organization (Corrochano et al., 2013). However, as Baars and Torres (1991) admitted, intense research using cathodoluminescence have not been conducted for understanding the internal structures in most phylloid algae. Species of *Archaeolithophyllum* in the Mississippian are restricted to *A. lamellosum* Wray, 1964, with a typical shape with multiple sheets, however, in the early Serpukhovian of SW Spain, there are common recrystallized 'phylloid' algae, but it is not possible to decipher if they belong to a new species of *Archaeolithophyllum* or if they are certainly phylloid in the sense of the Codiacean algae. As in other groups, those problematic specimens have been excluded from this study.

Also included within the Rhodophycophyta, are the problematic 'Solenoporaceae'. This group have been traditionally included in the red algae (e.g., Maslov, 1956a; Johnson, 1960; Mamet and Roux, 1977; Wray, 1977), but it is currently considered as chaetetid porifera (Brooke and Riding, 1998; Riding, 2004). Nevertheless, as Aguirre and Barottolo (2001) and Cózar and Vachard (2006) suggested, the solenoporaceans are a heterogeneous group, artificially regrouping taxa which are morphological similar, but belonging to different phylums. Therefore, every genus and species should be investigated independently to see its porifera or corallinacea algal affinity. Some Lower Palaeozoic algae are for instance, *Graticula* Brooke and Riding, 2000, whereas in the Mississippian, we have considered as algae *Maimonachaetetes* Cózar and Vachard, 2006 and *Anchisolenopora* Vachard and Cózar in Vachard et al., 2016a. Although possibly, some species of Mississippian *Parachaetetes* might belong to the algae (e.g., Aguirre and Barottolo, 2001), but they need further evaluation.

The class Algospongia contains the most problematic Palaeozoic algae, even its name is the result of the confused original interpretation by Termier et al. (1977), who considered them as belonging to the sponges, although unfortunately, this confusing name has the priority (Vachard and Cózar, 2010). Representative of the class have been described as foraminifers, sponges, rhodophycophyta, codiacean chlorophycophyta, dasyclacales chlorophycophyta and cyanobacteria (Vachard and Cózar, 2010). It must be admitted that possibly the Algospongia are also a heterogeneous group, and different affiliations could exist, although the absence of any modern equivalent, as well as unconvincing palaeoecological interpretations, do not help solve the origin of the group. Different interpretations have been discussed in detail by Vachard and Cózar (2010).

Mississippian genera have been regrouped in orders or suborders, usually based on our own experience, which share similar ecological conditions, and thus, occurring in similar environments. Therefore, all the Moravamminida and Wetheredellina are grouped in a single category, whereas the other groups are the Donezellina, Calcifoliina and Aoujgaliina, whereas only *Ungdarella* Maslov, 1956a has been studied separately. Description of the genera, species and synonyms are described in detail by Vachard and Cózar (2010), and here, only the list of Mississippian genera are included in Appendix C.

As mentioned previously, there are still many uncertainties within these calcareous algae, the validity of some genera, undescribed genera, suprageneric classifications, geographic dispersion and stratigraphic distribution, and thus as used here the ecological diversity seems to be more representative than pure taxonomic diversity, which could give us unusual results.

In total, ten groups have been utilised:

1. Cyanobacteria: including common representatives of the genera *Girvanella*, *Ortonella*, *Renalcis*, *Aphralysia* and *Sparaphralysia*, and more rarely *Garwoodia*, *Mitcheldeania* and *Ortonellopsis.*

2. Bryopsidales (or Udoteaceans): which here include mostly *Saccamminopsis*, whereas *Pseudokulikia*, *Anatolipora* and *Richella* are rarer.

3. Dasycladales: including a great variety of species and genera, with more than 20 genera (details in above Information).

4. In the dasycladales only *Koninckopora* is analysed independently, owing to its abundance, and the particular features of its wall structure, which are slightly different to typical dasycladales.

5. Red algae are scarce, and mostly include *Archaeolithophyllum, Neoprincipia*, with more rarely *Principia*, *Hortonella* and *Anchisolenopora*.

6. Aoujgaliales genera including the families Aoujgaliidae, Ungdarellidae, Cuneiphycidae and Stacheiinidae, genera which are frequently interpreted as red algae (e.g., Mamet, 1991).

7. *Ungdarella* species are distinguished separately from group 6, due to its abundance in the studied platform successions.

8. The calcifoliids: including representative of the families Fasciellidae and Calcifoliidae and those traditionally interpreted as related to the bryopsidales (e.g., Skompski, 1981).

9. Donezellids: including representative of the families Claracrustidae (*Claracrusta* and *Asphaltinella*) and Donezellidae (*Kamaenella*, and *Praedonezella*), a group that many have considered to be related to the dasycladales (e.g., Horbury, 1987), but they commonly occur in bioconstructions in slope settings, where they occur in life position down to 300 m water depth (Della Porta et al., 2002). Such great depths do not indicate a dasycladal affinity for the group.

10. The moravamminids (rather similar to the donezellids, but never forming colony-like structures) include Mississippian representatives of the suborder Moravammina. These are mostly the Issinellidae and Palaeoberesellidae groups, commonly interpreted as dasycladales (e.g., Skompski, 1987; Mamet, 1991), although, their ecological restrictions were not as demanding as modern dasycladales, which are mostly restricted to less than 10 m depth (Berger and Kaever, 1992). In fact, some representatives of moravamminids are commonly recorded in deep-water settings in Waulsortian Banks during the late Tournaisian and early Viséan (Lees and Miller, 1995), possibly at some hundreds of metres water depth, as well as in the deepest and muddier settings in the microbial bioconstructions of the late Viséan-Serpukhovian (Cózar et al., 2019). Thus, apart from

some morphological similarities, ecological controls on the Carboniferous moravamminids are far more variable to equate them with modern dasycladales.

The selection of stratigraphic sections whilst providing complete coverage of the stratigraphic interval, does not provide the total diversity of species and genera recorded from each respective basin. For instance, in the Montagne Noire, 65 species are recorded in the selected stratigraphic sections, whereas the total number of species in this basin is more than 75, or 52 out of the total of 57 genera (compare Appendix A in Supplementary Information with figure 13 in Vachard et al., 2016a). A similar section-specific lower diversity is recognised in all the basins whose algal content have been studied in detail, such as observed in the Dublin Basin (Cózar and Somerville, 2005a), Sierra Morena (Cózar, 2004; Cózar and Rodríguez, 2004; Cózar et al., 2006a), Adarouch (Cózar et al., 2023a), and Valdediezma Platform (Cózar et al., 2018). Some calcareous algae used for this analysis have not been published previously, such as those of the Tindouf Basin and most of the succession from the northern England sections.

Biostratigraphic calibration

Precise biostratigraphic calibration of the successions is vital to properly interpret the timing of isotopic, sedimentological and macroevolutive data. Regional zonal schemes in Carboniferous basins have a long tradition, often defining regional substages for the main basins or cratonic areas (e.g., see Aretz et al., 2020, fig. 23.5; Alekseev et al., 2022, fig. 2). The calibration and correlation of these Carboniferous regional substages is still in progress (Fig. 1), and results, are yet to be harmonised. This fact has important implications for understanding global synchronicity of events, and thus, for the construction and comparison of isotopic and glacioeustatic curves. Chronostratigraphic mismatches (and alternative correlation options) can be common in the material selected for discussion here, leading to differently inferred timing of events during the onset of the LPIA.

For example, the succession in the Carboniferous of Northwest Ireland studied by Barham et al. (2012), although showing a marked increase in $\delta^{18}O$, is questionable in that: (i) the older samples from the bioclastic limestones within the Benbulben Shale Formation are really Holkerian and not Asbian, as shown by Somerville et al. (2009); (ii) the base of the Brigantian should be located in the Meenymore Formation (not in the Bellavally Formation); and (iii) the base of the Serpukhovian should be located at the base of the Bellavally Formation (not in the Dergvone Shale Formation) (Cózar et al., 2006b; Cózar and Somerville, 2021b). Therefore, the entire isotopic curve needs to be modified to a more precise timescale (Fig. 15E).

Barham et al. (2012) suggested the base of the Serpukhovian was equivalent to the base of the Namurian (thus, equating the base of the Tarusian with the base of the Pendleian regional substages), as traditional correlations assumed, and still currently inferred by some (e.g., Aretz et al., 2020; Lucas et al., 2021). Sevastopulo and Barham (2014) also used this basal Serpukhovian-Namurian correlation, recognising that the base of the potential new base for the Serpukhovian (based on the first appearance of the conodont *Lochriea ziegleri*) should be located in the P1c ammonoid subzone within the early Brigantian. This conodont is currently being investigated, but as yet, is not formally ratified as the primary marker for the base of the Serpukhovian in the GSSP (Richards and Task Group, 2017). However, as Cózar and Somerville

(2014, 2016) demonstrated, the base of the currently valid Serpukhovian (at the base of the Tarusian Substage) should be correlated with the base of the late Brigantian (P2a subzone), whereas *L. ziegleri* first occurs in older levels of the P1d subzone, within the uppermost part of the early Brigantian (main Fig. 3). In addition, Cózar and Somerville (2014) also considered the correlation of the American substages as proposed by Kulagina et al. (2008), with the equivalent of the basal Serpukhovian in the Beech Creek Limestone. In contrast the traditionally considered base for the Serpukhovian (the Menard Limestone; e.g., Lane and Brenckle, 2005), contains typical late Serpukhovian foraminifers (of the Protvian Substage) (Fig. 3). This latter limestone has been used as the base for the Serpukhovian in many publications (e.g., Eros et al., 2012). Readjustments of the biostratigraphy of each individual glacioeustatic cycle defined in the major cratonic areas (Moscow Basin, Ukraine, North America and England) with the revised uppermost Viséan-Serpukhovian calibration demonstrates a better match and correlation of the major cycles (Cózar and Somerville, 2014, fig. 4). Up to the Mississippian-Pennsylvanian boundary, which has been more widely investigated (e.g., Brand and Brenckle, 2001), there are significant mismatches in this part of the succession. Consequently, cycles, biota diversity and isotopic data recorded from this interval in the American craton and the Western Palaeotethys should be recalibrated and readjusted. It is quite likely that the variations in the foraminiferal diversity recorded by Groves and Wang (2009) in the early Serpukhovian (line C4 in main text Fig. 10C), are in fact restricted to the late Serpukhovian, and so indirectly, all the derived isotopic data using that biostratigraphy should be adjusted in age.

Also an issue is the questionable correlation of the Holkerian with the Livian and Tulian substages, are is related to the existence of the Cf5α foraminiferal biozone at the top of the early Viséan (defined in Cózar et al., 2020). This equates to a hiatus in some basins (Cózar et al., 2023b), which has led to regional timescale mismatches in the middle Viséan (Fig. 3).

The definition of the base of the early and late Asbian, and its correlation with other regional substages, is another questionable point, which has direct implications for understanding the onset of glaciogenic-driven cyclic sedimentation around the World. Cózar et al. (2022d) revised the biostratigraphy in cyclic successions from North America, Canada, Ireland and Britain (with some possible exceptions for Scottish sections), and showed that cyclicity started at the base of the late Asbian or its lateral equivalents. For example this has, direct implications in the sampling using in Bishop et al. (2009) (a curve commonly used in most isotopic curves), where the base of the Chesterian was considered as equivalent to the Mikhailovian (correlated with the late Asbian; Cózar et al., 2022d), although markers of the latter substages are recorded from older levels in the Meramecian (Fig. 3). If the Serpukhovian data needs to be chronostratigraphically adjusted, then nearly all the data in Bishop et al. (2009) needs to be readjusted before using them for the construction of any global isotopic curve. In addition, the proposed 1–30 m sea-level falls of Rygel et al. (2008) during the Asbian-early Brigantian based on data from England, have to be restricted to the late Asbian-early Brigantian interval.

Consequently, it is necessary to establish a precise and robust biostratigraphic scale in order to correlate cyclic sequences, biota events and to build isotopic curves linked to the onset of the LPIA.

References

Acordi, R., 1956. Calcareous algae from the Upper Permian of the Dolomites (Italy) with stratigraphy of the "*Bellerophon*-Zone". J. Palaeontol. Soc. India 1, 75–84.

Aguirre, J., Barattolo F., 2001. Presence of nemathecia in *Parachaetetes asvapatii* Pia, 1936 (Rhodophyta, Gigartinales?): reproduction in 'Solenoporaceans' revisited. Palaeontology 44, 1113–1125.

Alekseev, A.S., Nikolaeva, S.V., Goreva, N.V., Donova, N.B., Kossovaya, O.L., Kulagina, E.I., Kucheva, N.A., Kurilenko, A.V., Kutygin, R.V., Popeko, L.I., Stepanova, T.I., 2022. Russian regional Carboniferous stratigraphy in: Lucas, S.G., Schneider, J.W., Wang, X., Nikolaeva, S. (Eds.), The Carboniferous Timescale. Geol. Soc., London, Sp. Publ. 512, 49–117. https://doi.org/10.1144/SP512-2021-134

Antropov, I.A., 1950. New foraminiferal species of the Late Devonian of some areas of the eastern Russian Platform. Akademiya Nauk SSSR, Izvestiya Kazanskogo Filiala, Geologicheskiy Institut, 1, 21–33 (in Russian).

Antropov, I.A. 1955. Blue green algae from the Devonian of the central areas of the eastern Russian Platform. Utch. Zap. Kazansk. Inst. Obshch. Estest Trudy, 115, 41–53 (in Russian).

Aretz, M., Herbig, H.G., Wang, X.D., 2020. The Carboniferous Period, in: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), Geologic Time Scale 2020. Elsevier, Amsterdam, pp. 811–874. https://doi.org/10.1016/B978-0-12-824360-2.00023-1

Baars, D.L., Torres, A.M. 1991. Late Paleozoic phylloid lagae – A pragmatic review. Palaios, 6, 513–515.

Barham, M., Murray, J., Joachimski, M.M., Williams, D.M., 2012. The onset of the Permo-Carboniferous glaciation: reconciling global stratigraphic evidence with biogenic apatite $\delta^{18}O$ records in the late Viséan. J. Geol. Soc. London 169, 119–122. https://doi.org 10.1144/0016-76492011-102.

Bassoullet, J.P., Bernier, P., Deloffre, R., Génot, P., Jaffrezo, M., Vachard, D. 1979. Essai de classification des Dasycladales en tribus. Bulletin Centres Recherche Exploration-Production Elf-Aquitaine, 3, 429–442.

Berchenko, O.I. 1981. Calcareous algae from Tournaisian deposits of Donbass. Akademiya Nauk Ukrainskoi SSR, Institut Geologichesnikh Nauk "Naukova Dumka", Kiev. (in Russian).

Berger, S., Kaever, M.J., 1992. Dasycladales: an illustrated monograph of a fascinating algal order. Georg Thieme, Stuttgart.

Bergeron, M., Mamet, B., 1992. *Loomisella petryki,* gen. nov., sp. nov., une algue udotCacCe du Caronifère, Formation de Mount Head, Alberta. Can. J. Earth Sci. 29, 195–199.

Blanco-Ferrera, S., Cózar, P., Sanz-López, J., 2021. Development of a Mississippian–Lower Pennsylvanian isolated carbonate platform within the basinal griotte facies of the Cantabrian Mountains, NW Spain. Facies 67, 21 https://doi.org/10.1007/s10347-021-00629-w

Bishop J.W., Montañez, I.P., Gulbranson, E.L., Brenckle P.L., 2009. The onset of mid-Carboniferous glacio-eustasy: sedimentologic and diagenetic constraints, Arrow Canyon,

Nevada. Palaeogeogr. Palaeoclimatol. Palaeoecol. 276, 217–243. https://doi.org/10.1016/j.palaeo.2009.02.019

Bitter, P.H. von, Giles, P.S., Utting, J., 2007. Biostratigraphic correlation of major cycles in the Windsor and Codroy groups of Atlantic Canada with the Mississippian Stages of Britain and Ireland, in: Wong, Th.E. (Ed.), Proceedings of the XVth International Congress on Carboniferous and Permian Stratigraphy, Utrecht, the Netherlands, 10-16 August 2003: Amsterdam, Royal Netherlands Academy of Arts and Sciences, pp. 513–534.

Bogush, O.I., Ivanova, R.M., Luchinina, V.A., 1990. Calcareous algae from the late Famennian and Early Carboniferous of Urals and Siberia. Akademiya Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofiziki, 745, 1–160 (in Russian).

Bornemann, J.G., 1886. Die Versteinerungen des Cambrischen Schichtensystems der Insel Sardinien. Acad Caes Leopold-Carol N Acta, 51, 1–147

Brand, U., Brenckle, P., 2001. Chemostratigraphy of the Mid-Carboniferous boundary global stratotype section and point (GSSP), Bird Spring Formation, Arrow Canyon, Nevada, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 165 (3-4), 321–347. https://doi.org/10.1016/S0031-0182(00)00169-3

Brooke, C., Riding, R., 1998. Ordovician and Silurian coralline red algae. Lethaia 31, 185–195.

Brooke, C., Riding, R., 2000. *Graticula* and its derivatives, replacement name for the alga *Craticula* Brooke and Riding non Grunow. Lethaia 33, 82.

Bucur, I., 1999, Stratigraphic significance of some skeletal algae (Dasycladales, Caulerpales) of the Phanerozoic, in: Farinacci, A., Lord, A.R. (Eds.), Depositional Episodes and Bioevents. Palaeopelagos Sp. Publ. 2, pp. 53–104.

Chuvashov, B.I., Anfimov, A.L. 2007. On the taxonomy of the Paleozoic red algae of the family Ungdarellaceae. Paleontol. J. 41, 95–102.

Chuvashov, B.I., Luchinina, V.A., Shuysky, V.P., Shaikin, I.M., Berchenko, O.I., Ishchenko, A.A., Saltovskaya, V.D., Shirshova, D.I., 1987. Fossil calcareous algae, morphology, systematics, methods of study. Akademiya Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofiziki 674, 5–224 (in Russian).

Corrochano, D., Vachard, D., Armenteros, L., 2013. New insights on the red alga *Archaeolithophyllum* and its preservation from the Pennsylvanian of the Cantabrian Zone (NW Spain). Facies 59, 949–967. https://doi.org/10.1007/s10347-012-0347-8

Cózar, P., 2004. Foraminiferal and algal evidence for the recognition of the Asbian/Brigatian boundary in the Guadiato area (Mississippian, southwestern Spain). Rev. Esp. Micropaleont. 36, 367–388.

Cózar, P., 2005. Early Serpukhovian (late Mississippian) microflora from the Guadiato Area (SW Spain). Geol. J. 40 (4), 405–424. https://doi.org/10.1002/gj.1014

Cózar, P., Rodríguez, S., 1999a. Propuesta de nueva nomenclatura para las unidades del Carbonífero Inferior del sector Norte del Área del Guadiato (Córdoba). Bol. Geol. Min. 110, 237–254.

Cózar, P., Rodríguez, S., 1999b. Evolución Sedimentaria del Carbonífero Inferior del Área del Guadiato (España). Bol. Geol. Min. 110(6), 603–626.

Cózar, P., Rodríguez, S., 2004. Pendleian (early Serpukhovian) marine carbonates from SW Spain: sedimentology, biostratigraphy and depositional model. Geol. J. 39, 25–47. https://doi.org/10.1002/gj.942

Cózar, P., Somerville, I.D., 2004. New algal and foraminiferal assemblages and evidence for recognition of the Asbian–Brigantian boundary in northern England. Proc. York. Geol. Soc. 55, 43–65. https://doi.org/10.1144/pygs.55.1.43

Cózar, P., Somerville, I.D., 2005a. Significance of calcareous algae for the recognition of the Asbian and Brigantian Stages (Mississippian) in Ireland and Great Britain. Rev. Esp. Micropaleontol. 37, 71–94.

Cózar, P., Somerville, I.D., 2005b. Stratigraphy of upper Viséan carbonate platform rocks in the Carlow area, southeast Ireland. Geol. J. 40, 43–65. https://doi.org/10.1002/gj.984

Cózar, P., Somerville, I.D., 2005c. Late Viséan calcareous algal assemblages in south-eastern Ireland. Neues Jahrb. fur Geol. Palaontol. Mon., 2005(2), 95–117. https://doi.org/10.1127/njgpm/2005/2005/95

Cózar, P., Somerville, I.D., 2005d. A new species of Mississippian Diploporaceae alga (Chlorophyta, dasycladales) in southeastern Ireland. Rev. Esp. Micropaleontol. 37, 419–430.

Cózar, P., Somerville, I.D., 2014. Latest Viséan-Early Namurian (Carboniferous) foraminifers from Britain: implications for biostratigraphic and glacioeustatic correlations. Newsl. Stratigr. 47, 355–367. https://doi.org/10.1127/nos/2014/0052

Cózar, P., Somerville I.D., 2016. Problems correlating the late Brigantian-Arnsbergian Western Europen substages within northern England. Geol. J. 51, 817–840. https://doi.org/10.1002/gj.2700

Cózar, P., Somerville, I.D., 2021a. Serpukhovian in Britain: use of foraminiferal assemblages for dating and correlating. J. Geol. Soc., London 178, jgs2020-170. https://doi.org/10.1144/jgs2020-170

Cózar, P., Somerville, I.D. 2021b. Irish Serpukhovian revisited. Geol. J. 56, 1403–1423. https://doi.org/10.1002/gj.3981

Cózar, P., Vachard, D. 2003. *Neoprincipia* nov. gen., a new Mississippian Red alga, and remarks on the Archaeolithophyllaceae (Rhodophyta). Geobios 36, 505–517. https://doi.org/10.1016/S0016-6995(03)00060-3

Cózar, P. and Vachard, D. 2004. A new Mississippian dasyclad alga (Chlorophyta) from SW Spain; implications for the reproductive evolution of the dasyclads during the Late Paleozoic. Eclogae geol. Helv. 97, 175–181. https://doi.org/10.1007/s00015-004-1127-4

Cózar, P., Vachard, D. 2005. Comparaison d'"*Hortonella* (algue rouge du Carbonifère) avec une structure algaire problématique (racine?): *Lysvaella.* Rev. Paléobiol. 24, 243–249.

Cózar, P., Vachard, D. 2006. A new Mississippian red alga from southwestern Spain. Geobios, 40, 849–860. https://doi.org/10.1016/j.geobios.2005.09.002

Cózar, P., Somerville, I.D., Rodríguez, S., Mas, R., Medina-Varea, P., 2006a. Development of a late Viséan (Mississippian) mixed carbonate/siliciclastic platform in the Guadalmellato Valley (southwestern Spain). Sed. Geol. 183, 269–295. https://doi.org/10.1016/j.sedgeo.2005.09.018

Cózar, P., Somerville, I.D., Mitchell, W.I, Medina-Varea, P., 2006b. Correlation of Mississippian (Upper Viséan) foraminiferan, conodont, miospore and ammonoid zonal schemes, and correlation with the Asbian-Brigantian boundary in northwest Ireland. Geol. J. 41, 221–241. https://doi.org/10.1002/gj.1036

Cózar, P., Somerville, I.D., Rodríguez, S., Medina-Varea, P., 2007. New genera of late Viséan metaspondil dasycladales from the Fuenteobejuna section (Mississippian of the Guadiato Valley, southwestern Spain). Neues Jahrb. fur Geol. Palaontol., Abh. 246/1, 97–109.

Cózar, P., Vachard, D., Somerville, I.D., Berkhli, M., Medina-Varea, P., Rodríguez, S., Said, I. 2008. Late Viséan Serpukhovian foraminiferans and calcareous algae from the Adarouch region (central Morocco), North Africa. Geol. J. 43, 463–485. https://doi.org/10.1002/gj.1119

Cózar, P., Vachard, D., Somerville, I.D., Pille, L. & Medina-Varea, P. 2009. Revision and new species of the Late Palaeozoic dasyclad algae *Windsoporella* and *Eovelebitella*. Palaeontographica B 282, 39–67. https://doi.org/10.1127/palb/282/2009/39

Cózar, P., Said, I., Somerville, I.D., Vachard, D., Medina-Varea, P., Rodríguez, S., Berkhli, M. 2011. Potential foraminiferal markers for the Visean–Serpukhovian and Serpukhovian–Bashkirian boundaries— A case-study from Central Morocco. J. Paleontol. 85, 1105–1127. https://doi.org/10.1666/10-158.1

Cózar, P., García-Frank, A., Somerville, I.D., Vachard, D., Rodríguez, S., Medina-Varea, P., Said, I., 2014a. Lithofacies and biostratigraphical correlation of marine Carboniferous rocks in the Tindouf Basin, NW Africa. Facies 60, 941–962. https://doi.org/10.1007/s10347-014-0409-1

Cózar, P., Medina-Varea, P., Somerville, I.D., Vachard, D., Rodríguez, S., Said, I., 2014b. Foraminifers and conodonts from the late Viséan to early Bashkirian succession in the Saharan Tindouf Basin (southern Morocco): biostratigraphic refinements and implications for correlations in the western Palaeotethys. Geol. J. 49, 271–302. https://doi.org/10.1002/gj.2519

Cózar P., Vachard D, Somerville ID, Medina-Varea P, Rodríguez S, Said I. 2014c. The Tindouf Basin, a marine refuge during the Serpukhovian (Carboniferous) mass extinction in the northwestern Gondwana platform. Palaeogeogr. Palaeoclimatol. Palaeoecol. 394, 12–28. https://doi.org/10.1016/j.palaeo.2013.11.023

Cózar, P., Izart, A., Vachard, D., Coronado, I., 2017. A mid-Tournaisian-late Viséan carbonate ramp reconstructed from nappes and olistolites in the southern Montagne Noire (France). Sed. Geol. 358, 148–175. https://doi.org/10.1016/j.sedgeo.2017.07.007

Cózar, P., Somerville, I. D., Blanco-Ferrera, S., Sanz-López, J., 2018. Palaeobiogeographic context in the development of shallow-water late Viséan-early Bashkirian benthic foraminifers and calcareous algae in the Cantabrian Mountains (Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 511, 620–638. https://doi.org/10.1016/j.palaeo.2018.09.031

Cózar, P., Izart, A., Somerville, I.D., Aretz, M., Coronado, I., Vachard, D., 2019 Environmental controls on the development of Mississippian microbial carbonate mounds and platform limestones in southern Montagne Noire (France). Sedimentology 66, 2392–2424, http://dx.doi.org/10.1111/sed.12594

Cózar, P., Vachard, D., Somerville, I.D., Izart, A., Coronado, I., 2020. The lower-middle Viséan boundary interval in the Palaeotethys: refinements for the foraminiferal zonal schemes. Geol. Mag. 157, 513–526, https://doi.org/10.1017/S001675681900102X

Cózar, P., Coronado, I., García-Frank, A., Izart, A., Somerville, I.D., Vachard, D. 2022a. Alternating microbial mounds and ooidal shoals as a response to tectonic, eustatic and ecological conditions (late Viséan, Morocco). Sed. Geol. 431, 106109, https://doi.org/10.1016/j.sedgeo.2022.106109

Cózar, P., Somerville, I.D., Hounslow, M.W., 2022b. Foraminifers in the Holkerian Stratotype, regional substage in Britain: key taxa for the Viséan subdivision. Newsl. Stratigr. 55, 159–172, https://doi.org/10.1127/nos/2021/0674

Cózar, P., Somerville, I.D., Hounslow, M.W., Kamenikova, T., 2022c. A late Asbian (Mississippian) stratotype for England: Trowbarrow Quarry, S. Cumbria, UK. Pap. Palaeontol. e1451, https://doi.org/10.1002/spp2.1451

Cózar, P., Somerville, I.D., Hounslow, M.W., Coronado, I., 2022d. Far-field correlation of palaeokarstic surfaces in Mississippian successions using high-frequency foraminiferal diversity trends. Palaeogeogr. Palaeoclimatol. Palaeoecol. 601, 111088, https://doi.org/10.1016/j.palaeo.2022.111088

Cózar, P., Somerville, I.D., Rodríguez, S., El Houicha, M., Vachard, D., García-Frank, A., Coronado, I., Izart, A., Said, I. 2023a. Contrasting reef patterns during the evolution of the Carboniferous Azrou-Khenifra Basin (Moroccan Meseta). Facies 69, https://doi.org/10.1007/s10347-022-00657-0

Cózar, P., Somerville, I.D., Hounslow, M.W., 2023b. A potential global chronostratigraphic boundary for the subdivision of the Viséan. Newsl. Stratigr. 56, 357–376, https://doi.org/10.1127/nos/2023/0746

Cózar, P., Vachard, D., Somerville, I.D., 2023b. Foraminifers and calcareous algae in Brigantian rocks of Morocco as guides for the recognition of the Viséan-Serpukhovian boundary interval. C.R. Palevol. 22 (12), 207-232, https://doi.org/10.5852/cr-palevol2023v22a12

Della Porta, G., Kenter, J.A.M., Bahamonde, J.R., 2002. Microfacies and paleoenvironment of *Donezella* accumulations across an upper Carboniferous high-rising carbonate platform (Asturias, NW Spain). Facies 46, 149–168. https://doi.org/10.1007/BF02668079

Deloffre, R., 1988. Nouvelle taxonomie des algues dasycladales. Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine 12, 165–217.

Derville, H., 1931. Les Marbres du Calcaire Carbonifère en Bas-Boulonnais. Imprimerie O. Boehm, Strasbourg.

Elliott, G.F., 1988. A new alga from the Carboniferous Frosterley Marble of northern England. Palaeontology 31, 741–745.

Engel, W., Feist, R., Franke, W., 1981. Le Carbonifère anté-Stéphanien de la Montagne Noire: rapports entre mise en place des nappes et sédimentation. Bull. Bur. Rech. Géol. Min. (BRGM) section 1, 4, 341–389.

Eros, J.M., Montañez, I.P., Osleger, D.A., Davydov, V.I., Nemyrovska, T.I., Poletaev, V.I., Zhykalyak, M.V., 2012. Sequence stratigraphy and onlap history of the Donets Basin, Ukraine: Insight into Carboniferous icehouse dynamics. Palaeogeogr. Palaeoclimatol. Palaeoecol. 313-314, 1–25. https://doi.org/10.1016/j.palaeo.2011.08.019

Garwood, E.J., 1914. Some new rock-building organisms from the Lower Carboniferous beds of Westmorland. Geol. Mag. 51, 265–271.

Golubtsov, V.K., 1961. *Kulikia*, new genus of calcareous algae in the Viséan stage. In: Paleontologiya i stratigrafiya BSSR (Paleontology and stratigraphy of the SSR of Bielorussia). Minsk Izdateltsvo, Akademiya Nauk Beloruss SSR 3, 348–353 (in Russian).

Granier, B. 2012. The contribution of calcareous green algae to the production of limestones: a review. Geodiversitas 34, 35–60. https://doi.org/10.5252/g2012n1a3

Granier, B., Grgasovic, T. 2000. Les algues dasycladales du Permien et du Trias. Nouvelle tentative d'inventaire bibliograhique, géographique et stratigraphique. Geol. Croatica 53 (1), 1–197.

Groves, J.R., Wang, Y., 2009. Foraminiferal diversification during the late Paleozoic ice age. Paleobiology 35, 367–392.

Hance, L., 1983. Micropaléontologie du Moliniacien belge, trois nouveaux genres. *Halenopora* (Chlorophyceae), *Aranea* (Rhodophyceae) et *Globochernella* (Foraminiferida, Tournayellidae). Ann. Soc. Géol. Belgique 106, 111–119.

Horbury, A.D., 1987. The sedimentology of the Urswick Limestone in south Cumbria and north Lancashire. Ph.D. thesis, University of Manchester.

Hounslow, M.W., Somerville, I.D., Cózar, P., Chew, D., Drakou, F., 2022. A reassessment of Arundian-Holkerian carbonates in South Cumbria, UK. Proc. Geol. Assoc. 133, 227–249. https://doi.org/10.1016/j.pgeola.2022.04.005

Ivanova, R.M., 1988. Calcareous algae of the Viséan stage of the Urals, in: Chuvashov, B.I., Puchkov, B.N. (Eds.), Biostratigraphy and lithology of the Late Palaeozoic of the Urals. Akademiya Nauk SSSR, Uralskoe Otdelnye, Sbornik Nauchnyk Trudov, pp. 4–19 pp. (in Russian).

Ivanova, R.M., 2013. Carboniferous calcareous algae of the Urals. Ural Division RAS, Ekateringurg.

Johnson, E.W., Soper, N.J., Burgess, I.C., 2001. Geology of the country around Ulverston. Memoir of the British Geological Survey, Sheet 48 (England and Wales). HMSO, London

Johnson, G. A. L., Nudds, J. R. 1996. Carboniferous biostratigraphy of the Rookhope Borehole, Co. Durham. Trans. Roy. Soc. Edinburgh, Earth Sci. 86, 181–226.

Johnson, J.H., 1956. *Archaeolithophyllum*, a new genus of Paleozoic coralline algae. J. Paleontol. 30, 53–55.

Johnson, J.H., 1960. Paleozoic Solenoporaceae and related red algae. Quarterly Colorado School Mines 55(3), 1–77.

Johnson, J. H., 1966. New Mississippian algae from Alberta. J. Paleontol. 40, 1385–1387.

Johnson, J.H., Konishi, K., 1956. Mississippian algae from the Western Canada Basin and Montana, in: Johnson, J.H., Konishi, K. (Eds.), Studies of Mississippian algae. Quarterly of the Colorado School of Mines 51 (4), 85–107.

Kochansky-Devidé, V., Herak, M., 1960. On the Carboniferous and Permian Dasycladaceae of Yugoslavia. Geoloski Vjesnik 13, 65–94.

Konishi, K., 1956. *Anatolipora*, a new Dasycladacean genus, and its algal associates from the Lower Carboniferous of Japan, in: Johnson, J.H., Konishi, K. (Eds.), Studies of Mississippian algae. Quarterly of the Colorado School of Mines 51 (4), 109–127.

Kulagina, E.I., Gibshman, N.B. Nikolaeva, S.V., 2008. Foraminifer-based correlation of the Chesterian Stage in the Mississippian type region, Illinois, USA with the Serpukhovian Stage of Russia. Newsl. Carbonif. Stratigr. 26, 14–18.

Kulik, E.L., 1973. Cyanophyta, in: Einor, O.L. (Ed.), Stratigraphy and fauna from the Carboniferous of the Shartym River (southern Urals). Uralskoe Geologicheskoe Upravlenie, Kievskii Ordena Lenina Gosudarstvennyi Universitet, Izdatelskoe Obedisenie "Vishcha Shkola", pp. 39–48 (in Russian).

Lane, H.R., Brenckle, P.L., 2005. Type Mississippian subdivisions and biostratigraphic succession, in: Heckel, P.H. (ed.), Stratigraphy and Biostratigraphy of the Mississippian Subsystem (Carboniferous System) in its Type Region, the Mississippi Valley of Illinois, Missouri, and Iowa. Illinois State Geological Survey Guidebook, 34, pp. 76–105.

Lee, G.W., 1912. The British Carboniferous *Trepostomata*. Mem. Geol. Surv. Great Britain, Paleontology 1 (3), 135–195.

Lees, A., Miller, J., 1995. Waulsortian banks, in: Monty, C.L.V., Bosence, D.W.J., Bridges, P.H., Pratt, B.R. (Eds.), Carbonate mud-mounds: Their origin and evolution. International Association of Sedimentologists, Special Publication 23, pp. 191–271.

Lucas, S.G., Schneider, J.W., Nikolaeva, S., Wang, X., 2021. The Carboniferous chronostratigraphic scale: history, status and prospectus, in: Lucas, S.G., Schneider, J. W., Wang, X. and Nikolaeva, S. (Eds), The Carboniferous Time scale. Geological Society, London, Special Publications 512, pp. 1–19. https://doi.org/10.1144/SP512-2020-210

Luchinina, V.A., 2009. *Renalcis* and *Epiphyton* as different stages in the life cycle of calcareous algae. Paleontol. J. 43, 563–568.

Mamet, B., 1974. Sur deux dasycladacées carbonifères des cordillères nord-américaines. Rev. Micropaléont. 17, 38–44.

Mamet, B., 1986. Marine calcareous algae from the Devonian-Carboniferous transition beds. Ann. Soc. géol. Belgique,109, 61–64.

Mamet, B., 1991. Carboniferous calcareous algae, in: Riding, R. (Ed.), Calcareous algae and stromatolites. Springer-Verlag, Berlin-Heidelberg, pp. 370–451.

Mamet, B., 1996. Algues calcaires marines du Paléozoïque supérieur (Equateur, Bolivie). Ann. Soc. Géol. Belgique 117, 155–167.

Mamet, B., 1997. *Pseudokulikia*, a new Viséan green alga from Morocco. Rev. Micropaléont. 40, 331–338.

Mamet, B., 2002. Carboniferous marine algae, lower part of Akiyoshi Limestone Group, Japan, in: Hills, L.V., Henderson C.M., Bamber, E.W. (Eds.), Carboniferous and Permian of the World. Canadian Society of Petroleum Geologists, Memoir, 19, pp. 492–528.

Mamet B., Rudloff, B., 1972. Algues carbonifères de la partie septentrionale de l'Amérique du Nord. Rev. Micropaléont. 15, 75–114.

Mamet, B., Roux, A., 1975a. Dasycladales dévoniennes et carbonifères de la Téthys occidentale. Rev. Española Micropaleont. 7, 245–295.

Mamet, B., Roux, A., 1975b. Algues dévoniennes et carbonifères de la Téthys occidentale, Troisième partie. Rev. Micropaléont. 18, 134–187.

Mamet, B., Roux, A., 1977. Algues rouges dévoniennes et carbonifères de la Téthys occidentale, 4e partie. Rev. Micropaléont. 19, 215–266.

Mamet, B., Roux, A., 1978. Algues viséennes et namuriennes du Tennessee (Etats-Unis). Rev. Micropaléont. 21, 68–97.

Mamet, B., Roux, A., 1981. Note sur les Albertaporellinae (Dasycladaceae). Rev. Micropaléont. 23, 159–168.

Mamet, B., Roux, A., 1983. Algues dévono-carbonifères de l'Australie. Rev. Micropaléont. 26, 63–131.

Mamet, B., Roux, A., 1984. *Poncetellina* nomen novum (algue verte). Rev. Micropaléont. 27, 138.

Mamet, B.L., Roux, A., Nassichuk, W.W., 1987. Algues carbonifères et permiennes de l'Arctique canadien. Geol. Surv. Canada, Bull. 342, 1–143.

Maslov, V.P., 1956a. Fossil calcareous algae from USSR. Trudy Instituta Geologicheskikh Nauk, Akademiya Nauk SSSR 160, 1–301 (in Russian; French translation BRGM n° 3517).

Maslov, V.P., 1956b. New Carboniferous family of fossil red algae and two new Cyanophycean genera. Doklady Akademiya Nauk SSSR 107, 151–154 (in Russian; French translation CEDP 1381).

McLean, D., Owens, B., Bodman, D.J., McLean, F.D., 2018. Miospores from the Brigantian stratotype section at Janny Wood, Cumbria. Proc. York. Geol. Soc. 62, 89–100. https://doi.org/10.1144/pygs2017-00

Nicholson, H.A., Etheridge, R., 1878. A monograph of the Silurian fossils of the Girvan district, Ayrshire, with special reference to those contained in the "Gray Collection", I, 1. Blackwood, Edinburgh-London.

Pia, J. von, 1927. Thallophyta, in: Hirmer, M. (ed.), Handbuch der Paläobotanik. Band: Thallophyta, Bryophyta, Pteridophyta. Verlag R. Oldenburg, München-Berlin 1, pp. 31–136.

Pille, L., 2008. Foraminifères et algues calcaires du Mississippien supérieur (Viséen supérieur-Serpukhovien): rôles biostratigraphique, paléoécologique et paléogéographique aux échelles locale, régionale et mondiale. Lille, Université de Lille.

Pille, L., Vachard, D., 2011. Diploporaceae (calcareous Green algae dasycladales) from the late Visean (Mississippian) of Montagne Noire (southern France). Rev. Micropaléont. 54, 1–30. https://doi.org/10.1016/j.revmic.2009.02.001

Racz, L.G., 1965. Carboniferous calcareous algae and their associations in the San Emiliano and Lois-Ciguera Formations (Province of León, NW Spain). Leidse Geologische Mededelingen 31, 1–112.

Radoicic, R., 1959. Some problematic microfossils from the Dinarian Cretaceous. Bull. Serv. Géol. Géophys. Serbie 17, 87–92.

Riding, R., 1991. Calcified Cyanobacteria, in: Riding, R. (Ed.), Calcareous Algae and Stromatolites. Springer-Verlag, Berlin, pp. 55–87.

Richards, B.C., Task Group 2017. Report of the Task Group to establish a GSSP close to the existing Viséan-Serpukhovian boundary. Newsl. Carbonif. Stratigr. 33, 11–16.

Riding, R., 2004. *Solenopora* is a chaetetid sponge, not an alga. Palaeontology 47, 117-122. https://doi.org/10.1111/j.0031-0239.2004.00351.x

Riding, R., 2011. Calcified cyanobacteria, in: Reitner J., Hiel, V. (Eds), Encyclopedia of Geobiology. Springer Science+Business Media B.V. pp. 211–223.

Rose, W.C.C., Dunham, K.C., 1977. Geology and Hematite deposits of South Cumbria. Economic Memoir of the Geological Survey of Great Britain, Sheets 58 and part of 48. HMSO, London.

Rothpletz, A., 1913. Uber die Kalkalgen, Spongiostromen und einige andere Fossilien aus dem Obersilur Gotlands. Sver. Geol. Undersokning 10, 1–54

Roux, A., 1979. Revision du genre *Epimastopora* "Pia. 1922" (Dasycladaceae). Bull. Cent. Rech. Explor.-Product. Elf-Aquitaine 3, 803–810.

Rygel, M.C., Fielding, C.R., Frank, T.D., Birgenheier, L.P., 2008. The magnitude of late Paleozoic glacioeustatic fluctuations: a synthesis. J. Sediment. Res. 78, 500–511. https://doi.org/10.2110/jsr.2008.058

Sanz-López, J., Cózar, P., Blanco-Ferrera, S., 2018. Discovery of a Mississippian-early Bashkirian carbonate platform coeval with condensed cephalopod limestone sedimentation in NW Spain. Geol. J. 53, 2532–2557. https://doi.org/10.1002/gj.3087

Sevastopulo, G.D., Barham, M., 2014. Correlation of the base of the Serpukhovian Stage (Mississippian) in NW Europe. Geol. Mag. 151, 244–253. https://doi.org/10.1017/S0016756813000630

Shuysky, V.P., 1999. Problems of systematics and history of the phylum of the fossil red algae), in: Chuvashov, B.I. (Ed.), Materialy po stratigrafii i paleontologii Urala. Rossiiskaya Akademiya Nauk, Uralskoe Otdeleni, 2, pp. 248–260 (in Russian).

Skompski, S., 1981. Morphology and systematic position of the Carboniferous algal genus *Calcifolium*. Neues Jahrb. Geol. Paläontol Mon. 3, 165–179.

Skompski, S., 1987. The dasycladacean nature of Late Paleozoic palaeoberesellid algae. Acta Geol. Pol. 37(1/2), 21–31.

Skompski, S., Alekseev, A., Meischner, D., Nemirovskaya, T., Perret, M.-F., Varker, W.J., 1995. Conodont distribution across the Viséan/Namurian boundary. Cour. Forsch.-inst. Senckenb. 188, 177–209.

Sollas, W.J., 1921. On *Saccammina carteri* Brady, and the minute structure of the foraminiferal shell. Quart. J. Geol. Soc. London 77, 193–211.

Somerville, I D., Cózar, P., 2005. Late Asbian to Brigantian (Mississippian) foraminifera from south-east Ireland: Comparison with Northern England assemblages. J. Micropalaeontol. 24, 131–424. https://doi.org/10.1144/jm.24.2.131

Somerville, I.D., Cózar, P., Aretz, M., Herbig, H.-G., Mitchell, W.I., Medina-Varea, P., 2009. Carbonate facies and biostromal distribution in a tectonically controlled platform in northwest Ireland during the late Viséan (Mississippian). Proc. York. Geol. Soc. 57, 165–192. https://doi.org/10.1144/pygs.57.3-4.165

Stephenson, M.H., Angiolini, L., Cózar, P., Jadoul, F., Leng, M.J., Millward, D., Chenery, S., 2010. Northern England Serpukhovian (early Namurian) farfield responses to southern hemisphere glaciation. J. Geol. Soc., London, 167, 1171–1184. https://doi.org/10.1144/0016-76492010-048

Stolley, E., 1893. Üeber silurische Siphoneen. Neues Jahrb. fur Geol. Palaontol., Abh. 2, 135–146.

Termier, G., Termier, H., Vachard, D., 1977. Etude comparative de quelques Ischyrosponges. Géol. Méditerranéenne 4, 139–180.

Vachard, D., 1974. Sur les dasycladacées métaspondyles "vestibulaires", à propos d'un de leurs représentants viséens : *Eovelebitella occitanica* n. gen n. sp. CR Acad. Sci. Paris 279 (25), 1855–1858.

Vachard, D., 1993. Algues, pseudo-algues et microfaciès carbonatés du Dévonien du domaine Ligérien (Massif Armoricain, France). Paleontographica B 229, 53–113.

Vachard, D., Aretz, M., 2004. Biostratigraphical precisions on the Early Serpukhovian (Late Mississippian), by means of a carbonate algal microflora (cyanobacteria, algae and pseudo-algae) from La Serre (Montagne Noire, France). Geobios 37, 643–666. https://doi.org/10.1016/j.geobios.2003.05.008

Vachard, D., Beckary, S., 1991. Algues et foraminifères bachkiriens des coal balls de la Mine Rosario (Truebano, Léon, Espagne)*.* Rev.Paléobiol. 10, 315–357.

Vachard, D., Cózar, P., 2003. *Saccamminopsis*, Mississippian carbonate microproblematicum, a possible udoteacean algal gametophyte (Chlorophyta, Siphonales). Geobios, 36, 421–436.

Vachard, D., Cózar, P., 2010, An attempt of classification of the Palaeozoic incertae sedis Algospongia. Rev. Esp. Micropaleontol 42, 129–241.

Vachard, D., Hauser, M., Martini, R., Zaninetii, L., Matters, A., Peters, T., 2001. New algae and problematica of algal affinity from the Pennian of the Aseelah Unit of the Batain Plain, (East a man). Geobios 34, 375–404.

Vachard, D., Cózar, P., Aret, M., Izart, A., 2016a. Late Viséan-early Serpukhovian cyanobacteria and algae from the Montagne Noire (France); taxonomy and biostratigraphy. Bull. Geosci. 91, 433–466. https://doi.org/10.3140/bull.geosci.1613

Vachard, D., Cózar, P., Aret, M., Izart, A., 2016b. Late Viséan-early Serpukhovian foraminifers in the Montagne Noire (France): Biostratigraphic revision and correlation with the Russian substages. Geobios 49, 469–498. https://doi.org/10.1016/j.geobios.2016.09.002

Vachard, D., Izart, A., Cózar, P., 2017. Mississippian (middle Tournaisian-late Serpukhovian) lithostratigraphic and tectonosedimentary units of the southeastern Montagne Noire (Hérault, France). Géol. France, 1, 47–88.

Vologdin, A.G., 1932. Arkheotsiaty Sibiri (Archaeocyathids of Siberia) vol. 2: Fauna from the Cambrian limestones of Altai. Moscow-Leningrad, Gosudarstvennoe Naukno-Teknicheskoe Geologo-Razvedocne Izdateltsvo (in Russian).

Waters, C.N., Burgess, I.C., Cózar, P., Holliday, D.W., Somerville, I.D., 2021. Reappraisal of Arundian–Asbian successions of the Great Scar Limestone Group across northern England. Proc. York. Geol. Soc. 63, pygs2021-002. https://doi.org/10.1144/pygs2021-002Wethered, E., 1886. On the structure and organisms of the Lower limestone Shales, Carboniferous Limestone and Upper Limestones of the Forest of Dean. Geol. Mag. 23, 529–534.
Wood, A., 1940. Two new calcareous algae of the family Dasycladaceae from the Carboniferous Limestone. Proc. Liverpool Geol. Soc. 18, 14–18.

Wood, A., 1941. The Lower Carboniferous calcareous algae *Mitcheldeania* Wethered and *Garwoodia* gen. nov. Proc. Geol. Assoc. 52, 216–226.

Wray, J.L., 1977. Calcareous algae. Development in Palaeontology and Stratigraphy 4. Elsevier, Amsterdam.