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Diamond Anniversary Paper: Celebrating 60 years of Palaeo3

Paleobiogeography of early to middle Paleozoic phytoplankton: A review and synthesis ☆

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ABSTRACT

Phytoplankton form the foundation of marine food webs, and their fossil record provides key insights into ecosystem and climate evolution. We review the biogeography of Paleozoic phytoplankton based on data from the literature and new multivariate analyses of acritarch data that are georeferenced to paleolatitude and paleolongitude. Results show that acritarchs are rather cosmopolitan with wide geographic ranges, their distribution often differentiated into two broad latitudinal realms: a northern warm-water and a southern cold-water assemblage. Provincialism was most pronounced during the Ordovician and Devonian. The Ordovician provincial structure collapsed during the Hirnantian glaciation, resulting in a short-lived cosmopolitan phase that persisted into the early Silurian. Biogeographic differentiation re-emerged in the middle Silurian and was reorganized in the Devonian as plate movements closed ocean basins and enabled new intercontinental exchanges. Overall, climate change and plate tectonics appear to be the primary drivers of phytoplankton provincialism.

1. Introduction

Phytoplankton form the base of modern marine food webs and play a fundamental role in global biogeochemical cycles, including primary production and carbon sequestration (Falkowski et al., 2004; Boyce and Worm, 2015). Their distribution is closely linked to climate, particularly sea-surface temperature, nutrient regimes, and ocean circulation, and they respond sensitively to environmental change (Benedetti et al., 2021). Understanding phytoplankton diversity and biogeography in deep time therefore provides crucial insights into the co-evolution of life, oceans, climate; and possibly also plate tectonic movements and processes.

In the Paleozoic Era (539–252 Ma), phytoplankton were markedly different from today. Many of the groups that dominate modern oceans—dinoflagellates, coccolithophores, and diatoms—had not yet diversified (Knoll, 1992; Katz et al., 2004). Instead, the primary record of Paleozoic planktonic primary producers is provided by acritarchs, a polyphyletic group of organic-walled microfossils of uncertain affinity (Evitt, 1963). Acritarchs are generally interpreted as resting cysts of eukaryotic phytoplankton (Martin, 1993), although they may also include cysts of other protists, spores of other organisms or other biological entities. Despite their uncertain biological placement, they are widely regarded as fossil proxies for Paleozoic phytoplankton communities (Strother, 2008).

Alongside acritarchs, prasinophyte algae also contributed significantly to the Paleozoic phytoplankton (Molyneux et al., 1996). These green algae are known mainly from their resistant phycomata, such as *Tasmanites, Leiosphaeridia* (*pro parte*) and *Cymatiosphaera* (Guy-Ohlson, 1996). Because their morphology overlaps with acritarch forms and they are often recovered in the same palynological residues, prasinophyte cysts are frequently included in the acritarch category in Paleozoic studies. Prasinophytes appear to have been especially abundant during times of environmental stress (e.g. Eppley et al., 1969; Prauss, 1996, 2000) surviving the so-called Late Paleozoic “phytoplankton blackout”, suggesting ecological opportunism and resilience (Riegel, 2008). Their inclusion expands the scope of Paleozoic phytoplankton biogeography

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beyond acritarchs *sensu stricto*, but the two groups are commonly considered together in paleoecological reconstructions.

Acritarchs diversified dramatically during the late Cambrian and again during the Great Ordovician Biodiversification Event (GOBE), making them excellent tools for biostratigraphy and paleoenvironmental reconstructions (Strother, 1996; Molyneux et al., 1996; Kroeck et al., 2022; Shan et al., 2022). Their abundance, widespread distribution, and morphological diversity allow for both regional and global comparisons, and thus they have long been used to infer biogeographic patterns in early Paleozoic oceans. Key works synthesizing phytoplankton biogeography include Colbath (1990) for the middle Paleozoic, Le Hérissé et al. (1997) for the late Silurian and Devonian, Servais et al. (2003) for the Ordovician and Molyneux et al. (2013) for the early to middle Paleozoic.

Over the past half-century, interpretations of acritarch biogeography have evolved through several phases. Early studies emphasized qualitative comparisons and index taxa, leading to the recognition of distinct "provinces" such as the Baltic and Mediterranean (later Perigondwana) Provinces (Vavrdová, 1974; Li, 1989; Albani, 1989) in the Ordovician. Subsequent quantitative approaches, including cluster and ordination analyses, provided a more objective framework (e.g. Colbath, 1990; Le Hérissé and Gourvennec, 1995; Le Hérissé et al., 1997; Shen et al., 2019, 2025). More recently, the development of large-scale databases and georeferenced analyses have enabled spatially explicit assessment of phytoplankton distributions (e.g. Zacaï et al., 2021).

Despite these advances, major uncertainties remain. The degree to which observed patterns reflect true biogeographic differentiation *versus* facies control is debated (e.g. Colbath, 1990; Le Hérissé and Gourvennec, 1995; Le Hérissé et al., 1997). The timing and drivers of provincialism—whether primarily climatic, paleogeographic, or ecological—are not fully resolved. Furthermore, the Late Paleozoic "phytoplankton blackout" (Riegel, 1996, 2008) leaves the final 100 million years of the era poorly understood.

This work follows previous comprehensive reviews by Servais et al. (2003) for the Ordovician, Mullins and Servais (2008) for the Carboniferous, Lei et al. (2013) for the Permian and Molyneux et al. (2013) for the early to middle Paleozoic. In this review, we synthesize the state of knowledge on Paleozoic acritarch and prasinophyte biogeography and reassess it using new multivariate analyses of a georeferenced global database. Our objectives are to (1) review previous interpretations of Paleozoic acritarch biogeography, (2) test the robustness of previously proposed provinces using multivariate methods, and (3) reassess biogeographic patterns in the light of both.

2. Historical perspectives on Paleozoic acritarch biogeography

Research on the biogeography of Paleozoic acritarchs spans more than half a century, evolving from qualitative comparisons of key taxa to multivariate analyses and, more recently, to global, georeferenced database approaches. This progression reflects both the accumulation of fossil data and advances in analytical methods. Three main phases can be recognized: (1) early qualitative studies (1960s–1980s), (2) the application of quantitative and multivariate methods (1990s–2010s), and (3) the use of geospatial and database-driven approaches (2010s–present).

2.1. Early qualitative studies

The earliest attempts to recognize large-scale biogeographic patterns in Paleozoic phytoplankton were qualitative and relied on the distribution of selected index taxa. Following Evitt's (1963) definition of the acritarchs as a distinct microfossil group, the widespread acceptance of plate tectonics by the late 1960s (Dietz, 1977) provided a new framework for paleobiogeographic studies. Within this context, Cramer (1968, 1969, 1970, Cramer and Díez 1972a,b, 1974a,b, 1979) and Vavrdová (1974) were the most influential early contributors to Paleozoic phytoplankton biogeography.

Cramer (1968) and Cramer and Diez (1972a,b, 1974a,b) were the first to suggest a paleolatitudinal control on phytoplankton distribution. They identified six acritarch "biofacies" in the late Llandovery–Wenlock, which they interpreted as coinciding with paleoisotherms: the *Gloeocapsomorpha prisca* facies, *Deunffia eisenackii* facies, *Domasia* facies, *Neoveryhachium carminae* facies (subdivided into Iberian, Transitional, and Brazilian–Libyan realms), and the *Pulvinosphaeridium–Estiastra* facies. Cramer and Diez (1972b, 1974a, 1977) also distinguished two major Ordovician provinces: a cold African (also known as the *Coryphidium bohemicum* province) and a warm American Palynological Unit. However, these interpretations were based on outdated tectonic models. When their data were later replotted within more accurate paleogeographic frameworks (Colbath, 1990; Le Hérissé and Gourvennec, 1995), the Silurian "biofacies" did not coincide consistently with paleolatitudes and are now considered more likely to reflect local environmental controls rather than true latitudinal zonation.

Nautiyal (1976, 1977) used the Silurian example of Cramer (1968, 1970) and Cramer and Diez (1972a), including use of the same paleogeographical model, to generate "biofacies" belts for the Early to Late Devonian. The four "biofacies" belts are the *Cymatiosphaera/ Multiplicisphaeridium* (I), *Polyedryxium* (II), *Veliferites/Pterospermopsis* (III) and *Maranhites/Navifusa* (IV) belts. Belt I was located at low paleolatitudes and corresponds to warm climate conditions, Belt II to warmer to intermediate climate conditions, while Belt III and IV were placed in higher paleolatitudes with cooler conditions. Similar to the 'Cramer' model, later analysis by Colbath (1990) using a different plate reconstruction disproved Nautiyal's biofacies belts.

Vavrdová (1974) made a major contribution to early phytoplankton biogeography by proposing distinct Ordovician acritarch provinces: the Baltic and the Mediterranean Provinces. Initially, Vavrdová (1974) distinguished the two provinces by the prevalence of acanthomorphs in the former and the occurrence of diacromorphs in the latter, but representatives of both acritarch subgroups were found subsequently in both provinces by Vavrdová herself (Molyneux et al., 2013). Studies by Martin (1982) and Li (1989) extended the area of the Mediterranean Province to Avalonia and other parts of Gondwana such as South America and South China; Albani (1989) then renamed the Mediterranean Province as the Perigondwana Province to reflect its geographic distribution. Li (1989) proposed *Arbusculidium*, *Coryphidium* and *Striatotheca* as index taxa of the then-Mediterranean province, to which Albani (1989) added the occurrence of *Acanthodiacrodium* and *Dasydiacrodium* as diagnostic of the Perigondwana Province (replacing the original criteria of Vavrdová, 1974). Playford et al. (1995) split Perigondwana into three subprovinces: the Mediterranean (with the original extent of Vavrdová, 1974, including Belgium, France, Spain, North Africa, southern Germany, central Bohemia and Bulgaria), the South America, and the South China subprovinces. Baltica on the other hand is more problematic; proposed index taxa such as species of *Peteinosphaeridium* and *Liliosphaeridium* (Playford et al., 1995; Tongiorgi and Di Milia, 1999) exhibit a large amount of within-species morphological variation with wide overlaps between the species as they were defined. The distribution of morphotypes within this group could be due to local environmental factors rather than biogeographic controls (Li and Servais, 2002; Kroeck et al., 2021). Consequently, Baltica is noted for the lack of important Perigondwanan taxa (such as *Arbusculidium*, *Arkonia*, *Aureotesta*, *Dicrodiacrodium*, *Striatotheca*, and *Frankea*); Servais and Fatka (1997) used their presence/absence to delineate the Trans-European Suture Zone between Perigondwana and Baltica.

Although qualitative approaches remain widely used because of their relative simplicity — relying primarily on the identification of key taxa in samples — quantitative methods began to gain momentum in paleoecology and paleobiogeography during the 1970s, particularly following the publication of Reyment's (1971) influential book on quantitative paleoecology. However, their application to Paleozoic phytoplankton studies developed more slowly and only became established many years later.

2.2. Quantitative and multivariate approaches

Qualitative approaches are practical but can be challenging if key taxa are missing due to preservation or sampling biases. A possible approach is to calculate beta diversity between localities, and usually an additional step of applying multivariate approaches such as cluster analysis and ordination to extract biogeographic patterns.

Colbath (1990) was the first to apply multivariate methods and ecological similarity indices to Paleozoic acritarch biogeography. Using the Simpson similarity index on ten Frasnian localities spanning Australia, Ghana, the United States, Canada, France, Belgium, Germany, Algeria and Brazil, he identified clusters through weighted average linkage pair-group analysis. The results revealed a distinct grouping of Ghana, Brazil and Algeria, while Euramerican localities formed another large cluster together with the Canning Basin of Australia. In contrast, the Carnarvon Basin locality of Australia plotted separately from both Euramerica and the Canning Basin. These patterns supported Scotese's (1984) Famennian plate reconstruction model B, in which North Africa and Europe were separated by a broad seaway, rather than model A, where the two regions are juxtaposed (see Colbath, 1990, figs. 5, 6).

Le Hérissé and Gourvennec (1995) applied cluster analysis using Jaccard's coefficient to investigate late Llandovery and Wenlock acritarch biofacies along the eastern margin of North America. Their analysis, which also incorporated global comparisons, did not formally define bioprovinces but revealed clusters that generally aligned with geographically contiguous regions—for example, Jordan with Libya, the Carnic Alps with Bohemia, Gotland with Great Britain, Norway with Podolia, and a Laurentian cluster grouping all localities from eastern North America. These close associations were supported by relatively high coefficients of similarity (Le Hérissé and Gourvennec, 1995, figs. 6, 7). The study also highlighted several potential paleogeographic index taxa, including *Dilatisphaera williereae*, *Gracilisphaeridium*, *Dactylofusa maranhensis*, and *Tyrannus giganteus* (see Section 3.3.3).

Building on this work, Le Hérissé et al. (1997) extended the same approach to late Silurian–Early Devonian assemblages, comparing their biofacies clusters with the classical Malvinokaffric, Eastern American, and Old-World Realms of Boucot (1975, 1990), superimposed on the paleogeographic reconstructions of Scotese and McKerrow (1990). Their results showed that one Ludlovian–Pridoli cluster corresponded to the Malvinokaffric Realm (including Bolivia, Algeria, and Florida; Le Hérissé et al., 1997, figs. 2, 3), while in the Lochkovian a large Gondwanan cluster encompassed the Iberian Peninsula, the Armorican Massif, North Africa, and Bolivia (figs. 4-5 of Le Hérissé et al., 1997).

Molyneux et al. (2013) generated the most comprehensive review of Paleozoic acritarch biogeography to date, from the Cambrian to the Devonian. Molyneux et al. (2013) applied quantitative multivariate analysis (unweighted pair group method with arithmetic mean [UPGMA] clustering with the Jaccard similarity index) to acritarch assemblages from several time intervals. For the Furongian, data from Laurentia (Missouri–Arkansas), Baltica (Kolguev Island, East European Platform, Norway), Avalonia (eastern Newfoundland, England–Wales, Belgium) and Gondwana (North Africa, Iran, Spain, Algeria, Tunisia, NW Argentina) were compared, showing many cosmopolitan genera, but with Laurentia and Kolguev Island least similar to other regions (see fig. 23.4 of Molyneux et al., 2013). For the Dapingian, assemblages from the Canning Basin (Australia) were analyzed alongside Perigondwanan localities in western Gondwana, Avalonia, and South China, revealing a distinct, partly endemic Australian microflora that clustered apart from the Perigondwanan assemblages (fig. 23.12 of Molyneux et al., 2013). Finally, for the latest Katian–Hirnantian, pairwise comparisons of Jaccard indices from Anticosti Island (Laurentia), Estonia (Baltica), and Perigondwanan/high-latitude Gondwanan localities (based on Delabroye et al., 2011) showed declining similarities across pre-glacial, glacial, and post-glacial phases, marking the development of distinct Gondwanan versus Baltic/Laurentian paleoprovinces under glacially forced oceanographic restriction.

Shen et al. (2019) carried out the first comprehensive quantitative analysis of Late Devonian (mainly Famennian) phytoplankton paleobiogeography using a global dataset of 95 genera from 15 geographic units. They applied multivariate methods including hierarchical cluster analysis, non-metric multidimensional scaling (NMDS), and minimum spanning tree (MST) analysis, employing several similarity coefficients (Jaccard, Ochiai, Kulczynski, and Yule's Y) to test the robustness of their results. The analyses consistently revealed three phytoplankton realms (fig. 4 of Shen et al., 2019): a West Gondwana Realm (subdivided into Perigondwanan and high-latitude provinces), an East Gondwana Realm (with Australia–Iran and Perigondwanan provinces), and a Boreal Realm (Laurussia and western Junggar). Results showed closer affinities between East Gondwana and Laurussia than between those two realms and West Gondwana, and highlighted that high-latitude genera gradually dispersed into lower latitudes. The study demonstrated how multivariate statistical methods can identify large-scale biogeographic structures and link them to paleocurrent systems and paleotemperature gradients as the primary controls on Late Devonian phytoplankton distribution (Shen et al., 2019).

Askew (2019) analysed early Givetian phytoplankton assemblages from several locations in northern Spain. Three measures of similarity were used for comparison with other locations in Laurussia, Gondwana and China: a simple percentage of similarity (Wicander and Playford, 2017a, 2017b), coefficient of similarity (*sensu* Clark and Hatleberg, 1983) and the Jaccard index. Results show low similarities between northern Spain and the other Givetian assemblages, possibly due to its situation as an island chain between Laurussia and Gondwana containing many predominant taxa from both and lacking others. Ocean currents and temperature gradients may also have played a role in shaping an endemic character for the northern Spanish assemblages.

Taherian et al. (2021) applied the Dice similarity index to marine palynomorph assemblages from Late Devonian-early Carboniferous localities in Iran. The results generally show a high degree of similarity between assemblages from localities in the Alborz Mountains and Kerman Basin of north and central Iran, but relatively low similarity between those assemblages and assemblages from southwest Iran.

Recently, Shen et al. (2025) updated the taxonomy in Shen et al. (2019) and extended quantitative paleobiogeographical analysis to Famennian phytoplankton from the Hongguleleng Formation (Western Junggar, NW China). Using a revised global dataset of 88 genera across 13 geographic units, several multivariate techniques were applied: hierarchical cluster analysis (HCA) with different similarity indices (Dice, Simpson, Raup–Crick), neighbor-joining (NJ) clustering, non-metric multidimensional scaling (NMDS), and analysis of similarities (ANOSIM) to assess biogeographic structure. These analyses consistently distinguished two major realms: a Laurussia Realm (including Western Junggar, Poland, Belgium, South Wales, USA, and Canada) and a North Gondwana Realm (Portugal, Spain, Morocco, Algeria, Turkey, and Iran). Despite a large cosmopolitan component (~20 % of genera), the Hongguleleng assemblages showed strongest affinities with Poland and other Laurussian localities, reflecting both paleogeographic proximity and floral exchange, similar to the results in Shen et al. (2019).

Multivariate analysis is more easily applied and reproducible compared to qualitative methods. The two most commonly used techniques (HCA and NMDS) have their drawbacks, which new methods have been developed to address.

2.3. Further advances on biogeographic analysis from the 2000s to present

HCA and NMDS are among the most widely applied multivariate techniques for identification of biogeographic clusters and patterns (e.g., Colbath, 1990; Le Hérissé and Gourvennec, 1995; Le Hérissé et al., 1997; Molyneux et al., 2013; Shen et al., 2019, 2025). These methods provide complementary perspectives on taxonomic assemblages but also have limitations (Brayard et al., 2007). HCA is well suited for detecting ultrametric or nested relationships, yet its algorithms may impose artificial discrete clusters on continuous gradients. By contrast, NMDS is designed to reveal gradients, though points that appear to cluster in two dimensions may in fact be distinct in higher dimensions. This issue can be mitigated by superimposing a minimum spanning tree and by using only plots with low stress values.

To overcome such drawbacks, network analysis (NA) has been proposed as an alternative, offering additional insights such as the geographic ranges of taxa (Vilhena et al., 2013). Two prominent NA approaches have been developed: the bootstrapped spanning network (BSN) (Brayard et al., 2007, 2015) and bipartite network analysis (Vilhena et al., 2013; Vilhena and Antonelli, 2015).

BSN, introduced by Brayard et al. (2007), begins with the construction of a minimum spanning network (MSN) based on a chosen dissimilarity metric. Bootstrapped support values are then estimated for each edge, and weakly supported connections are discarded until only robust edges remain. In addition to delineating biogeographic provinces, this method revealed a progressive contraction of trans-Atlantic ammonite ranges from the Griesbachian to the Spathian in the Early Triassic (see also Guenser et al., 2025 for another application).

Bipartite networks, pioneered by Vilhena et al. (2013), Sidor et al. (2013), and Vilhena and Antonelli (2015), represent different approaches. In such networks, two sets of nodes-localities and taxa are linked by occurrences, with no direct connections within the same set. A community detection algorithm (e.g., the map equation) is then applied: the algorithm simulates random walks through the network, spending more time in cohesive assemblies (i.e., provinces) and crossing into new clusters when taxa span bioregions. This approach can also identify transitional zones, as demonstrated in the synthetic dataset of Vilhena and Antonelli (2015). Bipartite networks have since been applied to a range of paleobiogeographic problems, including the identification of time-persistent provinces across space and temporal scales (Kocsis et al., 2018a, 2018b, 2021; Na et al., 2023). Penn-Clarke and Harper (2021) combined HCA, NMDS, and NA to resolve latitudinally controlled brachiopod bioregions in the Pragian–Eifelian of West Gondwana. Yan et al. (submitted) also used the same techniques to decipher the paleobiogeography of Upper Ordovician acritarchs.

Aside from network analysis, another quantitative method known as indicator species analysis (IndVal) was introduced in Paleozoic phytoplankton studies by Trindade and Carvalho (2018). IndVal was developed by Dufrêne and Legendre (1997) to identify indicator species and species assemblages that might be characteristic of specific sample groups. Trindade and Carvalho (2018) applied this to the Devonian (Pragian to Famennian) of the Parnaíba Basin and the resulting associations reflect the changes in paleoenvironment, from nearshore to open marine. While IndVal is useful for paleoecological reconstruction, it could also be used to extract paleobiogeographically useful taxa (provided that abundances are known).

Other methodological innovations continue to expand the toolkit. For example, Gibert et al. (2022) applied hierarchical clustering on principal components (HCPC) to Neogene and Pleistocene mammal faunas. This method clusters NMDS scores derived from a dissimilarity index, allowing identification of continental-scale bioregions, with the option to subdivide clusters further. Their results showed a shift from predominantly longitudinal partitioning in the Miocene to latitudinal structuring in the Pliocene.

One important innovation is the use of species distribution models (SDM) to reconstruct diversity, introduced into acritarch studies by Zacaï et al. (2021). The SDM is based on the 'macroecological theory on the arrangement of life' (METAL; Beaugrand et al., 2013, 2014, 2018), generating virtual species with various thermal niches which are then allowed to populate the globe with a given set of environmental parameters (for example sea surface temperature, a specific paleogeographic reconstruction, ocean salinity, etc.). Since the fossil record is biased, the technique provides a way to reconstruct theoretical diversity patterns in poorly sampled areas and time intervals. For example, large parts of Gondwana (central and southern Africa, the northern part of South America, Antarctica and India) and Siberia remain underexplored in terms of marine invertebrates compared to Europe or North America (Harper et al., 2021).

Together, these methodological advances illustrate how biogeographic analyses have moved beyond traditional clustering and ordination to incorporate more flexible frameworks capable of capturing both spatial structure and evolutionary dynamics across multiple scales. No less important than the methods are the sources of empirical data, which form the backbone of the biogeographic analysis.

2.4. Sources of acritarch data

The effectiveness of any biogeographic method ultimately depends on the quality and breadth of the underlying data. For acritarchs, data compilation began in the 1960s and 1970s with card indices and printed catalogues that provided the first systematic overviews of Paleozoic phytoplankton diversity. Georges Deflandre and Marthe Deflandre-Rigaud produced one of the earliest palynological card indexes, which included acritarchs (Deflandre and Delfandre-Rigaud, 1965a, 1965b). Around the same time, Gerhard Kremp (University of Arizona) initiated a palynological database in 1968 that was later managed by a consortium of petroleum companies and scientific organizations. From 1974 this became known as Palynodata, which remained a standard reference until the consortium was dissolved in 2007, with final entries uploaded in 2006 (Riding et al., 2012). Tappan and Loeblich Jr. (1973) published their own list of oceanic plankton from the Precambrian to the present.

In parallel, John Williams (then at British Petroleum) began compiling a card index in 1971 that eventually became the John Williams Index of Palaeopalynology, maintained until 2012 and now available online through the Acritax website (Pedder, 2014). During the same period, Alfred Eisenack, Fritz Cramer and Maria del Carmen Díez de Cramer produced their influential four-volume acritarch compendium (Eisenack et al., 1973, 1976, 1979a, 1979b), which provided systematic descriptions and illustrations of taxa. Later, Fensome et al. (1990) published an index of acritarchs and fossil prasinophytes through the American Association of Stratigraphic Palynologists (AASP), further consolidating the available taxonomic knowledge.

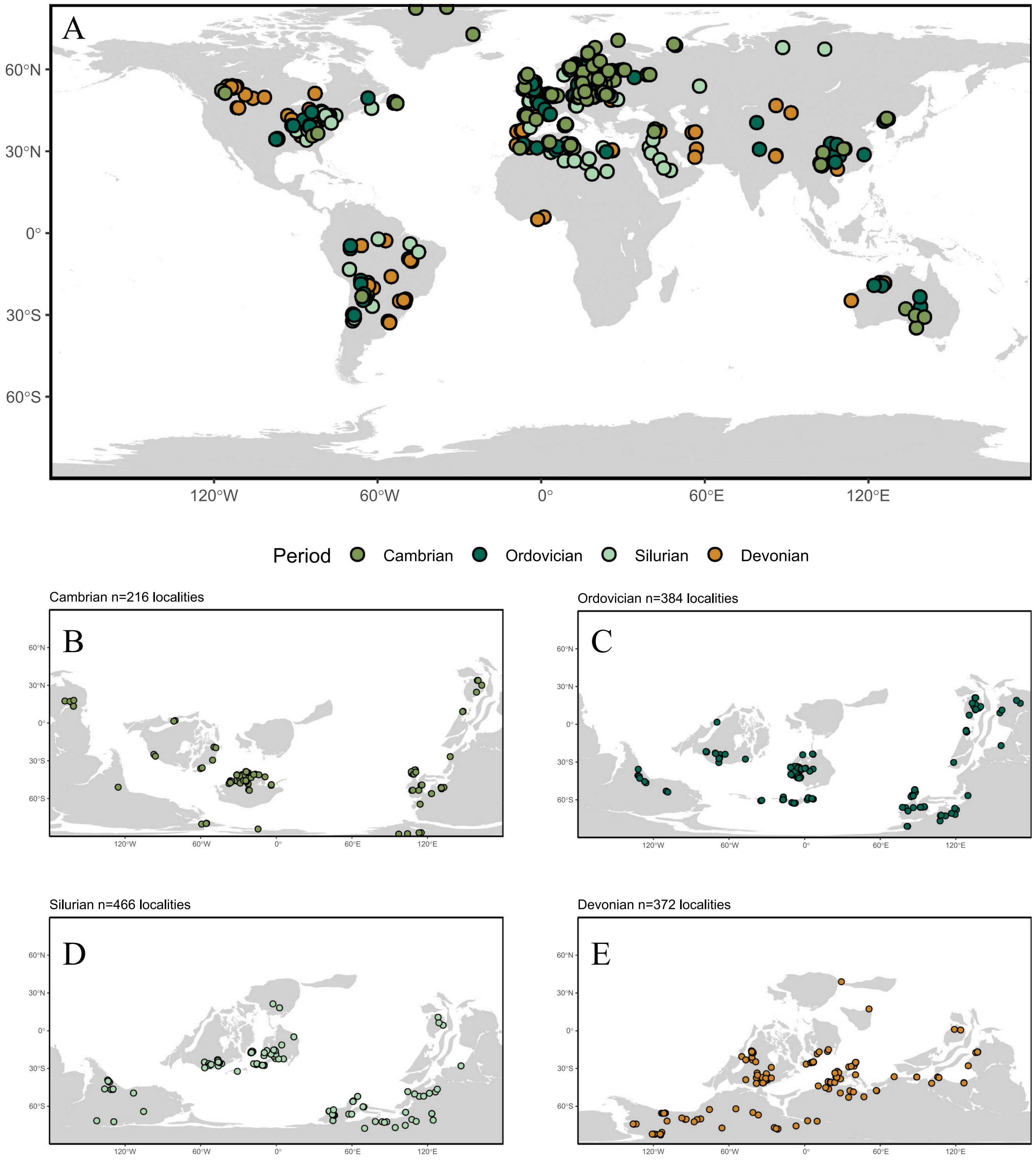
A major advance came in the 2000s with the Phytopal Project (Mullins et al., 2005, 2006), which created a new occurrence-based database of Paleozoic phytoplankton. It is presently stored at a Mendeley data repository (Mullins et al., 2022). Unlike earlier compilations, Phytopal was systematically cleaned, with synonymies and invalid taxa removed or reassigned, and regional chronostratigraphic schemes standardized to the international time scale. This made the database suitable for quantitative diversity studies such as Kroeck et al. (2022), which traced the trajectory of phytoplankton diversity for the whole Paleozoic. Phytopal contains 4053 species from 580 genera, obtained from 568 publications, however it was only updated until 2006. The database was initially presented at conferences, and portions have been used for previous studies on the Ordovician, Devonian, and the early Cambrian (Servais et al., 2008; Klug et al., 2010; Moczydłowska, 2011; Harper et al., 2021; Zacaï et al., 2021). Building on this foundation, Zacaï et al. (2021) georeferenced the Cambrian and Ordovician entries of Phytopal to explore latitudinal diversity gradients. Lately, Shu et al. (2025) extended this effort by georeferencing Palynodata entries and constructing the Global Acritarch Database (GAD) that integrates multiple sources. The GAD contains more than 111,000 entries from nearly 7800 references.

By contrast, the two most widely used general paleontological databases—the Paleobiology Database (PBDB; https://paleobiodb.org) and the Geobiodiversity Database (GBDB; www.geobiodiversity.com)—contain relatively few records of Paleozoic phytoplankton, highlighting the continued importance of specialist databases for global biogeographic analysis.

3. Re-evaluating acritarch biogeography with new multivariate analysis

The preceding sections reviewed the historical development of acritarch biogeographic research, the evolution of methodological approaches from qualitative to quantitative and network-based analyses, and the emergence of curated and georeferenced databases as primary data sources. Together, these advances highlight both the strengths and the persistent limitations of earlier syntheses and underscore the need for a systematic re-examination of Paleozoic phytoplankton biogeography.

Here we present a new multivariate analysis of acritarch distributions based on a global, georeferenced dataset compiled from Phytopal and updated literature sources. Our aim is to evaluate whether classical



Cambrian n=216 localities

Ordovician n=384 localities

Silurian n=466 localities

Devonian n=372 localities

Fig. 1. Distribution of sampled localities. (A) Present-day coordinates. Paleorotated localities based on the PALEOMAP reconstruction (Scotese & Wright, 2018) are shown for the (B) Cambrian, (C) Ordovician, (D) Silurian and (E) Devonian. (A) shows that Europe is the most densely sampled continent for the early to middle Paleozoic. In the Cambrian (B), Ordovician (C) and Silurian (D), the paleocontinent of Baltica is the best sampled, particularly the areas which are now the Nordic region of Europe. During the Devonian (E), present-day North America and southern Europe have the highest degree of sampling.

biogeographic provinces can be objectively recovered using modern methods, and to test the extent to which patterns reflect climate, paleogeography, or sampling biases. We employ HCA and NMDS (with minimum spanning trees) to identify broad-scale provincial structures and latitudinal gradients through the Cambrian to Devonian. The results are organized by period, with each section beginning with a synthesis of existing interpretations, before introducing the outcomes of our analyses. This approach allows direct comparison between traditional models and new data-driven insights, providing a robust framework for reassessing the spatial and temporal dynamics of Paleozoic phytoplankton.

3.1. Database and methods

The present database adapted Cambrian to Devonian occurrences from Phytopal. Zacaï et al. (2021) georeferenced Cambrian and Ordovician records; in the present study we extended georeferencing to Silurian and Devonian entries (See Fig. 1). To increase coverage, 66 additional references published between 2006 and 2024 were incorporated for the Silurian and Devonian, and all taxa were synonymized with the Phytopal taxonomy. Netromorph taxa were revised following Manzano et al. (2025), while questionable taxa were excluded.

Localities were merged into geographic units approximating paleoterranes similar to the methodology of Shen et al. (2019, 2025). To avoid distortion of multivariate analyses, geographic units with fewer than five genera were excluded, and singletons were discarded. All analyses were performed at the genus level, which provides a more stable taxonomic framework than species-level identifications. In total, the final dataset comprises 449 genera, derived from 195 references for the Cambrian and Ordovician (Zacaï et al., 2021) and 224 references for the Silurian and Devonian (Phytopal and post-2006 sources).

To delineate biogeographic regions, we applied HCA and NMDS using the Dice similarity index for each Cambrian epoch and each Ordovician–Devonian stage (see Supplementary Fig. 1). HCA employed Ward's method as the linkage algorithm, which minimizes within-group variance and produces compact clusters. Multivariate analyses were conducted in R using the vegan package (Oksanen et al., 2025). The paleogeographic model used is PALEOMAP by Scotese and Wright (2018), plotted in R using the rgplates package (Kocsis et al., 2024).

3.2. Biogeographic nomenclature

In interpreting the clusters derived from HCA and NMDS, we employ the terms "realm", "province," and "subprovince". The hierarchy of these units is not consistently defined in the literature, and different authors and taxonomic groups have applied varying terminologies (see Servais and Sintubin, 2009; Servais et al., 2013). Several frameworks have been proposed (Kauffman, 1973; McKerrow and Cocks, 1986; Westermann, 2000; Cecca, 2002; Cecca and Westermann, 2003). For example, Kauffman (1973), working on Cretaceous bivalves, suggested quantitative thresholds based on percentages of endemism: endemic centers (5–10 %), subprovinces (10–25 %), provinces (25–50 %), regions (50–75 %), and realms (>75 %). McKerrow and Cocks (1986) instead emphasized ecological and physical criteria, defining "provinces" as regions separated by barriers to migration and "realms" as climatically controlled floral and faunal zones. Cecca and Westermann (2003) proposed a more elaborate hierarchy: superrealm (used mainly in Russian literature), realm, subrealm or region, province, and subprovince.

In this study, while no explicit calculations of endemism were performed for the clusters identified, we follow McKerrow and Cocks (1986) in using the term "realm" to denote broad, climatically controlled phytoplankton distributions. Within these realms, smaller and geographically coherent HCA clusters are referred to as "provinces". Some of these provinces may reflect genuine biogeographic structuring, whereas others may be facies-controlled (e.g., the South Gondwana "Provinces 1 and 2" identified in the Miaolingian, Homerian, Gorstian, and Přídolí), where no obvious physical barriers can be demonstrated. Further investigation of the geological and environmental context is required to clarify these cases. Finally, the term "subprovince" is used for discernible subdivisions within provinces, where finer-scale differentiation can be recognized.

3.3. Results: literature vs. new analysis

Multivariate analyses reveal consistent patterns in Paleozoic acritarch biogeography that can be directly compared with earlier models. For each interval, we first summarize the literature and then present results from hierarchical cluster analysis (HCA) and non-metric multidimensional scaling (NMDS). Both methods, based on the Dice index, recover broad realms, reflecting climatic or latitudinal controls, and smaller, geographically coherent provinces, with occasional subprovinces. The expression of these units varies through time, with provincialism generally stronger under greenhouse conditions and reduced during glacial episodes. Results are presented chronologically from the Cambrian to the Devonian (See Fig. 2).

3.3.1. Cambrian

The paleobiogeography of Cambrian acritarchs remains poorly constrained and is generally regarded as cosmopolitan, with little evidence for stable provincialism (Molyneux et al., 2013). Most studies from the 1990s and 2000s relied on qualitative descriptions and concluded that Cambrian phytoplankton were broadly distributed (Moczydłowska, 1991, 1998; Zang and Walter, 1992; Rubinstein et al., 2003; Yao et al., 2005; Moczydłowska and Zang, 2006; Ghavidel-syooki and Vecoli, 2008; Dong et al., 2009; Nowak et al., 2015). Early Cambrian biozones such as *Asteridium tornatum–Comasphaeridium velvetum*, *Skiagia ornata–Fimbriaglomerella membranacea*, and *Heliosphaeridium dissimilare–Skiagia ciliosa* occur across Baltica, Laurentia, Gondwana, and South China (Dong et al., 2009; Palacios et al., 2011; Rushton and Molyneux, 2011; Yao et al., 2005), suggesting broad dispersal. Some genera hint at paleogeographic differentiation; for example, *Heliosphaeridium* is present in South China but absent from Baltica and eastern Canada, whereas *Granomarginata* occurs in Baltica and Canada but not South China in the Terreneuvian (Molyneux et al., 2013) but these patterns remain equivocal. Assemblages from South China, Australia, Baltica, Laurentia, and Siberia are generally comparable (Moczydłowska, 1998; Moczydłowska and Zang, 2006), and cosmopolitan taxa such as *Skiagia* are widespread (Molyneux et al., 2013). Later comparisons between Baltica, Avalonia, Gondwana, and Laurentia reinforced this broad cosmopolitanism, although Avalonia may have harboured more endemic species than other regions (Ghavidel-syooki and Vecoli, 2008).

Our multivariate analyses provide quantitative support for this general interpretation but also highlight transient structuring in the earliest Cambrian (Figs. 2A–D; Suppl. Figs. 1 A–D). In the Terreneuvian, HCA and NMDS distinguish two realms: a northern-hemisphere realm including a North Gondwana province, and a southern-hemisphere realm encompassing Baltica and a South Gondwanan locality. During Series 2, provincial differentiation becomes more apparent. The HCA resolves two Laurentia provinces, clustering with Baltica and parts of southern Gondwana (Suppl. Fig. 1B). Northern Gondwanan localities (Australia, South China) do not group with southern Gondwana (SW Poland–SE Germany, Spain); instead, some Baltica and Avalonia sites at high southern paleolatitudes cluster with northern Gondwanan assemblages. The NMDS reveals a latitudinal gradient, distinguishing North Gondwanan (equatorial), Laurentian (subequatorial), and Avalonian (high southern latitude) realms. Of these, only the Laurentian Realm forms a distinct HCA cluster (Fig. 2B), indicating weak but detectable partitioning.

By the Miaolingian, these signals disappear (Fig. 2C). The earlier Laurentia and North Gondwana provinces are no longer recognizable,

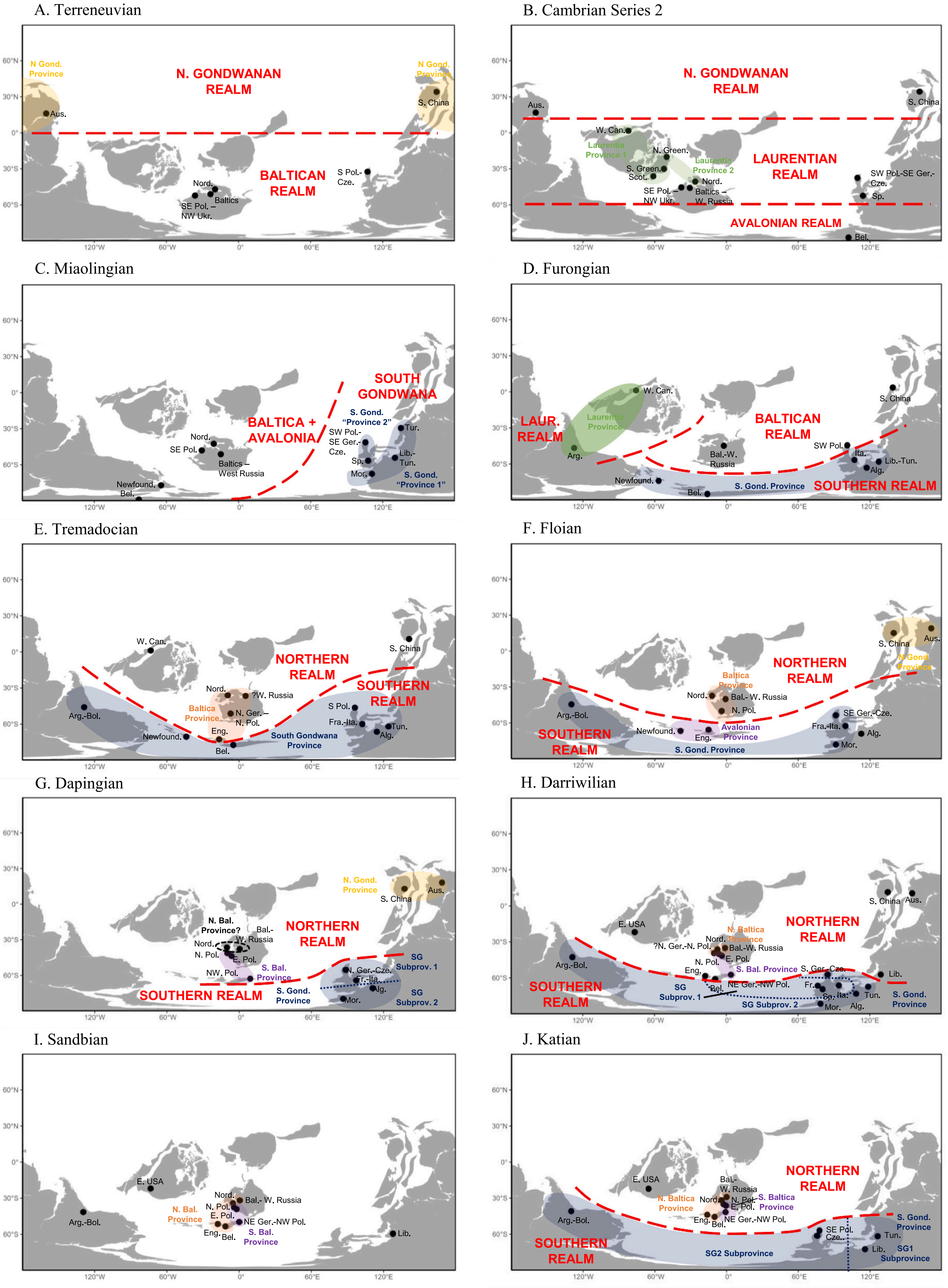


Fig. 2. Biogeography of early to middle Paleozoic acritarchs, based on the results of our multivariate analysis. The results are superimposed on the PALEOMAP reconstruction of Scotese and Wright (2018). The abbreviations are: Alg. — Algeria; Arg. — Argentina; Arg.-Bol. — Argentina-Bolivia; Aus. — Australia; Bel. — Belgium; Cze. — Czech Republic; E. Pol. — eastern Poland; E. USA — eastern USA; Eng. — England; Fr. — France; Ita. — Italy; Lib. — Libya; Lib.-Tun. — Libya-Tunisia; Mor. — Morocco; N. Ger.-N. Pol. — northern Germany-northern Poland; N. Green. — northern Greenland; N. Pol. — northern Poland; NE Ger.-NW Pol. — northeast Germany-northwest Poland; Newfound. — Newfoundland; Nord. — Denmark, Finland, Norway, Sweden; NW Pol. — northwest Poland; NW Ukr. — northwest Ukraine; S. China — southern China; S. Green. — southern Greenland; S. Pol. — southern Poland; S. Pol.-Cze. — southern Poland-Czech Republic; Scot. — Scotland; SE Ger.-Cze. — southeast Germany-Czech Republic; SE Pol. — southeastern Poland; SE Pol.-NW Ukr. — southeastern Poland-northwestern Ukraine; Sp. — Spain; SW Pol. — southwestern Poland; SW Pol.-SE Ger.-Cze. — southwestern Poland-southeastern Germany-Czech Republic; Tur. — Turkey; W. Can. — western Canada; W. USA — western USA.

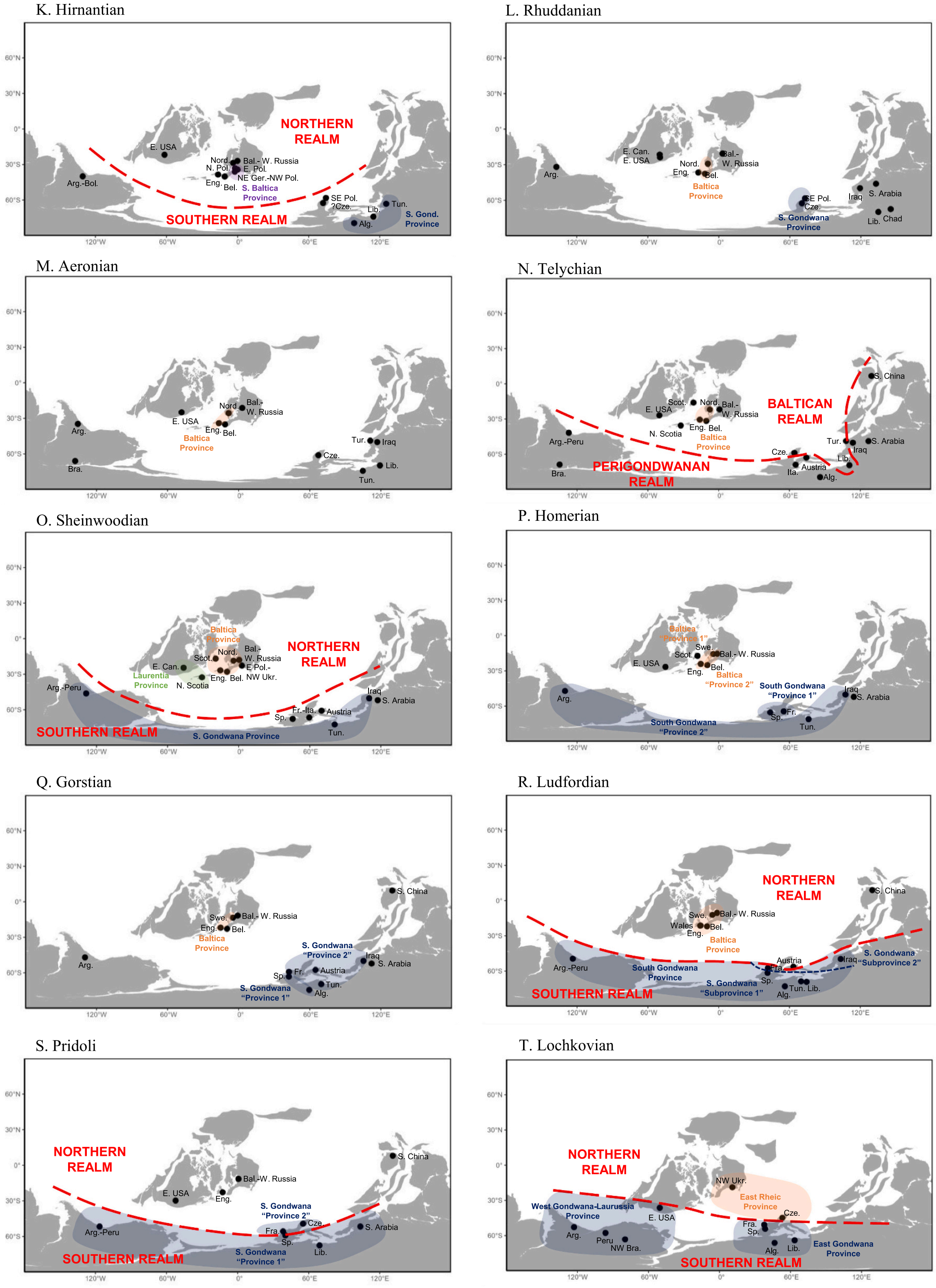


Fig. 2. (*continued*).

and clustering appears facies-controlled. Two South Gondwana clusters emerge (S. Gondwana "Provinces" 1 & 2), possibly reflecting inner- versus outer-shelf settings, comparable to Silurian facies clusters described by Le Hérissé and Gourvennec (1995). The Nordic region plots as an outlier in one of these groups (Suppl. Fig. 1C). Broader HCA clusters lack latitudinal coherence, while in NMDS, South Gondwanan localities form a coherent field, with Baltica and Avalonia outside.

The Furongian shows little latitudinal structuring but three realms can nevertheless be recognized (Fig. 2D; Suppl. Fig. 1D). In both HCA and NMDS, the Baltican and the Southern Realms are closely associated,

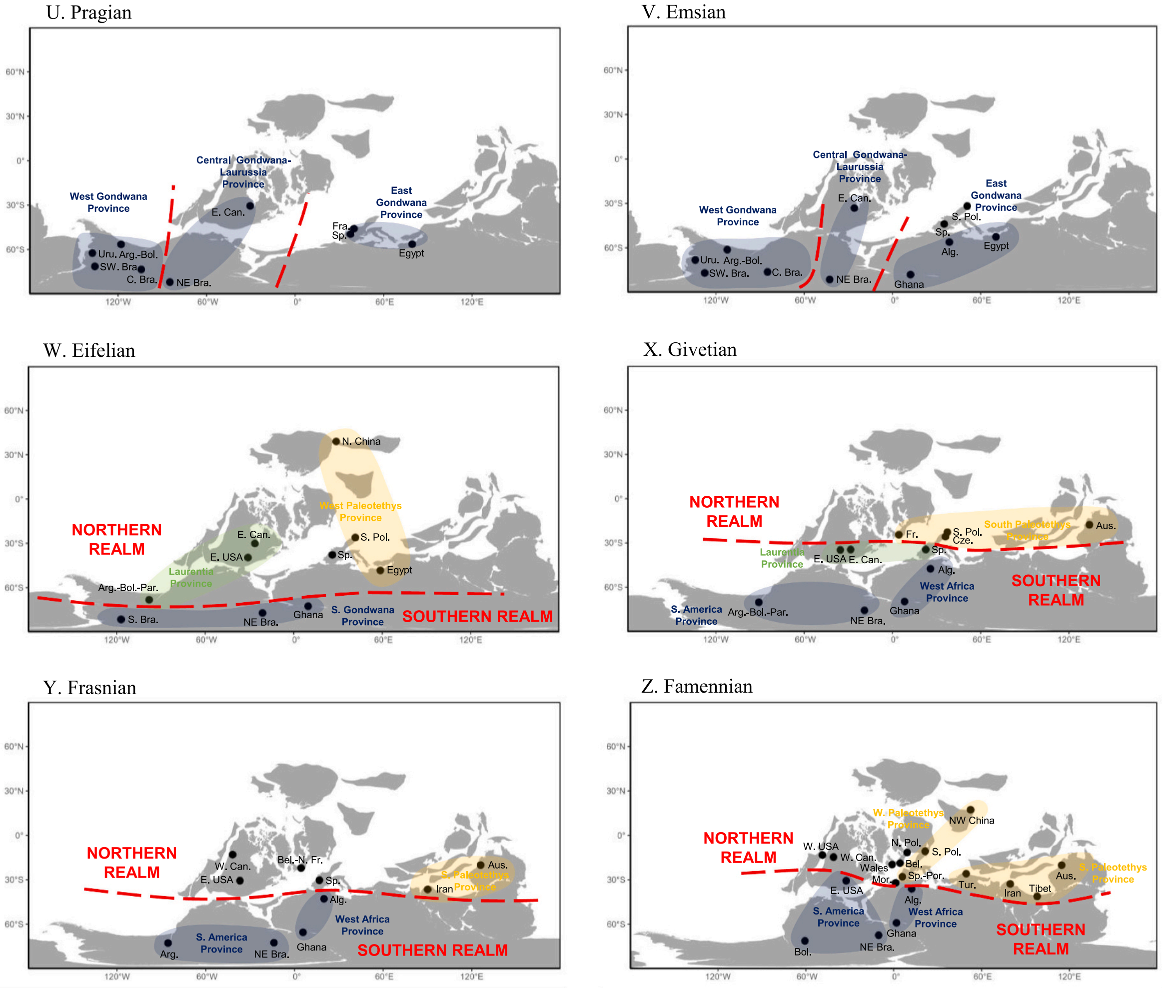


Fig. 2. (*continued*).

while the Laurentian Realm is isolated. The NMDS further reveals a westward gradient across assemblages. Most South Gondwana localities group within the Southern Realm, except SW Poland, which links to Baltica. Belgium plots inconsistently, clustering with Baltica in the HCA but within the Southern Realm in NMDS, and is therefore assigned to South Gondwana on paleogeographic grounds.

Overall, Cambrian acritarchs appear largely cosmopolitan, with only the Terreneuvian and Series 2 showing weak latitudinal partitioning. By the Miaolingian and Furongian, clustering reflects facies effects rather than true provinces. The Cambrian thus represents a phase of high dispersal ability and ecological tolerance among phytoplankton, with few effective barriers to migration, foreshadowing the stronger provincialism that developed in the Ordovician.

3.3.2. *Ordovician*

Classical interpretations emphasized two main provinces in the Early to Middle Ordovician: the Baltica and Perigondwana Provinces (see Section 2.1 above). These were defined qualitatively, with South China showing mixed affinities (Li, 1987, 1989). Later, Tongiorgi et al. (1998), in a study of the Yangtze platform, recorded stratigraphically alternating Perigondwana and Baltica-dominated assemblages in the Arenig (Floian-early Darriwilian). In addition to Baltica and Perigondwana, Playford et al. (1995) recognized provinces in North America and Australia, and a possible province in North China. Volkova (1997) proposed an additional warm-water province in the Tremadocian distinguished by the co-occurrences of *Aryballomorpha*, *Athabascaella* and *Lua*. However, *Athabascaella* has been reported subsequently from high southern paleolatitudes in Perigondwana such as Tunisia (Vecoli, 2004) and Belgium (Breuer and Vanguestaine, 2004).

Certain taxa, such as *Frankea*, were considered restricted to high southern latitudes during this interval (Colbath, 1990; Molyneux et al., 2013). This bi-provincial model suggested strong differentiation in the Early to Middle Ordovician, followed by a breakdown of provincialism during the Sandbian–Katian (Wicander, 2004) and a renewed split into Baltic/Laurentian and Gondwanan provinces in the Hirnantian (Delabroye et al., 2011). On the other hand, recent work by Yan et al. (submitted) using HCA, NMDS and NA show weak paleobiogeographic differentiation in the Sandbian; a subequatorial province in the Katian, with Laurentia, Baltica and central Gondwana, and another province straddling the equator with Tarim, North China and South China; and increased cosmopolitanism again in the Hirnantian.

Our multivariate analyses broadly support the existence of distinct biogeographic structuring in the Early to Middle Ordovician, but the patterns differ from the classical Baltica–Perigondwana model (Figs. 2E–K; Suppl. Figs. 1E–K). In the Tremadocian, HCA and NMDS distinguish two large realms: a Northern Realm, including Baltica, Laurentia, and North Gondwana localities, and a Southern Realm, corresponding to South Gondwana. While most of Baltica falls under a single province within the Northern Realm, a discrete Perigondwana Province *sensu stricto* is not recovered; instead, southern Gondwanan assemblages cluster together as a single South Gondwana Province (Fig. 2E). The ranges of *Athabascaella*, *Aryballomorpha* and *Lua*, which

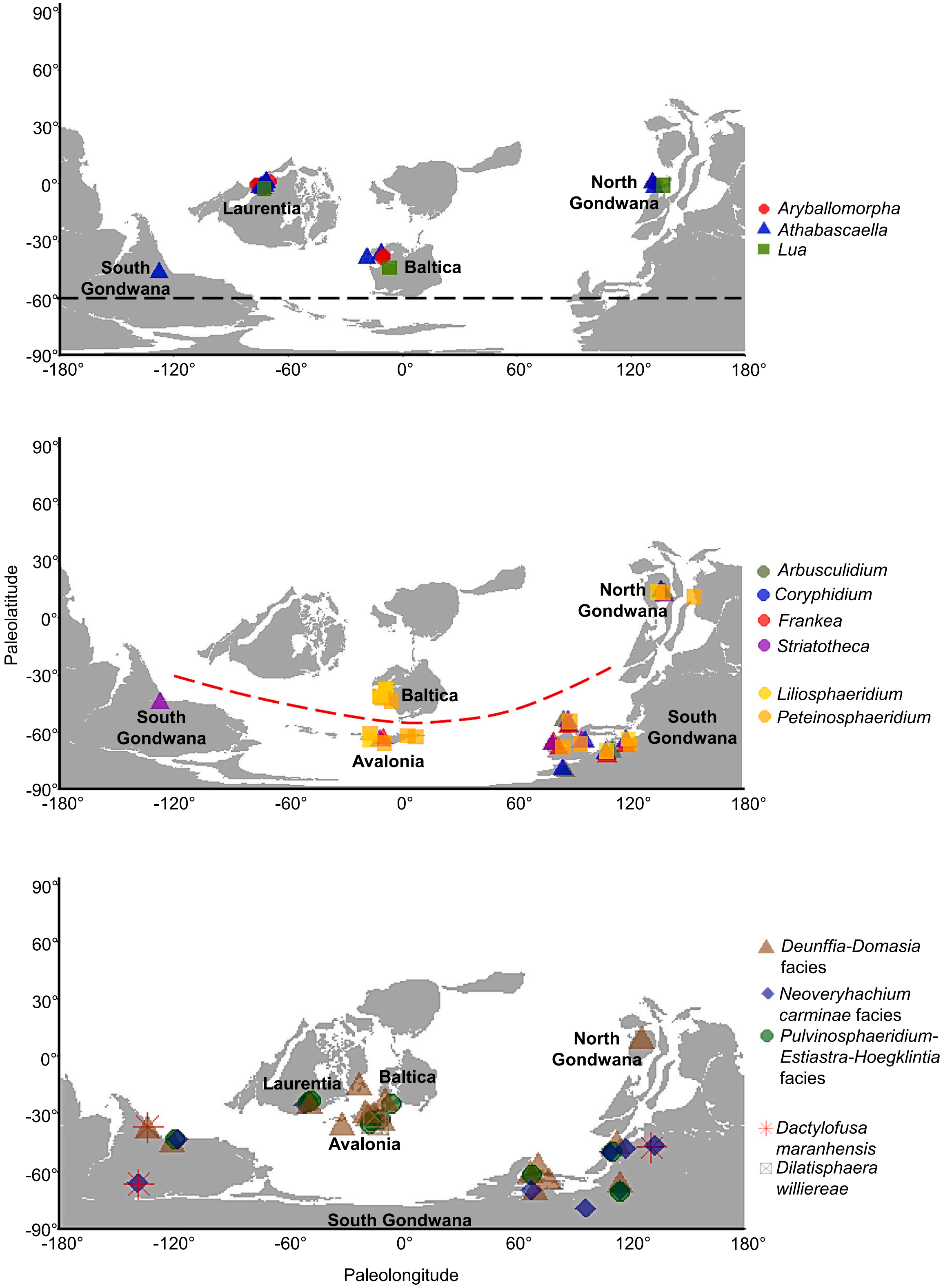


Fig. 3. (a) Distribution of warm-water taxa (*Aryballomorpha*, *Athabascaella* and *Lua*) in the Tremadocian, based on Volkova (1997). The occurrences were taken from the database used for this study and plotted on the plate model of Scotese and Wright (2018). Dashed line approximates northern limit of high southern paleolatitudes.

(b) Selected taxa reportedly characteristic of Baltic and Perigondwana provinces in the Middle Ordovician plotted on the PALEOMAP model of Scotese and Wright (2018). The red dashed line represents the northern limit of the genus *Frankea*. The squares and triangles indicate taxa ascribed to Baltica and Perigondwana, respectively (see text).

(c) The Silurian biofacies of Cramer (1970) and Cramer and Díez (1972a,b; 1974a,b) with possible biogeographically limited taxa (*D. maranhensis* and *D. willieraeae*) according to Le Hérissé and Gourvennec (1995); replotted using occurrences from the present database on the PALEOMAP model of Scotese and Wright (2018).

delineate the warm-water province of Volkova (1997), roughly correspond to the Northern Realm, except for Argentina-Bolivia (Fig. 3A).

In the Floian, the distinction between Northern and Southern Realms persists. Avalonia and South Gondwana cluster to form the Southern Realm, while Baltica and North Gondwana form the Northern Realm (Fig. 2F). Again, the Perigondwana Province of earlier literature is not clearly distinguished, as northern Gondwanan assemblages do not consistently separate from Baltica. As with the Tremadocian, most of Baltica falls under one province.

The Middle Ordovician (Dapingian–Darriwilian) shows further refinement. A South Baltica Province, including parts of Poland in Avalonia, emerges as an isolated cluster, while the remainder of Baltica clusters with Avalonian, Laurentian, and Gondwanan assemblages (Figs. 2G–H). Northern and Southern Realms remain visible in NMDS, but the HCA indicates more complex relationships than a simple Baltica–Perigondwana dichotomy. A North Gondwana Province is weakly expressed in the Dapingian, but less clear in the Darriwilian, while South Gondwana fragments into two subprovinces, echoing Miaolingian patterns. The ranges of four well-known Perigondwanan genera, *Arbusculidium*, *Coryphidium*, *Frankea* and *Striatotheca,* are reconstructed in Fig. 3B. The northern limit of *Frankea* (red dashed line in Fig. 3B) approximates the Northern-Southern Realm boundary while the other three genera are found along Perigondwana; on the South American side only *Striatotheca* was identified. The plot of peteinosphaerids (Fig. 3B) reaffirms their cosmopolitan range and they are thus not useful as paleogeographic indicators.

In the Late Ordovician, our results concur with the conclusions of Kui et al. (submitted). Previous interpretations suggested cosmopolitanism in the Sandbian–Katian and a re-emergence of Baltic/Laurentian and Gondwanan provinces in the Hirnantian. In our analyses, the South Baltica Province persists as a distinct cluster in the HCA across the Sandbian to Katian (Figs. 2I–J). A North Baltica Province is also evident in these stages but disappears in the Hirnantian. The Katian HCA can be subdivided into Northern and Southern Realms, with North and South Baltica in the former and South Gondwana in the latter. Czechia (the Bohemian Massif), although paleogeographically part of Gondwana, plots anomalously with the Northern Realm although it is something of an outlier. By the Hirnantian, the South Gondwana Province contracts markedly, and the HCA no longer resolves latitudinal realms. Nevertheless, NMDS plots delineate Northern and Southern Realms, with the Northern Realm subdivided into South Baltica and a composite Baltica–Laurentia–Avalonia field (Fig. 2K; Suppl. Fig. 1 K).

Overall, our results confirm strong Early to Middle Ordovician provincialism but suggest that the classical Baltica vs. Perigondwana dichotomy is oversimplified. Baltica is a single province in the Early Ordovician, and splits into two for the rest of the period. Perigondwanan affinities in general are not reproducible as a coherent province in the multivariate analyses. Instead, Gondwanan assemblages cluster primarily into South Gondwana, occasionally subdividing into subprovinces. The apparent collapse of provincialism in the Sandbian–Katian is less pronounced in our results, as North Baltica and South Baltica remain recognizable, while the Hirnantian shows contraction of Gondwanan provinces rather than a simple bipolar split. These findings indicate that Ordovician provincialism was more dynamic and geographically nuanced than suggested by earlier qualitative models.

3.3.3. Silurian

Silurian acritarch biogeography has been interpreted as a mix of facies control and true provincialism. While early "latitude–biofacies" models have been discounted (Colbath, 1990; Le Hérissé and Gourvennec, 1995; see also Fig. 3C), later studies identified consistent provincial signals. Cluster analyses by Le Hérissé et al. (1997) revealed Ludlow–Přídolí clusters comparable to the Malvinokaffric and Old World Realms of Boucot (1975), likely reflecting paleogeographic reorganization as North Africa drifted northward and the Rheic Ocean narrowed. Potential paleogeographic indicator taxa also support differentiation (Fig. 3C): *Dactylofusa maranhensis* is confined to Gondwana, while *Dilatisphaera williereae* occurs only in subtropical latitudes across the Llandovery–Wenlock boundary (Le Hérissé and Gourvennec, 1995). Other taxa, such as *Multiplicisphaeridium bonitum*, *M. jardinei*, and *Deflandrastum*, suggest Malvinokaffric affinities extending northward during the late Silurian.

Our multivariate analyses reveal a dynamic Silurian biogeography, with alternating phases of weak and strong provincialism (Figs. 2L–S; Suppl. Figs. 1 L–S). In the Llandovery (Rhuddanian to Telychian), provincialism was subdued, with only a small Baltica Province (including Avalonia) and a minor South Gondwana Province. By the Telychian, HCA resolved two broad clusters—one combining Baltica, Avalonia, and some South Gondwanan localities, and another dominated by Perigondwanan assemblages—though NMDS shows little latitudinal structure.

In the Wenlock (Sheinwoodian to Homerian), provincial structuring strengthened. The Sheinwoodian saw the re-establishment of a large South Gondwana Province, alongside smaller Laurentia and Baltica provinces (Fig. 2O; Suppl. Fig. 1O). NMDS suggests a Northern–Southern Realm division, though HCA is less distinct. In the Homerian, provincial signals weakened again (Fig. 2P; Suppl. Fig. 1P), with South Gondwana splitting into possibly facies-controlled "Provinces 1 and 2" and Baltica fragmenting into two provinces.

The Ludlow (Gorstian to Ludfordian) shows renewed provincialism. In the Gorstian, Baltica and South Gondwana formed distinct but restricted provinces (Suppl. Fig. 1Q; Fig. 2Q). By the Ludfordian, latitudinal structuring re-emerged: a Southern Realm dominated by South Gondwana, and a Northern Realm dominated by Baltica, although outliers (e.g., Sweden, England, Austria) complicate the pattern (Suppl. Fig. 1R; Fig. 2R).

By the Přídolí, provincial signals weakened once more. HCA does not recover a coherent Baltica Province, while South Gondwana is divided into two provinces that fall into separate realms: South Gondwana "Province 1" aligns with a Southern Realm, while South Gondwana "Province 2" clusters with Baltica and northern Gondwana in a Northern Realm (Suppl. Fig. 1S; Fig. 2S). This bipartite structure is clearer in NMDS than in HCA.

Overall, the Silurian was characterized by shifting patterns of provincialism: weak in the Llandovery, stronger in the Sheinwoodian and Ludlow, and diminished again by the Přídolí. These patterns roughly parallel faunal realms identified in other groups such as brachiopods (see fig. 7 of Cocks and Fortey, 1990). For example, the distribution of the *Clarkeia* fauna and the clastic diverse fauna coincides with the Southern Realm, and that of the carbonate diverse fauna with the Northern Realm (Cocks and Fortey, 1990). This suggests that despite strong facies effects, genuine phytoplankton provincialism persisted, especially in the late Silurian.

3.3.4. Devonian

Provincialism is still present in the Devonian. Throughout the Early Devonian, Gondwana is distinguished by various taxa such as *Schizocystia pilosa, Winwaloeusia distracta, Cordobesia uruguayensis, C. oriental* and *Bimerga* spp. (García Muro et al., 2017). *Bimerga* seems to be restricted to the Malvinokaffric realm (Daners et al., 2017). Middle Devonian assemblages have often been described as cosmopolitan, though certain taxa—such as *Bimerga bensonii*, *Duvernaysphaera radiata*, *Maranhites mosesii*, *Pterospermella pernambucensis*, and *Umbellasphaeridium deflandrei*—appear restricted to mid- to high-paleolatitudes of Gondwana (Molyneux et al., 2013 and references therein), with *Umbellasphaeridium* particularly noted as a Southern Hemisphere endemic (Wood, 1984). On the other hand, *Uncinisphaera acantha* and *Villosacapsula compta* are endemic to North America (Wicander and Playford, 2017a). Island chains such as those of northern Spain also show endemic assemblages (Askew, 2019). For the Late Devonian, Colbath (1990) demonstrated two distinct Frasnian bioprovinces

(Laurussia with parts of western Australia, and South America-West Africa) through cluster analysis (though these were not explicitly indicated as such). In the Famennian, Shen et al. (2019) recognized three realms—West Gondwana, East Gondwana, and Boreal—using multiple similarity indices in HCA and NMDS, and Shen et al. (2025) further resolved two robust clusters, Laurussian and North Gondwanan, broadly corresponding to the earlier Boreal and East Gondwana divisions.

Our multivariate results confirm persistent latitudinal structuring throughout most of the Devonian, punctuated by transient collapses and reorganizations (Figs. 2T–Z; Suppl. Figs. 1T–Z). In the Lochkovian, HCA and NMDS reveal Northern and Southern Realms (Fig. 2T; Suppl. Fig. 1T). The Southern Realm included southwestern Laurussia (eastern USA), while the Northern Realm featured an East Rheic Province linking southern Baltica and northern Gondwana. Argentina and Libya plot as outliers in HCA but cluster with contiguous Gondwanan provinces in NMDS, and are therefore assigned to West Gondwana-Laurussia and East Gondwana, respectively.

In the Pragian, all localities are from Gondwana or south Laurentia, and no clear Northern–Southern division is detected. Instead, Gondwana is subdivided into West, Central-Laurussia, and East Gondwana Provinces (Fig. 2U; Suppl. Fig. 1U). Egypt appears as an outlier but is assigned to East Gondwana on paleogeographic grounds. In the Emsian, West and Central Gondwana-Laurussia Provinces persist, while East Gondwana reorganizes with a different set of localities and shifts southward (Fig. 2V; Suppl. Fig. 1 V).

At the start of the Middle Devonian, a new West Paleotethys Province appears along the western margin of the Paleotethys Ocean, clustering with Laurentia to form a Northern Realm (Fig. 2W; Suppl. Fig. 1 W). A South Gondwana Province occupied high southern latitudes. By the Givetian, provincialism strengthens again: HCA and NMDS both delineate Northern and Southern Realms (Fig. 2X; Suppl. Fig. 1X). The Southern Realm extended north to ~30°S, incorporating Laurentia, while the South Gondwana Province fragmented into South American and West African Provinces, and a South Paleotethys Province emerged at the southern Paleotethyan margin.

In the Late Devonian, NMDS reveals a clearer latitudinal distinction than HCA. In the Frasnian, HCA shows two broad clusters that subdivide into northern and southern groups (Fig. 2Y; Suppl. Fig. 1Y). The South American Province clusters with South Paleotethys (with eastern USA as an outlier), while the West African Province groups with Spain and western Canada. NMDS clearly separates Northern and Southern Realms. In the Famennian, the South Paleotethys Province forms an isolated cluster with parts of Laurussia (Fig. 2Z; Suppl. Fig. 1Z), while West African, South American, and West Paleotethys Provinces group more closely. NMDS again distinguishes two realms.

Overall, the Devonian record highlights enduring latitudinal structuring, with short-lived disruptions in the Pragian–Emsian and reorganizations associated with the Paleotethys Ocean.

4. Discussion

The multivariate analyses presented here provide the first systematic, stage-level assessment of Cambrian–Devonian acritarch biogeography, revealing alternating intervals of cosmopolitanism, latitudinal structuring, and facies-controlled clustering. These results, when compared with previously proposed paleobiogeographic models, clarify where earlier models hold and where they are undermined by broader geographic coverage and standardized taxonomy. Complementary to these quantitative patterns, the distribution of reported paleobiogeographic marker taxa has been reevaluated using the updated Phytopal database. While some taxa (e.g., *Frankea*, *Dactylofusa maranhensis*) retain restricted ranges and biogeographic value, others such as the peteinosphaerids confirm earlier interpretations of cosmopolitan distributions and limited utility for delineating provinces. Together, these lines of evidence provide a more nuanced understanding of phytoplankton provincialism and its paleoenvironmental drivers.

4.1. Biogeographic Markers and Index Taxa

Plotting previously reported biogeographically significant taxa against the updated Phytopal database shows that some genera retain their value as paleobiogeographic indicators, while others appear more widespread than earlier assumed. The Tremadocian warm-water genera identified by Volkova (1997) remain consistent markers when replotted on PALEOMAP reconstructions (Fig. 3A).

By contrast, peteinosphaerids, proposed by Playford et al. (1995) and Tongiorgi and Di Milia (1999) as criteria for delineating Baltica in the Middle Ordovician, appear to be too widely distributed for paleobiogeographical use. Both *Peteinosphaeridium* and *Liliosphaeridium* occur across Baltica, Avalonia, as well as northern and southern Gondwana (Fig. 3B), suggesting cosmopolitan ranges. Tongiorgi et al. (1998) reported alternating Perigondwanan and Baltican assemblages in South China during the Arenig (Floian to Darriwilian), proposing two hypotheses to explain the shifts in biogeographic affinities: the first invokes periodic infringement of warm-water transporting Baltic taxa into the Yangtze platform while the second suggests a change in assemblage related to sea-level. Calero Gordon et al. (2025) described transitional changes in acritarch morphology and assemblages due to ecophenotypism in the Middle Ordovician of Öland, Sweden, linked to local regression. Thus, the second hypothesis of Tongiorgi et al. (1998) seems more likely than the first in explaining the Arenig assemblages of South China.

In addition to the three classical Early to Middle Ordovician Perigondwanan genera (*Arbusculidium*, *Coryphidium*, *Striatotheca*), *Frankea* emerges as the most latitudinally restricted and thus the most reliable cold-water marker (Fig. 3B), reaffirming earlier interpretations (Servais and Fatka, 1997; Servais et al., 2003; Molyneux et al., 2013). In South Gondwana, *Arbusculidium*, *Coryphidium*, *Frankea*, and *Striatotheca* commonly co-occur, though only *Striatotheca* is recorded from South America. In Avalonia, only *Frankea* is present, while none of these taxa are recorded in Baltica. The absence of *Frankea*, *Arbusculidium*, and *Coryphidium* from South America may reflect either poor sampling in the Middle Ordovician or, in the case of *Frankea*, a genuine biogeographic boundary separating cold- from warm-water realms. At lower latitudes, no single genus appears to provide a reliable positive criterion for warm-water conditions, as *Striatotheca*, *Coryphidium*, and peteinosphaerids all display cosmopolitan distributions.

In the early Silurian, Cramer's biofacies were reported widely across continents but show no consistent paleolatitudinal trends (Fig. 3C). Among potential indicators, *D. maranhensis* is restricted to South Gondwana, with its northernmost limit near ~30°S, although it remains uncommon even within its range. *D. williereae* also has a limited distribution, mainly within Avalonia and Baltica, though it is rare in both areas. By contrast, *N. carminae* and the *Pulvinosphaeridium*–*Estiastra*–*Hoegklintia* facies appear absent from regions north of the paleoequator, although this pattern may partly reflect uneven sampling coverage, and partly because most of the northern hemisphere is covered by the Panthalassic Ocean.

Taken together, these results suggest that some acritarch taxa—particularly *Frankea* in the Ordovician and *D. maranhensis* and *D. williereae* in the Silurian—function as robust paleobiogeographic markers, whereas many others once regarded as diagnostic are best interpreted as cosmopolitan or facies-controlled.

4.2. Biogeographic structure and controls in the Early–Middle Paleozoic

Across the Cambrian–Devonian, acritarch biogeography oscillated among three end-members: weakly structured latitudinal realms, possible facies-controlled clustering, and phases of cosmopolitanism. In the earliest Cambrian (Terreneuvian–Series 2), multivariate analyses already resolve a northern vs. southern partition with an equatorial boundary (Figs. 2A–B). That structure dissipates in the Miaolingian and Furongian, when clustering is dominated by facies effects (Fig. 2C–D).

Provincialism re-emerged decisively in the Ordovician, when long-term cooling sharpened a warm Northern Realm and a cold Southern Realm (Figs. 2E–H). The Hirnantian crisis dismantled this arrangement (Fig. 2K), leading to early Silurian cosmopolitanism, with realms and provinces reappearing through the Wenlock and Ludlow (Figs. 2O–R). By the Devonian, realm boundaries fluctuated and South Gondwana fragmented repeatedly, while new provinces formed along the margins of the Paleotethys (Figs. 2T–Z).

4.2.1. *Cambrian cosmopolitanism and weak latitudinal structure*

Even with limited sampling, the Cambrian reveals intriguing but transient provincial signals. In the Terreneuvian, both HCA and NMDS distinguish two coherent clusters around the paleoequator (Fig. 2A). A compact North Gondwana Province, represented by Australia and South China, contrasts with a more diffuse Baltican Realm encompassing Baltica and a South Gondwanan locality. This early partition may reflect latitudinal gradients, with equatorial waters supporting one realm (North Gondwanan realm) and higher-latitude settings another (Baltican realm).

By Series 2, provincial differentiation becomes more evident. Laurentia develops internal structure, splitting into multiple provinces, while some of its localities cluster with Baltica because of paleogeographic proximity (Fig. 2B). At the same time, NMDS suggests a three-band latitudinal pattern: equatorial Northern Hemisphere localities, subequatorial to low-latitude Southern Hemisphere sites, and high-latitude Avalonian and Gondwanan occurrences. This marks one of the earliest signs of realm-scale structuring in phytoplankton.

However, these patterns weaken by the Miaolingian. South Gondwana appears to have fragmented into two provinces (Fig. 2C), but the distribution of sites and their paleoenvironmental context (inner- vs. outer-shelf) suggest facies control rather than true paleogeographic partitioning. The Furongian continues this trend, with three broad clusters (Laurentia, Baltica, and South Gondwana; Fig. 2D), but without strong latitudinal coherence. Overall, Cambrian phytoplankton remain largely cosmopolitan, their weak provinciality reflecting high dispersal potential and broad ecological tolerance.

4.2.2. *Rise of provincialism in the Ordovician*

The onset of the Ordovician radiation marks a turning point, coinciding with global cooling. From the Tremadocian onward, both HCA and NMDS resolve into two large, stable realms: a warm Northern Realm spanning equatorial to ca. −30° paleolatitudes, and a cold Southern Realm extending from ca. −30° to the pole (Figs. 2E–F). This bipartite structure is one of the clearest features of our dataset and suggests that climate-driven latitudinal differentiation had become a primary control on phytoplankton distributions.

Baltica consistently formed a distinct province in the Tremadocian. Drifting northwards, Avalonia separated from the South Gondwana province in the Floian and eventually merged with Baltica in the Middle Ordovician. Differentiation into North and South Baltica provinces in the Sandbian and Katian may possibly reflect facies.

Classical reconstructions emphasized a Perigondwanan Province spanning the Laurentia/Baltica/Siberia facing rim of Gondwana but our analyses do not support its existence as a discrete unit. Instead, North and South Gondwana localities consistently separate with their respective realms, with Perigondwanan index taxa (*Arbusculidium*, *Coryphidium, Striatotheca*) straddling the Northern and Southern Realms. This finding suggests that earlier models may have overstated provincial distinctiveness by relying too heavily on individual taxa rather than whole-assemblage data.

4.2.3. *Late Ordovician destabilization and Hirnantian breakdown*

The Late Ordovician presents a more unstable picture. The Sandbian record is sparse, especially for southern Gondwanan sites, and HCA results show limited structure beyond subdivisions within Baltica and Avalonia (Fig. 2I). This scarcity likely contributes to the absence of clear realm-scale differentiation in this interval.

By the Katian, provincialism is re-established. Northern and Southern Realms are once again distinguished (Fig. 2J), with Baltica splitting into a North and a South province and South Gondwana subdividing along the east–west axis. These patterns suggest both paleolatitudinal controls and regional differences in Gondwanan shelf environments. Such differentiation anticipates the complex ecological disruptions that would follow during the Hirnantian.

The Hirnantian mass extinction triggered a complete collapse of phytoplankton provincialism (Fig. 2K). North Baltica disappears as a recognizable unit, South Gondwana contracts sharply, and cosmopolitan assemblages dominate. This breakdown mirrors similar patterns in faunal groups, where cold glacial climates and sea-level fall reorganized ecosystems at a global scale. For the phytoplankton, the Hirnantian illustrates how severe climatic stress can override even robust provincial patterns.

4.2.4. *Llandovery cosmopolitanism and Silurian recovery*

The early Silurian begins in the wake of this disruption. Diversity and structure are low in the Rhuddanian–Aeronian, with only a remnant Baltica Province and little sign of a coherent Southern Realm (Figs. 2L–M). Assemblages are broadly cosmopolitan, consistent with a stressed post-extinction recovery phase. This pattern parallels faunal records such as those of brachiopods (e.g. Cocks and Fortey, 1990), where many groups also show reduced endemism and widespread taxa following the Ordovician extinction.

By the Telychian, recovery is underway. Phytoplankton diversity increases (e.g. Kroeck et al., 2022), and broad realm-scale partitioning re-emerges (Fig. 2N). A Baltica Province becomes recognizable again, and Gondwanan assemblages differentiate into northern and southern groups. The distribution of restricted taxa supports these patterns: *Dilatisphaera williereae* appears confined to subtropical settings in Baltica, while *Dactylofusa maranhensis* remains restricted to South Gondwana. These index taxa, though limited, demonstrate that provincialism was beginning to be re-established.

This recovery phase highlights the resilience of phytoplankton communities in re-establishing structure following mass extinction. At the same time, the uneven strength of provincial signals across localities underscores the continued influence of facies and sampling coverage.

4.2.5. *Dynamic provincialism in the Devonian*

The Devonian is characterized by highly dynamic provincialism, reflecting the paleogeographic reorganizations during this time. In the Lochkovian, the paleobiogeography consists of a Northern Realm containing an East Rheic Province, and a Southern Realm divided into West and East Gondwana (Fig. 2T). Interestingly, our analyses group eastern USA with South America into a West Gondwana-Laurussia Province, highlighting possible floral exchange along the closing Rheic Ocean.

In the Pragian–Emsian, all analysed sites cluster within the Southern Realm, with Gondwana subdivided into West, Central, and East Provinces (Figs. 2U–V). Continued closing of the Rheic Ocean further enhanced the biogeographic link between North and South America, resulting in the formation of the Central Gondwana province between the East and the West. The lack of northern hemisphere data hampers proper identification of the Northern Realm at this time.

The Middle Devonian witnessed the rise of the Paleotethyan provinces. In the Eifelian, a West Paleotethys Province emerged along the ocean's western margin, clustering with Laurentia in the Northern Realm (Fig. 2W). By the Givetian, provincial structuring intensified, with South Gondwana fragmenting into South American and West African provinces, and a South Paleotethys Province forming on the ocean's southern margin (Fig. 2X).

Late Devonian patterns combine strong realm-scale structuring with complex provincial mosaics. In the Frasnian, Laurussian assemblages are broadly cosmopolitan, but Gondwanan provinces remain distinct: South America clusters with South Paleotethys, while West Africa groups with

Spain and western Canada (Fig. 2Y). By the Famennian, provincial boundaries reorganize again, with the South Paleotethys forming an isolated cluster and West African, South American, and West Paleotethys provinces grouping together (Fig. 2Z). These results broadly agree with the investigations of Shen et al. (2019, 2025) but highlight additional transient collapses and fragmentations.

The Devonian thus represents the most dynamic phase of Paleozoic phytoplankton biogeography, marked by shifting realm boundaries, longitudinal fragmentation of the South Gondwana Province and the emergence of Paleotethyan provinces.

4.3. Environmental controls on acritarch biogeography

Paleolatitude and paleoclimate emerge as primary controls on phytoplankton distribution throughout much of the Paleozoic. NMDS plots consistently show gradational structures between warm (Northern) and cold-water (Southern) assemblages, with HCA often reinforcing this bipartite division. The Southern Realm was relatively stable, typically occupied by one or more large provinces, whereas Northern Realm provinces were smaller and more ephemeral. A modern analogue can be found in the distribution of dinoflagellates, which form broad latitudinal assemblages with only a few truly endemic or bipolar taxa (Goodman, 1987; Mudie and Harland, 1996; Marret et al., 2020). Similarly, multivariate analyses of modern planktonic foraminifera (Rillo et al., 2022) reveal bioregions structured primarily by mean sea-surface temperature, underscoring the importance of climate as a persistent driver. Climatic perturbations correlate with disruptions in phytoplankton structure: provincialism weakened during the Hirnantian glaciation, collapsed in the Llandovery, and was destabilized during Wenlock cooling events, only to re-emerge during subsequent warming phases. Paleogeography also exerted a strong influence, particularly through the drift of Avalonia toward Baltica, the closure of the Rheic Ocean, and the formation of the Paleotethys. These tectonic changes fragmented or merged provinces and facilitated the emergence of new Paleotethyan realms in the Devonian. Together, these findings emphasize that phytoplankton provincialism was shaped by a dynamic interplay of latitude, climate, and plate configuration, rather than by any single controlling factor.

5. Conclusions and Perspectives

This synthesis of Cambrian–Devonian phytoplankton biogeography demonstrates that acritarchs were neither uniformly cosmopolitan nor strictly provincial, but instead oscillated between these states in response to climatic and paleogeographic changes. Multivariate analyses confirm that broad latitudinal structuring into warm- and cold-water realms was a recurrent feature, while glacial episodes and rapid environmental perturbations destabilized or erased this structure. Provinces were most robust in mid to high southern latitudes, particularly in South Gondwana, while Northern Realm provinces were generally smaller and shorter-lived.

The utility of certain taxa as paleobiogeographic markers is reaffirmed, such as *Frankea* in the Ordovician and *Dactylofusa maranhensis* or *Dilatisphaera williereae* for Perigondwana and Baltica respectively in the Silurian. This reevaluation underscores the importance of systematically testing marker taxa with standardized, georeferenced databases.

Despite these advances, several key questions remain. One challenge is to distinguish clusters reflecting true provincialism from patterns produced by local facies effects, as in the case of inner–outer shelf “subprovinces” in South Gondwana. Future studies should integrate the sedimentological and geochemical context into biogeographic frameworks to disentangle environmental versus biogeographic controls. Another frontier lies in resolving the degree of congruence between phytoplankton provinces and those identified for other planktonic groups such as graptolites, chitinozoans, and radiolarians. Multi-group syntheses would test whether provincial structures were ecosystem-wide or taxon-specific.

The role of climate and oceanography also warrants closer scrutiny. While paleolatitude and global temperature clearly structured phytoplankton distributions, the influence of ocean circulation, nutrient regimes, and upwelling zones remains less well constrained. Coupling fossil occurrence data with general circulation models and paleocurrent reconstructions would allow more explicit tests of dispersal barriers and migration pathways. Temporal resolution is another limitation: many of the patterns observed here are based on stage-level bins, which may obscure short-lived structures or transitions. Higher-resolution analyses, particularly around extinction and recovery intervals, could reveal more transient but ecologically significant provinces.

Geographic coverage remains uneven. Much of South America, Africa, India, Antarctica, and parts of Asia are undersampled, limiting the global resolution of Paleozoic phytoplankton provinces. Systematic sampling in these regions, tied to robust chronostratigraphy, is essential, as new localities could substantially alter current interpretations of global provincial structure. At the same time, taxonomic issues continue to hinder synthesis. Synonymies, inconsistent usage, and incomplete revisions obscure diversity signals. Renewed taxonomic syntheses, morphometric work, and integration with biomarker or molecular-clock data could clarify the ecological and evolutionary roles of key groups.

Finally, methodological innovation is likely to reshape the field. Traditional clustering and ordination remain valuable, but emerging approaches—such as network analysis and species distribution modelling—offer ways to quantify uncertainty, identify transitional zones, and predict diversity in unsampled areas. These tools, combined with improved data infrastructure through open and continuously updated databases such as Phytopal, will enable more robust global syntheses.

Altogether, Paleozoic phytoplankton biogeography is moving beyond descriptive frameworks toward predictive models. By integrating taxonomic revisions, expanded geographic sampling, multiproxy paleoenvironmental data, and new analytical approaches, future work can resolve the processes that structured ancient planktonic ecosystems. Such studies will not only refine our understanding of Paleozoic ocean dynamics but also provide a long-term perspective on how marine primary producers respond to global change—a perspective highly relevant to forecasting the future of modern phytoplankton under ongoing climate warming.

CRediT authorship contribution statement

Eiver Gelan Manzano: Writing – review & editing, Writing – original draft, Methodology, Data curation. **Claude Monnet:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **David M. Kroeck:** Writing – review & editing, Funding acquisition, Conceptualization. **Stewart Molyneux:** Writing – review & editing, Conceptualization. **Hendrik Nowak:** Writing – review & editing. **Paulina Nätscher:** Writing – review & editing. **Thomas Servais:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no competing interests in the writing of this paper.

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Appendix A. Supplementary data

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Data availability

Data available in this repository: https://doi.org/10.5281/zenodo.17815258

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