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Diversité du phytoplancton dans l'espace et dans le temps au Paléozoïque inférieur et moyen

Thèse préparée et soutenue publiquement par

Eiver Gelan O. MANZANO

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Composition du jury :

Frédérique EYNAUD

Maître de conférence, Université de Bordeaux, *Rapporteur*

Emanuela MATTIOLI

Professeure, Université de Lyon, *Rapporteur*

Catherine CRÔNIER

Professeure, Université de Lille, *Président du jury*

Muriel VIDAL

Maître de conférence, Université de Bretagne Occidentale, *Examineur*

Claude MONNET

Ingénieur de recherche, Université de Lille, *Directeur de thèse*

Thomas SERVAIS

Directeur de recherche, Université de Lille, *Co-Directeur de thèse*



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Doctoral School – 104
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Claude MONNET,

Ingénieur de recherche, Université de Lille, *Thesis director*

Thomas SERVAIS,

Directeur de recherche, Université de Lille, *Thesis co-director*

Université de Lille
CNRS-UMR 8198 Évo-Éco-Paléo
Bâtiment SN5
Avenue Paul Langevin
Cité Scientifique
59655 Villeneuve d'Ascq CEDEX
France

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Résumé

Le présent travail retrace l'évolution de la diversité et de la répartition du phytoplancton du Paléozoïque inférieur au Paléozoïque moyen (du Cambrien au Dévonien) et tente d'élucider les facteurs environnementaux influençant la dynamique de la diversité. Pour ce faire, une base de données a été créée à partir des travaux d'auteurs précédents, enrichie par une littérature plus récente et géoréférencée.

Une reconstitution correcte et pertinente de la paléodiversité et de la paléobiogéographie nécessite une révision des biais taxonomiques. Ainsi, l'auteur a participé à deux études publiées sur ce biais: la première porte sur un sous-groupe d'acritarches, les netromorphes, en proposant un système de classification des genres et une réaffectation des morphotypes apparentés ; la seconde revisite la plasticité morphologique des assemblages d'acritarches de l'Ordovicien moyen sur l'île d'Öland, en Suède.

L'étude aborde la diversité sous trois angles : global, latitudinal et par mailles (cellules de grille). L'analyse de la diversité générique globale met en évidence l'effet des extinctions massives, notamment après l'extinction massive de la fin de l'Ordovicien (LOME), période durant laquelle la diversité chuta drastiquement. Ce creux se prolongea presque tout au long du Silurien, probablement en raison d'événements positifs d'isotopes du carbone qui perturbèrent les cycles marins du carbone et réduisirent la résilience du phytoplancton. Les tendances globales des taux d'apparition et d'extinction sont corrélées à la disponibilité des habitats. La diversité latitudinale révèle une migration des pics de diversité en fonction du climat changeant, et un gradient de diversité latitudinale plus marqué a été observé lorsque l'écart de température entre les pôles et les tropiques était très important. Les résultats montrent également un scénario de type « sortie des tropiques » pour le phytoplancton du Paléozoïque inférieur à moyen. La diversité par cellule de grille a révélé l'existence de points chauds de diversité du phytoplancton, mais des recherches supplémentaires sont nécessaires pour en identifier les causes.

Pour l'analyse biogéographique, l'auteur a également participé à deux études (l'une soumise, l'autre publiée), adoptant des approches différentes : une description qualitative de la paléobiogéographie du Gondwana sud pendant le Floien (dans le cadre d'une étude du biote de Cabrières), en utilisant les taxons pour marquer les provinces ; et une approche quantitative du Famennien (fin du Dévonien) basée sur une analyse multivariée.

Pour le travail principal, une analyse multivariée a été réalisée sur la base de données du phytoplancton afin de déterminer les schémas biogéographiques. Les résultats ont montré une différenciation large en domaines latitudinaux, correspondant grossièrement à des assemblages d'eaux chaudes (équatoriales à subéquatoriales) et d'eaux froides (hautes paléolatitudes australes). Le provincialisme s'est affaibli durant l'Hirnantien, phénomène attribuable à la LOME et aux glaciations ; cette situation a perduré jusqu'à la fin du Silurien, période marquée par une faible diversité générique globale. Le réarrangement continental au Dévonien a fragmenté et reconfiguré le domaine des eaux froides en plusieurs provinces, tout en en formant de nouvelles en bordure de l'océan Paléotéthys.

Dans l'ensemble, cette thèse montre comment divers facteurs peuvent affecter la diversité et la répartition du phytoplancton. Les travaux futurs devront aborder deux enjeux principaux : une meilleure représentation spatiale et temporelle ; ainsi que l'application d'autres corrections spatiales pour mieux cerner les schémas de diversification.

Mots-clés: *acritarches, biogéographie, diversité, netromorphes, macroécologie, Paléozoïque, phytoplancton*

Abstract

The present work traces the evolution of phytoplankton diversity and distribution in the early to middle Paleozoic (Cambrian to Devonian) and attempts to elucidate environmental factors which affect diversity dynamics. In order to do so a database was created based on the work of previous authors, expanded with more recent literature and georeferenced.

Proper and meaningful reconstruction of paleodiversity and paleobiogeography warrants a review of taxonomic bias and thus the author engaged in two published studies related to this bias: the first reviews an acritarch subgroup, the netromorphs, proposing a system for classifying genera and reassigning related morphotypes while the second revisits morphological plasticity in Middle Ordovician acritarch assemblages in Öland, Sweden.

The study approached diversity from three perspectives: global, latitudinal and grid-cell diversity. Analysis of global generic diversity shows the effect of mass extinctions, particularly after the Late Ordovician mass extinction (LOME) when there was a drastic drop in diversity, but this trough persisted nearly throughout the whole of the Silurian and possibly attributed to positive carbon isotope events which disrupted marine carbon cycles and lowered phytoplankton resiliency. Global trends of origination and extinction rates are correlated with habitat availability. Latitudinal diversity shows the migration of diversity peaks with the changing climate, and a stronger latitudinal diversity gradient was observed for very high polar-tropical temperature differences. The results also showed an out-of-the-tropics scenario for early to middle Paleozoic phytoplankton. Grid-cell diversity revealed the occurrence of phytoplankton diversity hotspots, but further investigation is needed to ascertain causative factors.

For the biogeographic analysis the present author also participated in two studies (submitted and published respectively) with different approaches: a qualitative description of southern Gondwana paleobiogeography during the Floian (part of a study of the Cabrières biota), using taxa to mark provinces; and a quantitative approach to the Famennian (end-Devonian) using multivariate analysis.

For the main work, multivariate analysis was performed on the phytoplankton database to determine biogeographical patterns. Results showed broad differentiation into latitudinal realms; roughly equated to warm-water (equatorial to sub-equatorial) and cold-water (high southern paleolatitudes) assemblages. Provincialism weakened in the Hirnantian, which is attributable to the LOME and the glaciations, but this situation persisted until the late Silurian at the same time there was low global generic diversity. Continental rearrangement in the Devonian fragmented and reconfigured the cold-water realm into several provinces and formed new ones at the margins of the Paleotethys Ocean.

Overall, this thesis shows how various factors can affect the diversity and distribution of phytoplankton. Future work will need to address two main issues: better spatial and temporal representation; and the application of other spatial corrections to better constrain diversification patterns.

Keywords: *acritarchs, biogeography, diversity, macroecology, netromorphs, Paleozoic, phytoplankton*

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CHAPTER 1

INTRODUCTION

Phytoplankton are important and fundamental components of marine ecosystems. They form the base of the marine trophic structure, providing food for micro- and macroscopic consumers. Phytoplankton affects and are affected by changes in the environment. Photosynthetic activity of cyanobacteria transformed life and environments on Earth by triggering the Great Oxygenation Event (GOE, 2.4 Ga; Schirrmeister et al., 2015; Olejarz et al., 2021), changing the composition of our atmosphere and resulting in the deposition of banded iron formations (Konhauser et al., 2002). Marine phytoplankton continues to be a major source of atmospheric oxygen (around half) despite being only around 1% of global plant biomass today (Behrenfeld, 2014). Also, phytoplankton is sensitive to changes in environment and thus indicative of water quality such as those due to eutrophication, when diversity decreases dramatically with nutrient saturation (Bužančić et al., 2016). Furthermore, experiments show species loss with higher temperatures, which can affect ecosystem functioning (Bestion et al., 2020). Therefore, the current global warming scenario due to anthropogenic activities will significantly impact global phytoplankton distribution and has consequences for important areas such as carbon sequestration, fisheries and marine conservation (Ibarbalz et al., 2019). Climate change is by no means a modern event, with multiple occurrences in deep time particularly in the Paleozoic Era, with three mass extinctions linked to global cooling and warming (the end-Ordovician; end-Devonian, and end-Permian mass extinction events). Understanding phytoplankton response in deep time is, thus, crucial to decipher possible future scenarios.

Although modern oceans consist of phytoplankton with organic, calcareous and siliceous tests, only the first type has been preserved in Paleozoic sediments. It is evident that we do not have the full picture of Paleozoic phytoplankton diversity due to taphonomic and sampling biases. The closest possible analogue of acritarchs are dinoflagellates, with which they share superficial morphological similarities. There are also important differences, for example Neoproterozoic and the Paleozoic phytoplankton are speculated to be derived from the green algal lineage (chlorophyll a + b) and were replaced in the Mesozoic and Cenozoic by the red lineage (chlorophyll a + c) which includes the dominant modern groups (Falkowski et al., 2004; Katz et al., 2004). Nevertheless, if acritarchs are phytoplanktonic (or at least most of them), they should have had a similar life cycle to modern dinoflagellates (e.g. Martin, 1993) which also have an organic-walled test; producing fossilizable cysts in their sexual phase. Dinoflagellates also appear to thrive with high diversity in warm, stratified, oligotrophic waters (e.g. Margalef, 1978; Martin, 1996). Modern latitudinal diversity gradients show peak diversity in the equator (Chen et al., 2011). Some modern plankton groups, such as planktonic foraminifera, show biogeographic partitioning along latitudinal regions (Rillo et al., 2022). Thus, it can be hypothesized that Paleozoic phytoplankton behaves like modern-day dinoflagellates: with a cyst-producing life cycle; their diversity and distribution controlled by climate and environmental factors such as temperature and nutrient availability.

Acritarchs are some of the most common microfossils in Paleozoic sediments with proven utility in biostratigraphy, paleoecology and paleoenvironmental reconstructions in extensive investigations since the 1960's, driven by the worldwide need for fossil fuels (see **Fig. 1.1** and **1.2A**). And yet, few studies have viewed them from a macroecological lens to provide insights on the effects of changing environmental conditions in the deep past (e.g. Zacaï et al., 2021). The current global warming scenario is set to alter phytoplankton distribution and reorganize marine assemblages (Benedetti et al., 2021). The Paleozoic Era, which spans almost 290 Ma of earth's history punctuated by climate swings and mass extinction events, may offer clues into how phytoplankton adapt (or not) to an ever-changing world.

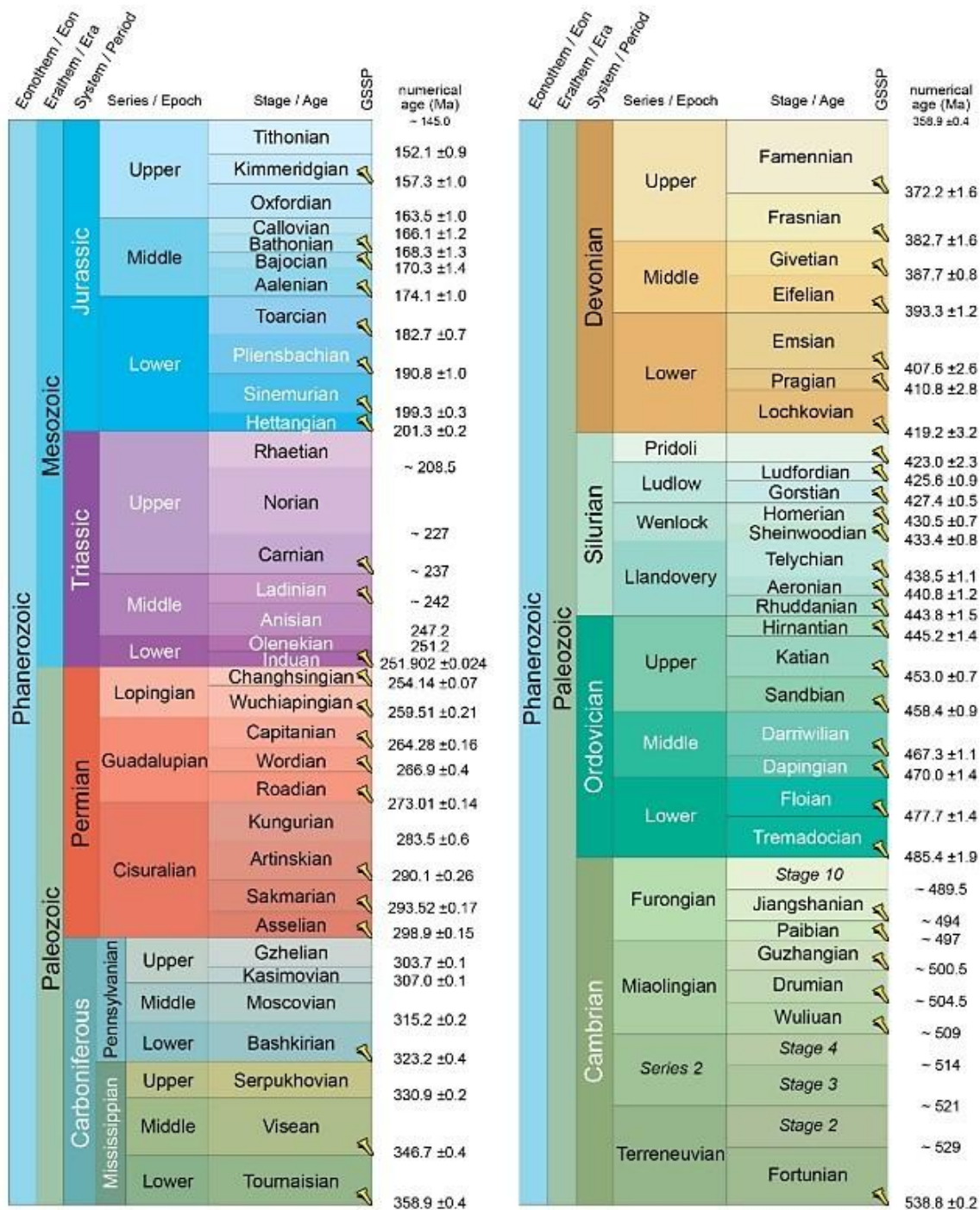


Figure 1.1 The Paleozoic era, 2022/02 version of the International Chronostratigraphic Chart from the International Commission on Stratigraphy (Cohen et al., 2013).

However, the macroecology of acritarchs both in space and time have scarcely been studied in detail and with appropriate quantitative methods. This thesis picks up the tempo set by recent work on acritarch diversity and distribution by Kroeck et al. (2022) and Zacaï et al. (2021), regarding temporal and spatial dimensions, respectively. Kroeck et al. (2022) gathered an exhaustive occurrence database of Paleozoic acritarchs and provided a broad temporal picture (diversity through time) on the trajectory of global acritarch diversity for the entire Paleozoic. Zacaï et al. (2021) complemented the space component of a part of this database and revealed what is perhaps the earliest evidence of the latitudinal diversity gradient of phytoplankton in the Cambrian and Ordovician in a first attempt to understand the spatial

distribution. The main objective of this thesis is to continue to fill the space component (geographic coordinates of occurrences) of this acritarch database, then to determine how the diversity and distribution of phytoplankton evolved and transformed in the early to middle Paleozoic, particularly during intervals of climate change and mass extinction events. The thesis is structured as follows:

Chapter 1 is an introductory chapter presenting the environmental context in the Paleozoic and the state of the art on phytoplankton. Next, **Chapter 2** describes how the present database is constructed, the multivariate statistical methods used and possible biases which can affect diversity counts and biogeographical reconstructions.

An example of this is a taxonomic bias due to improper classification. Some acritarch groups have no established or confusing criteria for classification; while in some cases transitional forms can exist which do not necessarily represent different species. These are explored in two published studies the present author participated in: Manzano et al. (2025) in *Palynology* (attached as **Appendix 1**) and Calero Gordon et al. (2025) in *Palaeogeography, Palaeoclimatology, Palaeoecology* (attached as **Appendix 2**). Manzano et al. (2025) is summarized in **Section 2.2.1**; Calero Gordon et al. (2025) in **Section 2.2.2**. Manzano et al. (2025) reviews the classification of netromorphs, a small acritarch subgroup with relatively simple morphology but with numerous taxa and confusing criteria; here we propose a classification scheme. Calero Gordon et al. (2025) revisits the Middle Ordovician sections of Öland, Sweden; documenting changes in acritarch morphology and assemblages which suggest an environmental response to sea level fall rather than a biostratigraphical signal.

Thanks to the previously established database, **Chapter 3** tracks the evolution of phytoplankton diversity both in space and time. This chapter represents the most innovative part of the thesis, especially because the space component will be addressed both by means of its latitudinal structure and, for the first time, by means of a 2D partitioning with equal-area grid-cells. Then, the resulting diversity patterns are attempted to correlate with possible control factors such as temperature, extinction events and paleogeography.

Chapter 4 reviews and discusses the paleobiogeography of phytoplankton. This historical biogeography is done using either a qualitative approach, based on the occurrence of certain taxa or a quantitative approach, which is based on multivariate analysis. The first approach is discussed in **Section 4.1**, and the latter in **Section 4.2**. I also present a quantitative analysis for the early and middle Paleozoic. The analyses performed during this PhD thesis enabled collaboration on several papers, here attached as **Appendices 3** and **4** and summarized in **Section 4.3**: In **Appendix 3** Caillaud et al. (2025; in prep.) analyzed the acritarch component of the Cabrières Biota in southern France and discusses the implications of the results on biostratigraphy and paleobiogeography. This is also summarized in **Section 4.3.1**; as of writing the work is being prepared for submission to *Lethaia*. In **Appendix 4**: Shen et al. (2025) revisits the phytoplankton content of the Famennian Hongguleleng formation in northwest China in order to establish a biostratigraphical framework for the Gennaren section. Biogeographical affinities were determined using multivariate analysis. The work is published in *Review of Paleobotany and Palynology* and summarized in **Section 4.3.2**. The conclusions and future perspectives from **Chapters 3** and **4** are presented in **Chapter 5**.

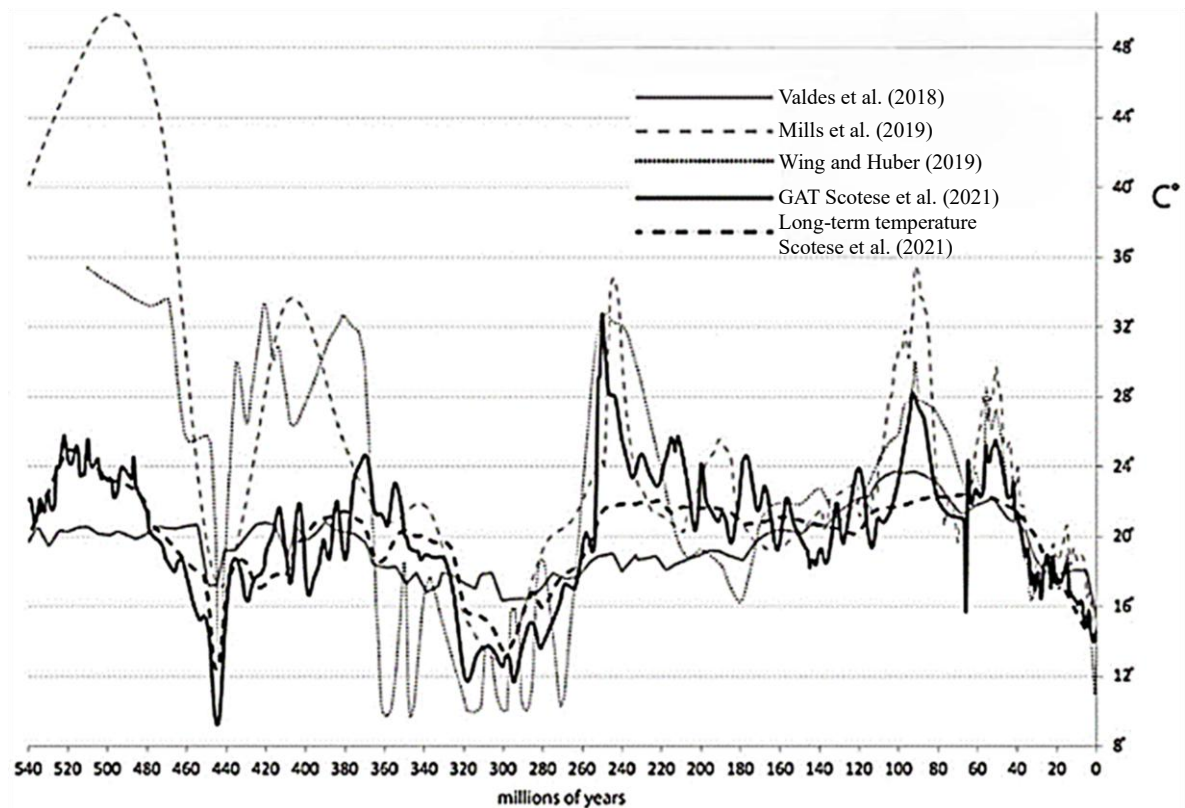


Figure 1.2 Models of global temperatures from several authors (fig. 1 of Scotese et al. 2021 and references therein; slightly modified).

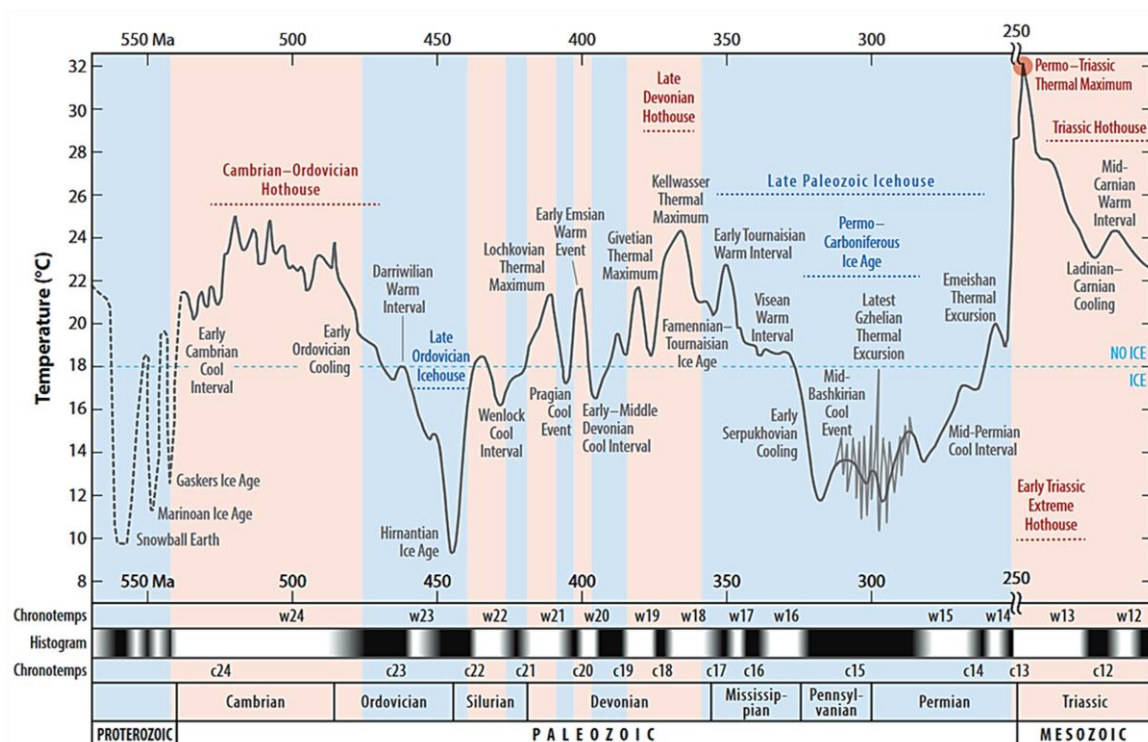


Figure 1.3 Paleozoic global average temperatures (fig. 12 of Scotese et al., 2021).

1.1 Environmental context: the Paleozoic era

The Paleozoic era is an important interval of the Earth's history, spanning nearly 287 million years (**Fig. 1.1**) from the start of the Cambrian (~539 Ma) to the end of the Permian (~252 Ma). The Paleozoic is mainly known for the major biotic events which affected biodiversity: the radiations in the Cambrian (the so-called Cambrian explosion) and the start of the Ordovician (the Great Ordovician Biodiversification Event, GOBE); and the three major extinctions at the end-Ordovician, Late Devonian and the end-Permian. In contrast to modern-day, most of the continents are clustered in the southern hemisphere from the Cambrian to the Silurian, with the northern hemisphere occupied by the Panthalassic Ocean. In the Devonian and the Carboniferous the continents gradually started to merge, culminating in the formation of the supercontinent Pangea by the end of the Permian. The climate was warmer than present-day in the early Paleozoic and started to cool to modern-day levels by the Middle Ordovician until the Hirnantian glaciations; rising steadily again until the end of the Devonian before cooling down again.

1.1.1 Paleoclimate

Paleotemperature estimates are obtained using the ratio of oxygen isotopes ^{18}O and ^{16}O (also known as $\delta^{18}\text{O}$) from apatite or carbonate microfossils, which is controlled by the water temperature in which the shell was formed. For example, ^{18}O decreases by 0.1‰ per 4.3°C rise in temperature in benthic foraminifera (Epstein and Mayeda, 1953). The oxygen isotope record is highly biased towards the tropical areas (with a scarcity of data in latitudes higher than 40° N and S), reflecting tropical rather than global temperatures; recent studies therefore adjust the isotopic temperatures or use non-isotopic information to account for the difference (see **Fig. 1.2** for examples of adjusted Phanerozoic temperature curves). The range of climate belts (Köppen, 1918) can also be mapped using various lithologic indicators such as bauxites and laterites (which form in tropical to subtropical wet climates), caliche (semi-arid areas), glacial deposits, glendonite (a CaCO_3 polymorph which forms at near freezing conditions), etc. Long-term global temperatures are controlled by three main factors (e.g., Scotese, 2021): the level of greenhouse gases in the atmosphere (primarily CO_2), the paleogeographic configuration of continents and the albedo effect of the earth's surface.

The trend of Paleozoic global temperatures is shown in **Fig. 1.3**. Scotese et al. (2021) divided the Phanerozoic Eon into eight climate modes which consist of 3-4 pairs of warming and cooling episodes. In the Paleozoic the Cambro-Ordovician (458-541 Ma) and the Siluro-Devonian (365-426 Ma) represent “hothouse” periods while the Late Ordovician-Silurian (426-458 Ma) and the Late Paleozoic (253-365 Ma) are “icehouse” periods (characterized by the presence of permanent ice caps at one or both poles). There is a large uncertainty for the maximum temperature estimates of the Cambro-Ordovician hothouse due to varying interpretations of the $\delta^{18}\text{O}$ values, ranging from > 50°C (Bergmann et al., 2018) to > 40°C (based on near polar phosphatic euconodonts, (Wong Hearing et al., 2021) to cooler 28-32°C. The latter “cool” scenario is consistent with the zonation of “Bahamian-type” carbonate reefs in the low latitudes and archaeocyaths in the tropics and subtropics (McKerrow et al., 1992); latitudinally controlled trilobite provinces (Cocks & Fortey, 1990; McKerrow et al., 1992); and the identification of unweathered mica flakes in the polar and temperate latitudes which indicate cooler climatic conditions in these areas (Boucot et al., 2013). Temperatures lowered further to 26-32°C (Trotter et al., 2008) in the Middle Ordovician, coinciding with the Great Ordovician Biodiversification Event (GOBE), then culminating in the Hirnantian glaciation with the formation of a southern ice cap in Gondwana during the Late Ordovician-Silurian

icehouse. There was no equivalent ice cap on the north pole due to the absence of a landmass, preventing a “Snowball Earth” scenario (Scotese et al., 2021). Warm, shallow-water tropical faunas were replaced by cosmopolitan planktic or cool-water benthic taxa (Sheehan, 2001).

The Silurian-Devonian hothouse spans the early Ludlow to the early Lochkovian. No permanent polar ice caps were present even during the cool intervals (Boucot et al., 2013). The cool interval in the Pragian coincides with a widespread sea-level fall; while a late Givetian warming corresponded with the Taghanic onlap (Brett et al., 2009), initiating a global transgressive cycle with the highest sea levels in the late Frasnian (Haq and Schutter, 2008). Early Devonian to Eifelian climate was “moderate” with a climatic gradient, evidenced by unweathered mica in the high southern latitudes of Gondwana and the presence of cool-water Malvinokaffric fauna (Boucot et al., 2013), and the absence of warm water conodonts (Girard et al., 2005) and stromatoporoid reefs (Stock, 2005) in the temperate shallow seas of Gondwana. The Malvinokaffric fauna was replaced by warm-water taxa with rising global temperatures in the Frasnian and Famennian (Stock, 2005). A major mass extinction event (the combined early and late Kellwasser Events) occurred in the Frasnian-Famennian.

The remaining part of the Paleozoic was subjected to an icehouse starting in the latest Devonian, interrupted by brief warming events in the Mississippian, latest Pennsylvanian and late Permian (Scotese et al., 2021). Global average temperatures ranged from 13°C during the Permo-Carboniferous Ice Age to ~22°C in the early Tournaisian Warm Interval. Polar ice caps were generally present (except for warm events), but the southern ice caps disappeared when temperatures started warming in the middle Artinskian (285 Ma). By the beginning of the Mesozoic the average tropical temperatures are ~40°C. This warming may have triggered the largest known extinction event, the Permo-Triassic mass extinction.

1.1.2 Paleogeography

Reconstructing paleogeography can be extremely challenging the further one goes back in time, with greater discrepancies between various global plate models (GPMs) in the Paleozoic (especially > 300 Ma) compared to the rest of the Phanerozoic (Buffan et al., 2023). This affects paleobiological analyses, such as paleobiogeographical distributions and the latitudinal diversity gradient (see Jones et al., 2025 in press). While paleolatitude can be reconstructed using paleomagnetic data and climatically sensitive lithological (the occurrence of bauxite, glacial deposits, etc.) and biological (such as coral reefs for example) indicators, paleolongitude is far less constrained (Vérard, 2019). Buffan et al. (2023) recommends the use of GPMs with paleomagnetic reference frames. While a review of the GPMs is beyond the scope of this paper (see Buffan et al., 2023 and Jones et al., 2025 in press for recent assessments of the various GPMs), we use the PALEOMAP model of (Scotese and Wright, 2018). Phanerozoic paleogeography is discussed in detail by Scotese (2021) and the Paleozoic is summarized herein (see also **Fig. 1.4**).

At the end of the latest Precambrian (~600 Ma) the continents are massed into a supercontinent called Pannotia (fig. 9 of Scotese, 2021 p. 699), which is centered on Gondwana (Africa, South America, Madagascar, India, Antarctica, Australia and Arabia). Northern Pannotia (which is in the northern hemisphere) consists of Cathaysia (North and South China), Indochina, Cimmeria, India and Antarctica. East and south of Gondwana are Laurentia, Baltica and Siberia. By the start of the Cambrian Pannotia was already breaking apart, forming new oceanic basins such as the Iapetus and the Rheic oceans.

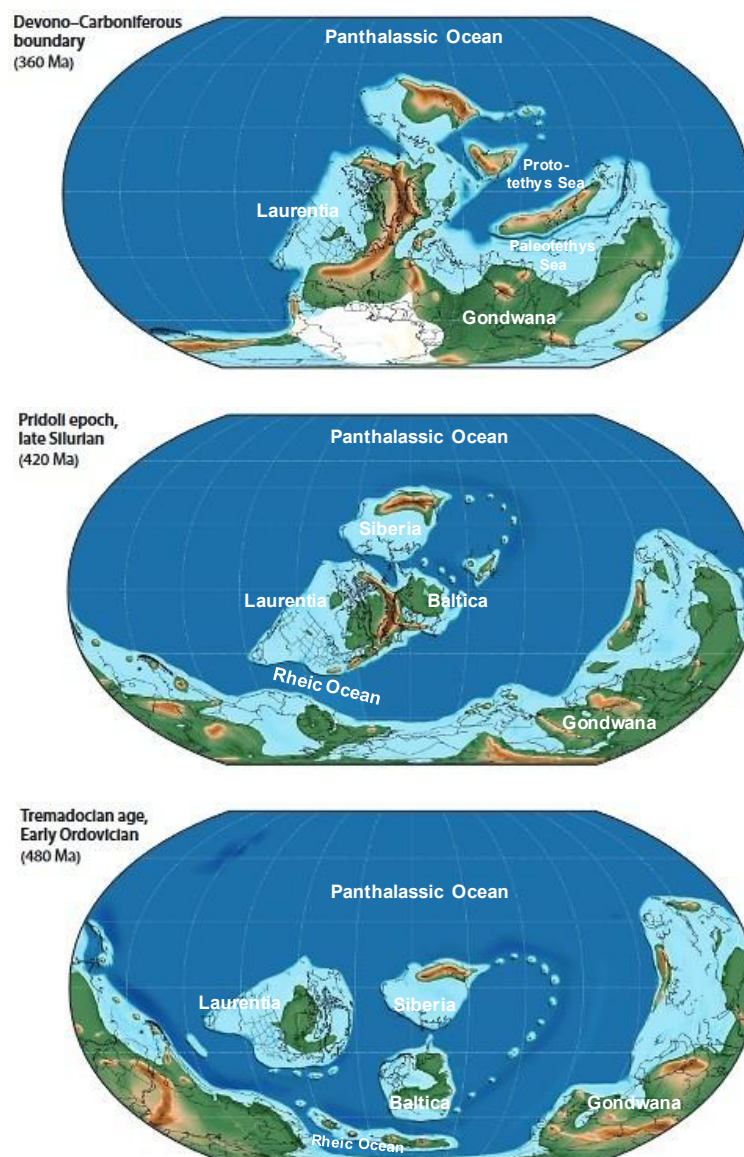


Figure 1.4 Paleogeography of the Paleozoic (modified from Scotese, 2021).

During the Cambrian and Ordovician, Australia, South China and Malaysia were situated in the northern hemisphere which is by ~90% dominated by the Panthalassic Ocean (fig. 10 of Scotese, 2021 p. 701). Gondwana occupies the South Pole and is oriented in a north-south direction (**Fig. 1.4**). Because of this orientation it is not easy to designate “western” or “eastern” Gondwana; but here the South American side can be referred to as “southwestern” Gondwana and to the southern European-North African side as “southeastern” Gondwana. Avalonia borders Gondwana near the south pole. Located North of Avalonia was Baltica, while parts of Laurentia and Siberia straddle the equator. Baltica and Laurentia moved northwards towards the equator and merged with Laurentia, closing the Iapetus Ocean by the latest Silurian (fig. 10 of Scotese, 2021 p. 702). Siberia and Kazakhstania were also drifting northward. Southeastern Laurentia and northwestern South America starting colliding in the Early to Middle Devonian, and by the latest Devonian the Rheic Ocean separating them had been closed (fig. 10 of Scotese, 2021 p. 702).

In the early Carboniferous the continents Gondwana, Laurentia, Baltica and Siberia are consolidating to form the western part of Pangea, while to the east Kazakshtania, Amuria, the

Urals and Cathaysia were separated by oceanic basins (fig. 14 of Scotese, 2021 p. 705). Pangea continued drifting northward into the early Permian while the eastern terranes merged. Southern Africa occupied the South Pole with no equivalent landmass in the northern polar latitudes until the end of the Permian, when northeastern Siberia crossed the Arctic Circle. By the end of the Permian and the start of the Triassic the eastern part of Pangea is marked by the Paleotethys Sea bounded by Cimmeria to the north, Arabia to the west with India and Australia to the south; and the Neotethys Sea north of Cimmeria with Cathaysia to the east and opening to the Panthalassic, and a narrow seaway to the west bordered by Europe and the Iranian segment of Cimmeria (fig. 14 of Scotese, 2021 p. 705).

1.1.3 Biotic radiations and crises

The early Paleozoic is marked by two major marine bioradiations (see **Fig. 1.5** for the major biotic events of the early Paleozoic), the Cambrian explosion and the Great Ordovician Biodiversification Event (GOBE), that are possibly belonging to a single long-term radiation (Servais et al., 2023). The Cambrian Explosion is possibly an extension of a recovery (represented by the Nama Biota) after a major extinction in the Ediacaran (Darroch et al., 2018). The Cambrian Explosion is characterized by the origin of bilaterian phyla (Smith and Harper, 2013; Harper et al., 2019) such as ecdysozoans (arthropods and related groups), deuterostomes (echinoderms and hemichordates) and lophophorates (brachiopods, molluscs and bryozoans) in contrast to simpler metazoans dominating the Ediacaran such as rangeomorphs and possibly cnidarians and sponges. Furthermore, there was a substrate revolution (Bottjer et al., 2000) with the typical Ediacaran microbial seafloor mats giving way to bioturbation with the evolution of burrowing organisms; dramatically changing the oxygenation and redox environment of the shallow marine substrate (Canfield and Farquhar, 2009). Marine invertebrate radiation roughly correlates with those of phytoplankton in Stage 3 (see fig. 10 of Nowak et al., 2015), though this could be the result of increased sampling (Nowak et al., 2015). The end of the Cambrian is marked by the so-called Furongian Biodiversity Gap (Harper et al., 2019), which appears clearly to be an artifact due to lack of examined material. This was followed by the GOBE, an “explosion” in diversity in the Early to Middle Ordovician which occurred over a more or less long time depending on the interpretation (Servais et al., 2023). Although the Cambrian “explosion” and the Ordovician “biodiversification” were traditionally considered to be distinct “events,” recent review of early Paleozoic marine diversities show possibly only a single long-term radiation which started in the Precambrian possibly triggered by the breakup of the supercontinent Pannotia (Servais et al., 2023).

Regarding the phytoplankton, new morphotypes appeared with the rise in diversity, such as the diacromorphs and galeate acritarchs (Servais et al., 2008, 2016, 2023). Increased phytoplankton availability in the late Cambrian-Early Ordovician triggered a diversification of zooplankton and suspension feeders (Servais et al., 2008). Important paleocological changes include the transition from trilobite-dominated Paleozoic evolutionary fauna to suspension-feeder dominated ones, evolution of deep-mobile burrowers, above-substrate tiering and the formation of reefal communities around corals and stromatoporoids (Bottjer et al., 2000).

After the long-term radiation in the Cambrian and Ordovician, three major mass extinction events and several minor biotic crises occurred in the Paleozoic. The first of the so-called “Big Five” extinctions is the Late Ordovician Mass Extinction Event (LOME). Based on some diversity counts, it is the second most severe mass extinction which eliminated almost 90% of marine invertebrate species, up to 61% of genera and nearly 30% of families (Jablonski, 1991; Sepkoski, 1996; Sheehan, 2001; Harper, 2010). According to some authors, the LOME

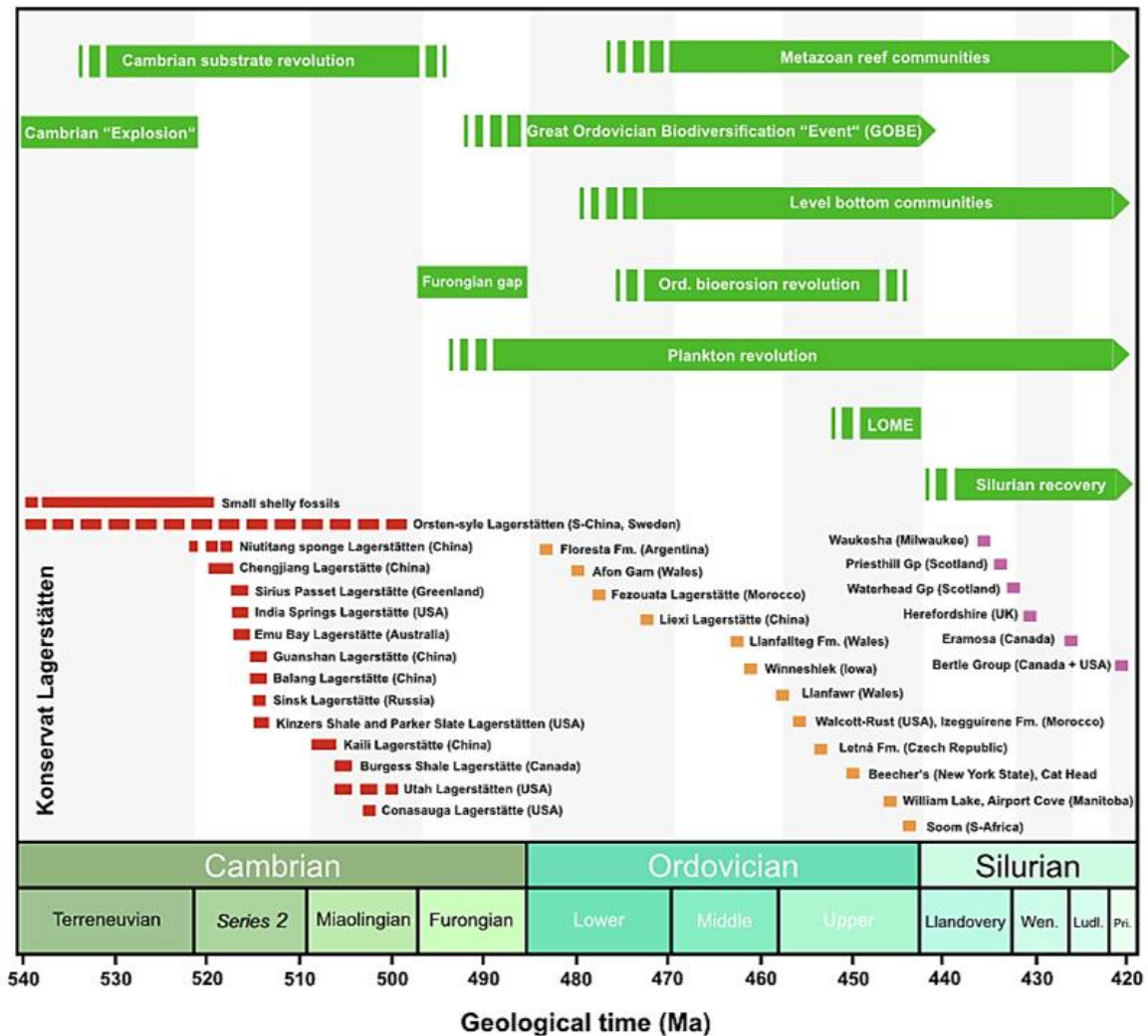


Figure 1.5 Major biotic events in the early Paleozoic and the stratigraphic position of major lagerstätten sites (fig. 1 of Servais et al., 2023).

occurred in two pulses (Brenchley et al., 1994). The first pulse is dated to the *N. extraordinarius*-*N. osjuensis* graptolite Zone (~445 Ma) at the onset of the end-Ordovician glaciations, which affected planktonic species such as graptolites and nekton. The speculated kill mechanisms include changes in global oceanic temperature linked to rapid cooling, and increased oxygenation which may have reduced the habitat for eutrophic graptolites and dysoxic deep-dwellers (Sheehan, 1988; Stanley, 1988; Berry et al., 1990; Skelton, 1994; Brenchley et al., 2001; Finnegan et al., 2011; Algeo et al., 2016). Marine anoxia has also been invoked by some authors (Goodfellow and Jonasson, 1984; Zhang et al., 2009). The second phase occurred in the late Hirnantian during the *Metabolograptus perscultus* Zone (~444 Ma) at the end of the glaciations and a corresponding rise in sea-level (Rong, 1984; Rong et al., 2002; Nielsen, 2004; Fan et al., 2009; Harper et al., 2014). Conodonts and cool-water specialists were nearly wiped out; leaving simple ecosystems (Brenchley et al., 2001; Sheehan, 2001; Rong et al., 2002; Zhan et al., 2010). Sea-level rise aided the spread of marine anoxia onto continental shelves (Rong and Harper, 1988; Brenchley et al., 2001; Melchin et al., 2013), which limited the supply of fixed nitrogen (LaPorte et al., 2009; Melchin et al., 2013; Luo et al., 2016) and further affected the already stressed graptolites (Bond and Grasby, 2017).

Marine life recovered after the LOME in the Silurian but the period is marked by three minor extinctions: the Ireviken, Mulde and Lau events (Bond and Grasby, 2017). The Ireviken Event occurred at the Telychian-Sheinwoodian boundary which affected graptolites, conodonts

and trilobites but not shallow-water reefs (Calner, 2008). Marine anoxia is a leading cause (Munnecke et al., 2003; Smolarek et al., 2017). The Mulde and Lau Events occurred in the Ludlow and involve a minor extinction in conodonts and graptolites (Jeppsson & Aldridge, 2000; Jeppsson and Calner, 2002; Loydell and Frýda, 2007). These two events coincide with eustatic sea-level falls and positive carbon isotope events (Samtleben et al., 2000). Jeppsson and Calner (2002) suggest that these extinctions were caused by starvation of planktonic larvae in non-coastal settings due to a reduction in primary phytoplankton productivity.

Transgressive events during the Devonian facilitated marine anoxic pulses which also triggered several biotic crises (Bond and Grasby, 2017). These include the Zlichov and Daleje Events in the Emsian; the Chotec Event at the Emsian-Eifelian boundary; the Kačák Event of the Eifelian and the Taghanic Event in the Givetian. These minor events affected goniatitic ammonites. Around 75% of them went extinct at by the end of the Emsian events (Walliser, 1996). The Kačák Event also affected conodonts and tentaculitids (House, 1996; DeSantis and Brett, 2011). The Taghanic Event wiped out Devonian reefs of low-latitude corals and stromatoporoids and other benthic groups such as brachiopods (House, 1985; Ebert, 1993; Walliser, 1996). The biotic crisis of the Late Devonian at the Frasnian-Famennian boundary, ranks among the largest in terms of “ecological severity” (McGhee et al., 2013). The Kellwasser Events also occurred at this time (Beard et al., 2017). Similar to the Taghanic Event the reefs were once again affected, but they never fully recovered (Kiessling et al., 2000; Copper, 2002). Terrestrialization may have amplified the Kellwasser Events, with the increased diversity of deep-rooted plants in the Middle to Late Devonian leading to enhanced weathering and runoff, which caused eutrophication and eventually marine anoxia (Algeo et al., 1995; Algeo and Scheckler, 1998). The ultimate cause seems to be large-scale volcanism associated with the formation of the Viluy Traps in Siberia and the Pripyat-Dnieper-Donets rift system in southeastern Europe, which affected global climate patterns (Bond and Grasby, 2017). The final anoxic event in the Devonian is the Hangenberg Crisis at the end of the Famennian, which showed high extinction rates in trilobites, conodonts, brachiopods, cephalopods and corals (Paproth et al., 1991; Becker et al., 2016). It is possibly at par with the Frasnian-Famennian extinction with the loss of 21% of marine genera and 16% of families (Simakov, 1993; Sepkoski, 1996).

Two huge mass extinction events punctuated the late Paleozoic. The first is the Capitanian mass extinction in the Middle Permian, which has been previously lumped with the end-Permian but was recognized by Stanley and Yang (1994) and Jin et al. (1994) as a separate event. Around 62% of species and 33-35% of genera went extinct, making it the fourth largest biotic crisis in terms of magnitude (Stanley, 2016) and a contender to be one of the “Big Five.” The Capitanian extinction saw losses not just in the marine realm with ammonoids, foraminifera, sponges, corals, bryozoans, brachiopods and bivalves (Jin et al., 1995; Wang and Sugiyama, 2000; Weidlich, 2002; Isozaki, 2009; Bond et al., 2010a) but also in plants and tetrapods (Bond et al., 2010a; Lucas, 1998, 2009). A possible trigger is the volcanism associated with the Emeishan Large Igneous Province in South China (Bond and Grasby, 2017). Proposed kill mechanisms include cooling (Isozaki et al., 2007); photosynthetic shutdown (Bond et al., 2010a,b); ocean acidification (McGhee et al., 2013); marine anoxia (Bond et al., 2015); and toxic metal poisoning (Grasby et al., 2015). The end-Permian event is thus generally considered the largest mass extinction in geologic history with ~90% marine species lost (Erwin, 1994), widespread terrestrial losses (e.g., Retallack, 1995; Smith and Ward, 2001) and the only mass extinction of insects ever recorded (Labandeira and Sepkoski, 1993). The timing is still equivocal with some authors considering a diachronous or multiphase extinction event (e.g. Xiong & Wang, 2011; Song et al., 2012) but regardless, there was extensive damage to both marine and terrestrial ecosystems in a short amount of time (Bond and Grasby, 2017). The

proposed kill mechanisms include global warming, anoxia, acidification on land and in the oceans, ozone depletion and toxic metal poisoning may be ultimately linked to volcanism associated with the Siberian Traps (see Bond and Grasby, 2017 and references therein).

1.1.4 Carbon isotope events

Carbon isotope excursions (CIE) are sudden, abrupt changes in the carbon isotope ratios ($\delta^{13}\text{C}$) recorded in marine carbonates and/or organic carbon deposits. Positive excursions are typically attributed to changes in primary productivity; with high primary production leading to accumulation of organic material which can cause anoxic events (Meyer and Kump, 2008) and deposition of black shales (Algeo and Scheckler, 1998; Delabroye and Vecoli, 2010; Stricanne et al., 2006; Gill et al., 2011). Not all positive CIEs are associated with high production; for example Stricanne et al. (2006) recorded a decrease in acritarchs and prasinophytes in the Lau event while Bickert et al. (1997) argued that the Ludfordian positive CIE amplitude is too high to be explained by greater primary productivity. These CIEs might have been related to humid-arid climate cycles in low-latitudes, where high $\delta^{13}\text{C}$ corresponds to arid conditions while with low terrestrial input and decreased productivity; while a humid climate promotes stratification and increased transport of terrestrial to the sea, which results in higher marine productivity and lower $\delta^{13}\text{C}$. Some positive CIEs coincide with extinction events such as the Steptoean Positive Carbon Isotope Event (SPICE) which caused an extinction of trilobites in the early Paibian (Gill et al., 2001) and the Ireviken, Mulde and Lae events mentioned above (**Section 1.1.3**). While negative CIEs can also be linked to changes in primary production as just stated, the causative factors are less understood and may be actually controlled by local depositional settings, diagenetic alteration and authigenic carbonate formation (Wu et al., 2022 and references therein). These are also correlated with extinctions and turnover, for example the Redlichiiid – Olenellid Extinction Carbon Isotope Excursion (ROECE) marks severe generic-level losses for the two namesake trilobite groups (Fagetter et al., 2017).

CIEs appear to influence phytoplankton diversity. High species turnover rates correlate with CIEs from the Cambrian to Silurian and from the Late Devonian to early Carboniferous (Kroeck et al., 2022) while new acritarch morphotypes appeared during the SPICE (Servais et al., 2008; Shan et al., 2022). The LOME also coincided with a strong positive CIE (Brenchley et al., 1995; Paris et al., 2000), which saw a major decline in phytoplankton diversity. Acritarch abundances also decreased during the Lau event in the late Silurian (Stricanne et al., 2006).

1.2 State of the art: Paleozoic phytoplankton

1.2.1 Definition, morphology and classification

Modern marine phytoplankton arose in the Mesozoic and consists of three main groups: the diatoms, coccolithophores and dinoflagellates (Webb, 2021). They roughly correspond to the siliceous, calcareous and organic-walled fractions commonly found in recent sediments and preserved as microfossils. For the Paleozoic the organic-walled fraction is the best preserved in the fossil record, little is known about the other fractions (e.g. Munnecke and Servais, 2008) and the smaller organisms such as pico- and bacterioplankton phytoplankton are largely unknown, because they are usually not studied by micropalaeontologists because of their reduced size. The two main groups present in the fossil record and considered as phytoplankton

in the Paleozoic are therefore the acritarchs and the prasinophytes (Martin, 1993; Playford, 2003; Martin et al., 2008).

Acritarchs were originally defined by Evitt (1963) as “small microfossils of unknown and probably varied biological affinities consisting of a central cavity enclosed by a wall of single or multiple layers and of chiefly organic composition; symmetry, shape, structure, and ornamentation varied; central cavity closed or communicating with the exterior by various means, for example: pores, a slitlike or irregular rupture, a circular opening (the pylome: see **Fig. 1.6**).” This informal group is considered “*incertae sedis*”, carved out from a larger grouping called the “Hystrichospheres” which formerly contained the organic walled microfossils with a central body and appendages (hystrichospheres: “spheres with spines”), a name coined by Otto Wetzel in 1963 (Playford, 2003). Evitt (1961) provided evidence that some Mesozoic and Cenozoic hystrichospheres are dinoflagellate cysts (Evitt, 1961). The remainder of the hystrichospheres that are not related to the dinoflagellate cysts were subsequently placed by Evitt (1963) in the artificial group of the acritarchs. Acritarchs, by definition, are polyphyletic (“probably varied biological affinities”), and despite the ambiguity of biological origin it is possible that most are actually phytoplankton cysts (Martin, 1993; Strother, 1996; Playford, 2003; Martin et al., 2008). Prasinophytes, on the other hand, are a primitive group of green algae which are still extant. Some acritarchs have been considered to be fossil prasinophytes, but these affiliations remain partly debated. In general prasinophytes have a motile and non-motile stage in their life cycle, with the non-motile stage producing cysts called phycoma, which are commonly fossilized. However, there are no satisfactory nor adequate criteria to distinguish between acritarchs and fossil prasinophyte phycoma (Fensome et al., 1990; Guy-Ohlson, 1996), hence they are considered here together as a single group (see **Fig. 1.7A** for examples of acritarchs).

Since the biological affinities of the acritarchs are unknown, their taxonomic classification is mainly based on morphology (see **Fig. 1.7B**). Various authors proposed different schemes (Downie et al., 1963; Evitt, 1969; Diver and Peat, 1979; Tappan, 1980) but the most widely accepted is that of Downie et al. (1963). Some of the subgroups include sphaeromorphs (simple spheres), acanthomorphs (spherical, with processes), netromorphs (fusiform outline), polygonomorphs (polygonal shape), oomorphs (egg-shaped with a possible ornamentation of small spines or tubercles), prismatomorphs (polygonal vesicle with flanges), diacromorphs (having two distinct polar areas with ornamentation), herkomorphs (spherical to subpolygonal vesicle subdivided into polygonal fields) and pteromorphs (spherical to

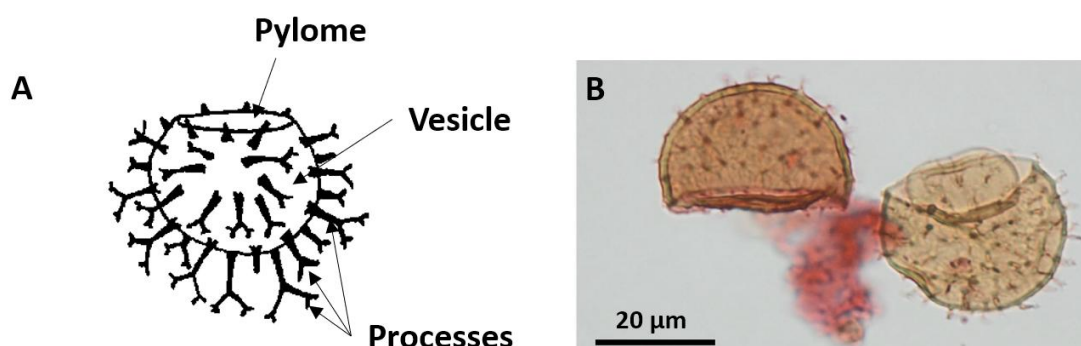


Figure 1.6 General morphology of an acritarch. (A) shows the basic morphology of a galeate acritarch *Priscogalea* sp. (from Servais et al., 2004). (B) are examples of *Priscogalea* in light photomicrographs (Agić et al., 2016), the specimen on the right shows an operculum hanging from the pylome.

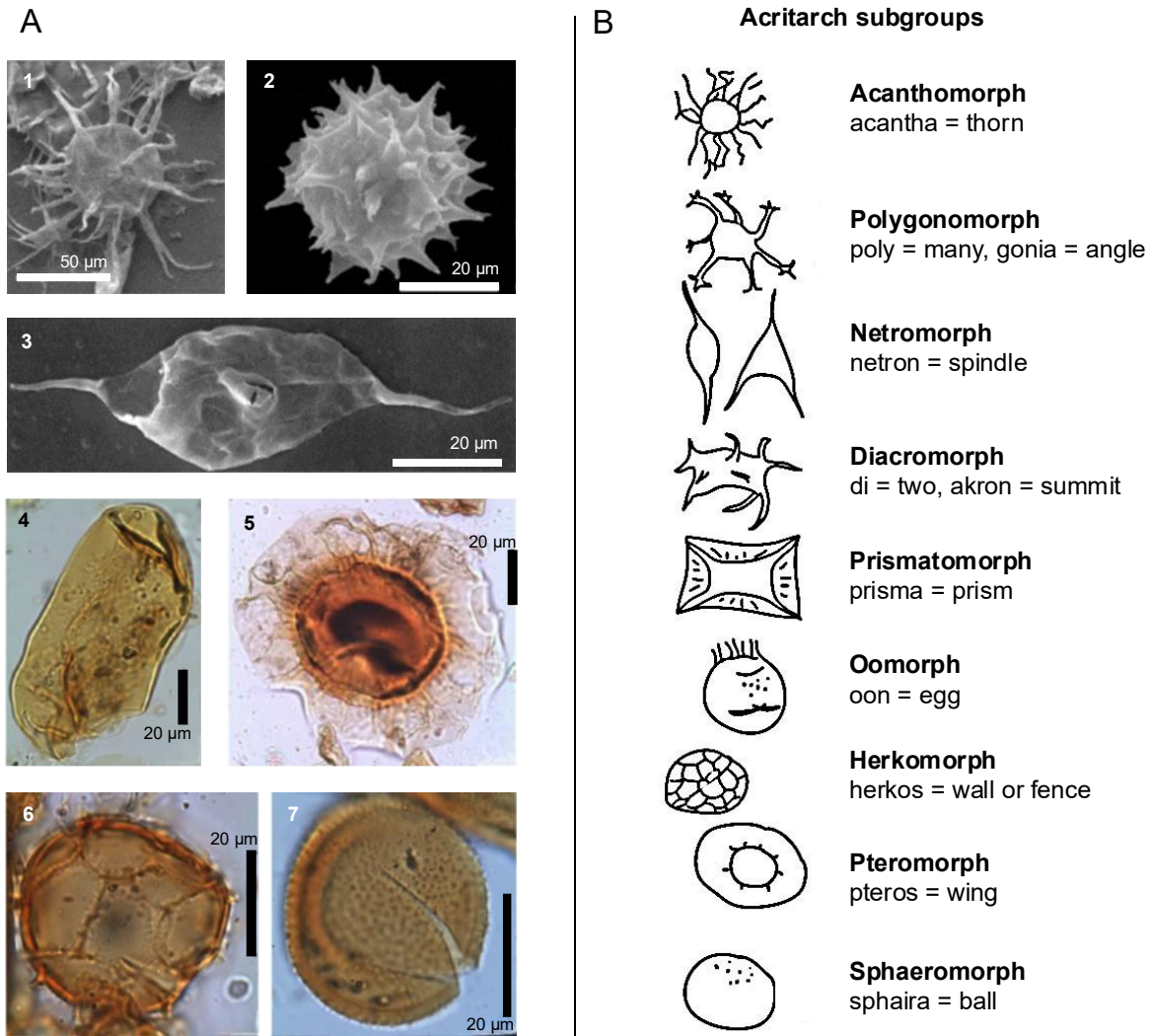


Figure 1.7 Examples of acritarchs (A) and the main subgroups of Downie et al. (1963) (B). In (A), 1-3 are SEM images of the following: *Baltisphaeridium* sp. aff. *B. aspersilumiferum* Tappan & Loeblich 1971, *Micrhystridium parinconspicuum* Deflandre 1945, *Leiofusa granulicatis* Loeblich 1970 forma *quincunx* Uutela 1989. 4-5: *Navifusa* spp. sensu García Muro et al. 2022, *Pterospermella crassimarginata* García Muro et al. 2022, *Polyedryxium carnatum* Playford 1977, *Filisphaeridium muscosum* (Wicander & Playford) Sarjeant & Stancliffe 1994. 1,3 are from Delabroye et al. (2011), 2 is from Stricane (2004), 4-7 from García Muro et al. (2022). (B) is modified from <https://www.ucl.ac.uk/GeolSci/micropal/acritarch.html>.

elliptical shape with a wing typically in the equatorial region). A split in the vesicle wall may be present, which could represent excystment (Strother, 1996). This could be a simple straight lateral or median rupture, a circular suture, called a pylome, which can have a plug or a lid known as the operculum, a split of trochospiral orientation or circinate (slightly offset, circular suture with an attached operculum). These structures are not very common, and thus are not commonly used in classification.

1.2.2 Are acritarchs dinoflagellates?

Acritarchs and dinoflagellates were originally classified together under the hystriospheres. Evitt (1961, 1963) demonstrated that majority of the post-Paleozoic hystriospheres are actually fossilized dinoflagellate cysts which formed during the motile stage, with the motile cell not preserved. Evitt (1961,1963) outlined the following features of a dinoflagellate: presence of a transverse furrow, with or without a longitudinal one; evidence

of tabulation (inferred from alignment of ornamentation or processes); presence of an archeopyle (excystment opening); and a “peridinioid” outline or the overall shape. Fossil diversity is likely underestimated: only about 15% of extant dinoflagellates are known to create fossilizable cysts and sometimes the cysts are not robust enough to be preserved geologically (Head, 1996). Dinoflagellates are known almost exclusively from the Mesozoic onwards (Fensome et al., 1996) but molecular clock and biomarker evidence suggest their lineage diverged around 650 Ma in the Neoproterozoic (Moldowan and Talyzina, 1998). However, there is no unequivocal dinocyst from the Paleozoic. Previously reported forms such as *Arpylorus antiquus* from the upper Silurian of Tunisia (Calandra, 1964) are not dinocysts but could instead be a storage structure or part of the anatomy of eurypterids or phyllocarid crustaceans (Le Herissé et al., 2012). Attempts to apply dinoflagellate morphological criteria to acritarchs to elucidate possible ancestral relationships were not successful (e.g. Lister, 1970). It is possible though that some acritarchs belong to extinct (proto?) dinoflagellates which do not necessarily display the criteria set by Evitt (1961, 1963 in Martin, 1993). Recent work by Meyvisch (2023) used Fourier-transform infrared (FTIR) spectroscopy to analyze the molecular composition of palynomorphs; comparison with other organic microfossils show that some Paleozoic acritarchs exhibit affinities with prasinophytes and dinocysts.

Aside from dinoflagellates, some workers also suspect a euglenid or fungal origin for some acritarch taxa such as *Moyeria* and *Strophomorpha*, respectively (Gray and Boucot, 1989). Analysis of the cell wall structure suggest similarities between Ordovician-Silurian *Moyeria* and extant euglenids (Strother et al., 2020). Others maybe fossilized eggs, such as the Ordovician acritarch *Baltisphaeridium spinigerum* which resembles those of the copepod *Centrophages hamatus* (Jan De Coninck, oral comm. in Martin, 1993). In addition, some other acritarchs are possibly related to land plant derived spores (Navidi-Izad et al., 2022). Acritarchs are thus clearly polyphyletic. More recently, some acritarch morphotypes have been related to fragments of animals, such as teeth of priapulid worms (Shan et al., 2023) or to loricate protists (Green et al., 2025). Not all acritarchs are thus related to phytoplankton.

1.2.3 Paleoeecology

The diversity and distribution of acritarch assemblages appear to be influenced by the environment. In a study of the Middle and Upper Ordovician sequences near Cincinnati, USA Jacobson (1979) identified a *Leiosphaeridia*-dominated assemblage nearshore; peteinosphaerid-*Dicommopalla* assemblage at the “shoal environment”; while the deeper water assemblage consist of acanthomorphs and polygonomorphs. Dorning (1981) analyzed the acritarch distribution in the Gorstian and Ludfordian shelf deposits of South Wales and the Welsh Borderland in the UK (see **Fig. 1.8**). Nearshore, offshore shelf and deep-water assemblages were identified. Nearshore assemblages have low diversity and low to moderate abundance, characterized mainly by sphaeromorphs. Thin-walled species of *Protoleiosphaeridium* are common. Offshore shelf assemblages have a high diversity and moderate abundance, with no dominant taxon. *Micrhystridium* forms have longer processes compared to inshore forms, while *Verhachium* species with four to six processes are more common than those with three. *Multiplicisphaeridium* is most diverse offshore. Deep water assemblages, like those of the nearshore environments are generally of low diversity and dominated by sphaeromorphs. *Protoleiosphaeridium* is also common, but they have thick walls. Dorning and Bell (1987) also noted morphological changes in some taxa from observations on other Paleozoic carbonate platforms. In general, sphaeromorphs have thin walls nearshore compared to offshore, and processes become longer and more branched or

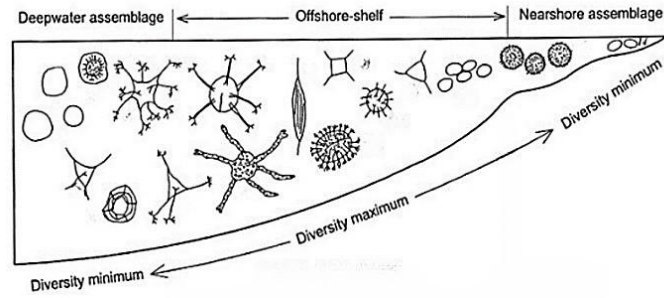


Figure 1.8 Acritarch facies in the Silurian, showing changes in acritarch morphotypes and assemblages from nearshore to deep water in Ludlovian assemblages (adapted from Dornig, 1981).

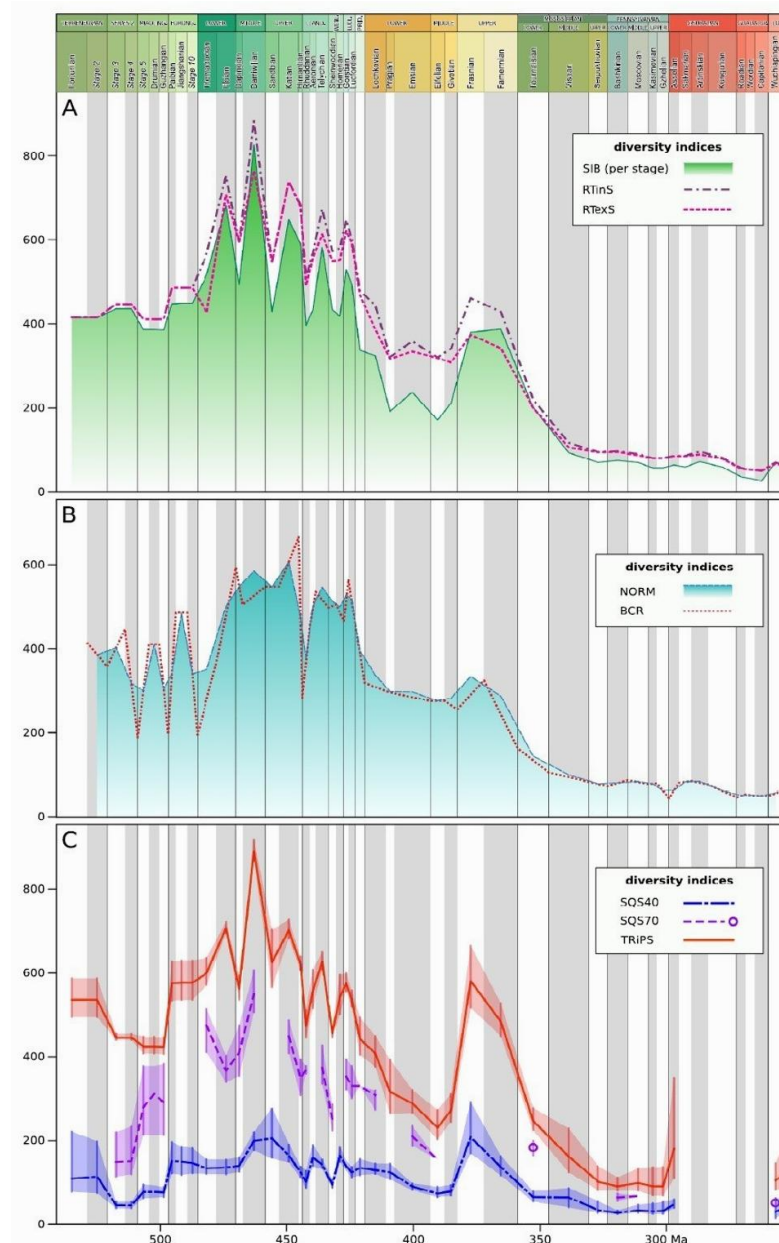


Figure 1.9 Global diversity of Paleozoic phytoplankton (fig. 1 of Kroeck et al., 2022). (A) shows standing in bin diversity (SIB), range-through including and excluding singletons (RTinS and RTexS respectively). (B) plots normalized diversity and boundary crossers while the indices in (C) use shareholder quorum sampling at $q = 0.4$ and 0.7 (SQS40, SQS70), and Poisson-based resampling.

complex from inshore to offshore. Li et al. (2004) worked on the Early to Middle Ordovician sections in southern China, which represent different environments of the Yangtze platform from nearshore to offshore settings. Recovered assemblages also showed low diversity nearshore and higher diversity offshore; the composition also changed with simple morphologies (leiosphaerids, micrhystrids and fusiforms) nearshore to longer and more complex branched processes (e.g. *Baltisphaeridium*, *Peteinosphaeridium*) offshore. Similarly, in the same special issue Stricanne et al. (2004) investigated a Gorstian (late Silurian) inshore-offshore transect from Gotland, Sweden, known for exceptional preservation of palynomorphs (Munnecke and Servais, 2008). Results show that the abundance of sphaeromorphs decrease from nearshore to offshore, while those of process-bearing acritarchs increase in the same direction. Proximal facies are characterized by taxa with shorter processes (*Micrhystridium* morphotypes) while distal facies feature longer and more ramified processes (for e.g. *Evittia*, *Percultisphaera* and *Oppilatala*). Thus, acritarch assemblages appear to be indicative of paleoecology and depositional environment.

1.2.4 Global diversity and distribution

Although the biological origins of acritarchs are not clear, the broad scale patterns in their diversity and distribution are starting to be better understood. The recent study of Kroeck et al. (2022) constitutes a comprehensive investigation and the most detailed study of global acritarch diversity for the whole Paleozoic (**Fig. 1.9**). This was enabled by the creation of a new occurrence database for Paleozoic phytoplankton, the Phytopal database, which was initiated by Mullins et al. (2005, 2006) and presently contains more than 6000 species from pre-2006 literature. The trajectory of global diversity correlates with some prominent biotic events (Fig. 4); there is a moderate diversity at the start of the Cambrian during the so-called Cambrian Explosion; the diversity is increasing during the Great Ordovician Biodiversification (GOBE) event at the start of the Ordovician and reaching a peak diversity in the Middle Ordovician; a drop of diversity is observed during the Late Ordovician Mass Extinction; a Silurian recovery is visible, followed by a gradual decrease in the Early and Middle Devonian before a slight increase in the Late Devonian; finally the diversities show a tapering off in the Carboniferous and Permian with very low diversities. The latter interval of low diversity is known as the Late Paleozoic Phytoplankton Blackout (Riegel, 2008). But Servais et al. (2016) argues that the lack of fossils does not necessarily imply absence: only a minority of modern phytoplankton produce cysts and the presence of marine invertebrate planktotrophic larvae suggests that the marine trophic system did not collapse following an absence of phytoplankton. In addition, there is evidence that many marine invertebrates continued feeding on phytoplankton during the so-called ‘phytoplankton blackout’ (e.g. Nützel, 2014).

Furthermore, the Ordovician and Silurian trends mirror those of zooplankton such as chitinozoans, radiolarians and graptolites which suggest trophic dependencies (discussed in Kroeck et al., 2022 and summarized in this paragraph). Although high phytoplankton diversity may have driven the GOBE, this is not clear for the Cambrian Explosion or the Devonian Nekton Revolution. In contrast, the Late Phytoplankton Blackout may have triggered a turnover resulting in the fall of Sepkoski Jr.’s (1981) Paleozoic Evolutionary Fauna and the rise of the Modern Evolutionary Fauna during the Late Paleozoic. Abiotic factors such as increased continental fragmentation, and intervals of high sea level which enlarged the area of flooded continental shelf contributed to high diversity. Atmospheric CO₂ concentrations correlated with diversity from the early to middle Paleozoic. Temperature is also an important control, with the highest phytoplankton diversity during colder climates up to a certain extent; very low temperatures reduce diversity and hinder growth and expansion.

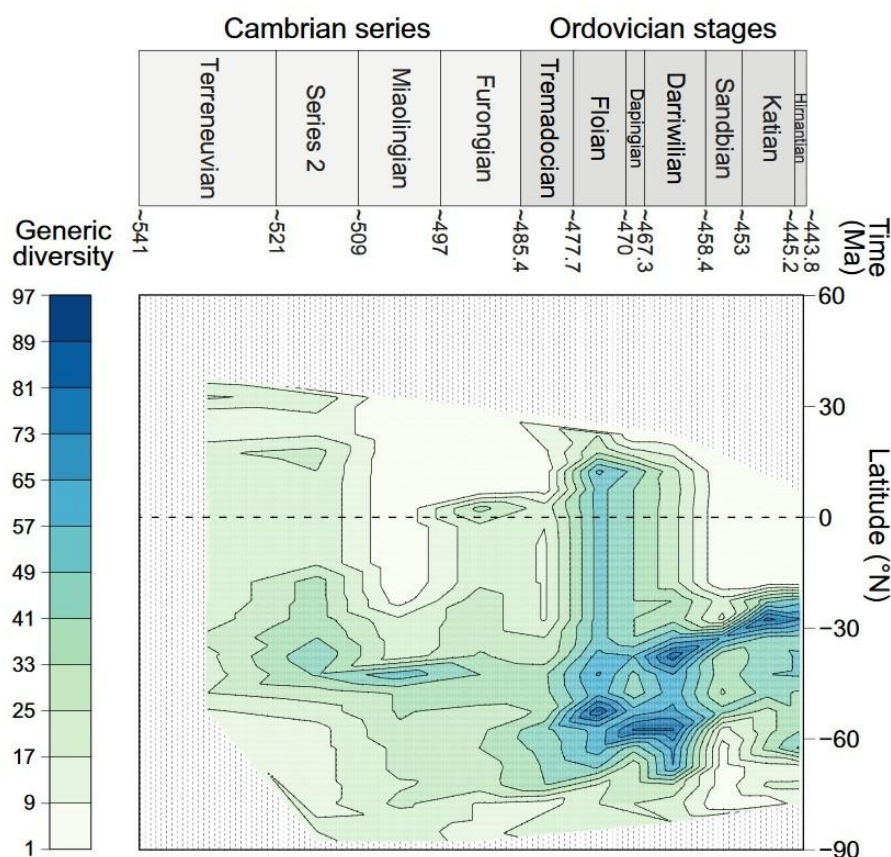


Figure 1.10 Range-through diversity excluding singletons, calculated for the Cambrian series and the Ordovician stages (fig. 1 of Zacaï et al., 2021).

Modern marine biodiversity is not uniformly distributed around the world. Various studies document the occurrence of a latitudinal diversity gradient (LDG; see also the **Chapter 3** introduction) in modern marine biotas (Powell et al., 2012) and groups such as planktonic bacteria (Fuhrman et al., 2008), planktonic foraminifera (Rutherford et al., 1999), brachiopods (Powell, 2009), bivalves (Flessa and Jablonski, 1995; Crame, 2000), copepods (Rombouts et al., 2009), dinoflagellates and coccolithophores (Chust et al., 2013) among others. Chaudhary et al. (2016) showed an asymmetrical LDG for modern marine species, with a peak at the northern hemisphere and a slight dip in the equator. Zacaï et al. (2021) mapped the distribution of phytoplankton in the Cambrian and Ordovician (**Fig. 1.10**). The results show a southern hemisphere peak of diversity, shifting northwards from mid-southern latitudes towards the equator and mirroring the continental drift of Baltica. However, modeled species reconstructions suggest a truncated bimodal peak in the early Cambrian and the Middle Ordovician with a dip in the equator; and a unimodal curve in the Hirnantian with the highest diversity at the equator (**Fig. 1.11**). The northward movement of the diversity peak coincides with the long-term climatic patterns from warm to cooler conditions, and reflects equatorial diversification when temperatures became more favorable (less warm) to phytoplankton growth. The discrepancy between the empirical and modeled diversity curves could be due to the incompleteness of the fossil record, with many time intervals and areas inadequately sampled and represented (fig. S2 in the supplementary material of Zacaï et al., 2021). Thus, interpretation of the LDG needs careful consideration to prevent erroneous conclusions due to biases. Despite the innovative approaches used by Zacaï et al., (2021), the study is restricted to the Cambrian and Ordovician, and do not cover the complete sequence of biotic events up to the Devonian Nekton Revolution; also the database is incomplete regarding spatial coordinates of occurrences.

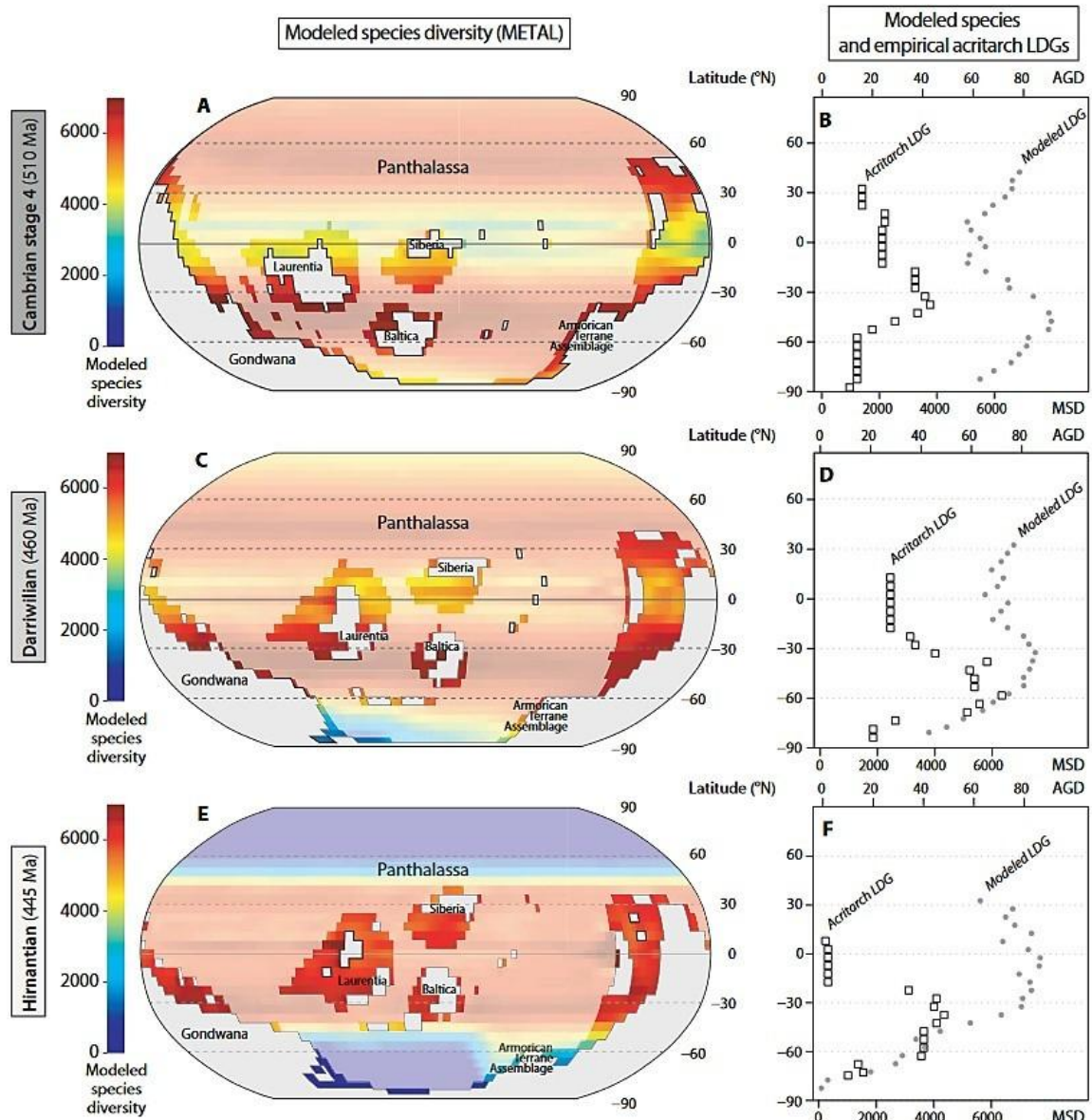


Figure 1.11 Modeled and empirical acritarch diversity across three intervals with different paleoclimate regimes (fig. 9 of Zacaï et al., 2021). Cambrian Series 2 represents a hothouse interval with 32 PAL (pre-industrial level) CO₂; the Darriwilian is cooler with 12 PAL CO₂, while the Hirnantian is an icehouse interval with 12 PAL CO₂. A, C and E are ecological niche models of global diversity based on METAL (Macroecological Theory of Life; see Beaugrand et al., 2020). Modelled and empirical latitudinal diversity gradients (LDG) are illustrated in B, D and F; calculated at 5° latitudinal bins.

CHAPTER 2

DATA AND METHODS

2.1 The database

Recent sources of information on acritarch occurrences are now readily available online. The largest and most comprehensive is Palynodata (<https://paleobotany.ru/palynodata>) which also includes other palynomorphs such as pollen, spores and dinocysts, but the references available are only those published until 2006. Fensome et al. (1990) compiled an index for acritarchs and prasinophytes with data up to the late 1980's; while the John Williams Index of Paleopalynology (JWIP) is a card catalogue with references until 2012 (Riding et al., 2012). The acritarchs and prasinophytes section of the JWIP has been scanned and uploaded in the website Acritax (<https://www.mikrotax.org/Acritax/index.html>) maintained. Very recently, Shu et al. (2025) generated their own database: the Global Acritarch Database (GAD) by adding recent literature and georeferencing Palynodata occurrences. The Paleobiology Database (PBDB) and the Geobiology Database (GBDB) are two of the most widely used databases in paleontology and biostratigraphy but both contain very few data on acritarchs and prasinophytes to be usable for diversity and biogeographical analyses.

To constitute a comprehensive database that could be utilized for diversity and biogeographical analyses, it should be “cleaned” and reviewed taxonomically to generate meaningful and more accurate measurements. It is important that a scientist who attempts diversity studies based on a database clearly understands the elements that constitute this database. Redundant and illegitimate names should be synonymized, while those with uncertain affinities can or should be eliminated, reviewed or reclassified pending further study. Robust morphological criteria should be used to distinguish taxa, especially for genera, which is considered to be the fundamental taxonomic unit for acritarchs (Strother, 1996). Transitional forms are common and can complicate classification. For some, their proper biological affinity will be discovered and can finally be properly reclassified. In this study, we call these errors arising from misclassification as a taxonomic bias. This is discussed further in **Section 2.2** below.

The present compilation of acritarch occurrences (**Fig. 2.1**) was derived from the PhytoPal database (Mullins et al., 2005, 2022) started by Gary Mullins and collaborators, with entries derived from pre-2006 literature. The taxonomy of the Paleozoic acritarch species in this dataset was reviewed by the collaborators that are acritarch experts of the different time periods. Kroeck et al. (2022) used this database to investigate the changes in diversity through time. Zacaï et al. (2021) georeferenced the Cambrian and Ordovician entries; and now combined with the present efforts for the Silurian and Devonian. The new database includes more recent acritarch literature (until 2022) for the Silurian and Devonian. For consistency, taxonomic nomenclature was synonymized using the PhytoPal scheme. Illegitimate, questionable and redundant nomenclature were eliminated. Netromorph taxa were revised based from Manzano et al. (2025; **Appendix 1**).

The present database records 45,838 phytoplankton occurrences from 687 localities (**Figs. 2.2** and **2.3**). Zacaï et al. (2021) used 195 references for their early Paleozoic database, and 224 references were utilized for the middle Paleozoic in this study. A total of 449 genera is reported.

reference	genus	species	period	stage	max_x	min_x	mid_pt	formation	locality	count	lat	long	rot_lat	p_lat
A. Combaz, G. Peniguel, Rhopalophora	Rhopalophora	pilata	Ordovician	Tremadocian	485.4	477.7	481.55	Nambeet Formation	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	162.7929
A. Combaz, G. Peniguel, Petenospaeridium	Petenospaeridium	furcatum	Ordovician	Floian	477.7	470	473.85	Willara Formation	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	159.1758
A. Combaz, G. Peniguel, Rhopalophora	Rhopalophora	palmeta	Ordovician	Floian	477.7	470	473.85	Willara Formation (=Thangoo)	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	159.1758
A. Combaz, G. Peniguel, Rhopalophora	Rhopalophora	pilata	Ordovician	Floian	477.7	470	473.85	Nambeet Formation	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	159.1758
A. Combaz, G. Peniguel, Petenospaeridium	Petenospaeridium	furcatum	Ordovician	Dapingian	470	467.3	468.65	Willara Formation	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	156.78
A. Combaz, G. Peniguel, Rhopalophora	Rhopalophora	palmeta	Ordovician	Dapingian	470	467.3	468.65	Willara Formation (=Thangoo)	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	156.78
A. Combaz, G. Peniguel, Rhopalophora	Rhopalophora	pilata	Ordovician	Dapingian	470	467.3	468.65	Nambeet Formation	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	156.78
A. Combaz, G. Peniguel, Comasphaeridium	Comasphaeridium	canningia	Ordovician	Darnwillan	467.3	458.4	462.85	Goldwyer Formation	Acacia-1 borehole Australia	19	-19.33	124.99	PALEOMA	155.8012
A. Combaz, G. Peniguel, Petenospaeridium	Petenospaeridium	furcatum	Ordovician	Darnwillan	467.3	458.4	462.85	Willara Formation	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	154.1519
A. Combaz, G. Peniguel, Rhopalophora	Rhopalophora	palmeta	Ordovician	Darnwillan	467.3	458.4	462.85	Willara Formation (=Thangoo)	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	154.1519
A. Combaz, G. Peniguel, Rhopalophora	Rhopalophora	pilata	Ordovician	Darnwillan	467.3	458.4	462.85	Nambeet Formation	Willara-1 borehole Australia	19	-19.18	122.07	PALEOMA	154.1519
A. Combaz, Un microbio Acanthodiodium	Acanthodiodium	angustum	Ordovician	Tremadocian	485.4	477.7	481.55		Hassi-Messaoud Algeria	31	31.61	6.07	PALEOMA	120.782
A. Combaz, Un microbio Attritisporites	Attritisporites	messaoudi	Ordovician	Tremadocian	485.4	477.7	481.55	Gres del Gassi	Hassi-Messaoud Algeria	31	31.61	6.07	PALEOMA	120.782
A. Combaz, Un microbio Attritisporites	Attritisporites	scabrus	Ordovician	Tremadocian	485.4	477.7	481.55	Gres del Gassi	Hassi-Messaoud Algeria	31	31.61	6.07	PALEOMA	120.782
A. Combaz, Un microbio Attritisporites	Attritisporites	velatus	Ordovician	Tremadocian	485.4	477.7	481.55	Gres del Gassi	Hassi-Messaoud Algeria	31	31.61	6.07	PALEOMA	120.782
A. Combaz, Un microbio Leiofus	Leiofus	simplex	Ordovician	Tremadocian	485.4	477.7	481.55	El Gassi Sandstone Formation	Hassi-Messaoud Algeria	31	31.61	6.07	PALEOMA	120.782
A. Di Milia, M. Tongiorgi Cymatogalea	Cymatogalea	trevisanii	Ordovician	Tremadocian	485.4	477.7	481.55	Solas Sandstone Formation	Riu Araxisi Italy	39	39.91	9.06	PALEOMA	103.506
A. Di Milia, M. Tongiorgi Dactylofusa	Dactylofusa	meanensis	Ordovician	Tremadocian	485.4	477.7	481.55	Solas Sandstone Formation	Riu Araxisi Italy	39	39.91	9.06	PALEOMA	103.506
A. Di Milia, Upper Cambri Acum	Acum	araxisi	Cambrian	Furongian	497	485.4	491.2	Solas Sandstone Formation	Riu Araxisi Italy	39	39.91	9.06	PALEOMA	107.673
A. Di Milia, Upper Cambri Cymatogalea	Cymatogalea	parvifera	Cambrian	Furongian	497	485.4	491.2	Solas Sandstone Formation	Riu Araxisi Italy	39	39.91	9.06	PALEOMA	107.673
A. Eisenack, Beiragze zu Baltisphaeridium	Baltisphaeridium	longispinosum	Ordovician	Darnwillan	467.3	458.4	462.85	Chasmoop-Serie	Boda Sweden	57	57.26	17.04	PALEOMA	-7.1671
A. Eisenack, Beiragze zu Chlamydochaeridia	Chlamydochaeridia	oelandica	Ordovician	Darnwillan	467.3	458.4	462.85	Vaginatensalk	Halludden Sweden	57	57.36	17.06	PALEOMA	-7.1415
A. Eisenack, Beiragze zu Tasmanites	Tasmanites	trematus	Ordovician	Darnwillan	467.3	458.4	462.85	Vaginatensalk	Halludden Sweden	57	57.36	17.06	PALEOMA	-7.1415
A. Eisenack, Beiragze zu Baltisphaeridium	Baltisphaeridium	longispinosum	Ordovician	Darnwillan	467.3	458.4	462.85	Expansus-Kalk	Leningrad Russia	59	59.87	30.15	PALEOMA	1.0759
A. Eisenack, Beiragze zu Pachysphaeridium	Pachysphaeridium	brevispinosum	Ordovician	Darnwillan	467.3	458.4	462.85	Vaginatensalk	Tallinn Estonia	59	59.46	24.67	PALEOMA	-2.1902
A. Eisenack, Beiragze zu Baltisphaeridium	Baltisphaeridium	longispinosum	Ordovician	Sandbian	458.4	453	455.7	Chasmoop-Serie	Boda Sweden	57	57.26	17.04	PALEOMA	-5.6627
A. Eisenack, Beiragze zu Baltisphaeridium	Baltisphaeridium	longispinosum	Ordovician	Katian	453	445.2	449.1	Chasmoop-Serie	Boda Sweden	57	57.26	17.04	PALEOMA	-4.7568
A. Eisenack, Beiragze zu Baltisphaeridium	Baltisphaeridium	longispinosum	Ordovician	Hirnantian	445.2	443.8	444.5	Chasmoop-Serie	Boda Sweden	57	57.26	17.04	PALEOMA	-4.3919
A. Eisenack, Die Mikrofa Petenospaeridium	Petenospaeridium	trifurcatum	Ordovician	Darnwillan	467.3	458.4	462.85	helle Ostseekalke	Kiesgrube Spandau Germany	52	52.54	13.2	PALEOMA	0.8006
A. Eisenack, Die Mikrofa Petenospaeridium	Petenospaeridium	trifurcatum	Ordovician	Sandbian	458.4	453	455.7	helle Ostseekalke	Kiesgrube Spandau Germany	52	52.54	13.2	PALEOMA	-2.4264

Figure 2.1 The database used for this study. Entries include references, the genus and species, age, localities, present and paleorotated coordinates (based on the PALEOMAP model of Scotese et al. 2016).

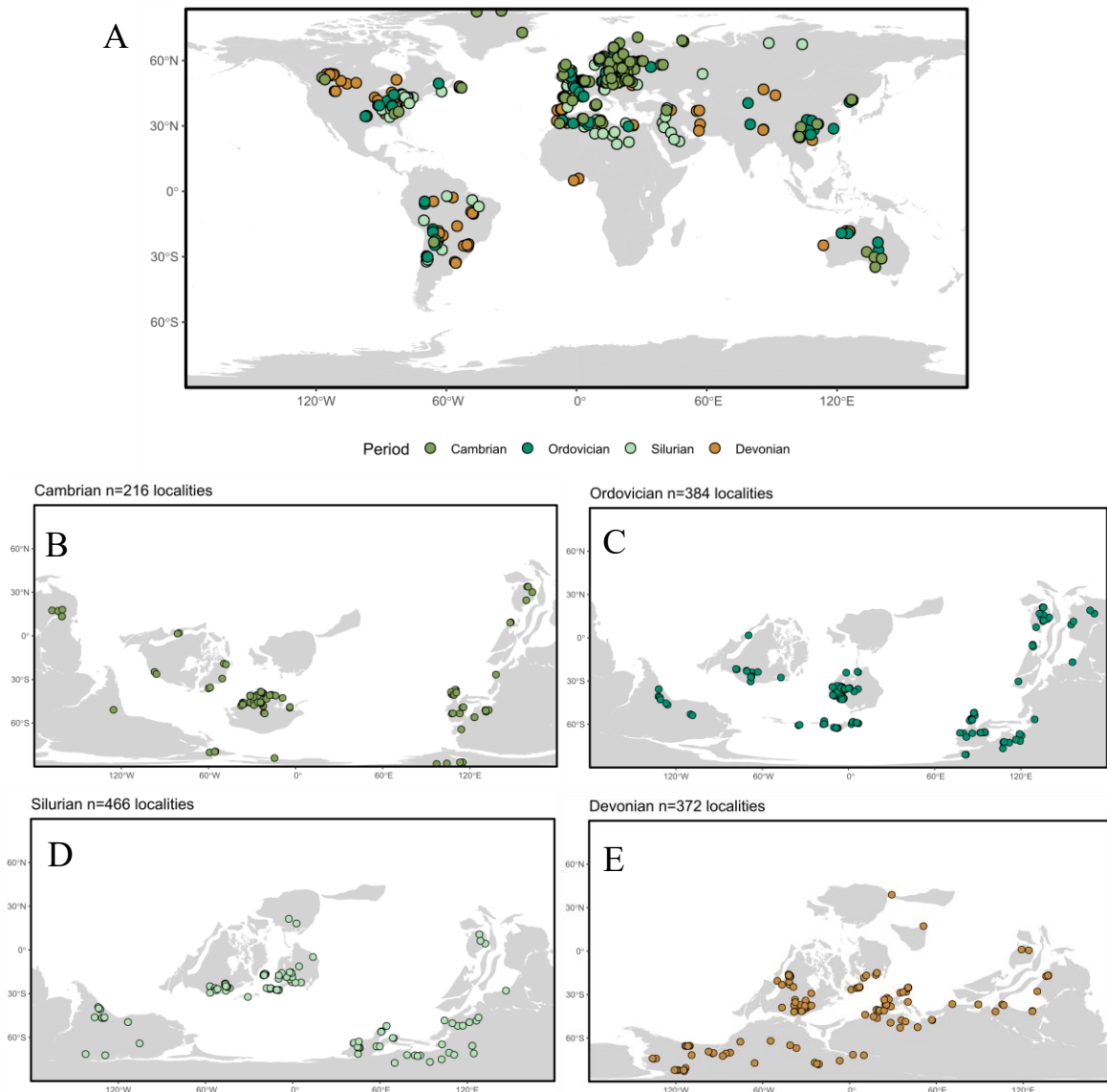


Figure 2.2 Distribution of sampled localities. (A) Present-day coordinates. Paleorotated localities are shown for the (B) Cambrian, (C) Ordovician, (D) Silurian and (E) Devonian. (A) shows that most Europe is the most densely sampled continent for the early to middle Paleozoic. In the Cambrian (B), Ordovician (C) and Silurian (D) the paleocontinent of Baltica is the best sampled, particularly the areas which is now the Nordic region of Europe. During the Devonian, the present-day North America and southern Europe have the highest degree of sampling.

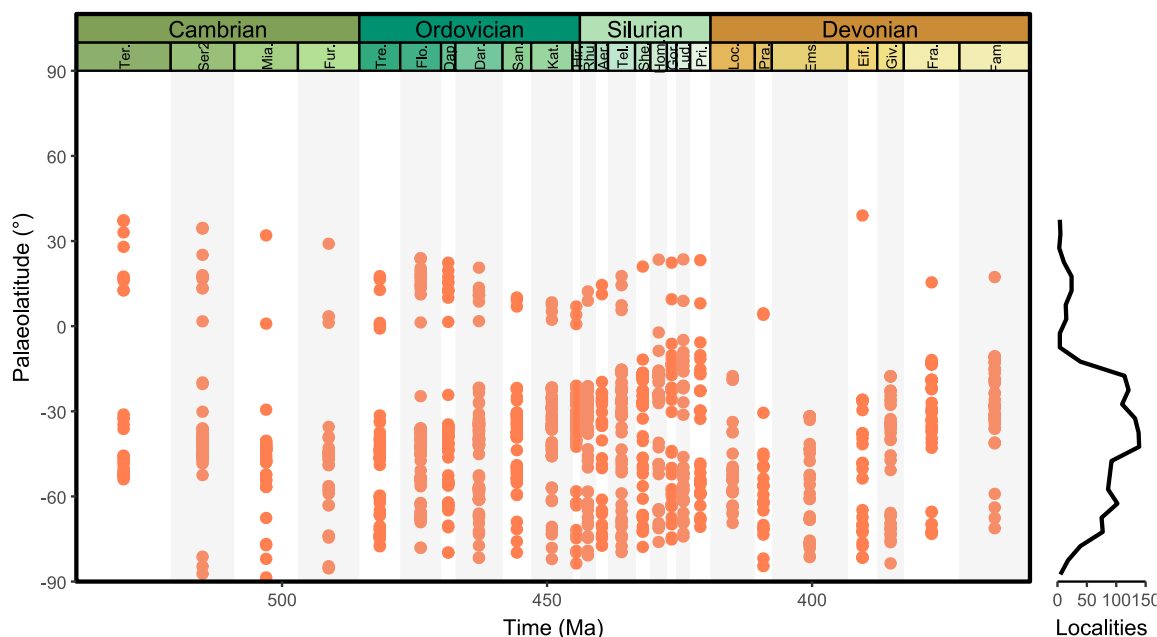


Figure 2.3 Paleolatitudinal coverage of sampled areas. (A) shows paleolatitude of areas sampled from the Cambrian (shown in epochs rather than stages) to Devonian. (B) tallies the number of localities per 5° paleolatitudinal bin.

2.2 Taxonomic bias

It is impossible to revise in detail the several thousands of acritarch taxa in the databases. Nevertheless, to get acquainted with the problematic of acritarch classification, an attempt was made to understand the taxonomy of a specific group. In this context, the netromorphs have been selected. The netromorphs are a subgroup of acritarchs defined as having a simple, spindle-shaped morphology. We reviewed the netromorphs in detail, by proposing a classification system and by reassigning the related *Deunffia*-*Domasia* morphotypes to the diacromorphs and other species to respective genera. This work is detailed in **Appendix 1**, as a separate scientific article published (Manzano et al., 2025). This is summarized in **Section 2.2.1** below.

Another problem that can affect taxonomic classification is the morphological plasticity of some acritarch species, leading to identification of numerous junior synonyms for the same variant of one species. For example, Fensome et al. (1990) lists more than 250 species, subspecies and varieties under the genus *Veryhachium* which does not necessarily reflect a high diversity or a high morphological disparity; Servais et al. (2007) suggests subdivision into only two informal groups (triangular *V. trispinosum* group and rectangular *V. lairdii* group) for the early Paleozoic veryhachids while for the late Paleozoic Lei et al. (2013) added another (the ellipsoidal *V. cylindrica* group). This problem of taxonomic splitting in literature became obvious when revising individual taxa. Several acritarch taxa have been revised in detail in recent years (e.g. Servais et al., 2018). More recently, Kroeck et al. (2020) emended and reduced the number of species in *Vulcanisphaera* from 32 previously published specific taxa to only three, recognizing the presence of transitional forms. Tongiorgi and Di Milia (1999) proposed peteinosphaerids (the three genera *Peteinosphaeridium*, *Cycloposphaeridium* and *Liliosphaeridium*) as a possible paleobiogeographic marker for the Baltica province in the Middle Ordovician, going as far as to identify alternating assemblages in South China as of either Baltica or Perigondwana Province affinity. However, Li and Servais (2002) already

argued that there is a high morphological variability between the different species for *Peteinosphaeridium*, and that this variability may reflect local rather than biogeographical conditions, which was confirmed by Kroeck et al. (2021). Recent studies on modern-day dinoflagellates demonstrate the effects of light, temperature and salinity on cyst morphology (e.g. Mertens et al., 2009; Zonneveld & Susek, 2007). In order to better understand the paleoecological influence on acritarch taxa, but also assemblages, a participation in a review of Middle Ordovician acritarchs from Öland, Sweden, published as Calero Gordon et al. (2025), is attached as **Appendix 2**. The results show that differing proportions in acritarch morphotypes are linked to progressive changes in characters such as process length; and that these changes in assemblages are correlated with sea-level fall rather than biogeography or biostratigraphy. The results are summarized below in **Section 2.2.2**.

2.2.1 A proposed classification of netromorph acritarchs and related morphotypes

The netromorphs were originally defined by Downie et al. (1963) as “acritarchs having an elongate to fusiform test, without an inner body. Surface is generally smooth, rarely granular. One or more spines, closed distally, may be present at one or both poles. Openings not observed (see **Fig. 2.4** below).” Downie et al. (1963) further subdivided the subgroup into three generic complexes: a fusiform complex (which includes the genera *Leiofusa*, *Dactylofusa* and *Baiomeniscus*), the *Deunffia*-*Domasia* complex and elliptical forms (represented by the genus *Leiovalia*). In terms of polar symmetry, the netromorphs can be classified as homopolar (taxa with symmetrical poles) or heteropolar (different ornamentation on both poles). The *Deunffia*-*Domasia* complex belongs to the latter, resembling some morphotypes of another group called the diacromorphs (see **Fig. 1.7** for an illustration of the different subgroups). *Domasia* resembles the Cambrian genus *Ninadiacrodium* while *Deunffia* has a similar outline to *Dicrodiacrodium* (see **Fig. 2.5** for illustrations of *Ninadiacrodium* and *Dicrodiacrodium*).

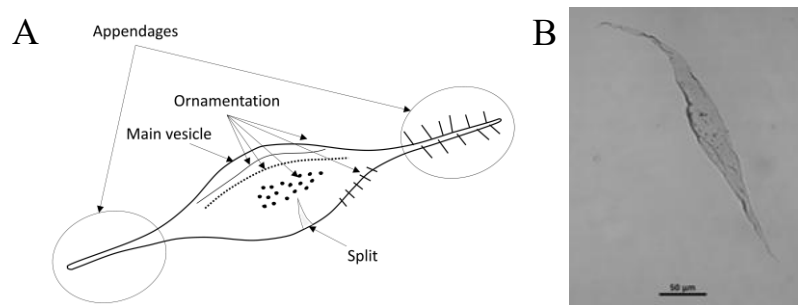


Figure 2.4 General morphology of a netromorph acritarch (A) and an example of *Leiofusa* sp., from the *L. estrecha* group. The specimen is from the När borehole (372m depth) in Gotland, Sweden, Silurian age.

The main point of contention among various authors are criteria for the three genera *Dactylofusa*, *Poikilofusa* and *Eupoikilofusa*. Some authors argue for full or partial synonymy (Combaz et al., 1967; Cramer, 1970; Fensome et al., 1990) while others argue that they are three separate genera (Cramer and Díez de Cramer, 1979; Rasul, 1979; Turner, 1984). *Dactylofusa* was originally defined by Brito and Santos (1965) as navicular shaped and covered with clavate processes arranged in longitudinal rows. Staplin et al. (1965) erected *Poikilofusa* in the same year as a genus of fusiforms having small spines or muri. *Eupoikilofusa* was established by Cramer (1970) to accommodate fusiforms with striations. The confusion between the three genera apparently lies on how to utilize the longitudinal arrangement or the type of ornamentation for classification. For example, Combaz et al. (1967) synonymizes *Dactylofusa* and *Poikilofusa*, both of which have processes and excluding *Eupoikilofusa*, which

does not. On the other hand, Loeblich and Tappan (1978) and Rasul (1979) retains these as three separate genera. Dorning (1994) proposed the most practical solution: smooth, non-ornamented fusiforms are classified under *Leiofusa*; forms with complex processes arranged in rows to *Dactylofusa*; those with random and simple processes to *Poikilofusa*; and striated forms to *Eupoikilofusa*.

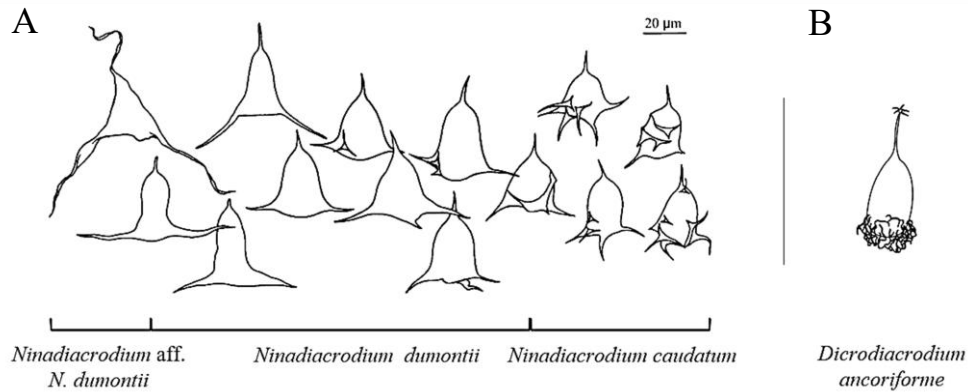


Figure 2.5 Diacromorph taxa similar to the *Deunffia-Domasia* complex (slightly modified from Raevskaya and Servais, 2009). (A) *Ninadiacrodium* morphotypes resembling *Domasia* and (B) *Dicrodiacrodium* which grossly resembles *Deunffia*. See also **Fig. 2.6** below for examples of *Deunffia-Domasia* morphotypes.

We build upon this classification by Dorning (1994) and propose our own scheme for taxa in the middle Paleozoic (Silurian-Devonian). But first we distinguish between the homopolar and heteropolar forms: we restrict the netromorphs to the former and consider the latter (the *Deunffia-Domasia* complex) as related morphotypes more appropriately described as diacromorphs. We divide the netromorphs into three categories (**Fig. 2.6**): Category 1 with the rod-shaped forms (*Navifusa*, *Deusilites*); Category 2 with reniform outlines (*Holothuriadegma*); spindle-shaped Category 3 (*Leiofusa*, *Dactylofusa*, *Poikilofusa*, *Eupoikilofusa*, *Disparifusa*); and crescent to half-moon shaped (*Baiomeniscus*, *Lunulidia*) in Category 4. These categories are then further subdivided into the type of ornamentation (whether the main vesicle is smooth or ornamented; and if ornamented whether these consist of simple, complex processes or just striations). For some taxa this is enough to differentiate the genera. Very similarly ornamented genera are united as a complex (*Poikilofusa-Disparifusa* complex). But we also acknowledge the possible occurrence of ecophenotypes (see **Section 2.2.2** below) and provide intra-generic groupings which pull together species which could represent transitional forms in terms of various characteristics such as appendage or process length (see section 3.2 of **Appendix 1** for terminology on the morphology of netromorphs).

We also provide a classification system for the related morphotypes based on the number, presence and type of polar appendices (**Fig. 2.7**). The Category 1 of related morphotypes only have an appendage on one side; in Category 2 there are appendices on both the anterior and posterior poles. The number and type of posterior appendage/s enable classification into genera and the different intrageneric groups.

Based on our proposed classification scheme several new combinations are proposed (see section 4 of **Appendix 1**). Some names have also been corrected based on the Shenzhen Code version of the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018).

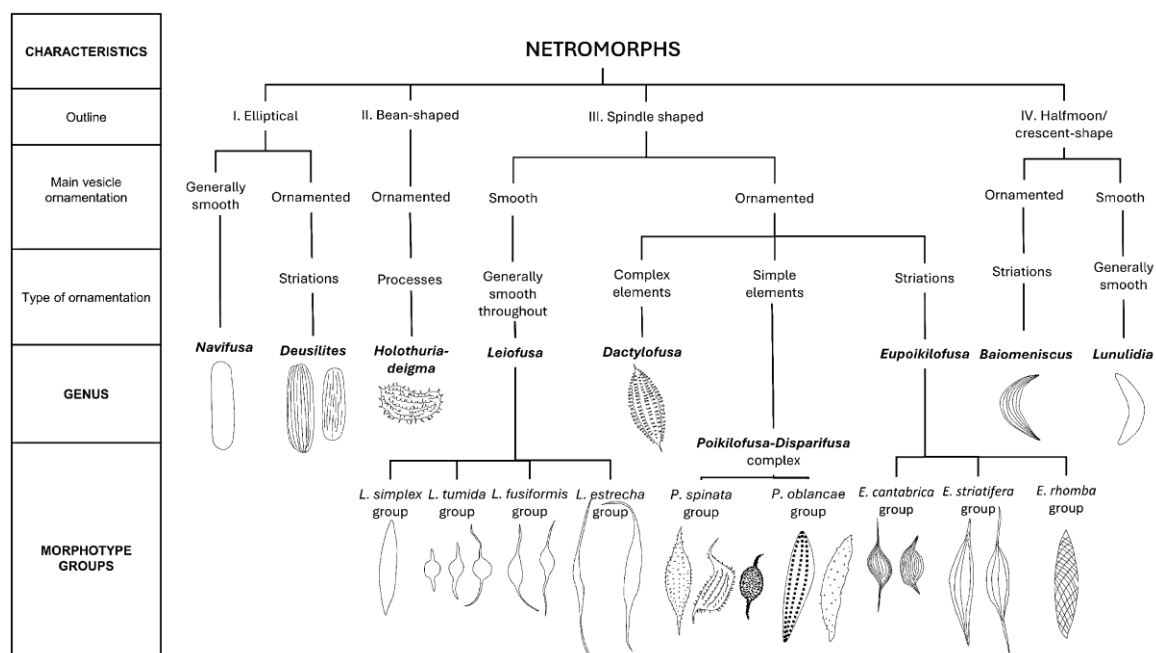


Figure 2.6 Proposed classification scheme for netromorph acritarchs (fig. 2 of Manzano et al., 2025).

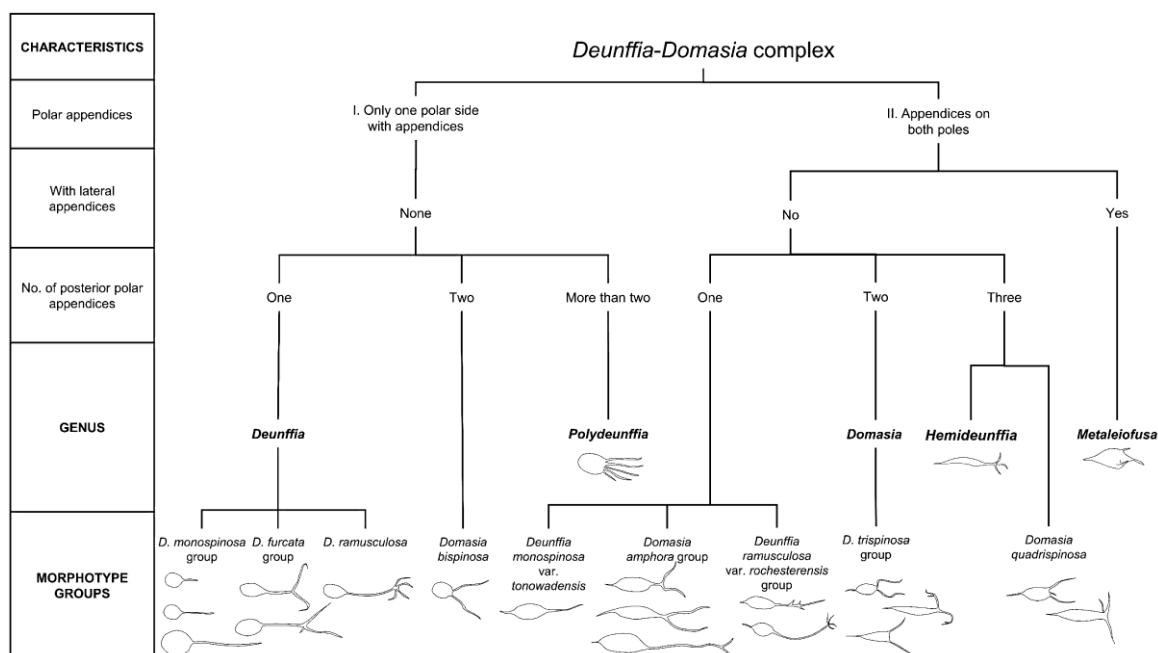


Figure 2.7 Proposed classification scheme for related morphotypes (fig. 3 of Manzano et al., 2025).

2.2.2 Ecophenotypism in Middle Ordovician acritarchs of Öland, Sweden

During the Middle Ordovician, the paleocontinent of Baltica is largely covered by an epicontinental sea (Torsvik and Cocks, 2017). Sediments from this interval are well-preserved and undisturbed in the island of Öland in Sweden, making the area key to the study of Ordovician stratigraphy and paleontology (Nielsen et al., 2023). These carbonate strata are successions of cool to temperate water deposits (Lindskog and Eriksson, 2017 and references therein). Sedimentological and petrographic investigations (by two of the co-authors AL and MEE) of the coastal sections in Hälludden and Hagudden (northern Öland; see **Fig. 2.8**)

indicate decreasing sea-levels through time and increasing water depth from northwest to southeast of the island.

Because of its favorable geology and high degree of microfossil preservation Öland became a center for reference studies on Ordovician palynology, which focuses not only on acritarchs but also on chitinozoans (Grahn, 1980, 1981, 1982) and scolecodonts (Eriksson et al., 2013, 2016). Initial studies on acritarchs by Eisenack (1958, 1959, 1968, 1976) were followed by detailed investigations prompted by interest in petroleum exploration (e.g. Kjellström, 1972). A group of palynologists (Righi, 1991; Ribecai, 1996; Ribecai and Tongiorgi, 1995, 1997; Bagnoli and Ribecai, 2000) from the University of Pisa (Italy) investigated Middle Ordovician sections (including Horns Udde, Hälludden and Hagudden) and published biozonation schemes based on acritarch assemblages. Bagnoli and Ribecai (2000) described four new peteinosphaerid species deemed biostratigraphically significant. Reinvestigations by Kroeck et al. (2021) and more recently by Valdivia-Covenas (2025) on the morphology of peteinosphaerids showed distinction of between genera is difficult, if not nearly impossible.

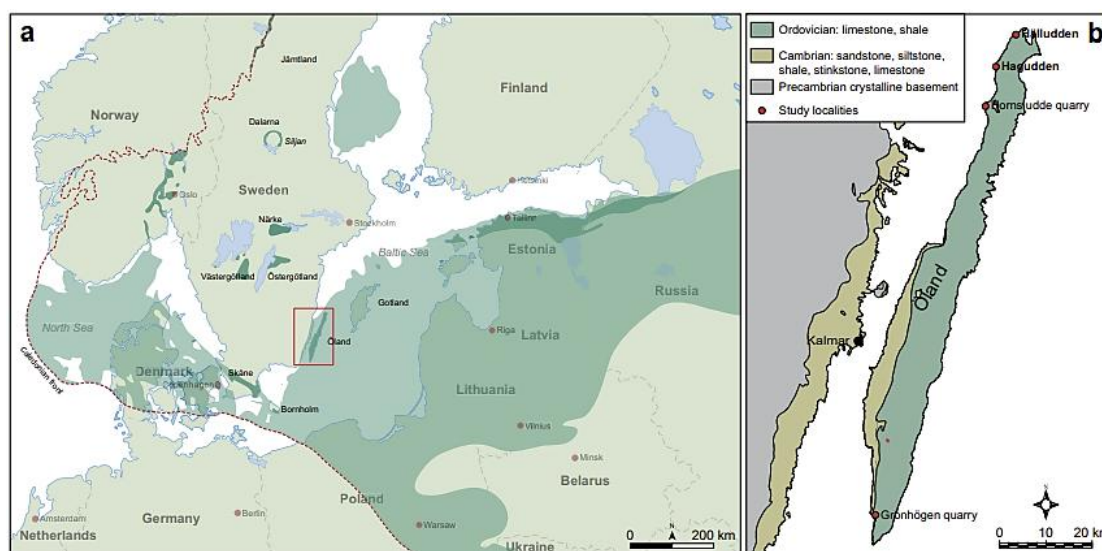


Figure 2.8 Map showing the geology of southern Sweden and the Baltoscandian region in northern Europe. Öland is indicated by a red rectangle in (A). The studied sections of Hälludden and Hagudden are shown in (B).

The composition of acritarch assemblages in Hälludden and Hagudden were investigated by two of the co-authors (JLCG and BC). During the first count (conducted by BC) acritarchs were separated into five ‘acritarch morphotype’ categories based on process length/type (1: long processes; 2: short processes; 3: complex processes; 4: few processes; 5: no processes). Vesicle and processes lengths were also measured. In the second count (by JLCG) specimens were classified into ‘acritarch groups’ roughly based on the scheme of Downie et al. (1963) (1: veryhachids with triangular and rectangular shapes; 2: sphaeromorphs, rounded vesicles; 3: polygonomorphs, polygonal outline; 4: multiplicisphaerids with complex, branched processes; 5: micrhystrids, acritarchs less than 20 μm in diameter; 6: baltisphaerids, rounded with very long processes). The second count also analyzed assemblages from two different fractions (15 to 51 μm and larger than 51 μm). These two counts provided a view of the relative proportions of acritarch morphologies in the different assemblages, independent from established classification schemes (not counting genera or species reported in literature). Data from the proportions of assemblages, morphometric measurements and sedimentological parameters (percentages of sediment matrix, cement, skeletal grains and glauconite grains)

were ordinated using correspondence analysis (CA) to evaluate a possible gradient through time coupled with attendant sea-level change (regression).

The main results are shown in the three figures below (**Figs. 2.9, 2.10, 2.11**). The results of the first count (**Fig. 2.9**) showed acritarchs with long processes making up the largest proportion of specimens, followed by short processes and no processes. Morphotypes with few or complex processes are less abundant or negligible. Acritarchs with long processes likely belong to the genus *Baltisphaeridium*; in general, their relative proportion decreases from more than half in the lower sections (but not the lowermost) to around 35% at the top of the sequence. Short process morphotypes commonly belong to genera such as *Solisphaeridium* and *Comasphaeridium*; the values fluctuate but they appear to slightly decrease upwards. Spherical acritarchs (no processes) are usually attributed to *Leiosphaeridia*; they exhibit lower proportions (around 20%) at the base and increasing 30% at the top. The second count (**Fig. 2.9**) shows stronger trends. Baltisphaerids have very high abundances of up to 70% at the base of the section, continuously decreasing towards the top. Multiplicisphaerids also show the same trend. In contrast, sphaeromorphs and micrhystrids show increasing proportions the base to the top. Polygonomorph abundances fluctuate with very low abundance at the base. Veryhachids registered only a single occurrence near the top.

The distribution of the six acritarch groups in the two sieving fractions show that some groups are more abundant in one fraction compared to the other (see fig. 4 of **Appendix 2**): for example micrhystrids (being small acritarchs) are more abundant in the smaller fraction while multiplicisphaerids and baltisphaerids have higher proportions in the larger fraction. Multiplicisphaerids show decreasing upward trends in both fractions while baltisphaerids does not show a clear trend. Sphaeromorphs have similar proportions in both fractions and like the baltisphaerids, show no clear trend. Polygonomorphs have higher abundances in the larger fraction but the fine fraction shows a clearer trend diminishing towards the top of the sequence.

Three morphometric parameters were measured during the first count (**Fig. 2.10**): vesicle diameter (D), average process length (P) and the ratio of the first two parameters (D/P). Vesicle diameter ranges from 40 to 48 μm with no clear trends. Process length, on the other hand, became shorter from a mean length of 28 μm at the bottom of the section to 19 μm near the top. The trend becomes clearer for the D/P ratio: values range from 1.6 at the bottom to 2.0 near the top.

The CA showed a clear gradient that matches the stratigraphic sequence and the shallowing sea-level trend from the left to the right side of the CA plot (**Fig. 2.11**). Hälludden samples are more associated with veryhachids, micrhystrids and sphaeromorphs while Hagudden samples are more related to baltisphaerids, multiplicisphaerids and polygonomorphs. All these results corroborate previous studies, such as Stricanne et al. (2004), which show smaller and simpler acritarchs to be more abundant in shallower and nearshore settings, while larger and complex ornamented types dominate deeper-water conditions. The Öland sections are similar to inshore-offshore transects of Stricanne et al. (2004) for Gotland in the Silurian, and Li et al. (2004) for the Yangtze platform, also from the Middle Ordovician.

It is therefore essential to understand that some taxa, previously considered to be separate taxa, sometimes considered as palaeobiogeographically significant (for example some peteinoid acritarch species) are actually only ecophenotypes. Our databases must thus be analyzed and interpreted with care.

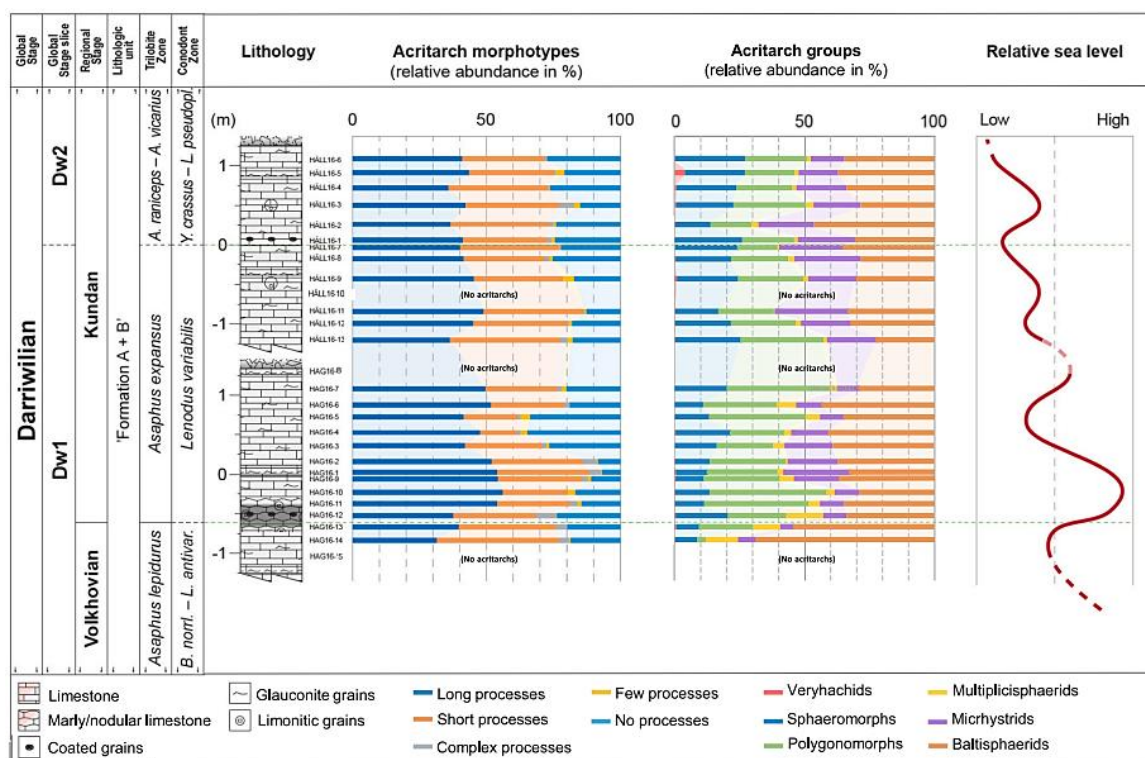


Figure 2.9 Relative abundances of acritarch morphotypes and groups from the Hälluden and Hagudden sections (fig. 3 of Calero Gordon et al., 2025).

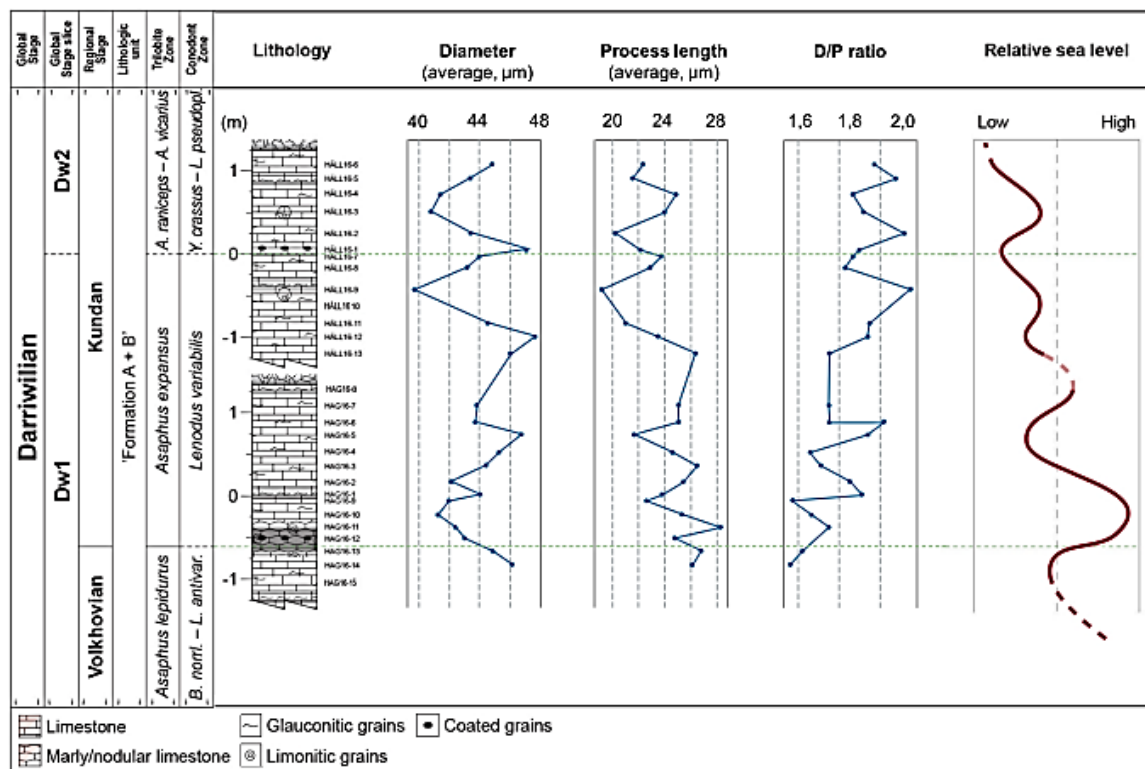


Figure 2.10 Morphological measurements of diameter, process length and their ratio taken from Hälluden and Hagudden samples during the first count (fig. 5 of Calero Gordon et al., 2025).

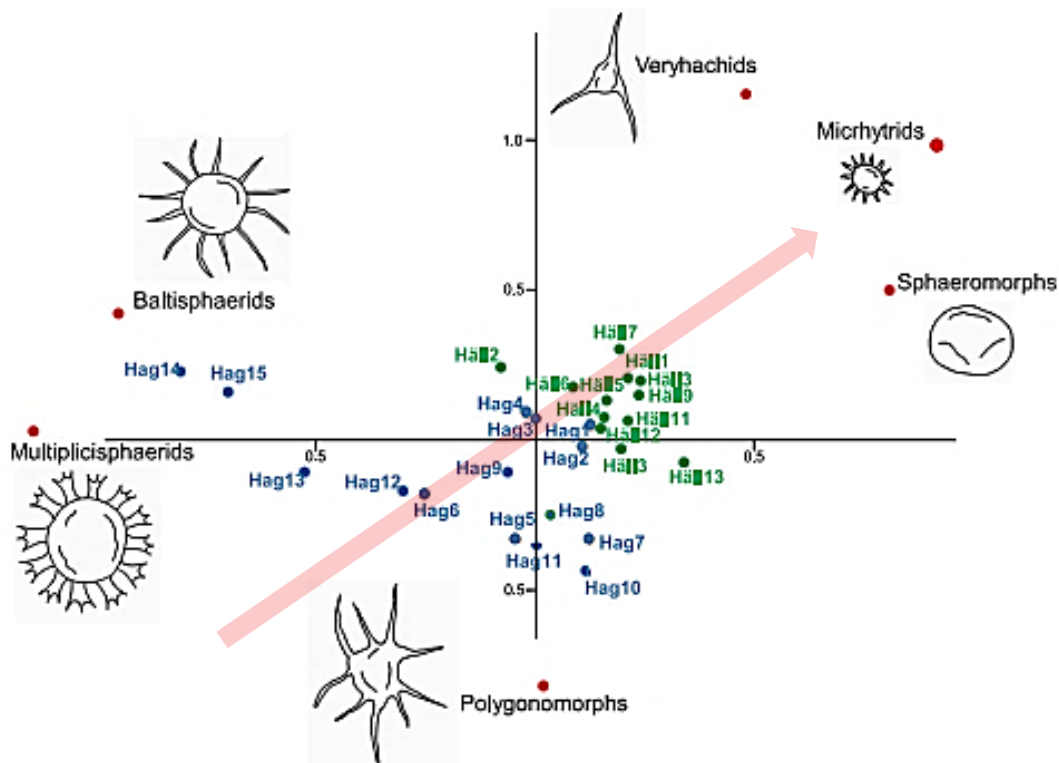


Figure 2.11 Correspondence analysis of Hälluden and Hagudden samples (fig. 6 of Calero Gordon et al., 2025). The red arrow illustrates the younging/shallowing trend, pointing towards shallower and younger sections.

2.3 Sampling bias

As emphasized by Darwin (1859), the fossil record is inherently incomplete and subject to biases due to various factors such as preferential preservation (due to the presence of resistant, fossilizable body parts), larger duration of the sampled interval, increased sampling effort, greater sampled area, among others (Raup, 1972).

Among these biases, the most studied one is the sampling effort. Within communities, species are not usually equally distributed with some abundant taxa and rare ones. This evenness among taxa causes this sampling bias, because documenting the rare taxa requires chance. Therefore, the higher the sample size/effort, the higher the recovered biodiversity. In this context, the extent of sampling effort or completeness can be compared using a species accumulation or rarefaction curve (e.g. Thompson et al., 2007); sampling is considered sufficient when the curve reaches a plateau. In this study sample completeness curves were generated using the R package *vegan* (Oksanen et al., 2025).

Estimates of total diversity, typically quantified as species or taxon richness, are inherently biased by the effects of sampling. Alroy (2010) highlights how traditional approaches, such as counting taxon ranges or using uncorrected occurrence data, are particularly susceptible to biases including the "Pull of the Recent," edge effects, and unequal sampling intensity across time intervals. Similarly, Foote (2000) demonstrates that commonly used interval-based metrics can be distorted by the inclusion of short-lived (single-interval or singletons) taxa, preservation biases, and varying interval durations. These studies underscore the critical need to correct for sampling biases when estimating taxonomic diversity,

particularly in paleontological datasets, to avoid conflating true biological patterns with artifacts of data collection.

Two subsampling methods have been used to counter the sampling bias in estimating paleobiodiversity. The first approach is known as classical rarefaction (CR), which standardizes samples to the same size (Sanders, 1968; Hurlbert, 1971; Gotelli and Coldwell, 2001). Although an efficient approach which has also the advantage of underlining time bins with a poor sampling coverage, it has the tendency to under-sample highly diverse assemblages, compress relative richness ratios and artificially flatten diversity curves (Alroy, 2010; Chao & Jost, 2012; Close et al., 2018). The second approach avoids the pitfalls of CR by standardizing samples to the same level of completeness or “coverage,” defined as the proportion of individuals in a community that belong to the represented species in the sample (Chao & Jost, 2012). This method is known as coverage-based rarefaction (CBR) or shareholder quorum subsampling (SQS). In this study, SQS is applied to diversity counts in order to correct for sampling biases.

2.4 Spatial biases

Previously described sample-standardized methods, however, do not take into account the differences in size of the sampled area for the time intervals, which can vary depending on the level of accessibility (Close et al., 2017). This spatial bias is due to the species area effect: larger habitat areas will hold more species than smaller ones, as the sampled area is extended total species recorded increases at a diminishing rate (Rosenzweig, 1995). In contrast to the sample bias, the spatial bias has only recently been accounted for in paleontology, starting with the key paper of Close et al. (2017); but the problem was already discussed by Sepkoski (1976).

Failure to account for spatial bias affects interpretations of diversification patterns: for example it can mask the true shifts in latitudinal diversity gradients through time (Antell et al., 2024 and references therein), or suggest unconstrained diversification (Close et al., 2017). It also prevents identifying “hotspots” of diversity and it is well known that diversity is not global but regional and not a simple sum (Flannery-Sutherland et al., 2022).

Currently, the methods to estimate paleobiodiversity by accounting for this spatial sampling bias are still in development and must cope with the highly uneven fossil record in space. To mitigate spatial bias the sampled areas can be standardized by superimposing equal area grids or circles on localities, or using minimum spanning trees set to a predefined length to limit dispersion (Close et al., 2017, 2020). **Fig. 2.3** shows that more localities are sampled from approximately -10° to -75° paleolatitudes, but this is not just due to sampling effort; most of the continents and landmasses are massed together in the southern hemisphere. Based on the species-area-effect, the southern hemisphere is projected to have higher total diversity.

To calculate latitudinal diversity, localities were partitioned into 5° latitudinal bins (see **Fig. 2.12**). This corrects for the sample bias. Further correction is made for the sampling effort by applying SQS on the latitudinal bins. Likewise, diversity “hotspots” were identified by superimposing an equal area hexagonal grid with 5° edge on the globe and applying SQS on each grid. Diversity metrics were calculated using the divDyn package of (Kocsis et al., 2022). The hexagonal grid was obtained from the package icoso (Kocsis et al., 2024).

One overlooked parameter which could be considered in the category of spatial bias is the background on which they are superimposed, which is paleogeography. Reconstructing past tectonic configurations becomes more challenging the further one goes back in time, due to

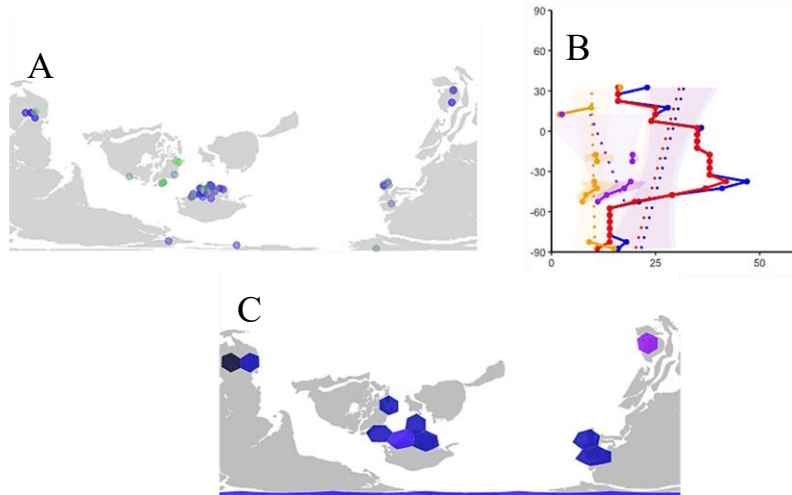


Figure 2.12 Application of spatial corrections, an example from the Cambrian series 2. (A) shows localities with raw diversity, from which the latitudinal diversity gradient is calculated (B). (C) shows equal-area grid cells used for spatial correction in two dimensions.

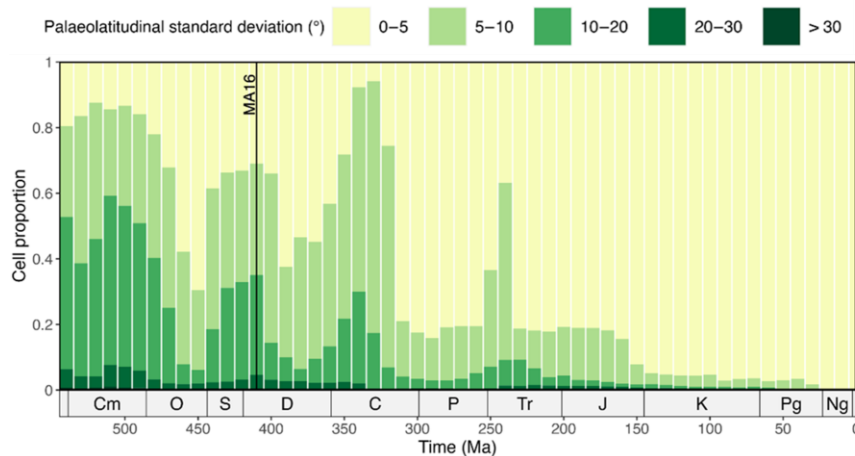


Figure 2.13 Paleolatitudinal standard deviation for paleocoordinates of reconstructed cell centroids in the Phanerozoic (fig. 3a of Buffan et al., 2023, p. 3012). The GPMs used are from Wright et al. (2013), Matthews et al. (2016), Torsvik and Cocks (2017), Scotese & Wright (2018) and Merdith et al. (2021). The dark line delineates the maximum temporal limit of the Matthews et al. (2016) GPM.

lack and incompleteness of paleomagnetic data preserved in oceanic crust, which tend to be consumed in subduction zones during collision events. The study of Buffan et al. (2023) comparing five open-access global plate models (GPMs) concluded that differences between various paleogeographic reconstructions increase with age, especially for those older than ~300 Ma (**Fig. 2.13**). For the early to middle Paleozoic the Cambrian exhibits the largest proportion of reconstructed cell centroids with standard deviation (SD) greater than 10°, but in general <10% have an SD > 30°. The study recommended using GPMs based on a paleomagnetic frame, as these require pure paleomagnetic constraints and report true paleolatitudes. Thus, we use the PALEOMAP model of Scotese & Wright (2018), which utilizes a paleomagnetic reference frame.

2.5 Multivariate analyses

The application of multivariate statistical techniques has significantly advanced the field of paleobiogeography. Initially, biogeographical analyses—especially for phytoplankton during the 1970s and 1980s—relied on subjective interpretation of species ranges (e.g. the

Perigondwana and Baltic provinces of Vavrdová, 1974 for the Middle Ordovician; the Silurian paleolatitudinal facies of Cramer and Díez, 1974b). The adoption of hierarchical cluster analysis (HCA) in the 1990s marked a turning point, with Colbath (1990) among the first to calculate inter-locality similarities using the Simpson index and produce taxonomic clusters. Le Hérissé and Gourvennec (1995) similarly used HCA to identify Late Llandovery and Wenlock acritarch biofacies in North America, and later compared their results with global localities (Le Hérissé et al., 1997). These studies showed that multivariate methods could recover meaningful, geographically coherent patterns aligning with established biogeographic realms.

Subsequent studies refined these approaches and incorporated additional metrics and time slices. Molyneux et al. (2013) reviewed the biogeography for the early to middle Paleozoic, applying HCA using Jaccard index to Furongian and late Dapingian-early Darriwilian Perigondwana localities; while Shen et al. (2019) expanded the methodological toolkit by introducing non-metric multidimensional scaling (NMDS) alongside CA to identify Famennian bioregions. While HCA effectively identifies nested or hierarchical structures, it can impose artificial boundaries in gradient-like distributions. NMDS better reveals continuous ecological gradients but may obscure fine-scale separations unless supported by stress evaluation and minimum spanning trees (Brayard et al., 2007).

In response to the limitations of HCA and NMDS, network analysis (NA) has emerged as a complementary or alternative approach. Bootstrapped spanning networks (BSNs), developed by Brayard et al. (2007), use minimum spanning trees and bootstrap values to reveal well-supported biogeographical relationships, as seen in Early Triassic ammonite distributions. Concurrently, bipartite networks introduced by Vilhena et al. (2013) treat localities and taxa as separate node types and detect modules using algorithms such as the map equation. This method not only identifies bioregions but also transitional zones and overlapping faunas (Vilhena and Antonelli, 2015), and has been applied in both spatial and temporal frameworks (e.g., Kocsis et al., 2017; Na et al., 2023).

More recently, hierarchical clustering on principal components (HCPC) has been used to define mammalian bioregions in the Neogene and Pleistocene (Gibert et al., 2022). HCPC clusters ordination scores to define bioregions at varying resolutions, offering a flexible alternative for continental-scale studies. Their results revealed a shift from longitudinal to latitudinal biogeographic structure among Old World mammals from the Miocene to the Pliocene, illustrating the method's capacity to capture dynamic spatial patterns.

Together, these approaches reflect a methodological progression in paleobiogeography—from discrete taxon-range interpretations to statistically robust, multivariate frameworks. The integration of clustering, ordination, and network-based techniques provides a more nuanced understanding of paleocommunity structure and regional differentiation. As computational tools and curated databases continue to improve, multivariate analyses will remain essential for resolving biogeographic patterns across both space and deep time.

In this study, HCA and NMDS were used to determine biogeographical regions, both based on the Dice index, for each epoch in the Cambrian and stage from the Ordovician to the Devonian. Ward's method was used as the linkage algorithm for HCA, since it minimizes within-group variance and tends to produce more compact clusters. The multivariate analysis was done using the *vegan* package in R (Oksanen et al., 2025).

2.6 Paleobiogeographical nomenclature

In interpreting the clusters from HCA and NMDS, the terms “realm”, “province” and “subprovince” are used. In literature the hierarchy of the units have not always been clearly defined and workers focusing on different taxa use different terminologies (Servais and Sintubin, 2009). Various authors (Kauffman, 1973; McKerrow & Cocks, 1986; Westermann, 2000; Cecca, 2002; Cecca & Westermann, 2003) proposed terminologies for various biogeographical units. Kauffmann (1973) noted that some workers use percentages of endemism to define provinces, as an example for Cretaceous bivalves: endemic centers contain 5-10%; subprovinces 10-25%; provinces 25-50%; regions 50-75% and realms have > 75%. McKerrow & Cocks (1986) defined “provinces” as regions separated by physical barriers to migration; and “realms” as climate-controlled flora and fauna. Cecca & Westermann (2003) recommended the following ranks: Superrealm (mainly used in Russian literature), realm, Subrealm or Region, Province and Subprovince. While for the moment there is no calculation of endemism between the biogeographic units/clusters identified, the term “realm” as used here is the same meaning as McKerrow and Cocks (1986). Under the “realms” are smaller, geographically continuous and distinct HCA clusters which are called here as “provinces.” While some maybe true biogeographical provinces as defined by McKerrow and Cocks (1986), some others may turn out to be facies controlled (for example the South Gondwana “Provinces 1 and 2” in the Miaolingian, Homerian, Gorstian and Pridoli) because of the apparent lack of physical barriers. Further investigation of the geologic and geographic setting is necessary to determine if it is indeed the case. “Subprovinces” are also occasionally invoked when there are discernable units within the identified “provinces.”

CHAPTER 3

DIVERSITY IN SPACE AND TIME

The diversity, growth and productivity of modern phytoplankton are strongly influenced by physical and biological factors (Boyce & Worm, 2015; and references therein). The physical factors mainly control nutrient flux, and these include temperature, wind intensity, salinity and even pH. Higher sea surface temperatures and changes in surface salinity enhances stratification and prevents upwelling of nutrients from greater depths while stronger wind intensity also promotes upwelling and consequently production. Swifter currents, faster dispersal and greater environmental variability enhances local diversity and creates diversity hotspots (Clayton et al., 2013). Prolonged favorable environmental conditions and maximal continent separation led to the formation of late Mesozoic and Cenozoic marine invertebrate diversity hotspots (Cermeno et al., 2022), and this might also apply to phytoplankton. Ocean acidification chiefly affects metabolic processes, such as formation of tests by calcareous phytoplankton. Biological controls include the presence of predators such as zooplankton, which keep production in check and enhance diversity in stable ecosystems; and environmental conditioning due to activities of other organisms which can supply (or withhold) nutrients (e.g. through the form of feces; or nektonic movement which can also promote upwelling).

Paleozoic phytoplankton are likely to be affected by the same drivers, but there are notable departures to modern oceanic and atmospheric conditions. The oceanic chemistry and atmospheric carbon dioxide concentrations are different in the Paleozoic, two factors which directly affect metabolic processes. Atmospheric CO₂ levels are much higher than in the present; and there is a shift from low Mg calcite to high Mg calcite + aragonite seas in the Carboniferous (see fig. 1 of Strother, 2008, p. 11). These are the environmental conditions to which Paleozoic phytoplankton must adapt. Strother (2008) suggested that the lack of carbon concentration mechanisms (CCMs) which make photorespiration more efficient in other algal groups rendered acritarchs less fit when atmospheric CO₂ drastically dropped in the Devonian; while the change in oceanic chemistry increased particulate and dissolved organic matter (which brought an influx of P) affected cyst production. Eventually, these contributed to the decline of acritarch diversity in the late Paleozoic and the takeover by dinoflagellates in the Mesozoic.

The distribution of species across the world is not uniform. Modern biodiversity patterns show a tropical peak and a poleward decline in species; this pattern is known as the latitudinal diversity gradient (LDG) (Hawkins, 2001). There are several hypotheses on the origin of the LDG which can be divided into two main categories: the first is related to diversification rates while the second is linked to dispersal history (Rolland & Freeman, 2023). The tropics is either a “cradle” with high speciation rates; a “museum” showing low extinction rates or even both with preferential origination in the tropics and expansion to the poles without losing their tropical presence (Jablonski et al., 2006). Higher productivity in the tropics may have allowed for a higher carrying capacity compared to extratropical regions, contributing to a tropical peak (Currie et al., 2004). On the other hand, species may have shifted from high to low latitudes through time to accumulate diversity (Wiens & Donoghue, 2004). Another view suggests that originations and net dispersal are more likely from the extratropics; in particular for Cenozoic marine plankton such as foraminifera, calcareous nannoplankton, diatoms and radiolarians (Raja & Kiessling, 2021). In modern marine phytoplankton the peak of the LDG varies from equatorial in dinoflagellates, and northern mid-latitudes for diatoms and coccolithophorids (Chen et al., 2011). Marine bacteria showed an LDG centered on the equator (Fuhrman et al., 2008). Long term climate appears to drive LDG patterns in deep time: cooler icehouse regimes result in a tropical peak while warmer greenhouse regimes show flatter gradients or peaks in temperate areas (Mannion, 2020; Mannion et al., 2014). Paleogeography also plays an important role in the distribution of diversity. For example marine biodiversity was highest in the West Tethys (Mediterranean region) during the Eocene, shifting further east

to Arabia and the Indo-Australian archipelago (IAA) when the Mediterranean Sea started to close by the early Miocene and leaving only the IAA when Arabia and Eurasia collided in the middle to late Miocene (Renema et al., 2008).

Here we investigated the role of two factors and their effect on diversity: temperature and productivity. The temperature data of Scotese et al. (2021) also included information on the poles and the tropics aside from the global average; it shows that polar temperatures contribute more to the global difference (the tropical temperatures are more stable) and are thus a potential major driver to changes in latitudinal diversity. The occurrence of positive carbon isotope events are used as a proxy for intervals of increased productivity (Pederson and Calvert, 1990). For the first time, grid-cell diversity is plotted for the Paleozoic phytoplankton to identify diversity hotspots, which will indicate local areas of favorable environmental conditions. The LDG plots using various diversity metrics for all time intervals are shown in **Appendix 6**. Maps of grid-cell diversity are shown in **Appendices 7, 8, 9, 10** and **11**. These illustrate measured diversity for SQS50, SQS70, origination rates, extinction rates and turnover respectively. Although grid-cell diversity was done for the four diversity metrics used, we utilized SQS50 to identify diversity hotspots since this is the metric with the least susceptibility to sampling effort bias (**Table 3.1**).

Table 3.1 Spearman correlation between global diversity measurements and number of localities sampled. * indicates significant p-values (< 0.05).

Diversity metric	Spearman ρ	p-value
RT (range-through including singletons)	0.57	0.0025*
RTex (range-through excluding singletons)	0.59	0.0015*
SQS50 (shareholder quorum sampling with $q=0.5$)	0.44	0.03*
SQS70 (shareholder quorum sampling with $q=0.7$)	0.50	0.01*

3.1 Sample completeness

A sample completeness curve was generated and shown in **Fig. 3.1**. The best sampled intervals are the Gorstian and Emsian while the Terreneuvian and Sandbian are the least sampled. Overall, the Silurian and Devonian show better sampling than the Cambrian and Ordovician intervals.

Results of the Spearman's correlation test between global diversity metrics and localities as proxy for sampling effort show moderate ρ values (**Table 3.1**). Spearman's ρ for RT and RTex are 0.60 while those for SQS are lower, at 0.4 and 0.5 for SQS50 and SQS70 respectively. Of the four diversity metrics, SQS50 is the least susceptible to sampling bias.

3.2 Global diversity

The unstandardized diversity (RT and RTex) both show increasing generic diversity from the Cambrian to the Early Ordovician (**Fig. 3.2**), dipping slightly in the Dapingian then recovering with a peak in the Darriwilian, another dip in the Sandbian and a plateau for the rest of the Late Ordovician before another dip in the Rhuddanian, just after the LOME. Both curves showed increasing trends and a peak at the Ludfordian before a steady decrease until the end-Devonian. The two SQS curves showed a different pattern, particularly for the Silurian (**Fig. 3.2**). Diversity is low in the Cambrian and the curve is nearly flat, except for an increase at the end-Cambrian. Diversity dipped in the Tremadocian and reached the highest levels from the

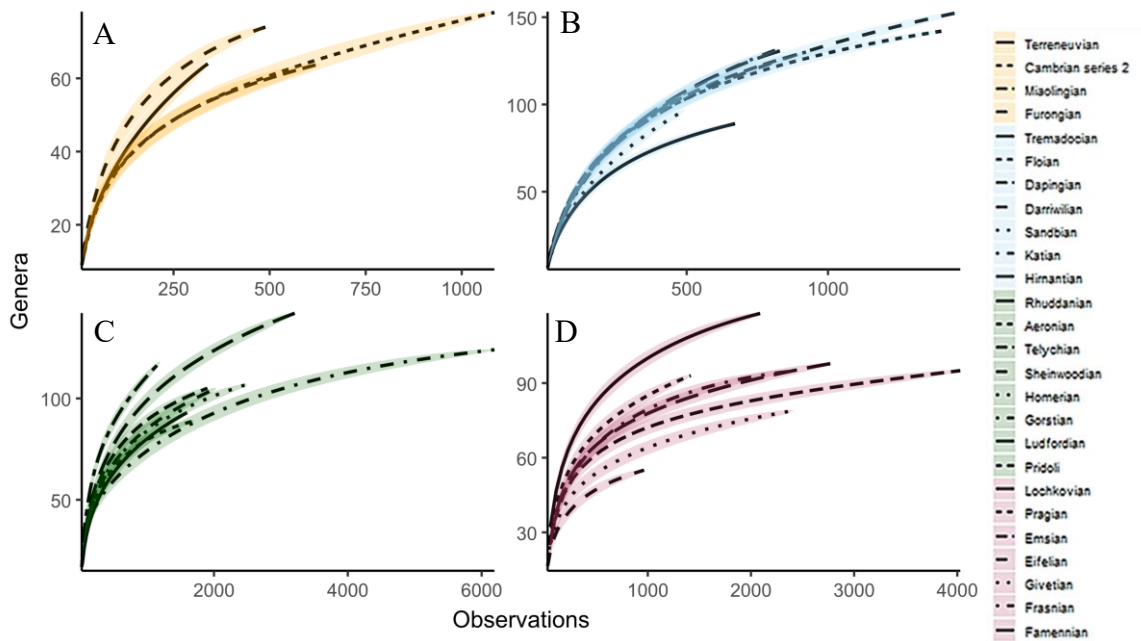


Figure 3.1 Sample completeness curves with the 95% confidence interval. The Cambrian was analyzed at system level and the rest at stage level. Orange = Cambrian, blue = Ordovician, green = Silurian, maroon = Devonian.

Floian and the Middle Ordovician, before dipping in the Sandbian and recovering for the rest of the Late Ordovician. Peak diversity was recorded in the Dapingian. As with the unstandardized curves the effect of the LOME is clear with a large dip in diversity at the start of the Silurian in the Rhuddanian, recovered slightly afterwards and plateaued with generally low diversity until the Ludfordian peaking again in the Pridoli. Afterwards the diversity steadily dropped and the curve is nearly flat up to the end-Devonian.

The Silurian trough is in contrast to the pattern of species diversity in Kroeck et al. (2022, see fig. 1, p. 4), which show a rebound in diversity after the LOME. Another notable discrepancy is a small diversity peak near the Frasnian-Famennian boundary, which is not documented in the present generic curve (**Fig. 3.2A**). An early to middle Devonian trough of species diversity is prominent in almost all diversity indices for Kroeck et al. (2022); also in Katz et al. (2004; fig. 3, p. C-3) for both species and genera. Strother (2008, fig. 1, p. 11) on the other hand shows a steep decrease in acritarch genera starting in the early Silurian, briefly interrupted in the Early and Middle Devonian before proceeding in a steep decline. However, the diversity curves from the two latter references have not been sample-standardized. Nevertheless the SQS40 trend in Kroeck et al (2022) shows relatively low diversity in the Silurian. The Frasnian-Famennian may need to be reviewed for cases of possible taxonomic “oversplitting.”

We compared diversity with temperature data from Scotese et al. (2021) using linear regression (**Table 3.2**). Results show a moderate R^2 value of ~ 0.4 for RT and RTex versus temperature difference (T_{diff} = tropical – polar temperatures), polar (T_{polar}) and tropical (T_{trop}) temperatures; and 0.5 with global average temperatures (GAT). SQS50 and SQS70 show weak correlation with all the temperature parameters with $R^2 \sim 0.1$. It seems there is a stronger correlation between GAT and RT, RTex, which is not corroborated by SQS analysis. It seems however that phytoplankton diversity (at the generic level) did not immediately recover after the LOME, and the depressed trend could be due to the stronger effects of environmental variables other than temperature. We redone the analysis without most of the Silurian, except

for the Pridoli when diversity recovered (**Table 3.3**). The results show a dramatic difference for SQS, with R^2 values several times higher than the previous analyses for all time intervals. All the diversity metrics showed stronger linear correlations with the temperature variables, except for RT vs. GAT where the R^2 is slightly lower. RTex vs. GAT had the highest R^2 value at 0.60, but in general unstandardized diversity did not show much change. SQS50 had better, but still weak correlation with R^2 between 0.2-0.3. SQS70 had a moderate correlation with R^2 of 0.40 against T_{diff} , T_{polar} and GAT, and weak (0.3) with T_{trop} .

The turnover rates show very strong swings, but some patterns emerge. From Cambrian series 2 to the Katian origination rates are greater than extinction (except for the Miaolingian, Dapingian and Sandbian). As expected, the Hirnantian had the highest extinction rate due to the LOME but the Darriwilian showed the second highest rate. Turnover was depressed in the Silurian with alternating higher origination and extinction rates until the Pridoli. From the Pridoli onwards extinction generally outstripped origination (except for the Pragian and Eifelian). Origination rates have clearly weakened in time while extinction does not show a trend, except for a trough from ranging nearly the entire Silurian (except for Pridoli). Overall, turnover is decreasing through time. Linear regression between the turnover rates and temperature parameters show weak correlation (**Tables 3.4 and 3.5**).

Table 3.2 Coefficient of linear regression for diversity metrics compared to temperature parameters, calculated for all time intervals. The values in red indicate a negative slope or inverse relationship. T_{diff} is the difference between tropical and polar temperatures; T_{pol} is the average polar temperature, T_{trop} are tropical temperatures while GAT is the global average temperature.

Diversity metric	T_{diff}	T_{pol}	T_{trop}	GAT
RT	0.4	0.4	0.4	0.5
RTex	0.4	0.4	0.4	0.5
SQS50	0.1	0.1	0.1	0.1
SQS70	0.1	0.1	0.1	0.1

Table 3.3 Coefficient of linear regression for diversity metrics compared to temperature parameters, excluding the Rhuddanian to Ludfordian. The values in red indicate a negative slope or inverse relationship.

Diversity metric	T_{diff}	T_{pol}	T_{trop}	GAT
RT	0.4	0.5	0.4	0.4
RTex	0.5	0.5	0.5	0.6
SQS50	0.3	0.2	0.2	0.3
SQS70	0.4	0.4	0.3	0.4

Table 3.4 Coefficient of linear regression for turnover metrics compared to temperature parameters. The values in red indicate a negative slope or inverse relationship.

Diversity metric	T_{diff}	T_{pol}	T_{trop}	GAT
oriPC	0.1	0.1	0.1	0.2
extPC	0.000007	0.001	0.05	0.009
turnover	0.09	0.1	0.1	0.1

Table 3.5 Coefficient of linear regression for turnover metrics compared to temperature parameters, excluding the Rhuddanian to Ludfordian. The values in red indicate a negative slope or inverse relationship.

Diversity metric	T_{diff}	T_{pol}	T_{trop}	GAT
oriPC	0.2	0.2	0.1	0.2
extPC	0.05	0.03	0.007	0.02
turnover	0.06	0.07	0.1	0.1

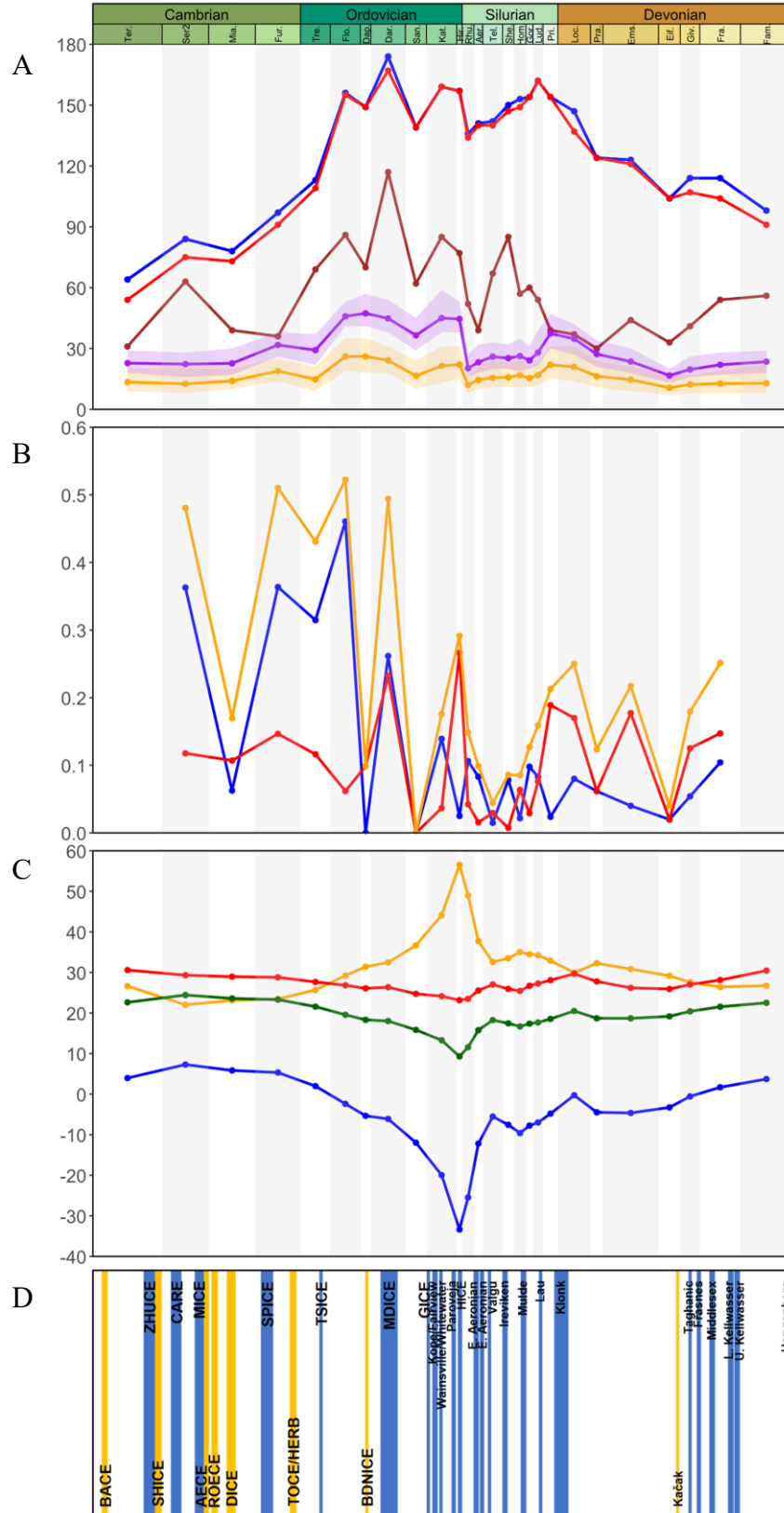


Figure 3.2 Global diversity metrics, along with temperature changes and carbon isotope events. (A) plots RT (blue), RTex (red), SQS70 (purple) and SQS50 (orange) with number of localities sampled (brown). (B) shows turnover metrics, total turnover (orange), origination rate (blue) and extinction rate (red). (C) is temperature data from Scotese et al. (2021), T_{diff} (orange), T_{trop} (red), GAT (green) and T_{polar} . (D) shows the timing of carbon isotope excursion events from Cramer and Jarvis (2020); positive excursions are shown in blue while negative ones are in yellow.

3.3 Latitudinal diversity

The LDG plots showed the movement of diversity hotspots through time (**Fig. 3.3**). For the unstandardized diversity both measurements (RT and RTex) exhibit the same broad pattern, but the peaks are more pronounced for RT. Throughout the Cambrian until the Tremadocian diversity is low with the peak of diversity generally in the Southern hemisphere from -30° to -75° paleolatitude, except for the Furongian which has peak diversity in the Northern Hemisphere at 3° . From the Floian until the Famennian the LDG is pronounced, except for the Eifelian in the early Middle Devonian. In the Floian and Dapingian peak diversity is between -50° and -60° before drifting north in the Darriwilian to -38° . From the Sandbian to the Telychian it drifted further north between -28° to -33° . The Wenlock (Sheinwoodian and Homerian) marks the northernmost location of peak diversity since Furongian, at -18° . During Gorstian peak diversity moved slightly south to -23° , while from the Ludfordian to the Lochkovian it ranged from -63° to -53° . In the Pragian and Emsian peak diversity is at the high, southern paleolatitudes from -73° to -78° . In the Eifelian and Givetian it was at -38° , in the Frasnian at -73° and was recorded at -33° in the Famennian. The same locations of peak diversity were also noted for the SQS measurements.

The origination and extinction rates show latitudinal preferences (**Fig. 3.4A, B**). High origination rates occur between $\sim 20^{\circ}$ to -40° (equatorial to subequatorial regions) from the Miaolingian to the Frasnian; except for the Floian, Darriwilian and from the Emsian to Givetian where there were low origination rates in the said latitudes. The Miaolingian had two peaks of origination at $\sim 0^{\circ}$ and -30° . During the Furongian and Tremadocian only the northern peak remained and in the Dapingian it was located further north at 15° . For the whole of the Late Ordovician until the Aeronian, the origination peak stayed at -25° . During the Telychian it was at $\sim 8^{\circ}$. In the Wenlock it was at -17° . There were two peaks in the Ludlow, the main peak is the same as the Telychian at $\sim 8^{\circ}$ while another peak is located -14° . In the Lochkovian and Pragian the peak was at $\sim -30^{\circ}$ while in the Frasnian it is approximately at -15° . The occurrence of peak originations can be divided into five phases, a northern hemisphere phase from the Miaolingian to the Dapingian, a stable period in the Late Ordovician to the Aeronian, instability from the Telychian to the Pridoli, and subequatorial southern hemisphere occurrences in the Lochkovian-Pragian and Frasnian. On the other hand, the extinction “hotspots” preferentially occur in a palaeolatitudinal band from -60° to $\sim -76^{\circ}$, and a continuous phase from the Lower Ordovician to the Pridoli coincides with two origination phases mentioned above. Outside of this interval, there are peaks in the Furongian and the Givetian.

The slopes of the LDG are shown in **Fig. 3.5**. Results show more positive slopes for standardized versus unstandardized diversity metrics. The SQS show peak positive slopes for the Late Ordovician and peak negative for the Lochkovian, while the unstandardized shows peak negative slopes at the Gorstian and Ludfordian. Turnover metric slopes are weak.

We tested the correlation between the slope of the LDG versus temperature with and without the Silurian (See **Tables 3.6** and **3.7**, respectively). RT and RTex have much lower R^2 values compared to SQS70 and SQS50. For SQS only SQS50 vs. GAT is not significant at $p < 0.05$. For the turnover metrics extPC showed larger R^2 values ~ 0.3 compared to oriPC and total turnover which are < 0.1 .

The results of the LDG analysis show movement of the diversity peak through time, and a latitudinal control for origination and extinction rates. The LDG slopes show weak correlation with temperature parameters, while for turnover only the slope for extinction rates is moderately controlled by temperature parameters.

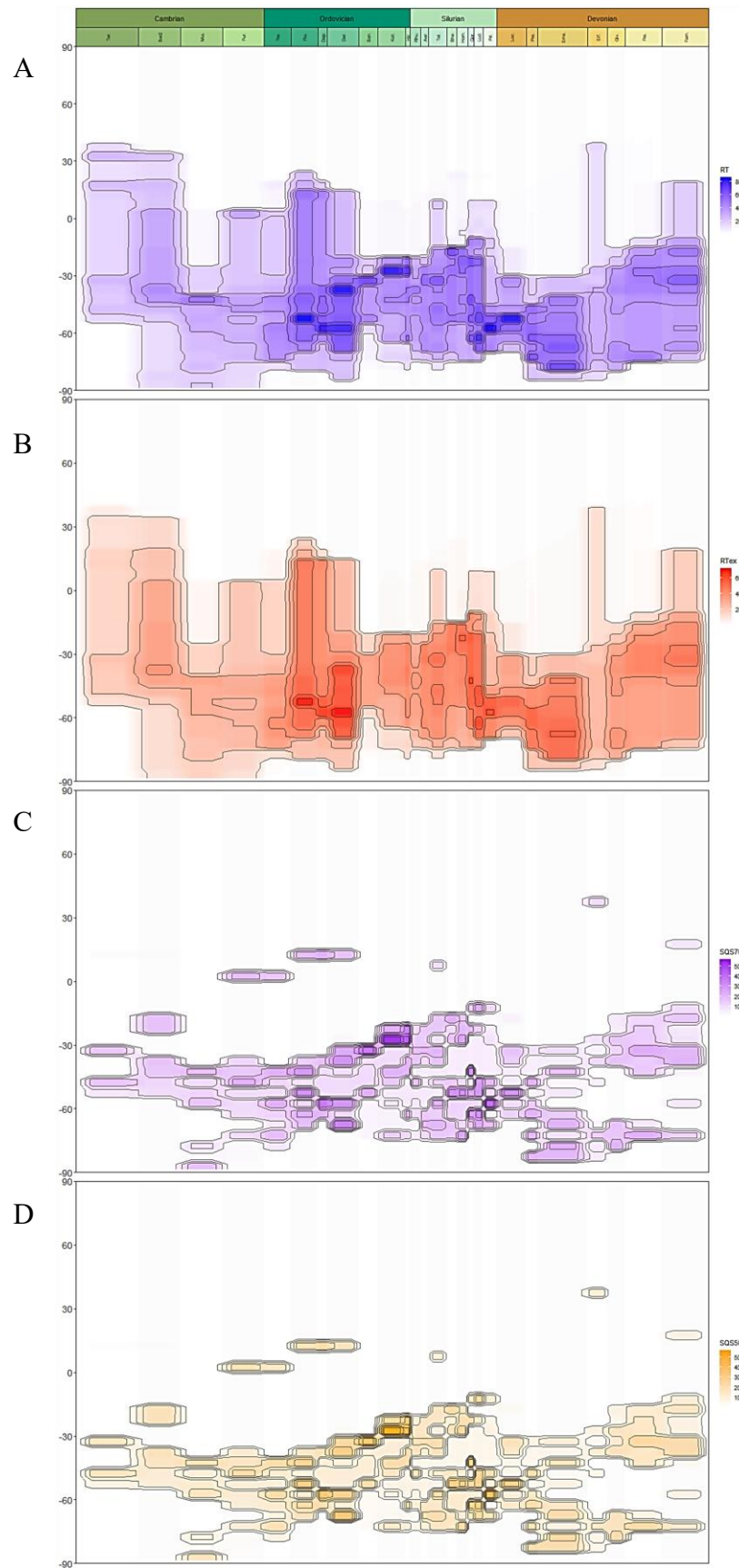


Figure 3.3 Latitudinal diversity showing RT (A), RTex (B), SQS70 (C) and SQS50 (D). The color shading represents the number of genera. SQS = shareholder quorum subsampling (at $q = 0.7$ for SQS70 and $q = 0.5$ for SQS50); RT = range-through diversity while RTex excludes singletons.

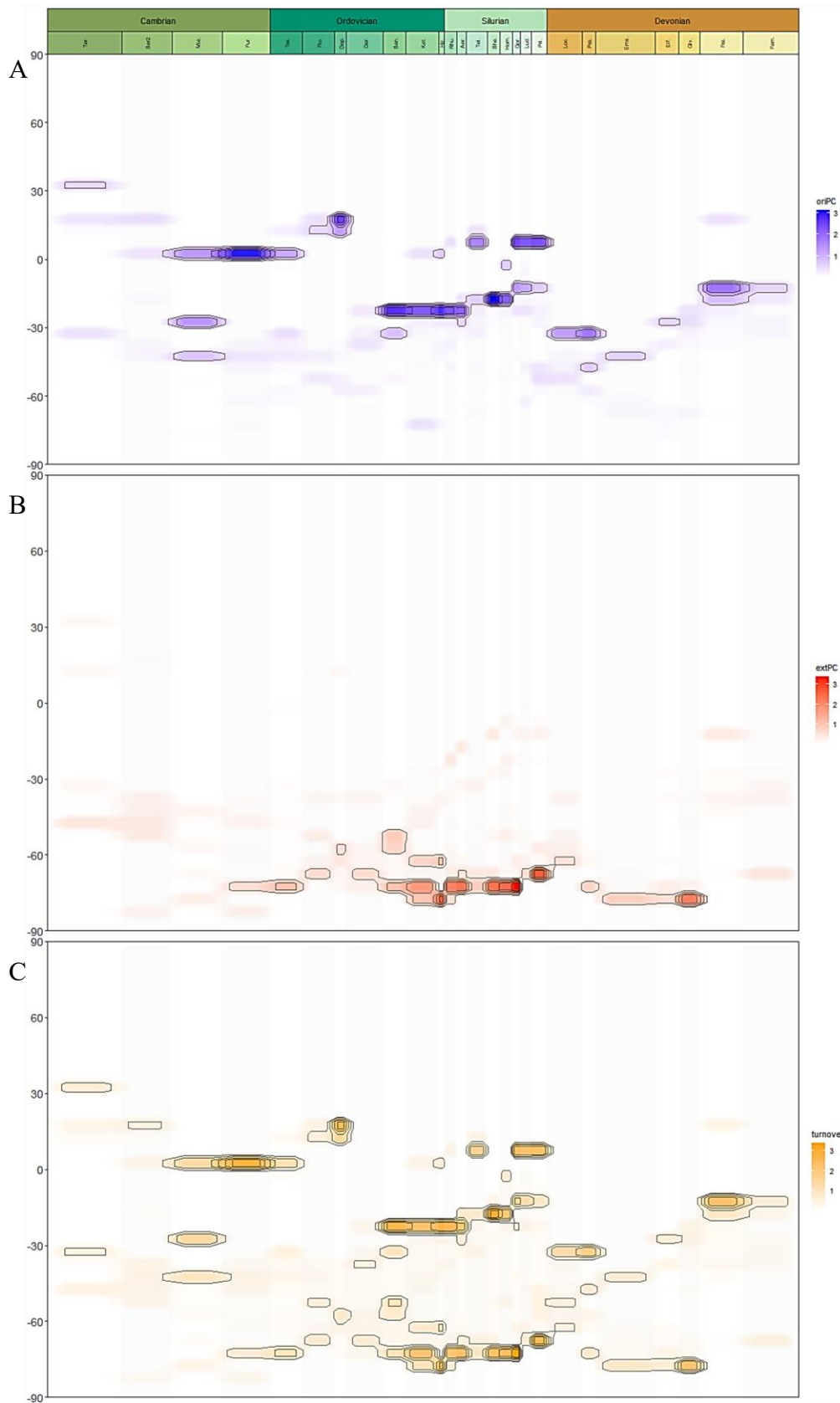


Figure 3.4 Latitudinal turnover metrics for originations (A), extinctions (B) and total turnover (C). The color range represents the number of genera.

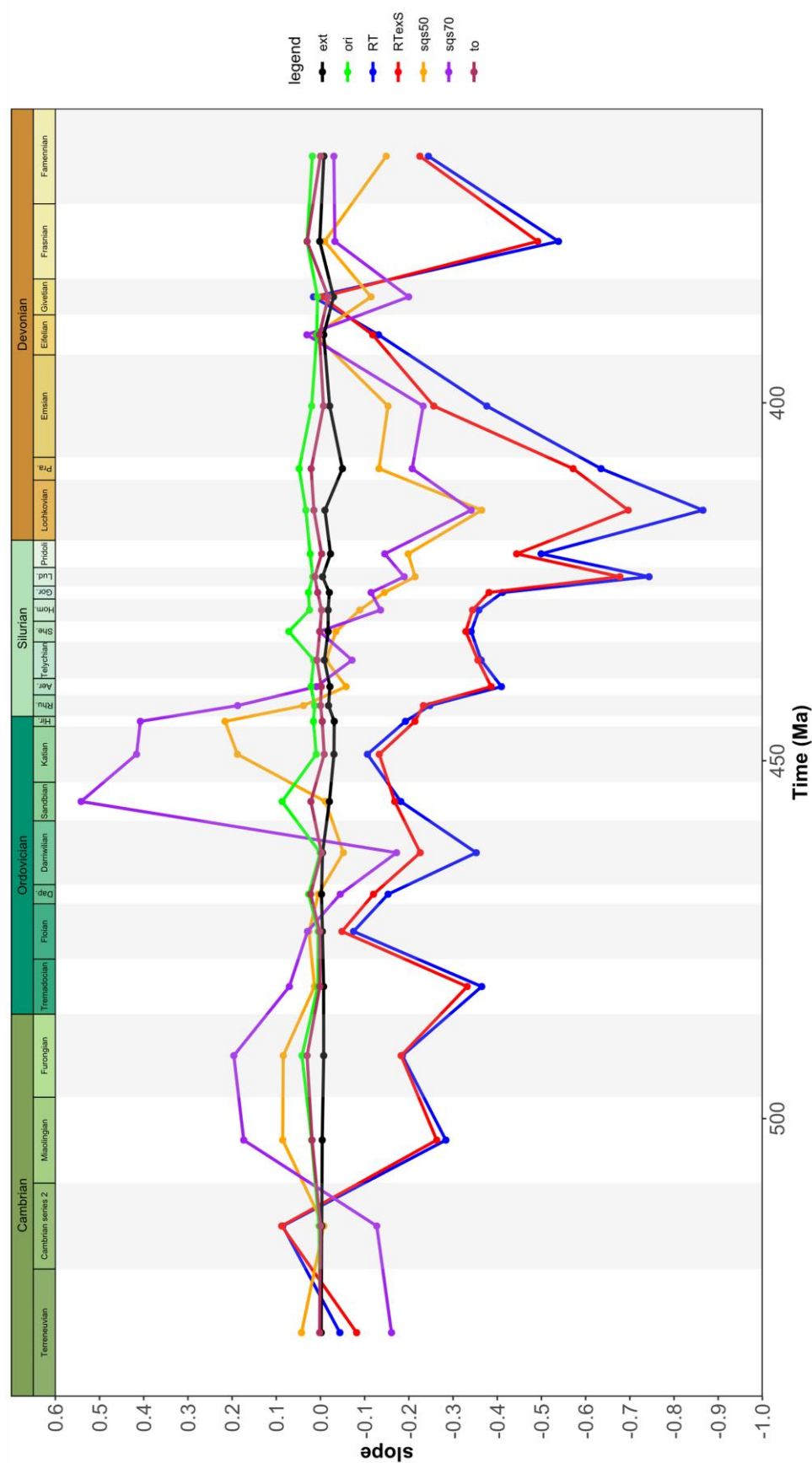


Figure 3.5 The slope of various diversity and turnover metrics plotted through time.

Table 3.6 Linear regression between the LDG slopes for diversity and turnover metrics versus temperature, for all time intervals. Significant p-values (<0.05) are indicated by *.

Metric	Parameter	Slope	R²	p-value
RT	T _{diff}	-0.0014	0.0024	0.81
	T _{pol}	0.00030	0.00016	0.95
	T _{trop}	-0.015	0.018	0.51
	GAT	0.0041	0.0044	0.75
R_{Tex}	T _{diff}	-0.0024	0.0093	0.64
	T _{pol}	0.0012	0.0033	0.78
	T _{trop}	-0.011	0.011	0.60
	GAT	0.0058	0.012	0.60
SQS70	T _{diff}	0.021	0.33	0.0022*
	T _{pol}	-0.018	0.35	0.0015*
	T _{trop}	-0.082	0.32	0.0025*
	GAT	-0.042	0.29	0.0045*
SQS50	T _{diff}	0.0072	0.17	0.037*
	T _{pol}	-0.0062	0.19	0.028*
	T _{trop}	-0.031	0.20	0.021*
	GAT	-0.014	0.13	0.073
oriPC	T _{diff}	9.3E-05	0.068	0.20
	T _{pol}	-7.4E-05	0.063	0.22
	T _{trop}	-0.00026	0.032	0.38
	GAT	-0.00021	0.071	0.19
extPC	T _{diff}	-0.00037	0.32	0.0028*
	T _{pol}	3.1E-04	0.33	0.0022*
	T _{trop}	0.0014	0.29	0.0049*
	GAT	0.00084	0.35	0.0016*
turnover	T _{diff}	0.0024	0.091	0.13
	T _{pol}	-0.0020	0.095	0.13
	T _{trop}	-0.0088	0.082	0.16
	GAT	-0.0052	0.094	0.13

Table 3.7 Linear regression between the LDG slopes for diversity and turnover metrics versus temperature, excluding the Rhuddanian to Ludfordian. Significant p-values (<0.05) are indicated by *.

Metric	Parameter	Slope	R ²	p-value
RT	T _{diff}	-0.00038	0.00017	0.96
	T _{pol}	-0.00073	0.00089	0.90
	T _{trop}	-0.022	0.037	0.43
	GAT	0.00089	0.00019	0.96
RTex	T _{diff}	-0.0014	0.0033	0.82
	T _{pol}	0.00019	8.4E-05	0.97
	T _{trop}	-0.017	0.032	0.46
	GAT	0.0025	0.0022	0.85
SQS70	T _{diff}	0.024	0.37	0.0060*
	T _{pol}	-0.020	0.39	0.0043*
	T _{trop}	-0.091	0.35	0.0078*
	GAT	-0.050	0.34	0.0092*
SQS50	T _{diff}	0.0083	0.19	0.059
	T _{pol}	-0.0072	0.21	0.046*
	T _{trop}	-0.034	0.22	0.043*
	GAT	-0.016	0.15	0.097
oriPC	T _{diff}	1.1E-04	0.089	0.22
	T _{pol}	-8.8E-05	0.089	0.21
	T _{trop}	-0.00035	0.062	0.30
	GAT	-0.00023	0.091	0.21
extPC	T _{diff}	-0.00038	0.30	0.016*
	T _{pol}	0.00031	0.31	0.014*
	T _{trop}	0.0013	0.24	0.034*
	GAT	0.00085	0.32	0.011*
turnover	T _{diff}	0.0023	0.073	0.26
	T _{pol}	-0.0019	0.073	0.26
	T _{trop}	-0.017	0.032	0.46
	GAT	0.0025	0.0022	0.85

3.4 Grid-cell diversity

Grid-cell diversity was calculated for SQS (**Appendices 6 and 7**) but the SQS50 metric was used mainly to interpret locations of diversity hotspots, as this is the measurement least likely to be affected by heterogeneous sampling intensity (see **Fig. 3.6; Appendix 6**). The results show low to moderate worldwide diversity from the Terreneuvian to the Tremadocian. During the Floian moderate to high diversity marked many areas along Perigondwana, including Avalonia and Baltica, with the highest diversity in “southeastern” Gondwana. In the Middle Ordovician, “southeastern” Gondwana is the center of phytoplankton diversity. This disappeared in the Late Ordovician, except for the Katian, when Baltica hosted greater diversity. Worldwide diversity is low to moderate during the early to middle Llandovery (Rhuddanian and Aeronian). From Telychian to the Wenlock (Sheinwoodian, Homarian) the phytoplankton hotspot returned to “southeastern” Gondwana, with low to moderate diversity in Baltica. From Ludlow (Gorstian, Ludfordian) to the Pragian (middle Early Devonian) the

paleolatitudinal band from approximately -30° to -75° hosted moderate to high diversity, as opposed to the lower southern latitudes (0° to -30°) which has low to moderate diversity. In the Emsian the peak of diversity is at the high southern latitudes, in the modern South American landmass. Diversity is low to moderate in the Eifelian. Starting in the Givetian until the end of the Devonian, peak diversity is in the high southern latitudes of southern Gondwana, specifically in South America.

The location of areas with high origination rates do not show apparent trends, aside from occurring roughly between the paleolatitudes $+30^{\circ}$ and -30° (**Appendix 8**). The early Cambrian had low origination everywhere while from the Miaolingian to the Early Ordovician there were elevated rates in “eastern” and northern Gondwana. The Middle Ordovician had low origination rates. Laurentia had high origination rates from the Sandbian to the Hirnantian, and for the whole Silurian peak origination rates shifted between Baltica and northern Gondwana (South China). The Devonian had generally low origination except for Laurentia in the Pragian and eastern Gondwana (Australia) in the Frasnian. Relatively higher extinction rates preferentially occur in higher southern paleolatitudes (**Appendix 9**), which can be observed in the colder Late Ordovician and the Rhuddanian. The Gorstian and Ludfordian had a high extinction rate in “southeastern” Gondwana. Elevated extinction rates shifted to western Gondwana (South America) in the Pragian, Emsian and Frasnian. Turnover trends (**Appendix 10**) merely follow origination and extinction rates.

The results of the grid-cell diversity analysis show where diversity is located (or not), and which localities contribute to observed latitudinal diversity. It also attempts to trace how diversity hotspots evolved through time.

3.5 Discussion

3.5.1 Paleoclimatic control

Many studies indicate that the diversity of phytoplankton is largely controlled by climate through temperature, with warmer climates harboring greater diversity because of enhanced speciation, metabolic rates and selecting for higher number of species (Benedetti et al., 2021 and references therein). The modern organic-walled representatives of phytoplankton, the dinoflagellates, show greater diversity in the equatorial regions rather than at the poles (Chen et al., 2011). Although species distribution models indicate that the present global warming might actually promote overall phytoplankton diversity (Benedetti et al., 2021), it will drastically alter the latitudinal diversity gradient with the poleward migration of species, creating an equatorial trough. The converse, global cooling, is likely to decrease diversity (Righetti et al., 2019).

The empirical global diversity metrics show an apparent correlation with decreasing global temperatures in the early Paleozoic, until the LOME. The Silurian is anomalous, with a dip in diversity despite apparently favorable climatic conditions. Superimposing the occurrence of carbon isotope events on the global diversity curves and turnover metrics show increased frequency of these events in the Silurian. This may have affected the diversity of phytoplankton, more than the effect of climate. Disregarding most of the Silurian shows a moderate to strong control of temperature on diversity (see **Table 3.3**), particularly GAT. Lower GAT and higher T_{diff} drives higher global diversity. T_{trop} is more stable than T_{polar} , therefore the difference relies on swings in polar temperatures rather than in the tropics. Extreme temperature difference due to colder polar temperatures in intervals of global cooling can cause extinction

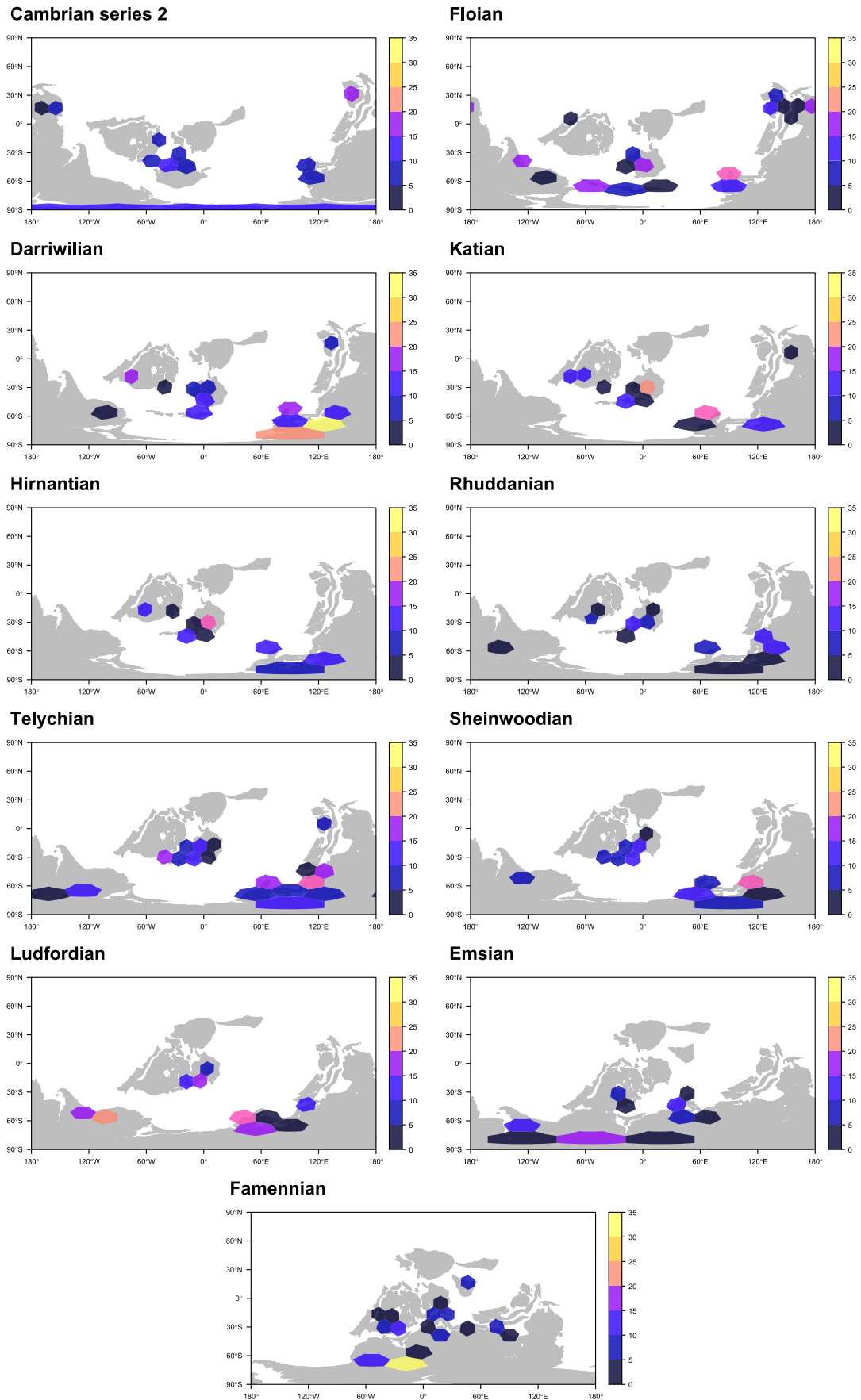


Figure 3.6 Selected grid cell diversity counted using SQS50 (see **Appendix 6** for the complete set). The color bar corresponds to number of genera.

events and drive extinction rates, as in the Hirnantian (see **Figs. 3.6A, B, C**). Compared to Kroeck et al. (2022; fig. 2, p. 5) the extinction rate for the Darriwilian is anomalously high. There are two possibilities: either it is an artifact due to poor sampling, or the extinction rate is naturally high due to a combination of one or several environmental factors. The Dapingian and Darriwilian coincide with carbon isotope excursions but the effects of these on diversity are not clear. The climate does not show strong linear correlation with turnover (**Tables 3.4 and 3.5**).

The early to middle Paleozoic results on global diversity appear to contradict the increase in global diversity predicted by Benedetti et al. (2021), but this increase is due to species tracking optimal thermal habitats and the predicted peak of latitudinal diversity migrates from the tropics to northern temperate areas (some tropical diversity hotspots remain due to upwelling). The GAT and average tropical temperatures in the Paleozoic are higher than the present-day, and the colder intervals in the Ordovician (except for the Hirnantian) and Silurian may represent thermally favorable regimes (Scotese et al., 2021).

Climate appears to have a moderate effect on sample-standardized latitudinal diversity with R^2 values of 0.2 to 0.4 (for correlations with $p < 0.05$), when the Rhuddanian to Ludfordian are not included in the linear regression (see **Tables 3.6 and 3.7**). The sign of the slope indicates whether diversity is increasing towards the north or southwards, the LDG will be flatter if the absolute value of the slope approaches 0 and more pronounced if it is greater. Sample-standardized diversity show weak to moderate correlation with temperature parameters, whether the Silurian is included or not, in contrast to standardized diversity (See **Fig. 3.5** for a plot of the LDG slopes). SQS70 shows significant relationship with both T_{diff} and GAT; while SQS50 does not. A positive relationship between SQS70 and T_{diff} suggests a more pronounced LDG with increasing T_{diff} . The main contributor to higher T_{diff} is higher polar temperatures; during cold intervals there is a migration of peak diversity northwards as can be seen for the Ordovician in **Fig. 3.3**. This is also reflected in the relationship between slopes of SQS latitudinal diversity and T_{polar} , colder temperatures tend towards more positive slopes and more northward movements of peak diversity. Both T_{trop} and GAT have an inverse relationship with the slopes of SQS latitudinal diversity; and these are evident in the Cambrian and the Devonian with warm temperatures. The Floian to the Emsian have high T_{diff} , the value of which exceed T_{trop} . For most of this interval there are clear and prominent diversity hotspots, except for the Rhuddanian to the Ludfordian when the differences are attenuated. In terms of turnover, only the extinction rates appear to be significantly affected by climate (**Tables 3.6 and 3.7**). The inverse relationship between the latitudinal extinction rate slopes with T_{diff} , and positive correlation with T_{polar} , T_{trop} and GAT suggest that during cooler climates the extinction rates are greater in higher paleolatitudes than low paleolatitudes versus warmer climates where the opposite trend occurs.

The grid cell diversity mirrors the movement of the latitudinal diversity hotspots, but diversity is not necessarily uniform across these paleolatitudes (**Fig. 3.6**). Grid cell diversity shows generally low diversity in the warm Cambrian to Tremadocian, and also for the Devonian. The onset of cooling and higher T_{diff} in the Floian triggered a burst of diversity along the Perigondwana margin, including Avalonia and Baltica. The southern Europe-North Africa side (“southeastern Gondwana”) of southern Gondwana is the main diversity hotspot for most of the rest of the Ordovician (except for the Sandbian), before being eliminated in the Hirnantian with cooling of the southern polar latitudes. In the Late Ordovician Baltica was moving north, and a more favorable climate could have provided sanctuary from the colder temperatures in the south. Low to moderate diversity was observed everywhere during the Rhuddanian and Aeronian despite apparently favorable temperatures. From the Telychian to

the Pragian hotspots primarily occurred along the southern Perigondwana margin, and occasionally in Baltica or southern Laurentia. The hotspot switched to higher southern paleolatitudes, on the South American side (“southwestern Gondwana”) of Gondwana by the Emsian until the Famennian, when the global climate is warm.

3.5.2 Correlation with carbon isotope events

The Silurian is an unstable period characterized by changing environmental conditions, with fundamental changes in the global carbon cycle happening more frequently than any other time in the Phanerozoic (Munnecke et al., 2010). The 25 myr span of the Silurian is plagued by six recorded positive carbon isotopic events (compared to the 41 myr long Ordovician with seven): these are the Early and Late Aeronian; Valgu, Ireviken, Mulde, Lau and Klonk events. Positive carbon isotope excursions (CIEs) are linked to primary productivity and oceanic anoxic events, and often accompanied by extinctions (Kroeck et al., 2022 and references therein). Even though the GAT rose and approximates pre-LOME values, global diversity did not bounce back in the Silurian until the Pridoli (**Fig. 3.2A**). The low global diversity despite apparently favorable climatic conditions and coincidence with frequent CIEs suggest that disruptions to the carbon cycle may have played a role in suppressing the immediate recovery of phytoplankton diversity.

Similar to results of Kroeck et al. (2022; fig. 11, p. 21), several of the carbon isotope excursions coincide with high turnover (**Fig. 3.2B, D**). These include the SPICE (Steptoean Positive Carbon Isotope Excursion) in the early Furongian; and the MDICE (Middle Darriwilian Carbon Isotope Excursion). The high extinction rate recorded in the Darriwilian may not be an artifact after all but could be related to the MDICE. Generic diversity dropped after the LOME, which also coincides with the HICE (Hirnantian Isotopic Curve Event). Low global diversity and turnover coincide with these CIEs. The strength of the latitudinal diversity gradient seems weaker from the Rhuddanian to the Ludfordian (**Fig. 3.5**), and these correspond to a dense temporal cluster of CIEs from the Early Aeronian to the Lau events, but this correlation will need further investigation. The intensity of extinction rates in the high southern paleolatitudes coincide with positive CIEs from the Katian to the Pridoli, and the Givetian (**Fig. 3.4B**).

No clear effects of the CIEs were observed on patterns of grid-cell diversity. While the lack of diversity hotspots in the Rhuddanian can be attributed to the loss of diversity after the LOME, it is not very clear if this also holds for the Aeronian which hosted two CIEs (Early and Late Aeronian events).

3.5.3 Effect of paleogeography on diversity patterns and turnover

Phytoplankton thrive on continental shelves with a higher diversity and abundance compared to proximal or distal marine environments (e.g. Stricanne et al., 2004). Biotic radiations are known to occur when the amount of habitable areas expands, and extinctions occur when they are reduced (Sepkoski Jr., 1984). Katz et al. (2004) noted that Proterozoic acritarch radiations occurred during supercontinent rifting, and the modern phytoplankton groups radiated after the Late Triassic to Early Jurassic breakup of Pangea. The early Paleozoic is a time of maximal continent separation, while towards the Devonian the continents have started to coalesce with the closing of the Rheic Ocean and the formation of the proto-Tethys ocean. Our results show higher origination than extinction rates in general for the early Paleozoic, ending in the LOME when extinction rates far outstrip origination and the extinction

rates are the highest for the studied time interval (**Fig. 3.2B**). Origination and extinction rates are alternately higher and lower compared to each other in the Silurian, and total turnover, as with global diversity is low. The Devonian is the opposite of the early Paleozoic: the extinction rates are generally higher than origination rates. Origination rates decrease through time, while for extinction there is no clear trend. Turnover also decreases in time. The abundance of habitable areas in the early Paleozoic allowed for high originations until it was ended by extreme global cooling in the end-Ordovician. This is most evident in the Floian (**Fig. 3.6B**), when there is a radiation of high diversity along the Perigondwana margin, from the mid-southern paleolatitudes to the equatorial regions. As discussed in the previous section, the alternating dominance of origination and extinction rates in the Silurian is possibly also the result of environmental instability due to frequent CIEs. In the Devonian the merging of Euramerica with Gondwana closed many habitable areas in the southern mid-paleolatitudes, which may have prompted the southern movement of peak diversity.

The non-latitudinal uniformity of diversity is clearly apparent when plotted in terms of grid-cell diversity (**Fig. 3.6; Appendices 7, 8**). The diversity hotspots could possibly represent a boost in diversity due to immigration facilitated by oceanic circulation, such as the Perigondwana margin in the Floian (**Fig. 3.6**), or areas of upwelling. Further investigation of continent-wide or even local environment conditions are needed to determine the cause of heterogeneity.

3.5.4 The tropics as cradle or museum?

The results show higher origination rates compared to extinction in tropical paleolatitudes for the whole of the early to middle Paleozoic; compared to extinction rates which tend to be greater in the high southern polar paleolatitudes and pronounced from the Katian to Pridoli and again in the Givetian. The results evoke an “out of the tropics” (OTT) dynamic (Jablonski et al., 2006); the tropics as both cradle and a museum of biodiversity for phytoplankton. In an OTT scenario, taxa preferentially originate in the tropics before expanding into higher latitudes without losing their initial tropical distribution. Tropical originations exceed those of the extratropics; tropical extinction rates are equal or less than extratropics; while immigration into tropical latitudes are less than those of the extratropics. While our results satisfy the first two conditions, the last one remains to be tested.

3.6 Summary

The results show how phytoplankton diversity evolved in the early to middle Paleozoic. While the existing data on occurrences is far from complete, some patterns still emerge. The changing climate influences fluctuations in global diversity, which is mostly driven by polar temperatures. A steeper latitudinal gradient forms during icehouse intervals. Diversity and turnover are not uniform throughout paleolatitudes, with the formation of diversity hotspots and areas of high turnover. It is not clear what causes the heterogeneity of diversity and rates, but these could be the result of upwelling or immigration due to oceanic currents. Patterns of turnover suggest an out-of-the-tropics dynamic with originations preferentially occurring in the equatorial regions and extinctions in the high southern paleolatitudes. Recurrent positive CIE events which affected ocean chemistry, marine productivity and stratification caused frequent environmental disruptions in the Silurian and may have played a role in reducing the resilience of phytoplankton. Maximal continent separation in the early Paleozoic promoted high

origination rates while the initiation of widespread continental mergence in Devonian reduced habitable areas and increased extinction rates.

CHAPTER 4

PALEOBIOGEOGRAPHY

Pioneering work on the paleobiogeography of acritarchs started in the early 1970s (Cramer, 1971; Cramer and Díez, 1972, 1974a,b; Vavrdová, 1974) following the development of plate tectonics in 1965. Throughout the 1970s and 1980s delineation of biogeographical units relied on the ranges of selected taxa; use of multivariate analysis only started with (Colbath, 1990). While the former method is practical and easily applicable in the laboratory, it is only useful if 1) classification of the taxa is robust (not part of a morphological plexus with many transitional forms which are difficult to assign to a species) and 2) if the geographical ranges or occurrences are relatively well-known (endemic taxa would be more useful than cosmopolitan taxa in discriminating between different biogeographical provinces). While the first criterion is easily applied, the second can be hard to assess due to the incompleteness of the fossil record, and sampling bias. On the other hand, multivariate analysis utilizes beta diversity metrics rather than an arbitrary selection of taxa, and is deemed more objective and easier to replicate. An ideal methodology would use both methods; biogeographically important taxa can be selected from clusters determined by multivariate analysis.

The first biogeographical analysis of Paleozoic phytoplankton were done by Cramer (1971) and Cramer and Díez (1972, 1974a,b) for the middle Silurian (late Llandovery to Wenlock). This work envisioned a latitude-parallel biofacies model for acritarchs (**Fig. 4.1**), suggesting that their distribution is strongly controlled by temperature. Since then, the plate model used has been superseded by more reliable reconstructions. This latitude biofacies model was reviewed and disproved by Colbath (1990) and by replotting selected assemblages into updated paleogeographic maps during the time (models by Scotese, 1986 and Scotese and McKerrow, 1990 respectively). Colbath (1990) concluded that the distribution of the *Neoveryhachium carminae* biofacies parallel to the depositional basin margins could reflect local environmental conditions rather than biogeography. Le Hérisse & Gourvennec, (1995) focused on the *N. carminae*, *Deunffia-Domasia* and *Pulvinosphaeridium-Estiastra* biofacies (**Fig. 4.2**). They concurred with Colbath (1990), noting that while *N. carminae* biofacies appears in high paleolatitudes it is found in clastic facies and turbid environments. The *Deunffia-Domasia* facies was previously confined mainly at low, tropical to subtropical latitudes (Cramer and Díez, 1974b), but were now found elsewhere in Gondwana and Laurentia with no real provinciality. Similar to *N. carminae*, the *Pulvinosphaeridium-Estiastra* group is possibly controlled by depositional environment, with its occurrence coinciding with climatically sensitive carbonate lithofacies in the equatorial zone. HCA of North American localities reveal four clusters (fig. 4 of Le Hérisse and Gourvennec, 1997; p. 123), which does not correspond with the “biofacies” bands of Cramer and Díez (1972, 1974b). Interpretation of HCA results with other localities worldwide are less straightforward. Although all American and Canadian localities coalesce in a Laurentian cluster, the remaining three has some problematic associations which does not make sense with the geographical proximities (e.g. Quebec with Carnic Alps and Bohemia; Algeria with northern European assemblages). It is possible that these “problematic associations” also reflect similarities in depositional environments. Le Hérisse and Gourvennec (1997 and references therein) suggested other possible palaeogeographical markers (see **Fig. 4.2**) such as *Dilatisphaera williereae* which appears to be confined to a restricted area in the subtropical zone; species of *Gracilisphaeridium* (*G. encantador* and *G. gracile*) which could be restricted to areas of Laurentia and Baltica; *Dactylofusa maranhensis* which occurs only in the southern high to moderate latitudes; *Tyrannus giganteus* in Northern Africa and the Middle East; and *Psenotopus chondrocheus* found in Euramerica (Baltica and Laurentia).

Another major figure is Vavrdová, who in 1974 defined the two main paleoplankton provinces in Europe during the early Ordovician (**Fig. 4.3**): the Baltic and Mediterranean provinces which are still recognized today. Later workers extended the Mediterranean province

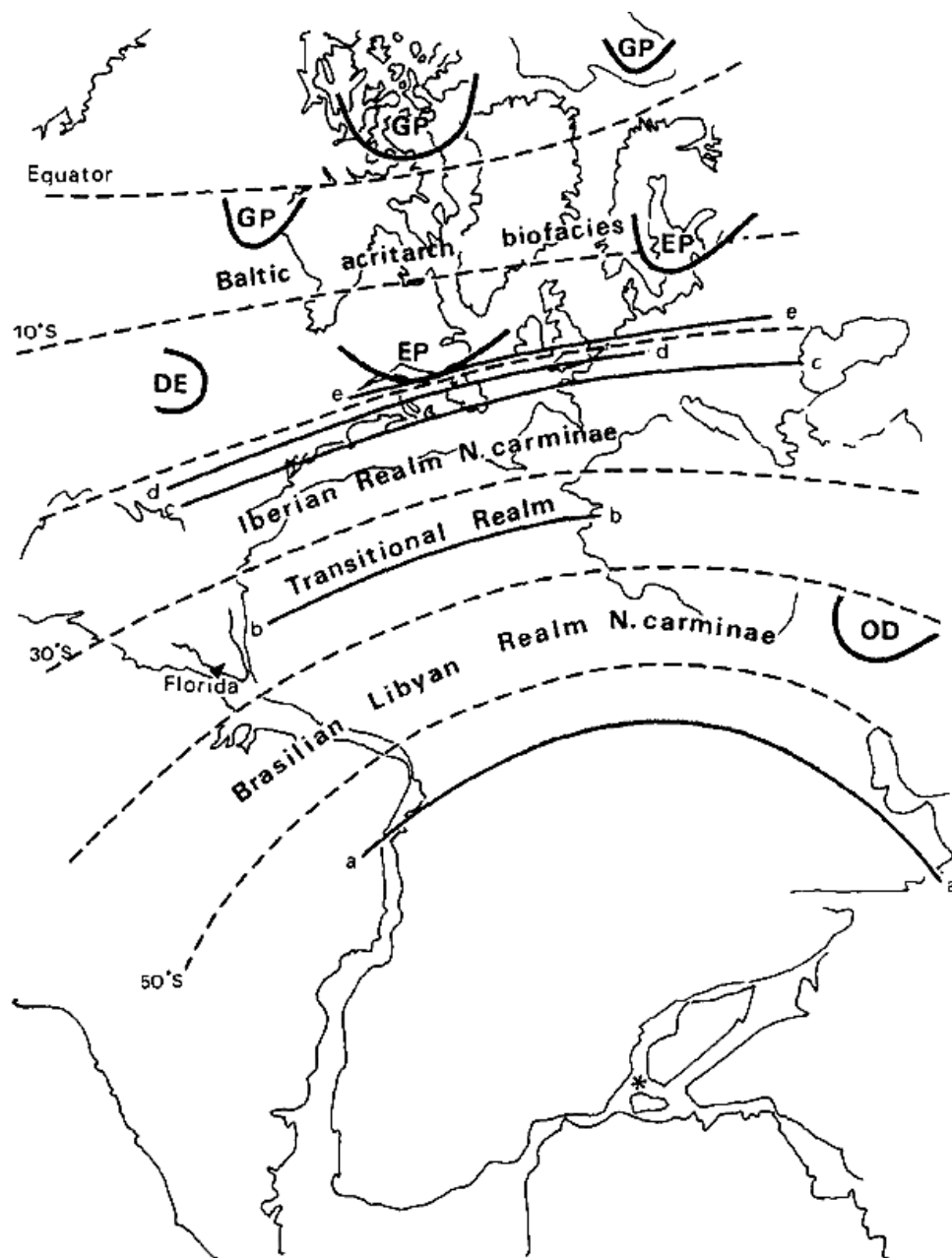


Figure 4.1 Silurian acritarch biofacies belts of Cramer (1971) and Cramer and Díez (1974b), plotted on an outdated paleogeographic model (fig. 1 of Le Hérisse and Gourvennec, 1995). DE = *Deunffia eisenackii* blooms, GP = *Gloeocapsomorpha prisca* facies, EP = *Estiastra-Pulvinosphaeridium-Hoegklintia* facies, OD = *Domasia* spp., aa = no data points below the line, bb = approximate boundary between the Brazilian-Libyan Realm and the Transitional Realm, cc = northern limit of abundant *Neoverhachium carminae*, dd = southern boundary of the *Deunffia-Domasia* facies, ee = southern boundary of the *Pulvinosphaeridium-Estiastra* facies. The * indicates the South Pole.

beyond Europe (Martin, 1982a; Li, 1989), and is now renamed Perigondwana (Albani, 1989). Vavrdová (1974) initially differentiated the provinces with the predominance of acanthomorph acritarchs in the Baltic Province, and diacromorphs in Perigondwana, but Li (1989) pointed out that supposedly Baltic species are present in the latter. Li (1989) and Albani (1989) suggested that the following taxa are diagnostic of Perigondwana: *Arbusculidium*, *Coryphidium*, *Striatotheca*, *Acanthodiacrodium* and *Dasydiacrodium*; to which can be added *Aureotesta* and *Frankea* (according to Vavrdová, 1974 these are not known from the Lower Ordovician of the Baltic province). the later work of Servais and Fatka (1999) was able to identify the early to middle Ordovician trans-European suture zone (separating Perigondwana from Baltica) based

on Perigondwana assemblages which include species of *Arbusculidium*, *Arkonia*, *Striatotheca*, *Aureotesta*, *Coryphidium*, *Vavrdovella*, *Dicrodiacrodium* and *Frankea*. The Baltic province is more problematic since the original diagnostic acanthomorph taxa have been found to have longer ranges (Playford et al., 1995; Tongiorgi and Di Milia, 1999; Molyneux et al., 2013) and the proposed replacements (Playford et al., 1995 and Tongiorgi and Di Milia, 1999 proposed several species of *Peteinosphaeridium* and *Liliosphaeridium*) have a high within-species morphological variability, and it is not clear whether this reflects local environmental or paleogeographical conditions (Li and Servais, 2002). No new taxa have been proposed yet to identify the Baltic province.

Throughout the 1970s and 80s phytoplankton biogeographical analysis relied on the ranges of a few key taxa. The use of multivariate analysis revolutionized ecology in the late 1970s (Legendre and Legendre, 1983) and was applied to phytoplankton starting in the 1990s with Colbath (1990). Colbath (1990) calculated similarities between 10 localities using the Simpson index and determined possible clusters with weighted average linkage pair-group analysis. Le Hérissé and Gourvennec (1995) also conducted cluster analysis (CA) and calculated the coefficient of similarity to identify Late Llandovery and Wenlock acritarch biofacies in the eastern margin of North America. Le Hérissé and Gourvennec (1995) also compared the North American localities with other areas worldwide but stopped short of defining bioprovinces; most of the clusters are geographically contiguous with few anomalies. Le Hérissé et al. (1997) used the same methods to compare late Silurian-early Devonian acritarch biofacies with the classical Malvinokaffric, Eastern American and Old-World Realms of Boucot et al. (1975), superimposed on the Scott and McKerrrow (1990) paleogeography. One acritarch cluster in the Ludlovian-Pridoli corresponds to the Malvinokaffric Realm (Bolivia, Algeria and Florida; see figs. 2 and 3 of Le Hérissé et al. 1997, p. 112) while in the Lochkovian the Iberian Peninsula, Armorican Massif and, North Africa and Bolivia comprise a large

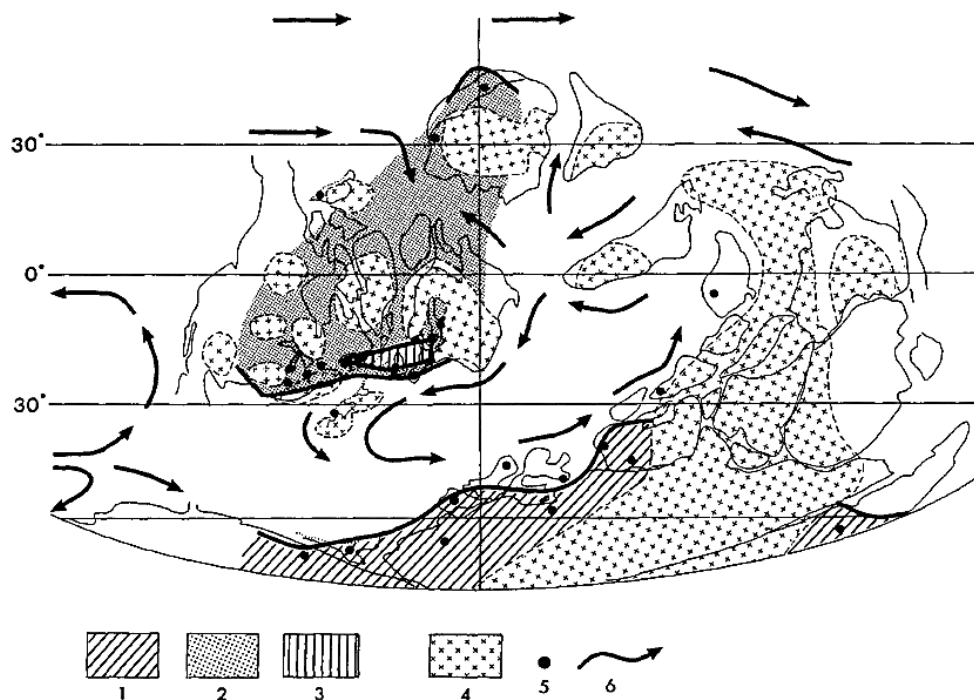


Figure 4.2 The biofacies model of Cramer (1971) and Cramer and Díez (1974b) replotted on the Scotese and McKerrrow (1990) map for the Upper Llandovery-Wenlock (fig. 1 of Le Hérissé and Gourvennec, 1995). 1 = range of *Dactylofusa maranhensis*, 2 = *Estiastra-Hoegklintia-Pulvinosphaeridium*, 3 = range of *Dilatisphaera williereae*, 4 = land, 5 = localities, 6 = ocean current circulation after Rickards et al. (1990).

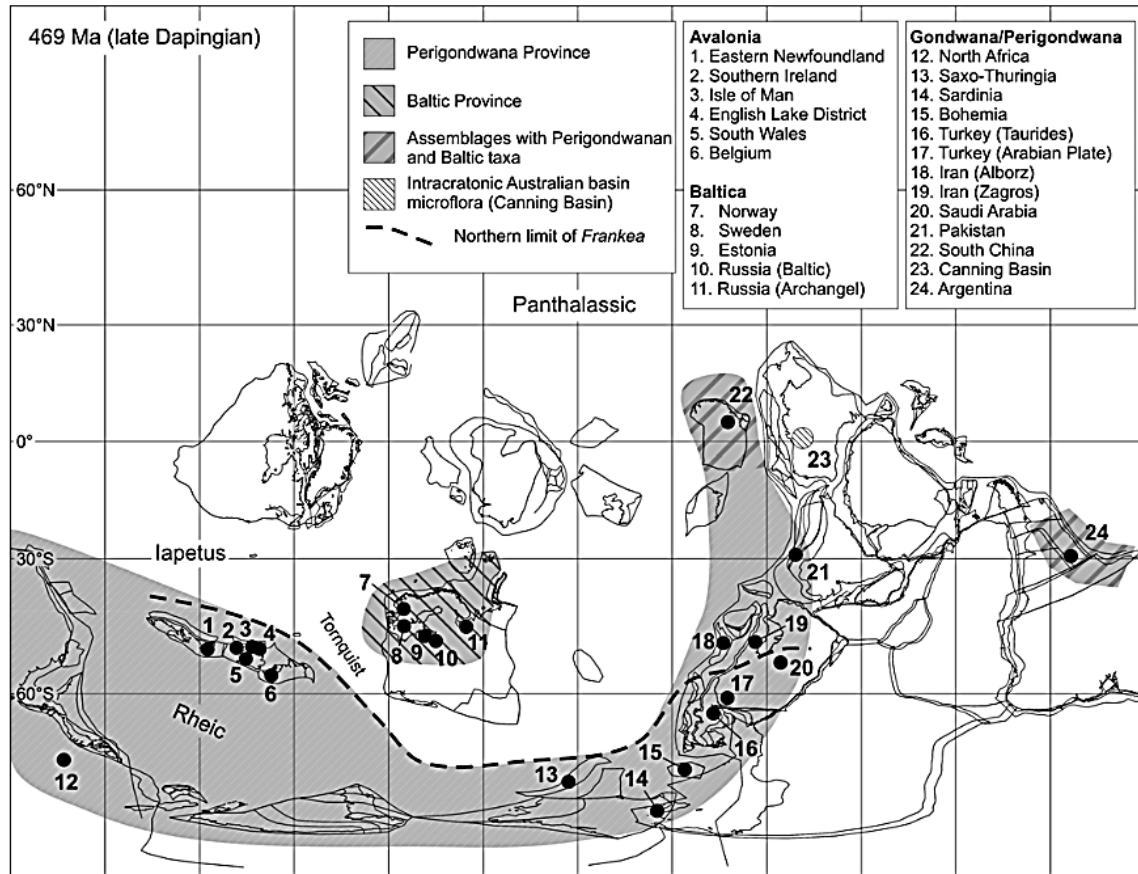


Figure 4.3 The two main provinces of the Early to Mid-Ordovician by Vavrdová (1974), Baltica and Perigondwana (fig. 23.5 of Molyneux et al., 2013; and references therein). The plate reconstruction used is by Torsvik and Cocks (2013).

Gondwana cluster (see figs. 4,5 of Le Hérissé et al. 1997, p. 114). Molyneux et al. (2013) reviewed the biogeography for the early to middle Paleozoic, applying CA using Jaccard index to Furongian and late Dapingian-early Perigondwana localities (check results). Shen et al. (2019) used CA on a variety of similarity indices (Jaccard, Yule's Y, Ochiai and Kulczynski indices) to identify three main realms in the Famennian, but it was also the first study to incorporate ordination methods such as nonmetric multidimensional scaling (NMDS) to reinforce clusters from the CA.

Work on Cambrian acritarchs progressed in the 1990s and 2000s with Moczyłowska (1991, 1998), Zang and Walter (1992), Rubinstein et al. (2003), Yao et al. (2005), Moczyłowska and Zang (2006), Ghavidel-Syooki and Vecoli (2008), Dong et al. (2009) involving qualitative descriptions of Cambrian assemblages. In general, the Cambrian remains poorly studied particularly at the stage level.

The latter part of the Paleozoic is likewise neglected. Mullins & Servais (2008) and Lei et al. (2013) reviewed acritarch literature for the Carboniferous and Permian, respectively. Mullins and Servais (2008) noted a general absence of high-resolution studies across the Devonian-Carboniferous boundary to test the various hypotheses for the late Paleozoic phytoplankton blackout. Lei et al. (2013) supersedes two short reviews of Permian acritarchs by Li et al. (2004) and Traverse (2007), noting that the taxonomy of the smaller Permian acritarchs have been neglected and in need of revision. Similar to the Carboniferous, many areas and time intervals lack data.

To date, there has not been a coherent analysis of acritarch biogeography throughout the Paleozoic. Different authors analyzing different time intervals use various databases, numerous methods (qualitative or quantitative) to identify biogeographic regions, and even several paleogeographic models which make direct comparison difficult. This can be addressed with the following: using a taxonomically reviewed database, application of uniform multivariate methods and diversity index for each time interval, and the use of a single paleogeographic reconstruction model. In this chapter a review of biogeographically important taxa is presented (**Section 4.1**), along with new multivariate analysis for the early to middle Paleozoic (**Section 4.2**). The present author also participated in two related studies (**Section 4.3**): the first is a qualitative description of acritarchs by Caillaud et al. (in prep.; 4th co-author) from the Cabrières biota which expands the phytoplankton diversity of southern Gondwana (**Section 4.3.1**), and a quantitative study of Famennian phytoplankton from South China by Shen et al. (2025; third co-author) (**Section 4.3.2**).

4.1 Paleobiogeographical markers

The distribution of the genera *Aryballomorpha*, *Athabascaella* and *Lua* in the Tremadocian are shown in **Figure 4.4**. The plot shows a predominantly warm-water occurrence north of -60° , corroborating Volkova (1997). The three genera occur together in Baltica and Laurentia, while in northern Gondwana *Athabascaella* and *Lua* are present. Only *Athabascaella* is present in South Gondwana. Notably, the South Gondwana locality (Arg.-Bol.) belongs to a South Gondwana Province, interpreted to be a cold-water (**Fig. 4.4**). *Athabascaella* has not been identified in other South Gondwana areas, and the Arg.-Bol. locality may represent the boundary between warm and cold-water realms. Thus, the co-occurrence of two or all three of these genera can be considered as possible warm-water indicators in the Early Ordovician (Tremadocian).

In the Middle Ordovician several taxa have been proposed to distinguish between Baltica and the Perigondwana Provinces. We replot the occurrences of commonly used taxa at the Dapingian-Darriwilian boundary in **Fig. 4.5**. Perigondwana is characterized by the appearance of *Arbusculidium*, *Coryphidium*, *Frankea* and *Striatotheca* (Vavrdová, 1974, 1977; Li, 1989; Albani, 1989; Servais and Fatka, 1997), with the main occurrences in southern

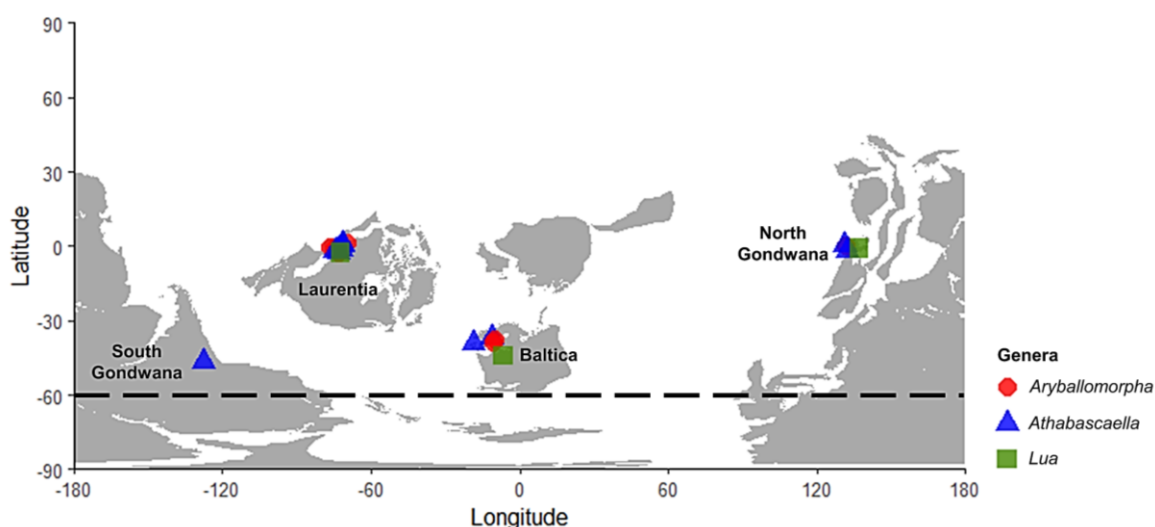


Figure 4.4 Distribution of warm-water taxa in the Tremadocian (*Aryballomorpha*, *Athabascaella* and *Lua*), based on Volkova (1997). The occurrences were taken from the present database and plotted on the plate model of Scotese (2016). Dashed line represents high south

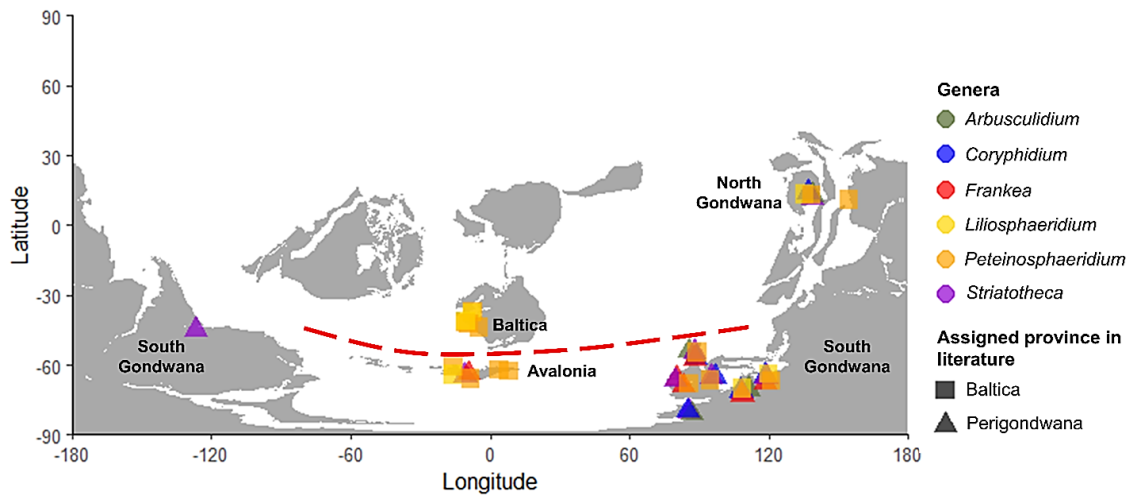


Figure 4.5 Selected taxa reportedly characteristic of Baltic and Perigondwanan provinces in the middle Ordovician plotted on the PALEOMAP model of Scotese (2016). The dashed line is the northern limit of *Frankea*.

Europe, northern Africa and the Middle East. Of the four genera *Frankea* is restricted to high southern paleolatitudes, with occurrences in South Gondwana and Avalonia. *Striatotheca* is noted in South America. Both *Coryphidium* and *Striatotheca* are present in South China. The peteinosphaerid genera (*Peteinosphaeridium* and *Liliosphaeridium*) are essentially cosmopolitan in distribution.

Colbath (1990) and Le Hérissé and Gourvennec (1997) reviewed Cramer's paleolatitude-parallel model and their results are reproduced in **Fig. 4.6** for the *Deunffia-Domasia*, *Neoveveryhachium carminae* and *Pulvinosphaeridium-Estiastra-Hoegkintia* facies in the Llandovery. Taxa from all three facies have a widespread distribution, in particular the *Deunffia-Domasia* facies extend from the equator in North Gondwana to high southern paleolatitudes of South Gondwana while the two latter facies co-occur from approximately -15° to higher southern paleolatitudes. *Dactylofusa maranhensis* seems to be widespread and restricted to southern Gondwana, from -30° to higher southern paleolatitudes. *Dilatisphaera williereae* appears endemic to Avalonia, in subtropical paleolatitudes approximately -30°.

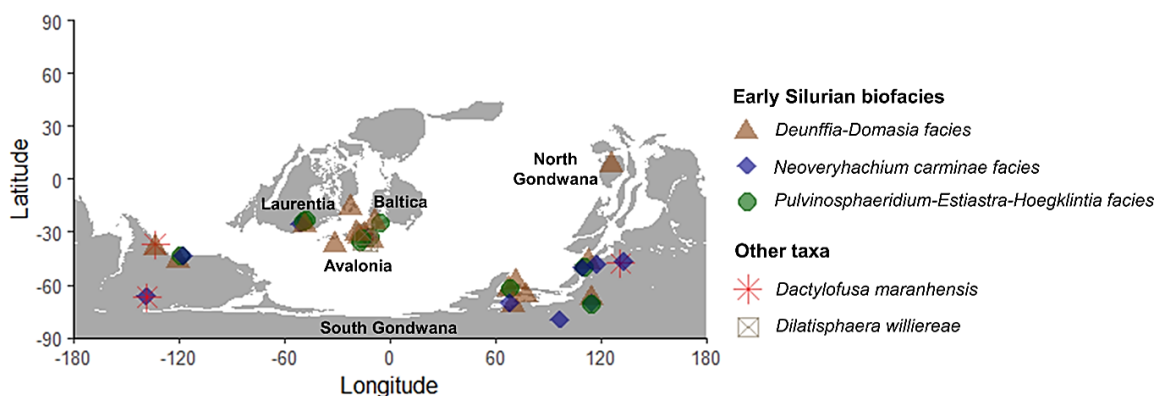


Figure 4.6 The middle Silurian biofacies of Cramer (1971) and Cramer and Díez (1972, 1974a,b) replotted using occurrences from the present database on the PALEOMAP model of Scotese (2016).

4.2 Results of the multivariate analysis

This section presents the results of the multivariate analysis using HCA and NMDS. The objective is to use, for the first time, a coherent set of techniques for all time intervals. The realms are geographically broad clusters identified from the HCA and NMDS.

Interpreted provinces are shown in **Fig. 4.7**. The results of the HCA and the NMDS are illustrated in **Appendix 11**.

4.2.1 Cambrian paleobiogeography

The multivariate results in the Cambrian show latitudinal partitioning in the Terreneuvian and for Cambrian Series 2, which is not apparent for the Miaolingian and Furongian (**Figs. 4.7A to D** and **App. 11A to D**). In the Terreneuvian two realms are distinguished in the HCA and NMDS, a northern hemisphere realm consisting of a North Gondwana province and a southern hemisphere realm of which includes all Baltica and the only southeastern Gondwana locality.

For the Cambrian Series 2 two provinces emerge from the HCA (**App. 11B**), between localities in Laurentia and Baltica (Laurentia Provinces 1 and 2; see **Fig. 4.7B**). These two provinces roughly group together in a broad cluster which contains localities from Baltica and southeastern Gondwana. The other clusters cobble together widely disparate areas. Noticeably, the northern Gondwana localities (Australia and South China) do not cluster with southeastern Gondwana (SW Poland-SE Germany and Spain). Some Baltican and even the Avalonian locality near the south pole cluster with north Gondwana areas. The NMDS shows an apparent latitudinal gradation from the north to south, similar to the Terreneuvian but with the addition of a high paleolatitude southern realm. These are named the Northern Gondwana (northern equatorial paleolatitudes), Laurentian (southern equatorial to subequatorial) and Avalonian Realms (high southern paleolatitudes), respectively. Of these three realms, only the Laurentian Realm is clearly differentiated with its own cluster in the HCA.

In the Miaolingian (**Fig. 4.7C**) there are no traces of the Laurentia (Provinces 1 and 2) and North Gondwana Provinces found in the Terreneuvian and the Cambrian Series 2, but the HCA and NMDS (**App. 11C**) shows two clusters in south Gondwana. It is not clear if these actually represent provinces or facies, with S. Gondwana “Province 1” representing inner facies while S. Gondwana “Province 2” is an outer shelf facies, similar to the Silurian North American facies of Le Hérissé and Gourvennec (1995). The Nordic area is an outlier in S. Gondwana “Province 2.” The broad HCA clusters do not show latitudinal coherence, which is also not apparent in the NMDS. However, in the NMDS, southeastern Gondwana localities form a field with Baltican and Avalonian localities outside.

Furongian multivariate results do not show apparent latitudinal structuring but three realms can be recognized (**App. 11D**, see also **Fig. 4.7D**). The Baltican and Southern Realms broadly cluster together in the HCA, while the Laurentian Realm is isolated. This is also illustrated in the NMDS, where a westward gradation is detected (left to right side of the NMDS plot, **App. 11D**). Most southeastern Gondwana localities belong to the Southern Realm except for SW Poland, which forms the southern frontier of the Baltican Realm. Belgium is an apparent outlier in the Baltican Realm HCA cluster but plots in the Southern Realm in the NMDS and hence classified with the South Gondwana Province since it is geographically continuous with the said province.

4.2.2 Ordovician paleobiogeography

Several provinces are present in the Early Ordovician and the multivariate results show a division between Northern and Southern Realms. This is also apparent for the Middle Ordovician. Multivariate analysis did not detect this paleolatitudinal structuring for the early Late Ordovician (Sandbian), possibly due to scarcity of analyzed localities in south Gondwana; but is again present for the Katian and Hirnantian.

In the Tremadocian the HCA and NMDS distinguishes between two large clusters (**App. 11E**; see also **Fig. 4.7E**), a Northern Realm which contains Baltica Province along with northern Gondwana and Laurentia localities; and a Southern Realm occupied by a South Gondwana Province. Parts of Avalonia (England) belong to Baltica Province while Western Russia is an outlier in the South Gondwana Province HCA and NMDS clusters. A northward gradation is present in the NMDS from left to right of the plot. For the Floian two groups of provinces appear in the HCA cluster and the NMDS (**App. 11F**). Avalonia and South Gondwana Provinces cluster together to form the Southern Realm, while Baltica and North Gondwana Provinces form the Northern Realm. The Nordic area is an outlier in the N. Gondwana Province HCA cluster but contiguous with the other Baltica Province localities in the NMDS and hence considered part of the latter province (**Fig. 4.7F**). There is an apparent clockwise trend from South Gondwana to North Gondwana Provinces in the NMDS plot.

The Northern and Southern Realms can be distinguished in the NMDS for the Middle Ordovician, but these are not clear in the HCA (see **App. 11G-H** and **Figs. 4.7G-H**). A South Baltica Province (which includes parts of Poland in Baltica and Avalonia) emerges as an isolated cluster in the HCA for the Dapingian and the Darriwilian. Other Baltican localities form a large group with Avalonian, Laurentian, northern and southeastern Gondwana units in the HCA and NMDS, but these readily split into Northern and Southern Realms with Avalonia classified as part of the Northern Realm. In the Dapingian a North Gondwana Province is present (with the Nordic area as an outlier) based on the HCA, but it is not very clear for the Darriwilian; conversely a North Baltica Province is present in the Darriwilian (with England as an outlier) but less clear in the Dapingian. The South Gondwana Province fragments into two subprovinces during the Middle Ordovician, harking to the South Gondwana “provinces” of the Miaolingian with similar boundaries. Northward trends in a clockwise direction from the South Gondwana Province fields are detected for the Dapingian and Darriwilian NMDS plots.

The South Baltica Province persists as an isolated cluster in the HCA during the Late Ordovician (**App. 11I-K**, see also **Figs. 4.7I-K**). A North Baltica Province is also present in the Sandbian and Katian but not in the Hirnantian. The larger cluster in the Katian HCA can be divided latitudinally into Northern and Southern Gondwana Realms; the former dominated by a North Baltica Province (Eastern USA as an outlier) and the latter by the South Gondwana Province. Czechia geographically belongs to South Gondwana but is an outlier in the Northern Realm. During the Hirnantian the South Gondwana Province appears greatly diminished in size. No latitudinal realms are apparent from the Hirnantian HCA results. The NMDS results for the Sandbian also does not show clear latitudinal gradients. The Northern and South Gondwana Realms can be delineated for the Katian and Hirnantian in the NMDS; the Northern Realm can be subdivided into separate fields for South Baltica Province and the other localities in Baltica, Laurentia and Avalonia.

4.2.3 Silurian paleobiogeography

The Llandovery epoch is notable for the presence of diminished provinces in Baltica and Southern Gondwana. The large South Gondwana Province re-established itself in the Wenlock, diminished shortly in the early Ludlow, then regained its extent until Pridoli. Baltica and parts of Avalonia form a province during the Wenlock and Ludlow, except for the Homerian where two Baltican Provinces appeared. From the Llandovery to early Ludlow there were no clear latitudinal clusters or gradients present similar to the Ordovician, it re-emerged again in late Ludlow and Pridoli.

A small Baltica Province consisting of some localities from Baltica and Avalonia persisted in the Llandovery (Rhuddanian to Telychian), based on the HCA (**App. 11L-N**). A small South Gondwana Province was present in the Rhuddanian. In the Telychian there are two broad HCA clusters: the first consisting of Baltica, Avalonia and some southern Gondwana localities; while the second is exclusively Perigondwana. The NMDS does not show a latitudinal gradient in the Llandovery, but in the Telychian the two large HCA clusters (tentatively named Baltican and Perigondwanan Realms) can be delineated.

In the Sheinwoodian (early Wenlock) the HCA shows South Gondwana Province restored to its typical territorial extent as in the Ordovician but excluding some localities (**App. 11O**). A small Laurentia Province including southern Laurentia and westernmost Avalonia is also present, along with a Baltica Province (**Fig. 4.7O**). The Sheinwoodian NMDS plot can be subdivided into Northern and Southern Realms, but this division is not clear in the HCA. For the Homerian a South Gondwana “Province 1” cluster (with Scotland as outlier) is isolated from the rest (**App. 11P**; **Fig. 4.7P**). Baltican “Province 2” clusters with South Gondwana “Province 2,” while in Baltican “Province 1” the East USA locality is an anomaly. There seems to be no continental or latitudinal partitioning in the latter part of the Wenlock, with the so-called “provinces” apparent facies in the vein of the Miaolingian South Gondwana “provinces” rather than actual biogeographic units.

HCA results for the Gorstian (**App. 11Q**) delineate the small Baltica and South Gondwana (1 and 2) Provinces (**Fig. 4.7Q**). South Gondwana “Province 1” is grouped with Baltica Province, while South Gondwana “Province 2” occupies most of the other broad cluster. A latitudinal structure returned in the Ludfordian (**Fig. 4.7R**) with one cluster for the Southern Realm with a South Gondwana Province (Sweden and England are geographic outliers), and another for the Northern Realm which is dominated by a Baltica Province (Austria appears as an outlier). The NMDS shows no gradient or pattern for the Gorstian, while the HCA clusters are reflected in the Ludfordian NMDS plot (**App. 11Q, R**).

By the end of the Silurian, the Baltica Province is not evident in the HCA, while southern Gondwana is divided into two “provinces” (**Fig. 4S**). South Gondwana “Province 1” is part of a Southern Realm while South Gondwana “Province 2” is part of the Northern Realm along with localities from Baltica and northern Gondwana. The two realms are more clearly differentiated in the NMDS than HCA (**App. 11S**).

4.2.4 Devonian paleobiogeography

The latitudinal structure and gradient observed in the previous geological periods were also present throughout most of the Devonian, with the exception of the mid-late Early Devonian (Pragian to Emsian). The boundary between the Northern and Southern realms shift from approximately -30° to below -60° , with the Southern Realm showing the smallest

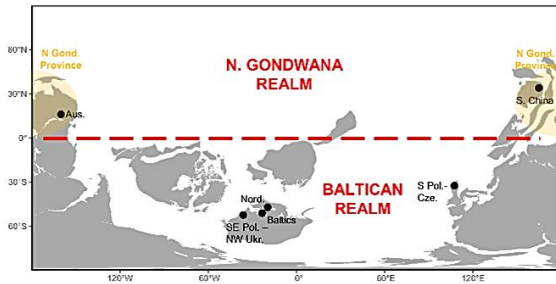
latitudinal extent in the Eifelian. South Gondwana fragmented into several bioprovinces for most of the Devonian (except for the Eifelian). Laurentian localities become biogeographically associated with those from South Gondwana from the Early Devonian to early Middle Devonian; and starting in the Eifelian, provinces emerged at the margins of the Paleotethys Ocean.

Despite the paucity of localities in Laurussia (the amalgamation of Laurentia, Baltica and Avalonia), the HCA still showed a latitudinal structure for the Lochkovian in the HCA and NMDS (**App. 11T**). The Southern Realm now included southwestern Laurussia (East USA). The Northern Realm features an East Rheic Province between southern Baltica and northeastern Gondwana (**Fig. 4.7T**). Argentina and Libya are outliers but in the NMDS they cluster with the bioprovince with which they form geographic continuities and are hence assigned to the West and East Gondwana Provinces, respectively. In the Pragian, all of the localities are Gondwana or South Laurentian, thus no Northern and Southern Realm emerged (**Fig. 4.7U**). Gondwana was subdivided into West, Central and East Gondwana Provinces. Egypt is an outlier in the central Gondwana Province HCA cluster and NMDS field (**App. 11U**), but it is geographically contiguous with the East Gondwana Province; hence this locality is assigned to the latter bioprovince. In the Pragian the West and East Gondwana Provinces remain intact from the multivariate analysis results, while East Gondwana has a different composition of localities (**App. 11V**) and moved southward (**Fig. 4.7V**).

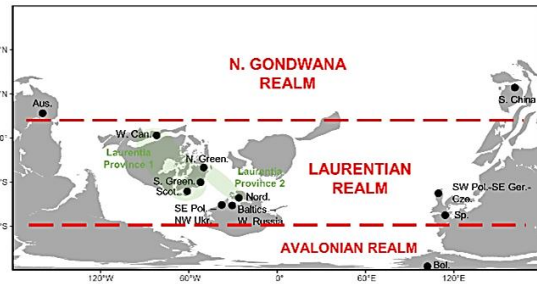
At the start of the Middle Devonian (Eifelian) a new bioprovince (West Paleotethys Province) along the western rim of the Paleotethys Ocean forms (**Fig. 4.7W**), and constitutes a Northern Realm HCA cluster along with the Laurentia Province to the west (**App. 11W**). The South Gondwana Province occupies the high southern paleolatitudes. In the Givetian two realms are again present (**App. 11X**) from the HCA and NMDS classification; the Southern Realm extends northward to -30° (**Fig. 4.7X**) incorporating the Laurentia Province to the north. The South Gondwana Province of the Eifelian fragments into South American and West African Provinces. A South Paleotethys Province also forms at the southern margins of the Paleotethys Ocean.

In the Late Devonian the latitudinal structure is more apparent in the NMDS than in the HCA, and the boundaries between the Northern and Southern Realms are placed approximately at -30° (see **Figs. 4.7Y, Z**). In the Frasnian the HCA shows two broad clusters, and each of the two broad clusters can be subdivided into northern and southern regions (**App. 11Y**). The South America Province clusters with South Paleotethys Province (East USA is an outlier), while the West Africa Province is grouped with Spain and West Canada. The Northern and Southern Realms are easily distinguished in the NMDS. In the Famennian the South Paleotethys Province is an isolated cluster (with other areas from Laurussia) in the HCA (**App. 11Z**), while the West Africa, South America, and West Paleotethys Provinces are closer in affinity. The distribution of the localities in the NMDS can be differentiated into a Northern and Southern Realm.

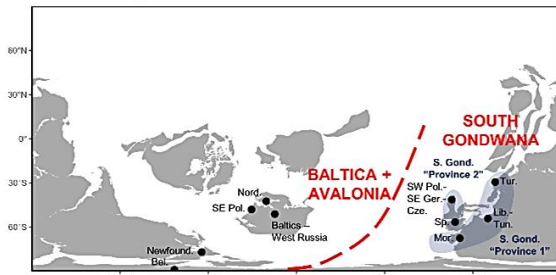
A. Terreneuvian



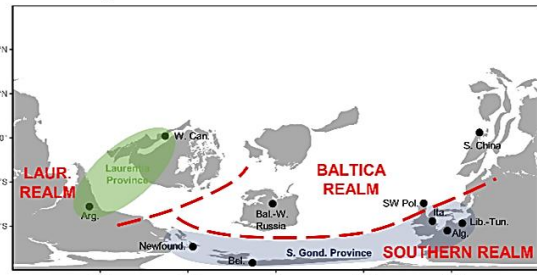
B. Cambrian Series 2



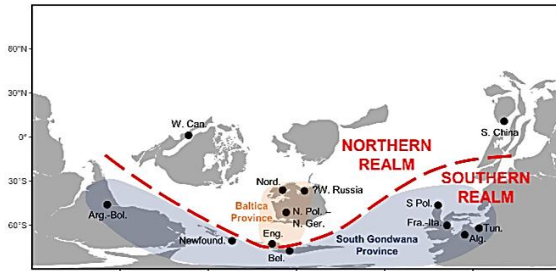
C. Miaolingian



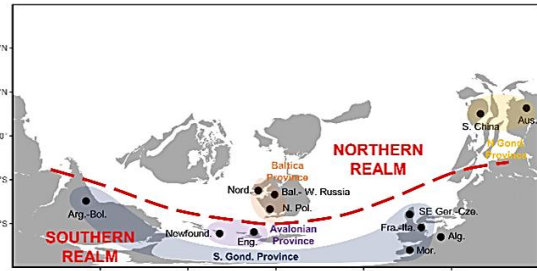
D. Furongian



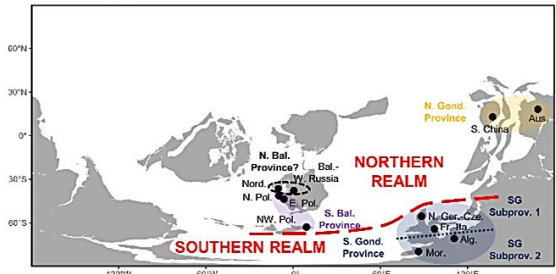
E. Tremadocian



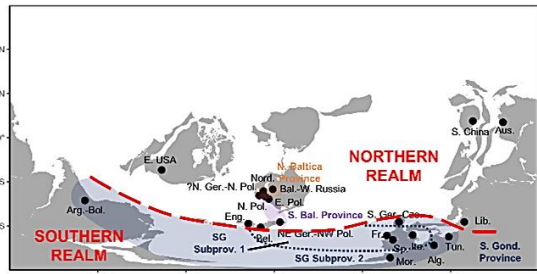
F. Floian



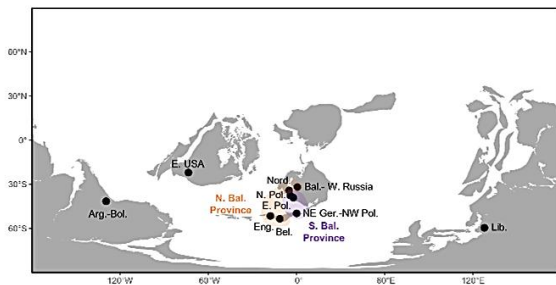
G. Dapingian



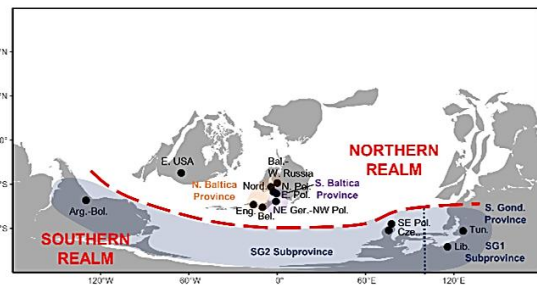
H. Darriwilian



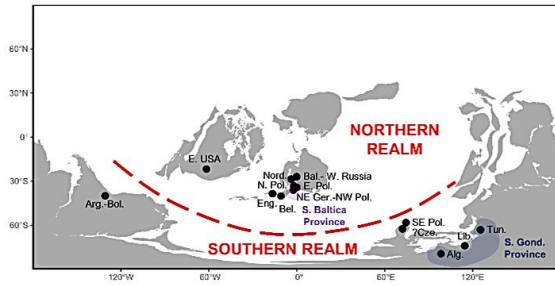
I. Sandbian



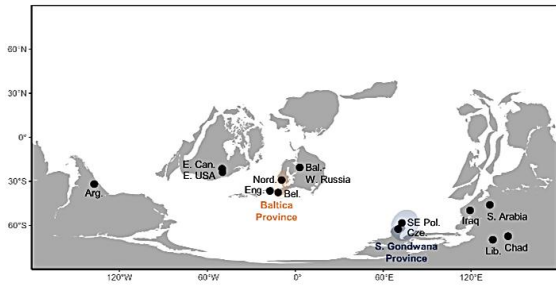
J. Katian



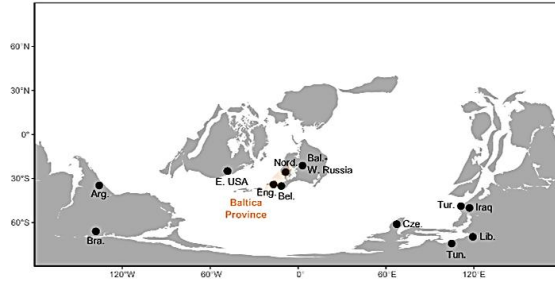
K. Hirnantian



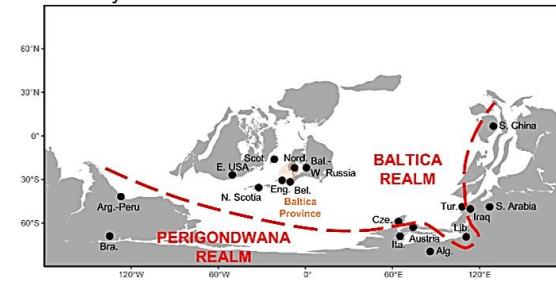
L. Rhuddanian



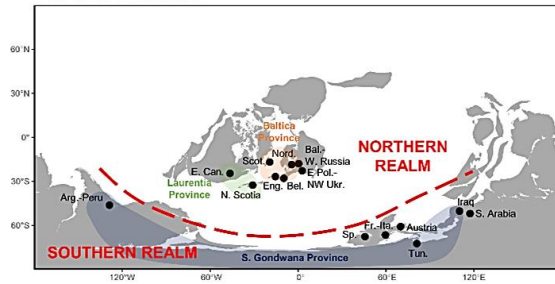
M. Aeronian



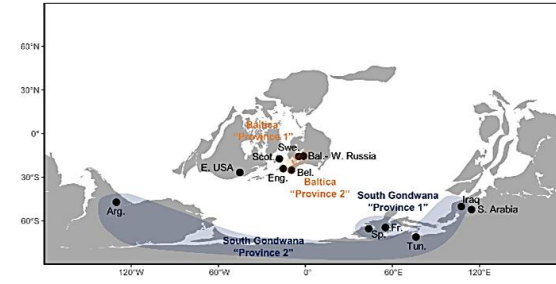
N. Telychian



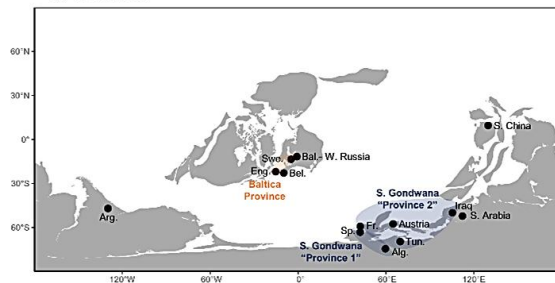
O. Sheinwoodian



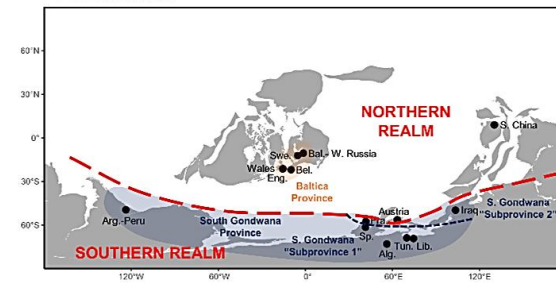
P. Homerian



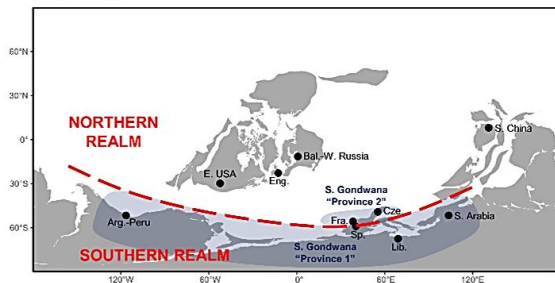
Q. Gorstian



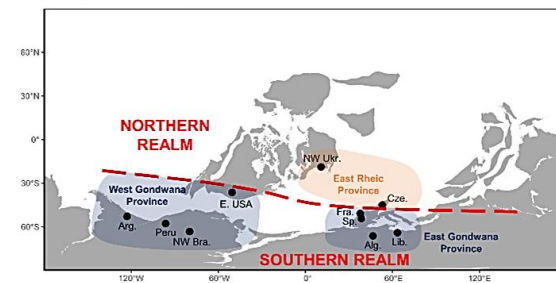
R. Ludfordian



S. Pridoli



T. Lochkovian



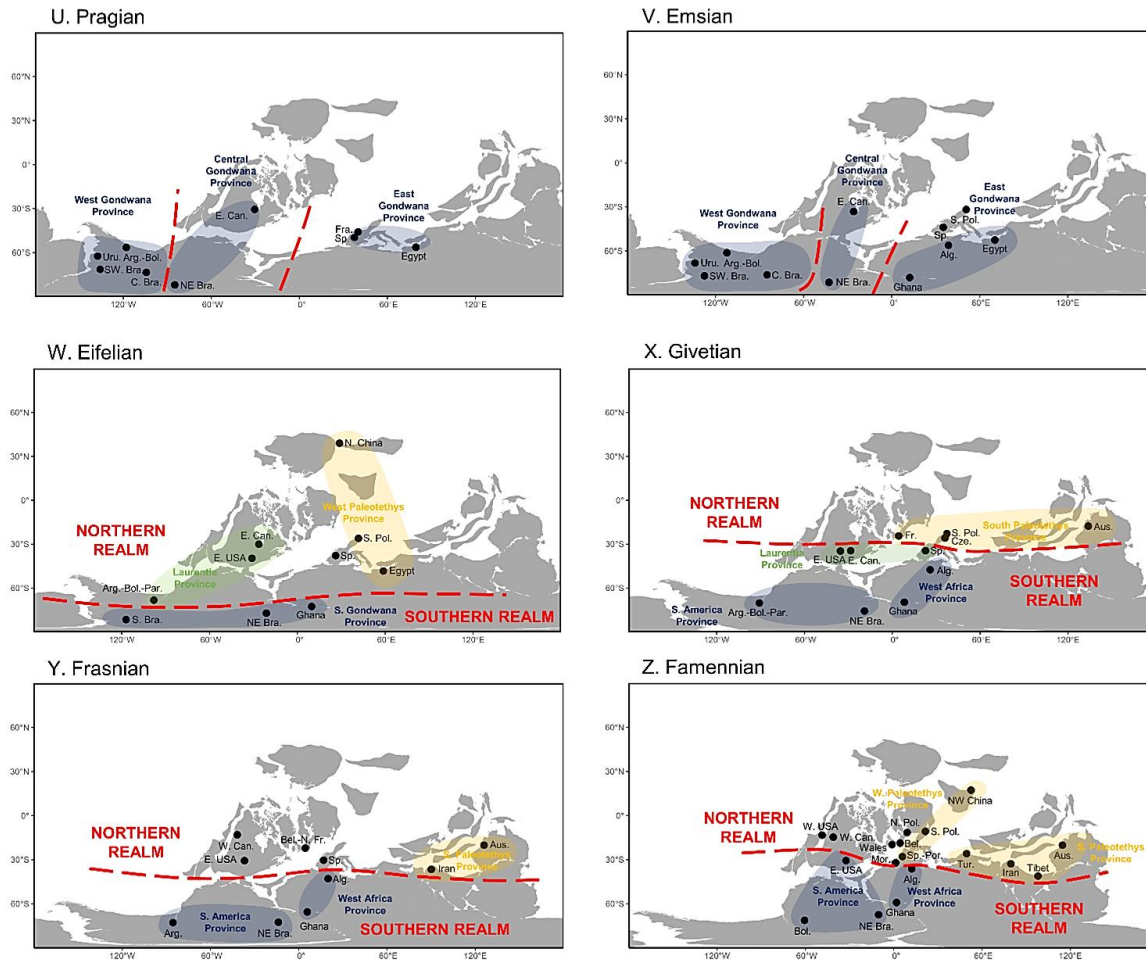


Figure 4.7 Biogeography of early to middle Paleozoic acritarchs, based the results of our multivariate analysis.

4.3 Related studies

As part of the doctoral exercise the author was engaged in two studies which involved paleobiogeographical analysis. The first is a study of the acritarchs from the Floian-age Cabrières biota which also determined paleobiogeographic affinities of the study area based on the occurrence of relevant taxa. The second study is an analysis of the Famennian-age Hongguleleng Formation in northwest China, which utilized similar multivariate methods in this thesis for the delineation of biogeographic clusters.

4.3.1 Acritarchs of the Cabrières biota in SE France

This study by Caillaud et al. (2025) investigates Early Ordovician (Floian) acritarch microfossils from the Montagne Noire region in southern France (**Fig. 4.8**), focusing on their biostratigraphical and palaeobiogeographical significance. The primary samples were extracted from the Landeyran Formation, specifically from the Cabrières Biota sites ("La Sangle" and "La Brouette") and a continuous reference section in the Landeyran Valley. These sediments, composed mainly of laminated siltstones and claystones, are indicative of a distal shelf environment, and their fossil content includes well-preserved palynomorphs, particularly acritarchs.

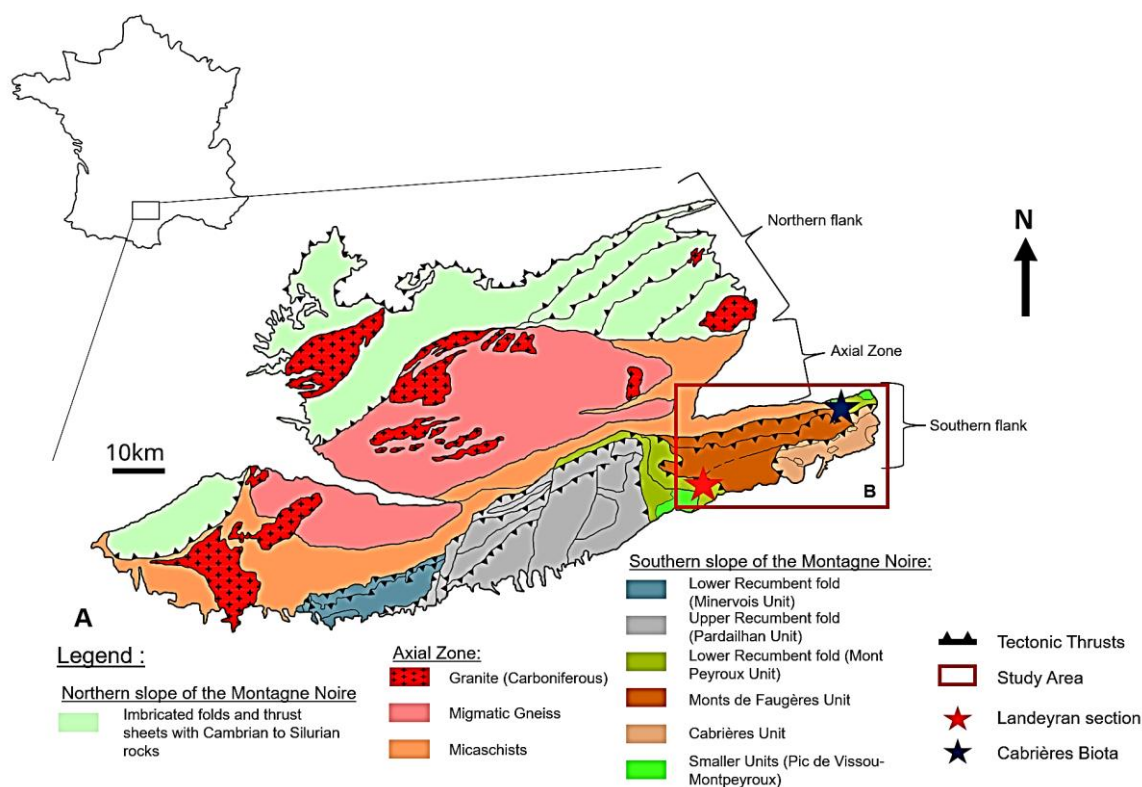


Figure 4.8 Geological context of the study area. (A) Localization of the Montagne Noire within the different Variscan massifs (modified from Demange, 1999; Faure et al. 2010; Montmartin et al. 2021); (B) Area of the southern slope part of the Montagne Noire including Pic de Vissou-Montpeyroux Unit, yielding the Cabrières Biota.

Acritarchs serve as valuable biostratigraphical tools in the Lower Paleozoic. The assemblages identified in this study are diverse and include key taxa such as *Coryphidium bohemicum*, *Ampullula crassula*, *Arbusculidium filamentosum*, *Barakella felix*, *Striatotheca*, and several *Acanthodiacrodium* species. The preservation quality varies across the section, with better-preserved and more abundant specimens occurring towards the top of the Landeyran Formation. Despite differences in preservation and abundance, the taxonomic composition across the sites remains consistent, allowing robust comparisons and interpretations.

Biostratigraphically, the assemblages are indicative of a middle to late Floian age (late Fl2 to early Fl3; **Fig. 4.9**). This conclusion is supported by the presence of key index taxa such as *Arbusculidium*, *Peteinosphaeridium*, *Veryhachium*, and *Striatotheca*, and the absence of younger taxa like *Arkonia* and *Orthosphaeridium* (Servais et al., 2018). The authors correlate these findings with trilobite and graptolite biozones from the same formation, notably the *Apatokephalus incisus* and *Hangchungolithus primitivus* trilobite zones and the *Baltograptus minutus* graptolite zone (Maletz, 2023), which also suggest a late Floian age.

One of the most significant outcomes of the study is the earliest southern peri-Gondwana appearance of *Ampullula crassula*, previously known only from Dapingian strata in Bohemia (Vavrdová, 1990). Its presence in middle-late Floian deposits in France revises its First Appearance Datum (FAD) in this region and underscores its value in refining biostratigraphical correlations across Gondwana margins. The broad geographical and environmental range of *Ampullula* also highlights its eurytopic nature (Kui et al., 2010), suggesting it was more widespread and adaptable than earlier assumed.

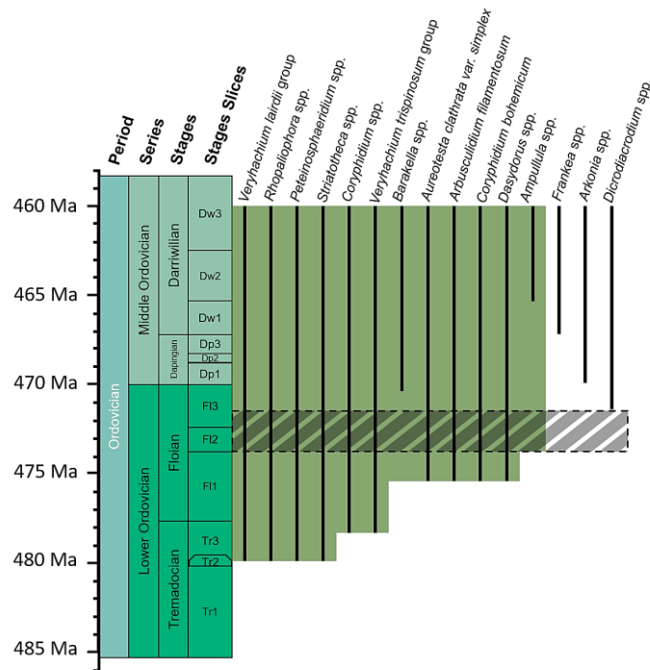


Figure 4.9 Age of the samples from the Landeyran section and the Cabrières Biota based on the acritarchs content and the First Appearance Datum (FAD) of selected taxa (Figure based and modified from Servais et al. 2018).

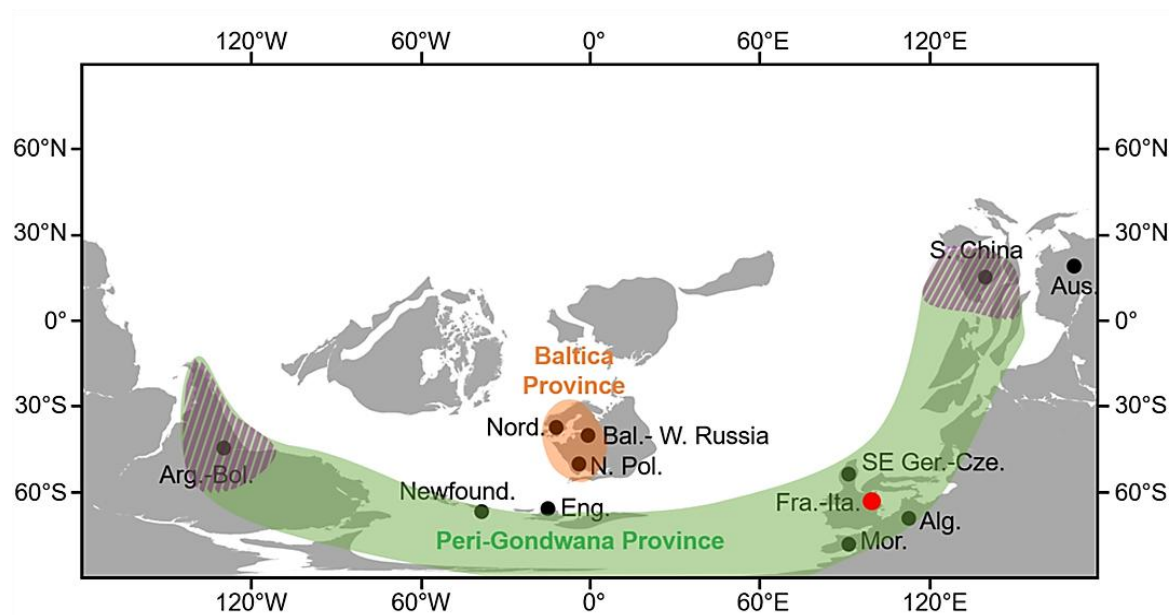


Figure 4.10 Floian (475 Ma) palaeogeographical reconstruction with the location of the Baltica Province (Nord.: Norway, Denmark, Sweden; Bal.-W. Russia: Estonia, St. Petersburg area, Finland; N. Pol.: northern Poland), and the Peri-Gondwana Province, including Eastern Gondwana (Arg.-Bol.: Argentina, Bolivia, Columbia), Western Gondwana (S. China: southern China), Northern Gondwana (Aus.: Australia), and the "southern peri-Gondwana subprovince" (Newfound.: Newfoundland; Eng.: England, Wales, Ireland; Fra.-Ita.: southern France, Sardinia, etc.; SE Ger.-Cze.: south-eastern Germany and the Czech Republic; Mor.: Morocco; Alg.: Algeria) Reconstruction based on the PALAEOMAP project (Scotese 2016).

Palaeobiogeographically, the assemblages are characteristic of the peri-Gondwana acritarch province (Fig. 4.10), particularly the Mediterranean subprovince as originally defined by Vavrdová (1974, 1997). Diagnostic taxa such as *Coryphidium bohemicum*, *Striatotheca principalis*, *Adorfia hoffmanensis*, and *Vogtlandia multiradialis* closely resemble those from Bohemia, reinforcing the strong biogeographical affinity. The Montagne Noire was located at

high southern latitudes ($\sim -68^\circ$) during the Floian, corroborated by palaeomagnetic and sedimentological data (Nysæther et al., 2002; Álvaro et al., 2008). The polar setting of the Cabrières Biota (which is dominated by sponges and algae and lacks echinoderms; Saleh, 2024) supports this interpretation and provides a rare glimpse into cold-water marine ecosystems during the early stages of the Great Ordovician Biodiversification Event (GOBE).

In a broader context, this study updates knowledge of Early Ordovician acritarchs in southern France, an area not re-investigated since the 1970s and 1980s (Rauscher, 1971, 1974; Martin, 1973). While earlier studies described general assemblages, this work refines the stratigraphy and adds important palaeobiogeographic detail. The newly recorded taxa and stratigraphic refinements have potential implications for global correlation and improve our understanding of phytoplankton evolution during a critical period in early Paleozoic history.

4.3.2 Famennian phytoplankton of the Hongguleleng formation, NW China

The Famennian Stage of the Late Devonian is marked by major biotic crises and that significantly impacted global marine ecosystems, such as the Frasnian-Famennian and the end-Devonian extinction events (see Bond & Grasby, 2017 and references therein). Understanding the causes and effects requires a robust biostratigraphic framework which can be correlated with other areas. Shen et al. (2025) revisits the Famennian Hongguleleng Formation in the Gennaren section of western Junggar in northwest China (**Fig. 4.11**), an area with extensive and well-exposed outcrops of Upper Devonian and Carboniferous strata but scarce reports on the Upper Devonian. Despite previous efforts of numerous workers focusing on various taxa such as ammonites, brachiopods, trilobites, palynomorphs and conodonts (Zhao and Wang, 1990; Xia, 1996; Chen et al., 2009; Ma et al., 2011; Zong and Ma, 2012, 2018; Wang et al., 2016; Zong et al., 2020; Zheng et al., 2020; Stachacz et al., 2021; Shen et al., 2021; Zhang et al., 2021), the precise location of the Frasnian-Famennian and the Devonian-Carboniferous boundaries are still disputed. The miospore content of the Gennaren section was recently discussed by Shen et al. (2024) while the results on the investigation of phytoplankton

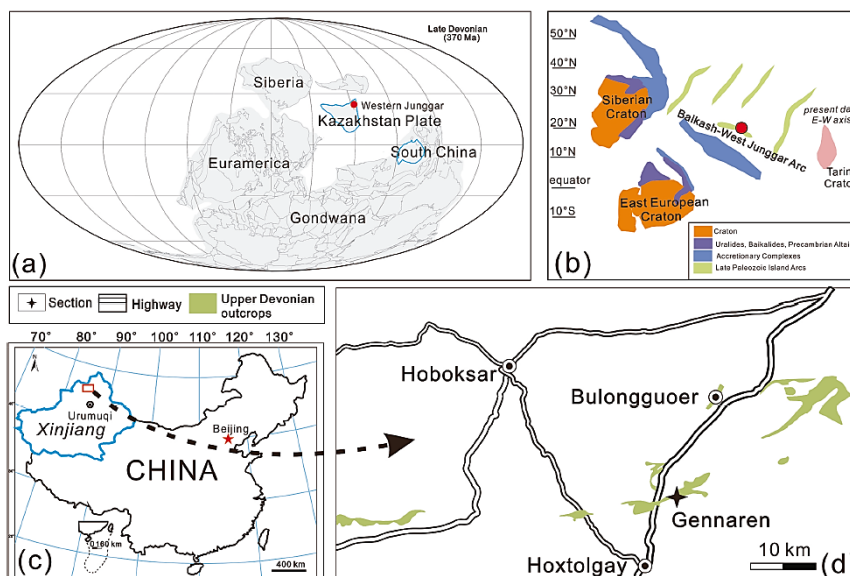


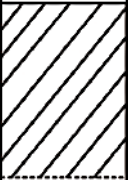
Figure 4.11 (a) Updated palaeogeographic reconstruction of the Late Devonian (adapted from Boucot et al., 2013), highlighting the position of the Kazakhstan Plate, from which palynological samples were obtained; (b) Conceptual tectonic model for the study region during the Late Devonian (red circle), illustrating the intricate assembly of island arcs and accretionary complexes typical of the era (modified after Xiao et al., 2010); (c) Regional map showing the study site's location in Xinjiang, northwestern China; (d) Map detailing the position of the sampled section and the distribution of Upper Devonian exposures in Western Junggar.

Acritarch and Prasinophyte taxa	SAMPLES														
	Ass. I	Assemblage II													Assemblage III
	GNR8	GNR50	GNR51	GNR52	GNR54	GNR55	GNR58	GNR59	GNR60	GNR61	GNR62	GNR63	GNR85	GNR86	
<i>Gorgonisphaeridium plerispinosum</i>	●														
<i>Somphosphragma miscella</i>	●														
<i>Michrhystridium pentagonale</i>	●														
<i>Pterospermella</i> sp.	●														
<i>Daillydium pentaster</i>	●									●					
<i>Cymatiosphaera rhacoamba</i>	●														
<i>Cymatiosphaera daioariochora</i>	●														
<i>Cymatiosphaera perimembrana</i>	●														
<i>Michrhystridium</i> spp.	●														
<i>Solisphaeridium</i> sp.	●														
<i>Solisphaeridium clavum</i>	●														
<i>Unellium piriforme</i>	●														
<i>Michrhystridium stellatum</i>	●														
<i>Michrhystridium flexibile</i>	●														
<i>Unellium winslowiae</i>	●														
? <i>Centrasphaeridium</i> sp.	●														
<i>Cymatiosphaera</i> cf. <i>melikera</i>	●														
<i>Gorgonisphaeridium savertonense</i>		●						●			●		●		
<i>Gorgonisphaeridium</i> sp.		●													
<i>Gorgonisphaeridium ohioense</i>		●	●	●	●	●	●	●		●	●	●	●		
<i>Gorgonisphaeridium elongatum</i>		●						●	●						
<i>Dasyptilula storea</i>		●													
<i>Leiosphaeridia</i> sp.		●			●	●	●					●			
<i>Ammonidium loriferum</i>		●			●	●				●		●			
<i>Perissolagonella</i> cf. <i>amsdenii</i>		●													
<i>Pterospermella capitata</i>		●													
<i>Pterospermella solis</i>			●												
<i>Multiplicisphaeridium</i> sp.				●											
<i>Lophosphaeridium</i> sp.				●	●							●			
<i>Divietipellis robusta</i>					●										
<i>Ammonidium sprucegrovense</i>						●									
<i>Ammonidium levigatum</i>					●	●	●			●	●		●		
<i>Veryhachium trispinosum</i> group	●		●				●	●		●	●				
<i>Saharidia lusca</i>									●						
<i>Leiofusa</i> sp.										●					
<i>Lophosphaeridium segregum</i>												●			
<i>Gorgonisphaeridium amplum</i>												●			
<i>Gorgonisphaeridium absitum</i>					●		●					●			
<i>Cymatiosphaera</i> sp. B												●			
<i>Exochoderma</i> cf. <i>irregularare</i>													●		
<i>Exochoderma</i> sp.														●	

Figure 4.12 Distribution of prasinophyte and acritarch species in the Gennaren section, showing the assemblages identified.

assemblages are reported in this study. The phytoplankton assemblage provide an alternative method of dating members of the Hongguleleng Formation, determine paleobiogeographic affinities and reconstruct the changes in the depositional environment.

Samples were prepared using standard protocol by Wood et al. (1996). Out of ninety-nine samples, fourteen yielded acritarchs. Forty-one species belonging to twenty genera were identified and were assigned to three phytoplankton assemblages based on their stratigraphic associations (see taxa belonging to each assemblage on **Fig. 4.12**). The first two belongs to the lower member (lower and upper parts, respectively) while the third belongs to the upper member of the Hongguleleng formation. These assemblages can be correlated to miospore and conodont biozonations from other parts of the world (see **Fig. 4.13**). Phytoplankton assemblage I shares species from northeastern Iran (Ghavidel-syooki and Owens, 2007) such as *Daillydium pentaster*, *Gorgonisphaeridium ohioensis*, *Ammonidium loriferum*, *Crassiangulina tessellita*, *Cymatiosphaera melikera*, and *Polyedryxium pharaonis*; and six species with the Iberian Pyrite Belt in Spain (González et al., 2005): *Gorgonisphaeridium ohioensis*, *Daillydium pentaster*, *Ammonidium sprucegrovense*, *Ammonidium levigatum*, *Michrhystridium stellatum*, and the *Veryhachium trispinosum* “group”. In terms of biostratigraphy the assemblage corresponds to the *Cyrtospora cristifer* – *Diaphanospora zadonica* (CZ) to *Lagenoisporites immensus* (Im) miospore zones of eastern Europe, delineated by Shen et al. (2024). Phytoplankton assemblage II shares the following species with the Holy Cross mountains in Poland (Racka et al., 2010): *Ammonidium loriferum*, *Gorgonisphaeridium ohioense* and the *Veryhachium trispinosum* “group.” Assemblage II is correlated with the *Grandispora gracilis* – *Grandispora famenensis* (GF) to *Rugospora versabilis* – *Grandispora cornuta* (CVo), as defined for western Europe (Shen et al., 2024). Phytoplankton Assemblage III has poor diversity with only two species of

	Richardson and McGregor 1986	Streel et al., 1987	Streel, 2009	Avkhimovitch et al., 1992	Avkhimovitch et al., 1993	Conodont zonation	Miospore zone	Phytoplankton assemblages
	Old Red Sandstone Continent and adjacent regions	Ardenne-Rhine regions	western Europe	Belarus		Ziegler and Sandberg, 1990 Spalletta et al. 2017	Shen et al. 2024	Western Junggar
Famennian	NV	LN	LN	PLE		Upper <i>expansa-praesulcata</i>		III
	PL	LE	LE	LE				
		LL	LL	LMb				
		LL						
		LV		LV				
		VH	LF			Upper <i>trachytera</i> -L. & M. <i>expansa</i>		
	FC	VCo	VCo	VF	<i>marginifera</i> -Lower <i>trachytera</i>			
	TG	GF	GF	CVa	<i>rhomboidea</i>	Ass. I	I	
		GH	DV	Im	<i>crepida</i>			
		"V"		CZ	<i>triangularis</i>			
		VV	<i>linguiformis</i>					
Fra.	OB	"IV"	BA	DE	<i>rhenana</i>			
		BM		OG				
		BJ						

 no data

 no data

Figure 4.13 Correlation of Famennian spore and phytoplankton zonation in Western Junggar with established miospore zonal frameworks from the Old Red Sandstone Continent (ORSC) and nearby regions (after Richardson & McGregor, 1986), western Europe (Streel et al., 1987; Streel, 2009), and eastern Europe (Avkhimovitch et al., 1992, 1993). For broader stratigraphic context, conodont biozones from Ziegler & Sandberg (1990) and Spalletta et al. (2017) are included. Abbreviations: Fra. = Frasnian; Ass. I = Assemblage I; Ass. II = Assemblage II.

Exochoderma and lack of age-diagnostic miospores except for a specimen of *Retispora lepidophyta*; the age could correspond to the LL miospore zone and part of the *expansa* conodont zone.

Multivariate analyses were performed to determine paleobiogeographic relationships (results in Fig. 4.14). Thirteen geographic units (corresponding to countries) were defined and used for comparison (see Figs. 4.14 and 4.15). Three similarity indices were calculated: Dice/Sørensen, Simpson and Raup-Crick indices. The analytical methods used are HCA with UPGMA linkage (Legendre and Legendre, 2012), neighbor-joining cluster analysis (NJ; Saitou and Nei, 1987), NMDS and one-way analysis of similarity (ANOSIM; Clarke, 1993). The results using Dice/Sørensen and Simpson are given priority; the former emphasizes similarities by giving double weight to shared occurrences while the latter is used to indicate possible spurious effects due to disparities in richness. Based on multivariate analysis, two main biogeographical realms can be recognized: Laurussia which includes Western Junggar, Poland, Belgium, South Wales, USA and Canada; and a North Gondwana Realm containing Portugal, Spain, Morocco, Algeria, Turkey and Iran. These results are similar to previous analysis by Shen et al. (2019). Western Junggar consistently clusters with Poland, sharing several taxa such as *Centrasphaeridium lecythium*, *Micrhystridium stellatum*, *Dictyotidium craticulum*, *Gorgonisphaeridium evexispinosum*, *Maranhites stockmansii*, *Polyedryxium embudum*, *Stellinium comptum*, *Stellinium micropolygonale*, *Unellium piriforme*, and *Unellium winslowiae*. Key indicator taxa for Laurussia are *Exochoderma*, *Ephelopalla*, *Muraticavea* and *Dasyopilula*; for North Gondwana these are: *Chomotriletes*, *Crassiangulina* and *Navifusa*. One-way ANOSIM of these two clusters show weak differentiation ($R = 0.16$, $p = 0.102$). Many taxa have a cosmopolitan range; around 20% out of 52 non-singleton genera are found in two-thirds of studied countries (Fig. 4.16).

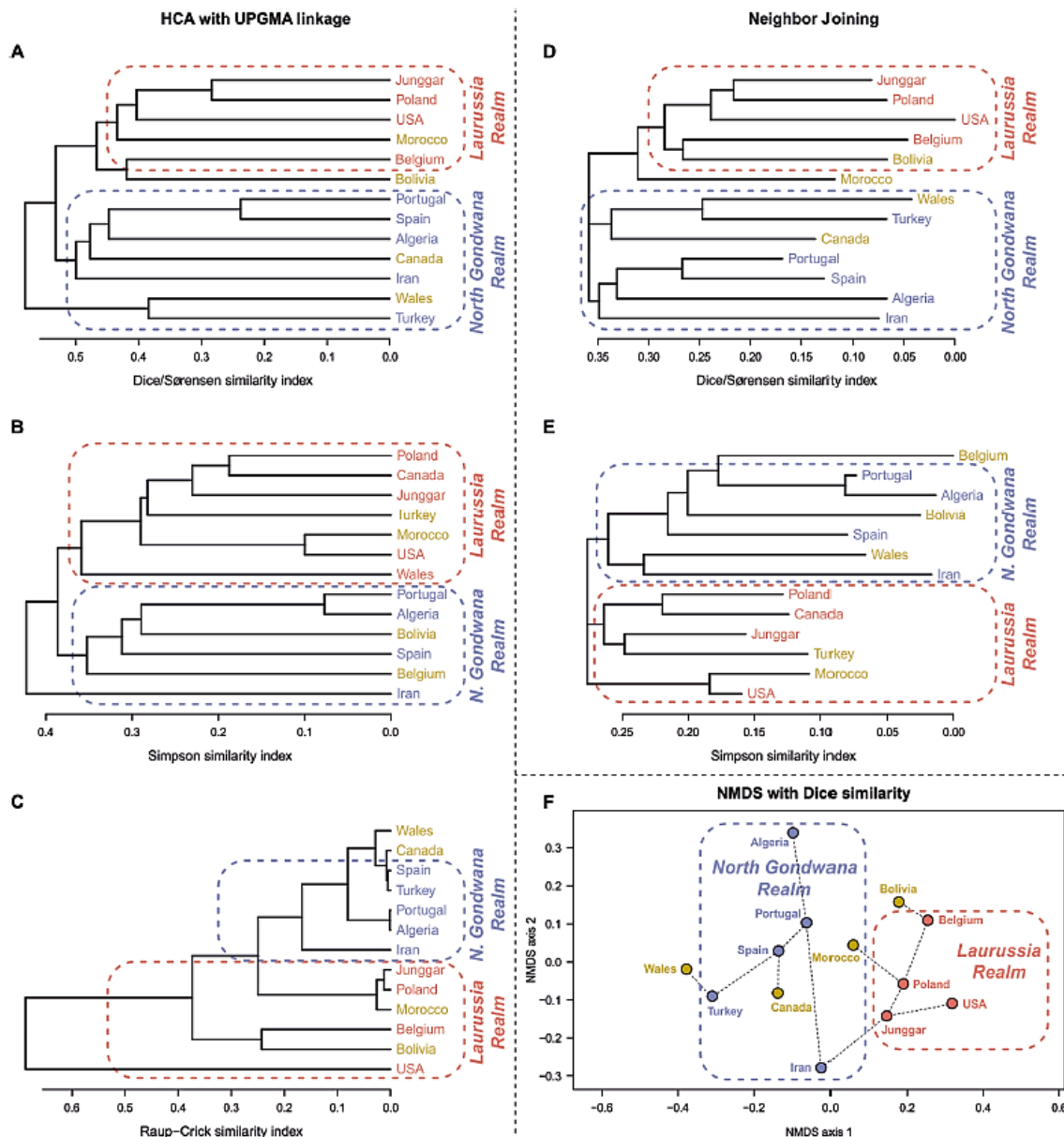


Figure 4.14 (A–C) Ultrametric hierarchical clustering (HCA) results based on the Dice/Sørensen, Simpson, and Raup-Crick similarity indices; (D–E) Metric additive trees generated using the Neighbor-Joining (NJ) method with Dice/Sørensen and Simpson indices; (F) Non-metric multidimensional scaling (NMDS) ordination of the phytoplankton dataset using the Dice/Sørensen index, with sample points connected by a minimum spanning tree.



Figure 4.15 Paleogeographic reconstruction of the Famennian (Late Devonian), adapted from Scotese and Wright (2018), illustrating the distribution of the geographical units analyzed in this study. These regions are broadly grouped into two major biogeographic realms: the Laurussia Realm and the North Gondwana Realm.

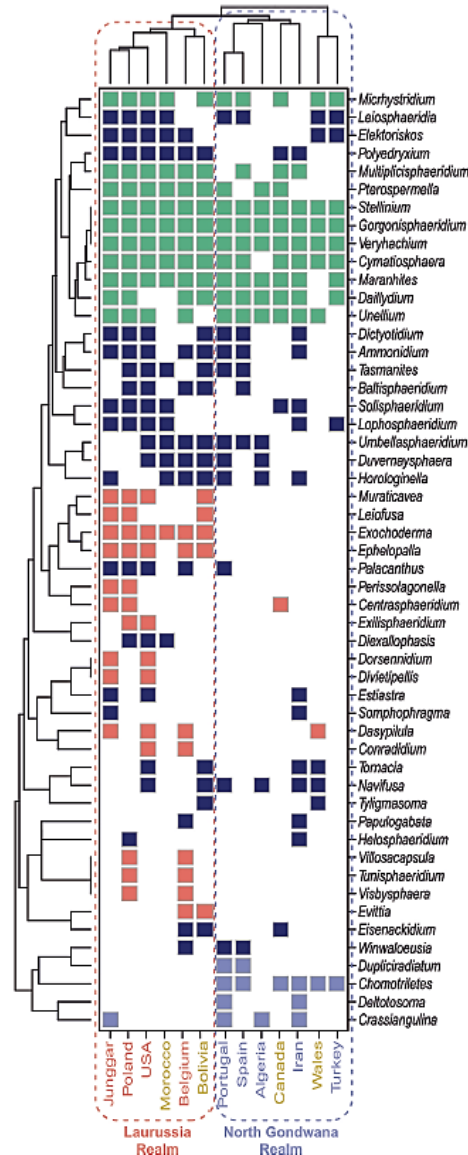


Figure 4.16 Distribution of the 52 non-singleton acritarch genera across the studied geographical units. Both taxa and regions are arranged based on results from a two-way cluster analysis using UPGMA linkage and the Dice similarity coefficient.

The delineated biogeographical realms in Shen et al. (2025; **Fig. 4.15**) differ slightly from this study (see **Fig. 4.7D**) for the Famennian. The North Gondwana Realm in Shen et al. (2025) nearly corresponds to the South Paleotethys Province in this study, though the latter doesn't include the southern European and North African localities. The West Paleotethys Province in this study roughly corresponds to the Laurussian Realm, but the former does not include localities on the Laurentian and Avalonian side of Laurussia. While the present study includes more localities and was able to detect additional provinces (South America and West Africa Provinces); they also differ in the database and linkage algorithm (UPGMA vs. Ward's) used.

Determination of the relative proportions between marine phytoplankton and terrestrial miospores allow for the determination of paleoenvironment (**Fig. 4.17**). Higher proportions of acritarchs indicate an off-shore marine environment while increased miospores indicate a shallower or nearshore setting (Wicander and Playford, 2013). The palynomorph abundances in the Gennaren section show fluctuations in the abundance of terrestrial and marine

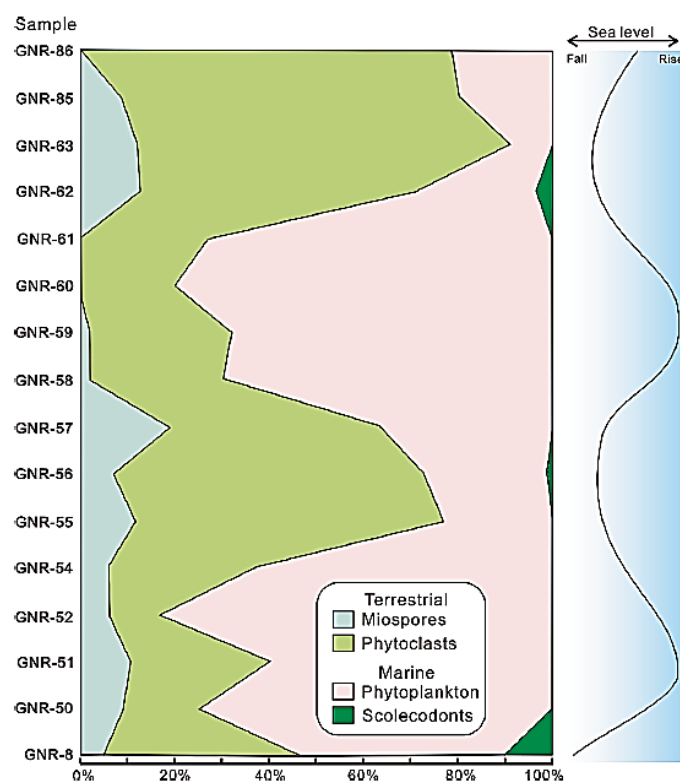


Figure 4.17 Palynomorph percentage abundance in the Famennian Hongguleleng Formation samples from the Gennaren section.

components. The base of the section only shows terrestrial organic matter and miospores. At GNR-8 (20.3m level of the Hongguleleng formation) marine components increased to 52%, suggesting a low-energy marine environment. From GNR9 to GNR49 there is a gradual increase in water depth. From GNR50 to GNR61 the abundance of terrestrial palynomorphs started low, peaking at GNR55 to around 80%, before falling back to around 40% in GNR61. This mirrors a transgressive-regressive cycle. From GNR58 to GNR61, at the top of the lower member, the environment shifts again from nearshore to normal marine. From GNR62 to GNR86 the terrestrial components increased again and reaching almost 90% at GNR63. These fluctuations suggest a initial coastal conditions which shifted to neritic, deeper water and finally back to neritic environments.

4.4 Discussion

4.4.1 Plausible biogeographic markers

Plotting of previously reported biogeographically significant taxa based on the updated Phytopal database shows that some genera/species retains their usefulness as biogeographic indicators. The Tremadocian warm-water genera of Volkova (1997) still holds when plotted on PALEOMAP (**Fig. 4.4**).

Playford (1995) and Tongiorgi and Di Milia (1999) proposed that the occurrence of peteinosphaerids can be considered a criterion to delineate Baltica in the Middle Ordovician, however *Peteinosphaeridium* and *Liliosphaeridium* appear to have a wide distribution from Baltica and Avalonia to northern and southern Gondwana (**Fig. 4.5**). They can thus be considered cosmopolitan. Reported alternation of biogeographical affinities in South China

from middle Arenig Perigondwana assemblages to upper Arenig Baltican flora (which includes *Liliosphaeridium kaljoi*) (Tongiorgi et al., 1998) could possibly represent ecostratigraphic changes related to environmental fluctuations (similar to Calero-Gordon et al., 2025; **Appendix 2**) rather than occasional invasions from distant bioprovinces.

Of the three Perigondwana genera in the Middle Ordovician, *Frankea* is the most latitudinally restricted (**Fig. 4.5**), reaffirming its status as a marker for cold-water paleolatitudes (e.g. Servais and Fatka, 1997). *Arbusculidium*, *Coryphidium*, *Frankea* and *Striatotheca* co-occurs in South Gondwana (but not in South America, where only *Striatotheca* is noted); *Frankea* and *Arbusculidium* are both absent from North Gondwana (South China) and Baltica; and only *Frankea* was present in Avalonia. The absence of *Frankea*, *Arbusculidium* and *Coryphidium* in South America is either due to the lack of sampled localities in the Middle Ordovician, or in the case of *Frankea*, marks the boundary of cold and warm-water realms. For warm-water latitudes, a positive criterion is needed since the distribution of *Striatotheca*, *Coryphidium* and peteinosphaerids are rather cosmopolitan.

In the early Silurian Cramer's biofacies were found on most continents, with no paleolatitudinal trend in their distribution (**Fig. 4.6**). *Dactylofusa maranhensis* appears to be a marker for South Gondwana, with a northern limit of distribution at -30° , though it is not commonly found in South Gondwana localities. *Dilatisphaera williereae* also has a limited distribution with a probable extent in Avalonia and Baltica, but it is not common in either area. *Neoveryhachium carminae* and the *Pulvinosphaeridium-Estiastra-Hoegklintia* facies does not appear to be present north of the equator, but this could be due to scarcity of sampled areas.

4.4.2 Latitudinal zonation in the early Cambrian (Terreneuvian and Cambrian Series 2)

There are few localities in the Terreneuvian but the multivariate results show an apparent zonation between the northern and southern hemisphere, and an approximate boundary at the equator (**Fig. 4.7A**). These two groups are interpreted to be realms. The northern cluster is also interpreted to be a province (North Gondwana Province) consisting of Australia and South China, which are paleogeographically close. The southern cluster includes areas widely separated from each other and hence retained as a realm (Baltican Realm).

In the Cambrian Series 2 there are provinces in Laurentia and between Laurentia and Baltica due to their proximity, but not apparent everywhere else (**Fig. 4.7B**). A latitudinal zonation is again present between localities from the equatorial northern hemisphere, equatorial to subequatorial southern hemisphere, and the high paleolatitude southern hemisphere.

4.4.3 Development of a distinct southern “cold-water” province (Miaolingian to Floian)

The latitudinal realms evident in the Early Cambrian were not prominent in the Miaolingian, although this could be due to the lack of analyzed localities in the northern hemisphere, but there is a division between southeastern Gondwana localities and those from Baltica and Avalonia (**Fig. 4.7C**). There seems to be a high degree of cosmopolitanism but the beginnings of provinciality in southeastern Gondwana emerges, divided into two “provinces.” Based on their location along the Gondwana continental shelf these “provinces” may represent facies: with an inner South Gondwana “Province 1” and the outer shelf South Gondwana “Province 2”. No other provinces (or geographically coherent clusters) are present.

In the Furongian, the broad divisions from the multivariate results are interpreted to be realms (the Laurantia, Baltica and South Gondwana Realms), but similar to the Miaolingian,

these do not seem to have a latitudinal control (**Fig. 4.7D**). A high-paleolatitude South Gondwana Province emerges, which includes southern Europe, North Africa and Avalonia. This is interpreted to be a “cold-water” province due to its position at the southern polar area. West Canada and Argentina form a Laurentian province, isolated from the two other realms. This seclusion could reflect patterns in oceanic circulation during that time. The Baltica Realm has a broad geographical extent which includes Baltica, and parts of Southern and Northern Gondwana.

The Ordovician is a period of continuous climate cooling, with global average temperatures starting to decrease from the Cambrian hothouse, culminating in the Hirnantian glaciations (Scotese et al., 2021). This affected the broad distribution of phytoplankton, showing clear division into Northern and Southern Realms. The Northern Realms extend from the northern equatorial regions to -30° while the Southern Realms extend from -30° to the Southern polar areas. All or most of the Avalonian localities are part of the Southern Realm in the Early Ordovician but became part of the Northern Realm starting by the Middle Ordovician due to its northward drift towards Baltica.

The cold-water province of South Gondwana becomes entrenched in the high southern paleolatitudes starting in the Tremadocian (**Fig. 4.7E**), and at that time it includes most of Avalonia. Baltica also appears as a distinct province in the Tremadocian, including parts of Avalonia (England). In the Floian, the cold-water realm also includes an Avalonia Province separates from South Gondwana Province, as it drifts northward towards the continent of Baltica (**Fig. 4.7F**). There is strong provincialism at this time, with the two provinces of the Southern Realm (South Gondwana and Avalonia Provinces) and two provinces in the Northern Realm (North Gondwana and Baltica).

4.4.4 Bioprovinces in the Middle Ordovician (Dapingian to Darriwilian)

Previous workers have defined two main bioprovinces in the Middle Ordovician: Baltica and Perigondwana, based on distribution of key taxa (see **Section 3** above and references therein). The Perigondwana Province extends from high southern paleolatitudes to the northern hemisphere equatorial region, including all of Avalonia (**Fig. 4.3**). Our analysis shows a slightly different picture; one which suggests a possible latitudinal control on distribution. Northern and Southern Gondwana localities do not cluster together, instead they fall between the Northern and Southern realms, respectively (**Figs. 4.7G, H**). Due to lack of sampled areas in the western hemisphere (primarily the South American landmass) the western extent of the South Gondwana Province is not documented in the Dapingian. The South Gondwana Province is divided into “subprovinces,” which, similar to the Miaolingian can instead represent facies. A North Gondwana Province is also present in the Dapingian. Baltica split into two provinces (North and South Baltica), a possible consequence of the closing of the Tornquist Sea and the northward drifting of Avalonia towards Baltica, enabling floral exchange these areas and fragmenting biogeographical uniformity (recorded in the Early Ordovician) in the latter.

4.4.5 Destabilization in the Late Ordovician (Sandbian to Hirnantian)

The Northern and Southern Realms are not differentiated for the Sandbian due to lack of localities in key areas, particularly in northern and southern Gondwana (**Fig. 4.7I**). Most of the analyzed areas are from Baltica and Avalonia, with only three from other paleocontinents. With only two far-flung localities from south Gondwana, the South Gondwana Province was

not defined for the Sandbian. But similar to the Darriwilian, Baltica and Avalonia are split between two provinces (North and South Baltica). The North Baltica Province extends to parts of western Avalonia.

In the Katian the familiar division between the warm-water Northern Realm and the cold-water Southern Realm is restored (**Fig. 4.7J**). The two Baltica provinces (North and South) are still present while South Gondwana Province is divided into two subprovinces, approximately along 95°E. The Hirnantian marks a global breakdown of the Ordovician biogeographical structure (**Fig. 4.7K**). Although the Northern and Southern Realms can still be recognized, North Baltica Province disappeared and South Gondwana Province became much smaller. Cosmopolitanism became the order of the day.

4.4.6 Cosmopolitanism in the Llandovery (Rhuddanian to Telychian)

The Late Ordovician mass extinction wiped out more than 80% of marine invertebrate species and is the second most severe biotic crisis in the Phanerozoic, after the end-Permian event (Bond and Grasby, 2017). The main cause has not been fully resolved but most of the proposed mechanisms involve changes in global ocean temperature and redox chemistry. Phytoplankton diversity dipped in the Hirnantian (Kroeck et al., 2022; see also **Fig. 3.2A**), along with zooplanktic groups such as graptolites (Fan et al., 2016), radiolarians (Danelian and Monnet, 2021) and chitinozoans (Grahm and Paris, 2011). Phytoplankton diversity was low in the Rhuddanian and Aeronian but it was on an increasing trend; during this time there was minimal biogeographic structure (**Figs. 4.7L, M**). Only a fraction of the Baltica Province survived, and the large cold-water province which dominated the southern polar areas has been all but extinguished.

The generic diversity of phytoplankton is still low in the Telychian (**Fig. 3.2A**), and the biogeographic structure has not fully returned (**Fig. 4.7N**). However, there is a broad differentiation of phytoplankton into Baltican and Perigondwanan realms. The Telychian also coincided with a rise in global average temperatures (**Fig. 1.3**).

The Baltica Province (**Figs. 4.7L, M**) in the Llandovery roughly coincides with the reported distribution of *Dilatisphaera williereae* (**Figs. 4.2, 4.6**) and may thus be indicative of the province. The limited distribution of *D. williereae* reflects the limited extent of Baltica Province. The distribution of *Dactylofusa maranhensis* does not seem to match with any cluster (or province for that matter) determined from the multivariate results but appears to be restricted to south Gondwana (**Fig. 4.6**), thus it can be an indicator of this area. However, this should be taken with caution, especially with few sampled localities in northern Gondwana during this time interval. The apparent absence of *D. maranhensis* in northern Gondwana could be due to sampling biases.

4.4.7 Re-establishment of bioprovinces (Sheinwoodian to Gorstian)

The South Gondwana Province re-established itself at the start of the Wenlock (Sheinwoodian). Baltica-Avalonia and Laurentia were drifting towards each other, and two provinces formed between them (Laurentia and Baltica Provinces, **Fig. 4.7O**). In the Homerian the Baltica and South Gondwana Provinces both split into two (Baltica “Provinces 1 and 2,” South Gondwana “Provinces 1 and 2” respectively) which could be representative of facies rather than provinces (**Fig. 4.7P**). Of the two Baltica Provinces, only “Province 1” remained

(named Baltica Province), while there are two provinces in South Gondwana but both are limited to the east (**Fig. 4.7Q**).

The multivariate results from the Sheinwoodian showed a broad differentiation into Northern and Southern Realms, similar to the Ordovician; but this was not apparent in the Homerian and Gorstian, although provinces can be delineated. There was a drop in global average temperatures during the Wenlock (Scotese et al., 2021) by the end of the Sheinwoodian, with a maximum dip at the Homerian-Gorstian boundary, then rising in the Ludfordian. As in the Hirnantian and the Llandovery, it appears that the drop in global average temperatures destabilizes the large-scale, latitudinal phytoplankton distribution.

4.4.8 Stabilization of warm and cold-water realms (Ludfordian to Pridoli)

By the end of the Silurian global average temperatures were rising, and phytoplankton distribution into Northern and Southern Realms stabilized. In the Ludfordian, a Baltica Province is present while South Gondwana Province is divided into two subprovinces (**Fig. 4.7R**). In the Pridoli the Northern Realm is more cosmopolitan (**Fig. 4.7S**), and there were two provinces in South Gondwana (“Provinces 1 and 2”). The South Gondwana “Provinces 1 and 2” could be manifestations of inner and outer shelf facies, respectively. Further investigations are necessary to assess whether these biogeographic units are actually facies.

4.4.9 The Early Devonian (Lochkovian to Emsian)

During the Early Devonian the Laurussian and western Gondwanan landmasses drifted closer with the closing of the Rheic Ocean, facilitating floral exchange. Our cluster analysis results are broadly similar to those of Le Hérissé et al. (1997a; see figs. 4 and 5, p. 114), except for East USA which is grouped with South American localities in our analysis instead of being isolated. Disregarding the Scott and McKerrow (1990) paleogeographic reconstruction, the two main CA clusters of Le Hérissé et al. (1997a) in fig. 4 can be reimagined as belonging into Northern and Southern Realms. Our results also show an apparent subdivision of south Gondwana into West and East Provinces (with East USA belonging to the West Province and the Southern Realm) in the Lochkovian (**Fig. 4.7T**). The Northern Realm is occupied by an East Rheic Province, with localities on both sides of the Rheic Ocean in Baltica and Gondwana.

In the Pragian and Emsian all the analyzed localities belong to the Southern Realm of the Lochkovian, thus no clear warm and cold-water realms can be determined (**Fig. 4.7U, V**). Southern Gondwana fragmented into West, Central and East Provinces in these time intervals. The climate does not appear to be stable, fluctuating between warm and cold (Scotese et al., 2021). However, there is also a lack of analyzed areas in the northern hemisphere, thus it hard to conclude if a latitudinal zonation existed for these times.

4.4.10 Formation of Paleotethyan bioprovinces (Eifelian to Famennian)

In the Eifelian the northern limit of the cold-water realm regressed southward below -60° . A Laurentian Province forms which incorporates Argentina-Bolivia-Paraguay (**Fig. 4.7W**). A bioprovince is forming at the western side of the Paleotethys Ocean (West Paleotethys Province), stretching from north Africa and southern Europe to northern China.

In the Givetian the Southern Realm regained its latitudinal extent up to -30° (**Fig. 4.7X**). The Southern Realm has three provinces: Laurentia Province which forms a southern

subequatorial belt just below -30° , the West Africa and South America Provinces. In the Northern Realm another province formed at the southern margin of the Paleotethys, the South Paleotethys Province.

The impending collisions between Laurussia and western Gondwana landmasses in the Frasnian (**Fig. 4.7Y**) appear to facilitate floral exchanges between the different continents, as a result the assemblages in North America, Baltica and northern central Gondwana are rather cosmopolitan; not classified into provinces. The Givetian South Paleotethys Province retreated eastward in the Frasnian while the South America and West Africa Provinces are preserved. The Northern Realm advanced slightly south of -30° , regaining Laurentia.

By the end of the Devonian West Africa was drifting closer towards Laurussia. The Southern Realm regained southern Laurentia (**Fig. 4.7Z**). In the Southern Realm, the West Africa Province remained the same since the Givetian, while South America Province extended northward into southern Laurentia. Both West and South Paleotethys Provinces are also present as part of the Northern Realm. The South Paleotethys roughly corresponds to the B2 Subprovince in the East Gondwana Realm and North Gondwana Realm of Shen et al. (2019; 2025) while the West Paleotethys Province corresponds to the eastern half of the Boreal and Laurussian Realms, respectively.

4.4.11 Environmental controls on Paleozoic paleobiogeography

Paleolatitude appears to be an important controlling factor in the distribution of phytoplankton. For most of the Early to Middle Paleozoic, with the exception of the Early to Middle Silurian, the NMDS results illustrate a gradational structure between warm (Northern) and cold-water (Southern) assemblages. In many cases these two realms are also demarcated in the HCA. Furthermore, the Southern Realm is generally stable (again with the exception of the Early to Middle Silurian), and for most of the Early to Middle Paleozoic is occupied by one or several provinces. In contrast Northern Realm Provinces are generally smaller in extent and more ephemeral. A possible modern-day analogue of Paleozoic acritarchs are the modern-day dinoflagellates, which form broad latitudinal bands: low, middle and high latitude assemblages (Goodman, 1987; Taylor, 1987). Mudie and Harland (1996) summarized the various geographic assemblages for late Holocene dinoflagellates and acritarchs (see text-fig. 6 in Mudie and Harland, 1996, p. 857). Qualitative analysis of global modern-day dinocyst distribution by Marret et al. (2020) show they are generally cosmopolitan, though less than a handful are truly bipolar (*Impagidinium pallidum*, *Islandinium minutum* and *Polarella glacialis*) and few taxa are endemic. Multivariate analysis of modern-day (pre-industrial) planktonic foraminifera by Rillo et al. (2021) also show latitudinally distributed bioregions with bi-hemispheric occurrence (fig. 1 of Rillo et al., 2021, p. 5). Various environmental factors exert control on the planktonic foraminifera distribution, but the most consistent for each bioregion is mean sea surface temperature (figs. 3c and supplementary fig. 9 of Rillo et al., 2021; pp. 7,5).

Drastic changes in climate influence phytoplankton distribution. Provincialism started to break down with the Hirnantian cooling, and marine ecosystems collapsed with the Late Ordovician Mass Extinction Event. Global phytoplankton diversity only recovered towards the end of Llandovery, in the Telychian (Kroeck et al., 2022). Provincialism also started to re-emerge during this time.

There is no correlation between CIE events and provincialism. While the lack of biogeographic structure in the Aeronian coincides with two positive CIE events (the Early and

Late Aeronian events; **Fig. 3.2D**), other time intervals with CIE events (both positive and negative) host provinces.

Like climate, paleogeography is a significant control on biogeographical patterns. The northward drift of Avalonia towards Baltica created an Avalonian Province, separating from South Gondwana Province but still part of the Southern Realm (**Fig. 4.7F**). Further interaction in the Middle Ordovician created a South Baltica Province, which is composed of both Avalonian and south Baltican localities (**Figs. 4.7G, H**). In the Early Devonian (**Figs. 4.7T-V**) the impending collision between the Euramerica and the South American landmass in Gondwana fragmented the South Gondwana Province 1 of the Pridolian, and which has occupied the high southern paleolatitudes since its restoration in the Sheinwoodian. While South Gondwana Province briefly returned in the Eifelian (**Fig. 4.7W**), it was once again broken up in the latter part of the Middle Devonian until the end of the Late Devonian. The formation of the Paleotethys Ocean also created new provinces along its margins (**Figs. 4.7W-Z**).

4.4.12 Correlation with diversity

The results of the biogeographic analyses do not show a clear correlation with global diversity. Initially, in the early Cambrian there was a broad latitudinal division in phytoplankton and there was high cosmopolitanism during a greenhouse interval, but even then, some provinces were delineated. The latter half of the Silurian and the Devonian in general also showed provincialism despite low diversities. Global turnover metrics and the LDG also did not show correlation with biogeographical results.

4.5 Summary

This chapter shows an overview of phytoplankton paleobiogeography for the early to middle Paleozoic. A review of potential biogeographic marker taxa shows that *Athabascaella*, *Lua* and *Aryballomorpha* comprise a trio of warm-water indicators in the Tremadocian, while *Dactylofusa maranhensis* is limited to south Gondwana during the early Silurian.

The present author was engaged in two related studies. While the results have not yet been incorporated in the present analysis, the study of the acritarch content of the Cabrières biota by Caillaud et al. (2025) allow the addition of another data point and enhances the diversity in the Floian. The study of Hongguleleng Formation by Shen et al. (2025) also adds to the diversity with the analysis of another section in northwest China, and while the biogeographic results are slightly different, it allows for confirmation of the existence of provinces along the Paleotethys during this time.

Although many regions are not represented and knowledge gaps exist, particularly in the northern hemisphere, robust patterns still emerge. Multivariate analysis shows that paleolatitudes exert significant control on the distribution of phytoplankton for most of the early to middle Paleozoic, with the establishment of northern and southern realms. This was disrupted by drastic climate changes associated with the Hirnantian glaciations, and a biotic turnover culminating in the Late Ordovician mass extinctions. It took approximately five million years for phytoplankton to recover and a semblance of provincialism returned in the Telychian, and was fully re-established by the Sheinwoodian. The continental drift and impending collision between Euramerica and southern Gondwana in the Early to Late Devonian also affected biogeographical patterns, enabling interactions between Euramerica

and the South American landmass and shifting the boundaries between the northern and southern realms. Thus, paleolatitude, climate change and continental drift appear to influence phytoplankton paleobiogeography.

CHAPTER 5

CONCLUSION & PERSPECTIVES

5.1 General conclusions

The primary objectives of this thesis are to trace the trajectory of early to middle Paleozoic phytoplankton diversity and to determine how their distribution varied during this interval, which encompasses mass extinctions and climatic changes. To address these aims, a comprehensive database was developed by merging data from previous authors. A substantial part of the project involved the spatialization of occurrence data, along with the incorporation of recent references for the Silurian and Devonian periods.

Phytoplankton diversity and paleobiogeography during the early to middle Paleozoic were shaped by a dynamic interplay of paleoclimatic, oceanographic, and tectonic processes. Despite gaps in the fossil record—particularly from the Northern Hemisphere—robust patterns emerge that reveal how they responded to large-scale environmental and paleogeographic changes.

Climatic fluctuations, especially those associated with polar temperature changes, played a major role in structuring global phytoplankton diversity. Icehouse conditions intensified latitudinal diversity gradients, and regional heterogeneity in diversity and turnover likely reflects the influence of upwelling zones and oceanic current-driven dispersal. Patterns of origination and extinction suggest an “out-of-the-tropics” dynamic, with new taxa emerging preferentially in equatorial regions and extinctions occurring more frequently at high southern paleolatitudes. Frequent positive carbon isotope excursion (CIE) events during the Silurian likely disrupted ocean chemistry and productivity, reducing ecosystem resilience.

Paleobiogeographic patterns were similarly complex. Distinct warm-water and cold-water phytoplankton realms were established early in the Paleozoic. This provincialism was temporarily disrupted by the Hirnantian glaciations and the Late Ordovician mass extinctions, with recovery and re-establishment occurring by the Sheinwoodian. Key taxa such as *Athabascaella*, *Lua*, and *Aryballomorpha* serve as markers of warm-water conditions in the Tremadocian, while *Dactylofusa maranhensis* highlights the persistence of regional endemism in South Gondwana during the early Silurian. In the Devonian, tectonic activity and the impending collision between Euramerica and southern Gondwana facilitated biotic exchange and shifted the boundaries between phytoplankton provinces.

Overall, this study underscores that climate change, CIE events and continental configuration were major drivers of phytoplankton evolution and distribution. The patterns observed not only reflect the ecological sensitivity of phytoplankton to global changes but also reinforce their value as indicators for reconstructing ancient marine environments.

5.2 Perspectives and future investigations

This study highlights key trends in Paleozoic phytoplankton diversity and paleobiogeography, but several unanswered questions and data limitations open promising avenues for further research. One of the most pressing needs is the improvement of geographic and temporal sampling. The fossil record remains uneven, with many regions—particularly in the Northern Hemisphere—underrepresented. Focused fieldwork and taxonomic revision in understudied areas such as northern Gondwana, parts of Laurentia, and Siberia could reveal additional diversity and improve biogeographic resolution. Similarly, intervals with poor sampling coverage, especially within the Cambrian and parts of the Silurian, need better temporal resolution to clarify diversity dynamics and evolutionary trajectories.

Further refinement of taxonomic frameworks and the ecological significance of proposed marker taxa is also necessary. While genera such as *Athabascaella*, *Lua*, *Aryballomorpha*, and *Dactylofusa maranhensis* show promise as indicators of warm-water or regional environmental conditions, their biogeographic value must be tested through integrative approaches. Combining detailed morphological analyses with geochemical and potential molecular-level data (e.g. FTIR) may enhance our understanding of their environmental tolerances and phylogenetic relationships, strengthening their utility in paleoenvironmental reconstruction.

Mechanistic modeling represents another key frontier. While correlations between diversity, paleolatitude, and temperature are evident, the causal drivers remain complex. Developing coupled climate-ocean-biological models that simulate phytoplankton distribution under different Paleozoic climate scenarios could help evaluate the influence of temperature, ocean currents, and upwelling zones on diversity patterns. These models would be especially valuable for reconstructing nutrient dynamics and testing hypotheses about migration and dispersal. Ultimately, ecological niche models can be generated to fill in the knowledge gaps in unstudied and sparsely sampled areas and time intervals.

Closely tied to this is the need for a better understanding of ancient ocean circulation and upwelling systems. Diversity hotspots and high-turnover regions may reflect zones of enhanced nutrient availability driven by upwelling. Future research should integrate paleoceanographic modeling with sedimentological and geochemical evidence, such as phosphorite deposits and isotopic proxies, to reconstruct ancient nutrient regimes and circulation patterns.

The impact of recurrent carbon cycle disruptions, particularly during the Silurian, is another critical area for exploration. The frequent positive carbon isotope excursions (CIEs) during this time are likely linked to shifts in marine productivity, ocean stratification, and ecosystem stress. High-resolution stratigraphic studies that integrate isotopic, redox, and organic geochemical proxies could help elucidate the ecological consequences of these events and explain the delayed post-extinction recovery of phytoplankton.

Further investigation into macroevolutionary dynamics, such as the “out-of-the-tropics” (OTT) model, is also warranted. The observed pattern of preferential origination in tropical paleolatitudes, combined with elevated extinction rates in high southern latitudes, suggests an OTT framework for Paleozoic phytoplankton. However, more data is needed to assess migration patterns and the rates of immigration between tropical and extratropical regions. Confirming this model would require a detailed analysis of spatial expansion histories and biogeographic range shifts.

Lastly, future studies should aim to integrate records of other planktonic groups, including radiolarians, graptolites, chitinozoans. This broader taxonomic scope would allow a more comprehensive understanding of primary producer evolution, biocalcification, and environmental sensitivity in Paleozoic marine ecosystems.

Together, these future directions promise to refine our understanding of the evolutionary history of phytoplankton and their responses to long-term environmental and tectonic changes. A multidisciplinary approach — combining paleontology, geochemistry, climate modeling, and biogeography — will be essential to unlocking the full complexity of early marine ecosystems.

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APPENDICES

Appendix 1. Netromorph acritarchs and related morphotypes in the middle Paleozoic: a proposal for classification by *Manzano, E. G., Monnet, C., Mertens, K. N., & Servais, T.* (2025). Journal article published in *Palynology*.

Appendix 2. Acritarch distribution in the Middle Ordovician of Öland, Sweden: Ecostratigraphical or biostratigraphical signal? by *Calero Gordon, J. L., Chaigneau, B., Lindskog, A., Eriksson, M. E., Manzano, E. G., Monnet, C., Munnecke, A., Régnier, S., & Servais, T.* (2025). Journal article published in *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Appendix 3. Acritarchs (organic-walled microfossils) from the Floian (Early Ordovician) of the Montagne Noire, France: biostratigraphical and paleobiogeographical implications by *Caillaud, V., Birolini, E., Lefebvre, B., Manzano, E. G., Michel, S., Régnier, S., Vaucher, R., & Servais, T.* Manuscript submitted to *Lethaia*.

Appendix 4. Famennian phytoplankton from the Hongguleleng Formation of Western Junggar, NW China by *Shen, Z., Monnet, C., Manzano, E. G., Gong, Y., & Servais, T.* (2025) Journal article published in the *Review of Palaeobotany and Palynology*.

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Netromorph acritarchs and related morphotypes in the middle Paleozoic: a proposal for classification

Eiver Gelan Manzano^a , Claude Monnet^a , Kenneth Neil Mertens^b  and Thomas Servais^a 

^aUniversité de Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, Lille, France; ^bCOAST, Ifremer, Concarneau, France

ABSTRACT

Acritarchs are organic-walled microfossils that dominate the phytoplankton in Paleozoic seas. The current classification subdivides acritarchs into subgroups based on the outline of the main vesicle. Among them, the netromorphs include the fusiform morphotypes showing peak diversity during the middle Paleozoic. More than 300 species and subspecies have been reported in the literature, many of which are probably synonyms or ecophenotypes. We review and emend the definition of netromorphs, restricting them to homopolar forms and reassigning related heteropolar morphotypes (*Deunffia*–*Domasia* complex) to another subgroup: the diacromorphs. We propose a simplified classification scheme as follows: (i) Category 1, for elliptical forms; (ii) reniform Category 2; (iii) spindle-shaped Category 3; and (iv) a Category 4 of crescent-shaped genera. Morphologically-similar species within *Leiofusa*, *Poikilofusa* and *Eupoikilofusa* are merged into intrageneric morphotype groups. Several new combinations are proposed. The *Deunffia*–*Domasia* complex is also classified based on the presence of appendages, their number and the distal branches. Possible biological affinities of netromorphs to fungal spores, euglenids and turbellarian (flatworm) oocytes are also discussed. However, clear biological affinities remain uncertain, and further investigation is needed to determine whether netromorphs are exclusively phytoplanktonic or belong in part to various animal, fungal or algal groups.

KEYWORDS

Acritarchs; diacromorphs; netromorphs; Paleozoic; phytoplankton

1. Introduction

The Acritarcha is an informal group of organic-walled microfossils (OWMs) with unknown biological affinities. The term was originally proposed by Evitt (1963) to accommodate taxa that remained unclassified after some hystrichospheres (an old term for OWMs with a spherical body and spines) were determined to be dinoflagellate cysts (Servais et al. 2004; Riegel 2008). Many researchers consider that most acritarchs may represent resting cysts of marine phytoplankton (Martin 1993; Martin et al. 2008), although it is clear that the group is heterogeneous and polyphyletic (Playford 2003). Acritarchs display a diverse array of morphologies but generally consist of a hollow vesicle 20 to 150 µm wide, and a plain or elaborate decorated exterior wall bearing processes, crests, granulae, etc. (e.g. Armstrong and Brasier 2005). They first appeared during the Proterozoic, becoming diverse and abundant in early to middle Paleozoic oceans (Strother 1996; Kroeck et al. 2022). There was a sudden decrease in global diversity during the Frasnian–Famennian mass extinctions, that continued throughout the rest of the Paleozoic, an interval known as the Late Paleozoic Phytoplankton Blackout (Riegel 1996, 2008; but see also Servais et al. 2006).

Due to the unknown origins of acritarchs, the classification of various taxa relies heavily on their morphology. Several authors have proposed different schemes to classify the acritarchs into subgroups (Downie et al. 1963; Evitt 1969; Diver and Peat 1979; Tappan 1980), though none of these

schemes have a formal taxonomic rank. Some of the most commonly recognized categories include the sphaeromorphs (spherical), polygonomorphs (polygonal), prismatomorphs (polygonal but with flanges or crests), oomorphs (egg-shaped), herkomorphs (spherical body divided into polygonal fields), pteromorphs (with an equatorial flange), diacromorphs (two-peaked with ornamentation mainly at the poles) and netromorphs (spindle-shaped forms).

There are probably more than 10,000 species of acritarchs reported in the literature (Servais 1996) but their taxonomy remains problematic. Some simple forms have seen a proliferation of species, making it necessary to streamline their classification. For example, Servais et al. (2007) subdivided the early Paleozoic genus *Veryhachium*, containing 250 species and subspecies, into two informal groups: the *V. trispinosum* group (morphotypes with three processes), and the *V. lairdii* group (with four processes). Subsequently, Lei et al. (2013) created a convenient classification scheme for the *Veryhachium*/*Michrhystridium* complex in the Permian of South China, dividing them into five informal categories according to basic morphology (disregarding the ornamentation): the *Veryhachium cylindricum* group (with ellipsoidal vesicles), *V. trispinosum* group (triangular), *V. lairdii* group (rectangular), *Michrhystridium pentagonale* group (pentagonal and hexagonal) and *M. breve* group (spherical).

The objective of the present paper is to review the classification of another group with a simple morphology, that

includes more than 300 reported taxa (Fensome et al. 1990): the netromorphs. These are the fusiform acritarchs, which were highly diverse during the Silurian and Devonian (Downie et al. 1963). We revise previous classification attempts and propose a practical scheme to differentiate between the genera and establish intrageneric morphotype groups for the middle Paleozoic.

2. The taxonomic history of netromorphs

2.1. First attempts at classification

Several authors have attempted to classify the subgroup Netromorphitae (Downie et al. 1963) but currently there is no universally accepted scheme encompassing the entire subgroup and related morphotypes. The endings ‘-idea’ and ‘-itae’ (used by some authors to name the subgroups) suggest a suprageneric classification (such as families or orders). However, similar to the group of the Acritarcha Evitt 1963, the subgroups have no formal taxonomical rank under the International Code of Nomenclature for algae, fungi, and plants (ICN). Therefore, we prefer to continue using the informal term ‘netromorphs’ in this study.

Eisenack (1934) identified the first known netromorph, *Ovum hispidum fusiformis* (now *Leiofusa fusiformis*), from Silurian rocks of the Baltic and later established the informal family Leiofusidae (Eisenack 1938). Members of this family are known as leiofusids, which were defined as having a more or less elongated spindle-shaped vesicle (central body) whose wall is reminiscent of hystrichospheres. Following Evitt’s (1963) definition of the group, Downie et al. (1963) proposed subdividing acritarchs into informal morphological subgroups and infragroups instead of families, equating the Leiofusidae Eisenack (1938) with a new subgroup, Netromorphitae. Netromorphitae is derived from the Greek word ‘netron’, meaning spindle shaped.

Downie et al. (1963) emended Eisenack’s (1938) definition by adding the lack of an inner body and a generally smooth exterior wall, rarely granular. One or more distally closed spines can be present at one or both poles. Downie et al. (1963) divided the netromorphs into three generic complexes: (i) a fusiform complex, which includes *Leiofusa*, *Dactylofusa* and *Baiomeniscus*; (ii) the *Deunffia*–*Domasia* complex; and (iii) the elliptical *Leiovalia* forms.

Combaz et al. (1967) retained Leiofusidae but redefined it as a category under the Netromorphitae, restricting leiofusids to forms with bilateral symmetry (perpendicular to the longitudinal axis) and excluding asymmetrical taxa such as *Metaleiofusa* (with a lateral appendage). Combaz et al. (1967) proposed three fundamental types of leiofusids. The first group consists of genera with rounded edges and elliptical to elongate outlines (such as *Navifusa* and *Leiovalia*). The second group has tapering ends but no polar processes, and a smooth, ribbed or ornamented wall (i.e. *Dactylofusa* and *Poikilofusa*), while the last type are those with a short or elongated outline and polar appendages (*Leiofusa*). Combaz et al. (1967) mentioned ‘crescent-moon’ shapes (such as *Lunulidia*), but it was unclear whether these were considered

a separate group or a sub-category of the *Navifusa*–*Leiovalia* grouping.

Downie (1973) attempted a phylogenetic classification for acritarchs which included two netromorph groups: the *Navifusa* group, which are elongated but without spines (e.g. *Navifusa* and *Leiovalia*), and the *Leiofusa* group, which are also elongate but with tapering ends forming spines (e.g. *Leiofusa* and *Deunffia*). Vavrdová (1978) reviewed the occurrence of netromorph acritarchs from the Lower Ordovician Klabava and Šárka formations near Beroun (Czech Republic). She distinguished three main morphological branches. The first are the spindle-shaped ‘true’ leiofusids such as *Dactylofusa* and *Leiofusa*. The second are heteropolar, flask-shaped forms with rounded ends such as *Pireia*, resembling diacromorphs in having a pylome at one pole. Vavrdová (1978) also mentioned *Deunffia ambigua* as a possible transitional form to branch 1. The third branch includes reniform to lenticular forms with asymmetrical processes, resembling the morphotypes of the *Deunffia*–*Domasia* complex, tentatively assigned to *Sylvanidium operculatum*. Finally, in a subsequent review of acritarch classification schemes, Strother (1996) retained the netromorph generic complexes of Downie et al. (1963). Despite these different attempts, there is currently no generally accepted scheme to classify the netromorph acritarchs.

2.2. The ‘true leiofusids’ complex

Netromorphs can be broadly classified into homopolar (with two similar poles) and heteropolar (with two morphologically distinct poles) forms. Leiofusidae *sensu* Combaz et al. (1967) considers all homopolar genera to be leiofusids while Vavrdová (1978) only retained spindle-shaped forms such as *Dactylofusa* and *Leiofusa* as ‘true leiofusids’. *Poikilofusa* and *Eupoikilofusa* can be added to this list of ‘true leiofusids’.

Three of the four ‘true leiofusid’ genera – *Dactylofusa*, *Poikilofusa* and *Eupoikilofusa* – have been the subject of frequent disputes among researchers due to their similar and overlapping morphological characteristics. *Dactylofusa* was established by Brito and Santos (1965, 12–13, 20) and was initially described as navicular (or naviform, essentially fusiform) in shape, and bearing regularly spaced claviform processes in longitudinal rows. In the same year Staplin et al. (1965, 185) erected the genus *Poikilofusa*, referring to fusiform acritarchs covered with small spines or muri. Slightly later, Cramer (1970, 83–84) proposed the generic name *Eupoikilofusa* for other fusiforms with striated exterior walls and longitudinally arranged echinate elements less than 1 µm in height.

Some authors advocate for full or partial synonymy between the three genera (e.g. Combaz et al. 1967; Cramer 1970; Fensome et al. 1990) while others distinguish among the three taxa (e.g. Cramer and Díez de Cramer 1979; Rasul 1979; Turner 1984; Dorning 1994; Mullins 2001; Rubinstein and Vaccari 2004). Combaz et al. (1967) included *Poikilofusa* spp. under *Dactylofusa* (without proposing new combinations) in a group characterized by forms with pointed ends, and a vesicle wall which can be smooth, ribbed or

ornamented. According to Fensome et al. (1990), Cramer (1970) synonymized the more senior generic names *Dactylofusa* and *Poikilofusa* into *Eupoikilofusa*, rendering the latter name illegitimate. However, Loeblich and Tappan (1978) interpret Cramer (1970) as agreeing with Combaz et al. (1967) in synonymizing echinate *Poikilofusa* species with *Dactylofusa* while excluding the striate forms, which led to the erection of *Eupoikilofusa*. In a later publication, Cramer and Díez de Cramer (1972) clearly listed *Dactylofusa* and *Eupoikilofusa* as distinct genera, thus supporting the view of Loeblich and Tappan (1978). Loeblich and Tappan (1978) and Rasul (1979) maintained *Poikilofusa* as separate from *Dactylofusa* and *Eupoikilofusa*. Turner (1984) also retained *Eupoikilofusa* as a distinct genus.

In contrast, Dorning (1994) found it practical to distinguish among the three genera, recognizing four distinct groups: those with smooth or laevigate walls (*Leiofusa*); vesicle walls ornamented with short, complex processes arranged in rows (*Dactylofusa*); fusiforms with randomly arranged, simple processes (*Poikilofusa*); and those with striated vesicle walls (*Eupoikilofusa*). Later authors (e.g. Mullins 2001; Rubinstein and Vaccari 2004) supported this view.

2.3. The *Deunffia*–*Domasia* complex

The heteropolar genera consist of members of the *Deunffia*–*Domasia* complex. Downie (1960) defined *Deunffia* as having a hollow, ellipsoidal shell with a spine at one end, while *Domasia* has one spine at one end and two at the other. In a study of Silurian acritarchs from Gotland, Sweden, Le Hérisse (1989) also included the following genera as part of the *Deunffia*–*Domasia* complex (see Le Hérisse 1989, fig. 7): *Metaleiofusa*, *Polydeunffia*, *Hemideunffia* and *Domasiella*.

Some authors exclude the *Deunffia*–*Domasia* complex from the netromorphs. For example, Deflandre and Deflandre (1964) considered them simplified polygonomorphs (polygonomorphs are a separate subgroup established by Downie et al. 1963). However, Brito (1967) retained them in the netromorphs, suggesting that these genera are closer to some *Leiofusa* species than to the polygonomorphs. *Domasia* also resembles the Cambrian genus *Ninadiacrodium* (see Raevskaya and Servais 2009, text-fig. 3) which is considered to belong to the diacromorph subgroup. Other members of the *Deunffia*–*Domasia* complex appear comparable to heteropolar diacromorph morphology. For example, *Deunffia* can also be considered a simplified morphotype of *Dicrodiacrodium* (see Raevskaya and Servais 2009, text-fig. 1). Thus, in agreement with Deflandre and Deflandre (1964) we exclude the heteropolar forms from the netromorphs and consider them ‘related morphotypes’ that can be classified as diacromorphs.

3. A new classification proposal

3.1. Database and methods

A literature review of the netromorph genera and species from the Silurian and Devonian was conducted for this study.

Valid taxa were identified using the acritarch index of Fensome et al. (1990) and the more recent John Williams Index of Palaeopalynology (JWIP), which is hosted on the Acritax website (<https://www.mikrotax.org/Acritax/index.html>). The JWIP lists more than 23,000 fossil palynomorph taxa compiled between 1971 and 2010 by Dr. John Williams (Riding et al. 2012); as of 2018, only the acritarch section is available online at the Acritax website. In addition to Fensome et al. (1990) and the JWIP, the Phytopal database of Mullins et al. (2022) was also utilized as a resource to reconstruct the biostratigraphic and paleogeographic ranges of netromorphs in the Paleozoic. The Phytopal database is a compilation of phytoplankton occurrence data from references prior to 2006, deposited in an open-access Mendeley Data repository. More than 6000 species of phytoplankton are reported in the database. More recent literature (post-2006) was also included for the present study. Data were cleaned and filtered to remove or reassign questionable and illegitimate taxa. Geographic coordinates were extracted from the references and rotated to their respective paleo-coordinates using the R package *palaeoverse* of Jones et al. (2023) and plotted on the paleogeographic maps of Scotese and Wright (2018).

Twelve netromorph and five related genera from the Silurian and Devonian mentioned or illustrated in the literature were analyzed. The 12 netromorph genera are: *Anomaloplaesium* Tappan and Loeblich 1971; *Baiomeniscus* Loeblich 1970; *Dactylofusa* Brito and Santos 1965; *Disparifusa* Loeblich 1970; *Eupoikilofusa* Cramer 1970; *Holothuriadeigma* Loeblich 1970; *Leiofusa* Eisenack 1938 emend. Combaz et al. 1967 emend. Cramer 1970; *Lunulidia* Eisenack 1958; *Navifusa* Combaz et al. 1967 ex Eisenack 1976; *Poikilofusa* Staplin et al. 1965; *Pseudolunulidia* Brito and Santos 1965; and *Saharifusa* Pöthe de Baldi 1997. The related morphotypes are *Deunffia* Downie 1960; *Domasia* Downie 1960; *Hemideunffia* Thusu 1973; *Metaleiofusa* Wall 1965; and *Polydeunffia* Cramer 1970 ex Eisenack et al. 1973. The accepted genera are described in the systematic paleontology section (Section 4), along with the list of included species and proposed new combinations.

3.2. Morphology and concept

We adopt a similar scheme to Combaz et al. (1967) in describing netromorph morphology (Figure 1). Netromorphs exhibit bilateral symmetry along the longitudinal axis, which is generally straight but can be curved (e.g. *Baiomeniscus* and some specimens of *Dactylofusa maranhensis*). The main body is referred to as the ‘vesicle’. We use the term ‘appendages’ to refer to the polar processes (analogous to horns in dinoflagellate terminology) – long, acuminate extensions of the vesicle found in some taxa, such as *Leiofusa* and *Anomaloplaesium*. Not all netromorphs have appendages; some taxa may have pointed (e.g. the *Leiofusa simplex* group, Section 3.3.2) or rounded ends (e.g. *Navifusa*). Netromorph length is measured along the longitudinal axis between the tips of the polar processes (when present), while the width is the maximum width of the vesicle perpendicular to the longitudinal axis.

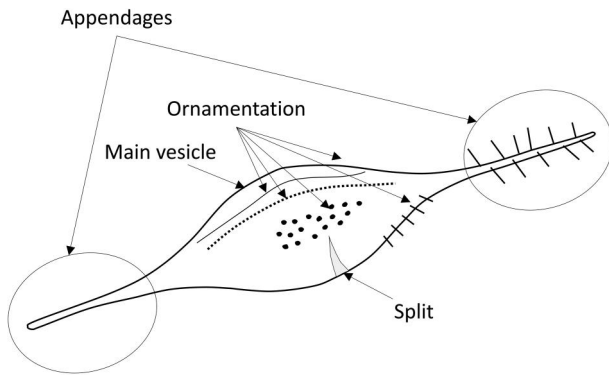


Figure 1. Basic morphology of a fusiform acritarch (modified after Combaz et al. 1967). Various examples of ornamentation are shown, including striations, granulations, tubercles and processes.

The main vesicle is generally single-walled, with or without ornamentation. The exterior wall may feature longitudinal ridges or furrows (e.g. *Eupoikilofusa*). Ornamentation can include crests, tubercles, granulations, spines, or simple or complex processes, among other forms.

Some acritarch specimens exhibit a rounded opening known as the pylome or a simple straight split in the vesicle wall, which can be oriented transversely, longitudinally or in a trochospiral manner. Some authors, considering the specimens to be cysts of algal origin, interpret these openings as excystment structures, thus implying a biological affinity. Specimens with a pylome or split are uncommon, and for the vast majority of acritarchs the type of possible excystment opening is unknown. Certain species may exhibit variations in the type or orientation of openings, potentially influenced by the phase of excystment (e.g. Fatka and Brocke 2008). As a result, these openings might not always serve as reliable features for classification.

3.3. A proposed classification for netromorphs

We propose a simple, practical scheme to classify netromorphs using easily recognizable criteria (Figure 2). The most obvious characteristics are shape or gross outline, the presence or absence of ornamentation (and if present, their arrangement or occurrence) and the type of processes/ornamentation. A tiered system of classification can be constructed based on these characters, which can be used for identification down to the genus level. Four categories were defined based on the outline: rod-shaped, reniform, spindle-shaped morphotypes, and half-moon or crescent-shaped genera. The type of ornamentation can then be used to distinguish between various genera. Genera with very similar characteristics are joined into an intergeneric complex (e.g. the *Poikilofusa*–*Disparifusa* complex; Section 3.3.3).

A genus can be further classified into informal morphotype groups, which bring together species with very similar morphologies. For example, the species in *Leiofusa* can be roughly subdivided into four (informal) groups based on their shape (see Figures 2 and 4 and Section 3.3.1 below). Within the *Poikilofusa*–*Disparifusa* there are two morphotype groups based on the type of ornamentation, while in *Eupoikilofusa*, one group is smaller than the other and has

denser striations, and a third differs in the orientation of striae (Section 3.3.3). The subdivisions proposed are purely utilitarian and do not reflect phylogenetic relations or position.

3.3.1. Category 1 netromorphs

Category 1 includes rod-shaped morphotypes with rounded ends and may have smooth or ornamented surfaces. The genus *Navifusa* has an elongated, cigar-like shape with rounded ends. Similar forms with a strongly curved longitudinal axis also exist (the genus *Lunulidia*, see Section 3.3.4 below) but it is not clear whether they are subspecies, varieties or ecophenotypes of *Navifusa bacilla* (Deunff 1955) Playford 1977. Elongated and rounded forms with striations (similar to *Eupoikilofusa*) are assigned to the genus *Deusilites*.

3.3.2. Category 2 netromorphs

A second category of netromorphs includes another morphotype with rounded polar areas but having a reniform outline. Ornamentation consists of numerous randomly arranged processes. The genus *Holothuriadeigma* belongs to this category.

3.3.3. Category 3 netromorphs

Category 3 includes the spindle-shaped netromorphs ('true leiofusids'), the largest and most diverse of the three netromorph categories, that comprises five genera subdivided into smooth-walled and ornamented types. The smooth-walled Category 3 netromorphs include *Leiofusa*, which is subdivided into four informal groups. The *Leiofusa simplex* group is named after a species originally defined from Ordovician rocks, comprised of forms with no or indistinct appendages. The *Leiofusa tumida* group has a globular main vesicle, with thin prominent appendages which can be short (e.g. *L. berneseana*) or long (*L. banderillae*). The *Leiofusa fusiformis* group has a more elongated and elliptical main vesicle compared to members of the *L. tumida* group, but also with prominent appendages. The *L. fusiformis* group includes the type species of the genus, *L. fusiformis* Eisenack 1934 ex Eisenack 1938, and *L. parvitatilis* Loeblich 1970. Extremely elongated forms, more than 100 µm in total length, are assigned to the *L. estrecha* informal group. Aside from *L. estrecha* Cramer 1964, this group also includes the species *L. filifera* Downie 1959.

Ornamented forms in Category 3 netromorphs are of multiple types. We follow a modified version of the scheme by Dorning (1994), differentiating *Dactylofusa*, *Poikilofusa*, and *Eupoikilofusa* based on ornamentation type and arrangement. Dorning (1994; in Rubinstein and Vaccari 2004, 1050) assigned species with complex short processes (often arranged in rows) to *Dactylofusa*; those with simple, randomly distributed processes to *Poikilofusa*; and those with striated ornamentation to *Eupoikilofusa*. In our scheme we consider processes (or ornamentation) with distal branches, outgrowths or bulbous parts (e.g. clavate, capitate, bifurcate or multifurcate processes) to represent complex

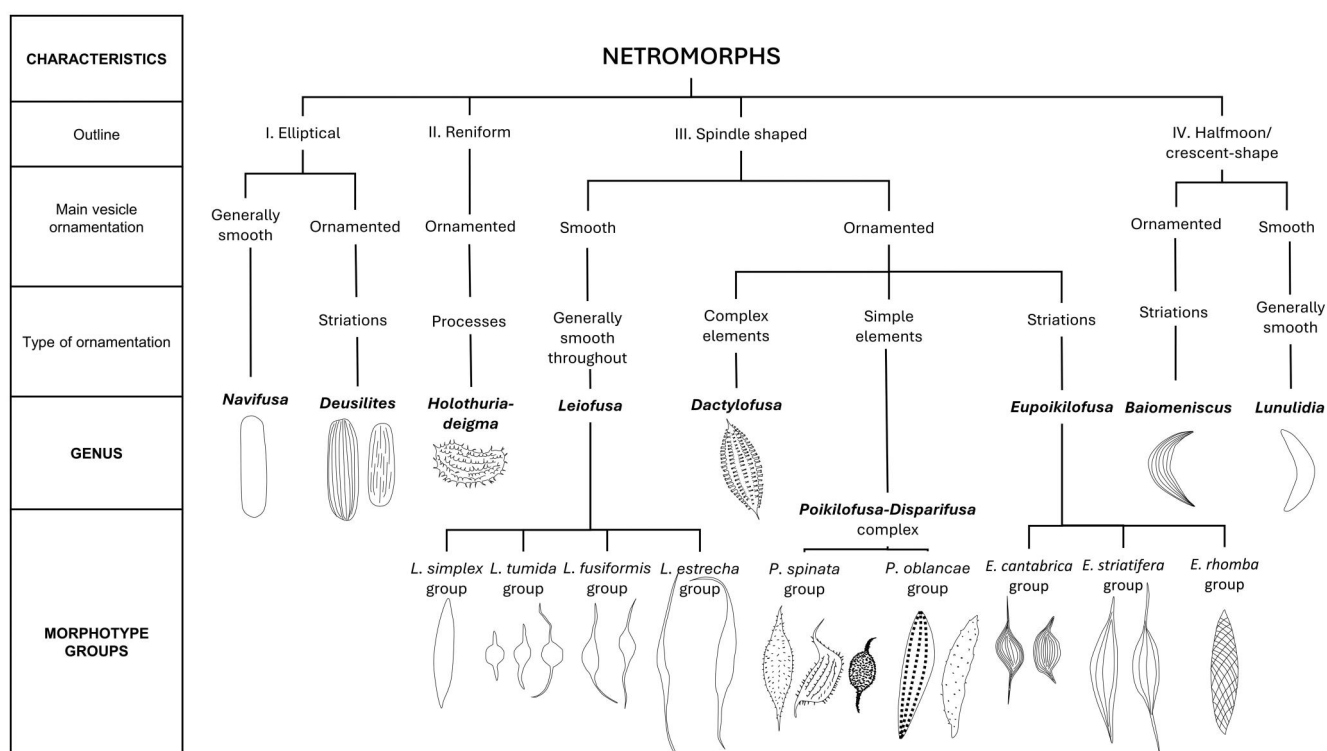


Figure 2. A proposed classification system for netromorph acritarchs. The intrageneric morphotype groups are explained in Section 4 (under the corresponding genera).

ornamentation, and those without to reflect simple ornamentation (e.g. acuminate, filose processes, granules or tubercles). Species with clavate processes are thus assigned to the genus *Dactylofusa*. The genera *Poikilofusa* and *Disparifusa* have similar outlines and ornamentation (both are spindle-shaped and can have processes and granulations); hence, they are combined into a *Poikilofusa-Disparifusa* complex (see Section 3.5 for further explanation). This includes netromorphs with simpler ornamentation such as acuminate or cylindrical spines, echinae or granules. The *Poikilofusa-Disparifusa* complex is subdivided into two informal groups: the *P. spinata* group, which is ornamented with spines/processes; and the *P. oblanceae* group, which has echinae, granulations or tubercles on the vesicle. Striated morphotypes are ascribed to *Eupoikilofusa*, which is composed of three informal groups: the *E. cantabrica* group, which is smaller but with distinct appendages and denser striations; the *E. striatifera* group, which is similar to the *L. estrecha* group, elongated and typically more than 100 µm in total length; and the *E. rhomba* group, with crisscrossing striations.

3.3.4. Category 4 netromorphs

Crescent-shaped forms with a curved longitudinal axis are classified under Category 4. Smooth, unornamented morphotypes are assigned to the genus *Lunulidia* while striated forms (similar to *Eupoikilofusa*) belong to the genus *Baiomeniscus*. Specimens of *Dactylofusa maranhensis* commonly have a curved longitudinal axis (e.g. Le Hérisse et al. 1995, pl. 2, fig. 6; Strother 1996, pl. 3, fig. 8; Le Hérisse 2000,

pl. 7, figs. e–f), although the cause of this variation is not clear.

Pseudolunulidia Brito and Santos 1965 was initially considered to belong to this category; however, similarities in vesicle wall microstructure to *Quisquilites* Wilson and Urban 1963 *emend.* Wilson and Urban 1971 (which has canals in the vesicle walls; Wilson and Urban 1971) suggest it is likely a chlorophyte. Therefore, it was not included in the netromorph classification scheme.

3.4. A classification for related morphotypes

The *Deunffia-Domasia* complex can be readily subdivided into main morphotype groups: the first group has an appendage on only one pole, while members of the second group feature appendages on both poles (Figure 3). The first category is further classified based on the number of 'posterior' appendages: single, two, or more (the term 'posterior' is used classically, although the vesicle does not have a defined anterior and posterior orientation). The genus *Deunffia* has one posterior appendage, which may have no bifurcations, two distal branches, or more, corresponding to three respective informal groups: *D. monospinosa* group, *D. furcata* morphotype and *D. ramusculosa* group. The species *D. bispinosa* has two posterior appendages, while the genus *Polydeunffia* has three or more.

The second category of *Deunffia-Domasia* morphotypes features one appendage on the 'anterior' side, and a single appendage, or multiple appendages, on the other. Single-posterior appendage types include taxa from both *Deunffia* and *Domasia*: *Deunffia monospinosa* var. *tonowadensis* has no distal branches; the *Domasia amphora* group has two distal

branches arising from a short posterior appendage; and the *Deunffia ramusculosa* var. *rochesterensis* group has multiple distal branches. The *Domasia trispinosa* group has two posterior appendages that can be simple or with short bifurcations, and a main vesicle outline ranging from elliptical to triangular or elongated. *Hemideunffia trifurcata* Thusu 1973 is the sole species in its genus, with three appendages arising from one point at its posterior pole. The *Domasia quadrispinosa* group also contains morphotypes with three appendages; however, these are placed farther apart than those of *H. trifurcata*. *Metaleiofusa arcuata* Wall 1965 has two lateral appendages in addition to the polar ones.

3.5. Discussion: taxonomic reassignments

An examination of various fusiform and related morphotypes shows that they can be classified into various informal morphotype groups, which may or may not correspond to their reported genera (see Figures 2 and 3). *Navifusa* has one of the simplest morphologies, yet there are nearly 30 reported species/subspecies described (see Fensome et al. 1990 and the JWIP), many of which are possibly ecophenotypes rather than distinct taxa. Some reported species of *Navifusa* (*N. multistriata* (Brito 1965) Eisenack et al. 1979 and *N. santanoniae* Cramer and Díez 1976) appear to share characteristics with the Early Carboniferous genus *Deusilites*, particularly in their striations. Therefore, these *Navifusa* morphotypes are assigned to *Deusilites*.

Within *Leiofusa*, there is also a wide spectrum of morphotypes (Figure 4): from no appendages (*L. simplex* group) to globular vesicles (*L. tumida* group) with thin, prominent appendages; to an intermediate *L. fusiformis* group where

the main vesicle is more compressed and the appendages transition gradually from the main vesicle; to extremely elongated forms (*L. estrecha* group). For the *L. tumida* and *L. fusiformis* groups the outline of the main vesicle is the same, varying only in size and the length of appendages for different species. In dinoflagellate cysts, the same species can display a spectrum of process lengths depending on environmental factors (e.g. Mertens et al. 2009; see also Section 5.2). It is possible that the reported species in each respective group actually correspond to a single taxon, responding to different environmental conditions.

Our classification for the ‘true leiofusids’ is similar to that of Dorning (1994); however, for *Dactylofusa*, it is not necessary for the ornamentation to be longitudinally arranged, and for *Poikilofusa*, some elements can have longitudinal orientation. For these two genera, we only consider the type of ornamentation, whether simple or complex. Thus, *Dactylofusa estillis* Cramer and Díez 1972 (acuminate spines), *Dactylofusa horrida* Le Hérisse et al. 1995 (filose processes), *Dactylofusa fastidiosa* (Cramer 1964) Fensome et al. 1990 (echinate), and *Leiofusa cucumis* Le Hérisse et al. 1995 (granulate to baculate) are reassigned to *Poikilofusa*. The first three species are placed in the *P. spinata* group, while the last is placed in the *P. oblancana* group.

Poikilofusa and *Disparifusa* are two genera with similar ornamentation, and in their original diagnoses (see Section 4) differ only in outline, with *Disparifusa* displaying asymmetry (one side is concave and the other convex); however, species later assigned to *Disparifusa* (such as the globular *Disparifusa quasibernesgana* Le Hérisse 2002) feature symmetrical vesicle outlines. Furthermore, *Disparifusa* specimens can be compressed at right angles to the asymmetric plane, showing a spindle shape (Miller and Eames 1982, 237) which can be

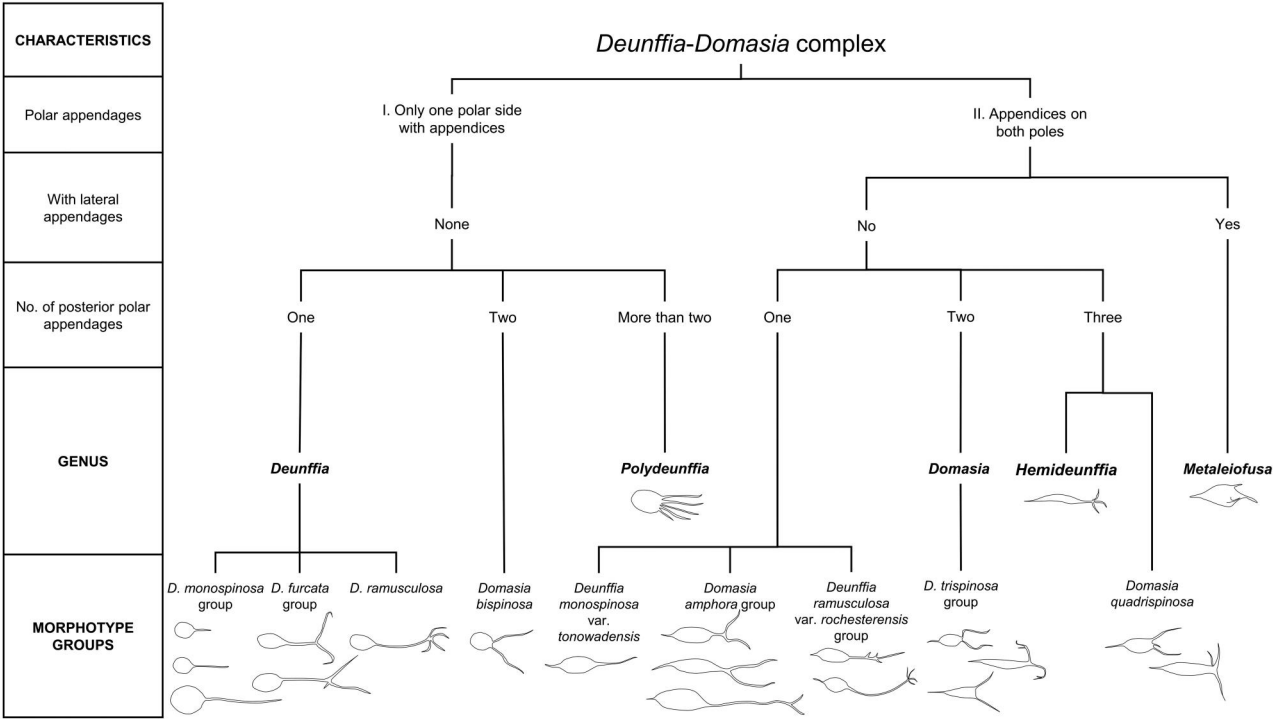


Figure 3. A proposed classification system for the *Deunffia*–*Domasia* complex. The intrageneric morphotype groups are explained in Section 4 (see corresponding genera).

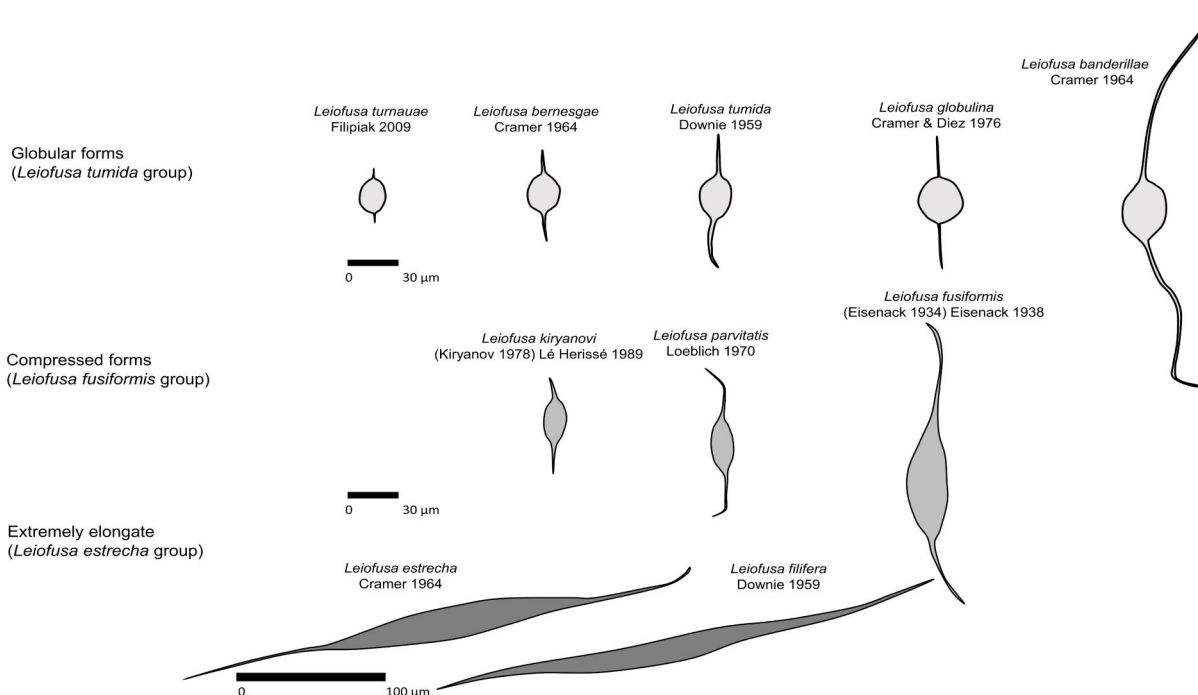


Figure 4. Transitional forms in the intrageneric morphotype groups of *Leiofusa*.

similar to that of *Poikilofusa*. Some specimens of *Poikilofusa estillis* comb. nov. also show a *Disparifusa*-type asymmetry (Eisenack et al. 1976). Thus, the two genera are tentatively classed together into a *Poikilofusa–Disparifusa* complex. Although the generic complex can be broadly divided into two informal morphotype groups based on ornamentation (processes versus granules/tubercles), some species may have a distinct arrangement of sculptural elements, in particular *Poikilofusa oblanca* Cramer and Díez 1968 ex Eisenack et al. 1976, in which they are longitudinally arranged. The differences between the two informal groups of *Eupoikilofusa* are based on size and density of striations: *E. cantabrica* morphotypes are smaller with denser striations, while *E. striatifer* are much larger with more widely spaced striations.

Despite attempts to create discrete categories, transitional forms can be difficult to classify. For example, *Anomaloplaesium johnsium* Lé Hérisse et al. 1995 overlaps with *Eupoikilofusa* in having a striated vesicle and *Anomaloplaesium* in having ornamented instead of smooth appendages. *Saharifusa rochesterensis* Pöthe de Baldi 1997 is also striated like *Eupoikilofusa* but has small digitate ornamentation on the vesicle, similar to *Poikilofusa*. Since striations appear to be the most dominant characteristic, we reassign both species to *Eupoikilofusa*, in the *E. striatifer* group (*S. rochesterensis* was previously classified as *E. rochesterensis* Cramer 1970). *Leiofusa punctalirella* Loeblich 1970 is striated and should also be classified under *Eupoikilofusa*. *Leiofusa ampulliformis* Martin 1966, which is densely covered in papillae, is transferred to *Poikilofusa*. Reassigned taxa are described below (Section 4).

In contrast to the netromorphs, a generic morphotype classification of taxa from the *Deunffia–Domasia* complex is less straightforward. Some reported subspecies of *Deunffia* (*D. monospinosa* var. *tonowadensis* Thusu 1973 and *D. ramusculosa* var. *rochesterensis* Thusu 1973) resemble *Domasia* in

having an apical appendage. A further review and subsequent redefinition of both genera may be necessary, one that considers the presence of apical appendages in some *Deunffia* morphotypes normally attributed to *Domasia*.

A major goal of the proposed classification scheme is to facilitate sorting into different entities, which have no clear boundaries in most instances (as discussed above). Transient forms may exist between one morpho-genus and another, as occurs also in the *Veryhachium/Micrhystridium* complex (Lei et al. 2013). Figure 4 graphically summarizes our classification scheme, while Section 4 describes the genera and proposed new combinations. Morphotype groups and included species are also listed in Section 4 below.

4. Systematic paleontology

In this section we present the various genera and species included in the netromorph subgroup and in the *Deunffia–Domasia* complex. The genera are arranged in the same order as in Figures 2 and 3, from left to right. The genera of the proposed *Poikilofusa–Disparifusa* complex are described separately.

Following Art. 60 of the International International Code of Nomenclature for algae, fungi and plants (referred to hereafter as the Shenzhen Code) (Turland et al. 2018), we correct some errors in the generation of specific epithets.

Informal Group **Acritarcha** Evitt 1963

Informal Subgroup **Netromorphitae** Downie, Evitt and Sarjeant 1963 emend. nov.

Original diagnosis (Downie et al. 1963, p. 9). 'Acritarchs having an elongate to fusiform test, without an inner body. Surface generally smooth, rarely granular. One or more

spines, closed distally, may be present at one or both poles. Openings not observed'.

Emended diagnosis. Homopolar acritarchs with elongated, fusiform or spindle-shaped vesicles, with similar morphologies at both ends (poles) of the vesicle. Vesicle outline can be straight, half-moon or crescent shaped. Each pole typically bears a single, simple appendage, open at its base and freely communicating with the vesicle, tapering to a distal end. Poles may also be rounded (lacking an appendage). The surface wall of the main vesicle is either smooth or ornamented with striae, rugulae, processes, smaller spines or other sculptural elements arranged randomly or longitudinally along the main axis. The appendages can be smooth or sculptured.

Remarks. Downie et al. (1963) originally defined netromorphs as possessing elongate to fusiform tests without an inner body and a generally smooth surface. One or more polar appendages, closed distally, may be present at either pole; however, openings were not observed. Strother (1996) later noted that specimens with openings (e.g. *Leiofusa tumida* Downie 1959 with trochospiral sutures) have since been found. Furthermore, numerous ornamented morphotypes have since been reported. Three generic complexes were included in the subgroup: the fusiforms with *Leiofusa*, *Dactylofusa*, *Poikilofusa* and *Baiomeniscus*; the *Deunffia*–*Domasia* complex; and *Leiovalia*.

We restrict the subgroup to homopolar forms, which include the genera *Baiomeniscus*, *Dactylofusa*, *Deusilites*, *Disparifusa*, *Eupoikilofusa*, *Holothuriadeigma*, *Leiofusa*, *Navifusa*, *Lunulidia*, *Poikilofusa* and *Pseudolunulidia* among others. Thus, we equate the definition of netromorphs with Leofusidae Combaz et al. 1967. The *Deunffia*–*Domasia* complex, with heteropolar symmetry, is here considered to belong to another group, the acritarch subgroup of the diacromorphs.

Genus *Navifusa* Combaz et al. 1967 ex Eisenack 1976

Type species. *Navifusa navis* (Eisenack 1938, 229, pl. 16, fig. 8) Eisenack 1976, 192

Original diagnosis (in French, from Combaz et al. 1967, p. 295). 'Coque en forme d'ellipse plus ou moins allongée, ou de bâtonnet à extrémités arrondies, sans appendices; membrane simple, lisse ou ornementée'.

Original diagnosis (translation, from Eisenack et al. 1979, p. 53). 'Shell in the form of a more or less elongated ellipse or of a rod with rounded extremities [without appendages]; vesicle wall simple, smooth or ornamented'.

Remarks. As mentioned above, It can be difficult to distinguish between *Leiovalia* (which has an elliptical outline) and *Navifusa*; numerous transitional forms can exist between the two. Both could be part of a single taxon with a spectrum of morphotypes, along with *Lunulidia*.

Silurian and Devonian species.

Navifusa bacilla (Deunff 1955) Playford 1977

Navifusa brasiliensis Brito and Santos 1965

Navifusa brasiliensis lingula Brito and Santos 1965

Navifusa cylindrica (Brito and Santos 1965) Eisenack et al. 1979

Navifusa drosera Wicander 1974

Navifusa eisenacki Brito and Santos 1965 (Eisenack et al. 1979)

Navifusa exilis Playford in Playford and Dring 1981

Navifusa minuta (Deunff 1955) Eisenack et al. 1979

Navifusa scrutilla Cramer and Díez de Cramer 1972

Navifusa sp. *sensu* Grahn et al. 2011

Navifusa sp. *sensu* Dufka and Pačtová 1988

Navifusa spp. *sensu* García Muro et al. 2022

Navifusa/Deusilites sp. *sensu* di Pasquo et al. 2017

Genus *Deusilites* Hemer and Nygreen 1967

Type species. *Deusilites tentus* Hemer and Nygreen 1967, p. 188, 190; pl. 2, figs. 17–18; pl. 3, fig. 19

Original diagnosis (Hemer and Nygreen 1967, p. 188).

'Test elongate, fusiform or terete, circular in cross-section, grooved. Wall 2 microns thick. Pigmentosae sometimes present at one end. Grooves multiple longitudinal or oblique, some wedge-shaped with point at or near one end and with low angle of separation. Surface matte to minutely granulate'.

Emended diagnosis. Elongated vesicle having rounded ends. The thin, organic wall (approximately 2 µm thick) is marked by numerous longitudinal grooves, and the wall surface can be smooth or with minute granulations.

Remarks. The characteristics of this genus are similar to some species of *Navifusa*, although the latter does not bear striations. It also differs from *Eupoikilofusa* in having an elongated outline with rounded ends.

Silurian and Devonian species.

Navifusa multistriata Brito 1965

Navifusa santanoniae Brito 1965

Genus *Holothuriadeigma* Loeblich 1970

Type species. *Holothuriadeigma heterakainum* Loeblich 1970, p. 722–723, figs. 16A–C

Original diagnosis (Loeblich 1970, p. 722). 'Central body variable in outline, reniform in shape, with blunt terminations; wall thin, granulate, ornamented by numerous spinose and granulate hollow processes freely communicating with the central body, processes of variable character, simple or terminally bifurcate, commonly arranged in rows, processes smaller and commonly simple on inner curve of central body; excystment probably by rupture of the body along the inner curve'.

Remarks. The genus differs from *Disparifusa* in its absence of appendages. *Pseudolunulidia* is also covered in ornamentation but has a strongly curved longitudinal axis (half-moon to crescent-shaped).

Silurian and Devonian species.

Dactylofusa neahgae Cramer 1970 ex Eisenack et al. 1976

Holothuriadeigma heterakainum Loeblich 1970

Genus *Leiofusa* Eisenack 1938 emend. Combaz et al. 1967 emend. Cramer 1970 emend. nov.

Type species. *Leiofusa fusiformis* Eisenack 1934 (p. 65–66, pl. 4, fig. 9) ex Eisenack 1938 (p. 28).

Original diagnosis (in German, from Eisenack 1938, p. 28). 'Ovale bis lang spindelförmige Zysten mit glatter Wand'.

Original diagnosis (translation from Eisenack et al. 1976, p. 863). 'Oval to elongate spindle-shaped cysts with smooth wall'.

Emended diagnosis. Spindle-shaped outline with pointed polar ends, with a thin vesicle wall. The central body can be spherical with thin appendages, or more compressed and elongate, with the appendages less prominent or even absent. The vesicle wall is smooth. A circular, trochospiral, longitudinal or an equatorial split can be present.

Remarks. Combaz et al. (1967) included it in their emendation forms with ribbed surfaces, now assigned to *Eupoikilofusa*. Cramer (1970) elaborated on the original diagnosis by adding that the vesicle wall can be microgranulate ($< 0.50 \mu\text{m}$ high) but not arranged longitudinally; and that the vesicle wall is unilayered and undifferentiated. Cramer (1970) also recognized the presence of pylomes.

The genus is distinguished from *Anomaloplaismium*, *Dactylofusa*, *Disparifusa*, *Eupoikilofusa* and *Poikilofusa* by its smooth vesicle and appendages. It is also differentiated from *Leiovalia* and *Navifusa* by its fusiform outline, which can have appendages.

Informal morphotype groups.

Remarks. The various species in *Leiofusa* can be assigned to four morphotype groups based on their outline, and presence or absence of appendages.

Leiofusa simplex group

Description. The *L. simplex* group consist of *Leiofusa* morphotypes with no appendages. The outline consists of a simple spindle shape.

Silurian and Devonian species.

Leiofusa aff. *fusiformis* Eisenack 1938 in Fang Xiaosi 1989

Leiofusa fusiformis Eisenack 1938 in Cramer 1964

Leiofusa sp. Fang Xiaosi 1989

Leiofusa tumida group

Description. The *L. tumida* group is characterized by globular main vesicles, with (generally thin) distinct appendages. The appendages can have variable lengths.

Remarks. The specific epithet of *Leiofusa berneseae* Cramer 1964 is hereby corrected to *berneseana*, according to Recommendation 60D of the Shenzhen Code (Turland et al. 2018). The name *berneseae* appears to be derived from the Bernesga River of the Cantabrian mountains in Spain, where the type locality of the species is found (Eisenack et al. 1976).

Silurian and Devonian species.

Leiofusa algerensis Cramer 1970 ex Eisenack et al. 1976

Leiofusa banderilla Cramer 1964

Leiofusa berneseana Cramer 1964

Leiofusa globulina Cramer and Díez 1976a

Leiofusa granulacutis Loeblich 1970

Leiofusa tumida Downie 1959

Leiofusa turnauae Filipiak 2009

Leiofusa fusiformis group

Description. The *L. fusiformis* group has an outline similar to the *L. simplex* group, but it has appendages which can also vary in length.

Silurian and Devonian species.

Leiofusa fusiformis Eisenack 1938

Leiofusa kiryanovii Le Hérisse 1989

Leiofusa parvitatit Loeblich 1970

Leiofusa pyrena Wicander and Wood 1981

Leiofusa sp. *sensu* Venckutė-Aleksienė et al. 2016

Leiofusa spp. *sensu* Rubinstein et al. 2017

Leiofusa estrecha group

Description. The *L. estrecha* group consists of species with an extremely elongated, spindle-shaped outline typically hundreds of microns in total length. They can resemble elongated versions of *L. simplex* in having no appendages, or *L. fusiformis* with subtler transitions from vesicle to appendage.

Silurian and Devonian species.

Leiofusa estrecha Cramer 1964

Leiofusa filifera Downie 1959

Leiofusa filifera Downie 1959 in Downie 1963

Poikilofusa–Disparifusa complex

Description. This informal grouping of these two genera includes spindle-shaped netromorphs with ornamentation described as simple, such as acuminate processes or granulations – ornamentation having no secondary outgrowths, distal branches or bulbous protrusions.

Genus *Poikilofusa* Staplin et al. 1965

Type species. *Poikilofusa spinata* Staplin et al. 1965, p. 186, pl. 18, figs. 25–26.

Original diagnosis (Staplin et al. 1965, p. 185). 'Vesicles fusiform, with small spines or muri; no openings (pylome) observed; wall firm but relatively thin, similar to that in micrhystrids'.

Remarks. We concur with Loeblich and Tappan (1978) in considering morphotypes with simple, longitudinally arranged microechinate elements to belong to *Poikilofusa* rather than *Eupoikilofusa*, assigning such forms to the *P. oblancana* group.

The genus differs from *Dactylofusa* and *Eupoikilofusa* by having simple ornamentation and a lack of striations, respectively. It is similar to *Disparifusa* in having simple sculptural elements and a fusiform outline (though in general *Disparifusa* has a more asymmetrical shape; see entry for *Disparifusa* below), hence we group them into a *Poikilofusa–Disparifusa* complex.

Poikilofusa ampulliformis (Martin 1966) comb. nov.

Basionym. *Leiofusa ampulliformis* Martin 1966a, p. 385, pl. 1, pl 1, fig. 21.

Holotype. Martin (1966, p. 385, pl. 1, fig. 21).

Type locality. Sondage de la Brasserie Lust, Courtrai, Belgium.

Type horizon. Sondage de la Brasserie Lust 158–172.50 m depth.

Stratigraphic range. Silurian.

Original diagnosis (Martin 1966, p. 385). 'The central body is stocky: $30 \mu\text{m}$ long and about $20 \mu\text{m}$ wide. The appendages are short, one third to one quarter the length of the entire body. The entire surface is bristling with papillae'.

Remarks. The spindle shape and the presence of papillae (simple ornamentation) are characteristic of *Poikilofusa*, hence the transfer. Furthermore, *Leiofusa* has smooth vesicle walls.

Poikilofusa cucumis (Le Hérisse et al. 1995) comb. nov.

Basionym. *Leiofusa cucumis* Le Hérisse et al. 1995, p. 67, pl. 3, fig. 1.

Holotype. Le Hérisse et al. (1995, p. 67, pl. 3, fig. 1).

Type locality. NYYM-2 well and subsurface material from different boreholes of the Rhuddanian of central Saudi Arabia.

Type horizon. Qusaiba member of the Qalibah Formation.

Stratigraphic age. Rhuddanian.

Original diagnosis (Le Hérisse et al. 1995, p. 67). ‘Based on 15 specimens. Vesicle fusiform, narrow and hollow, with very short terminal processes. There is no clear division between central body and processes. The wall is thin, less than 1 µm in thickness, and densely ornamented by a mixture of small grana and baculate ornaments, less than 0.5 µm in diameter and height, without particular arrangement. The ornamentation extends all over the vesicle and onto the processes. No excystment opening observed. Maximum length ranges from 115 to 170 µm and width from 15 to 20 µm’.

Remarks. *Leiofusa* has no ornamentation. This species notably has simple, dense ornamentation of short granules and baculae throughout its outer wall, which is more reminiscent of some *Poikilofusa* morphotypes (specifically the *Poikilofusa oblancana* group; see Section 3.3.2). Therefore, we reassign this species to *Poikilofusa* because of its ornamentation type.

Poikilofusa estillis (Cramer and Díez de Cramer 1972) comb. nov.

Basionym. 1972 *Dactylofusa estillis* Cramer and Díez, p. 160, pl. 34, fig. 47.

Holotype. Cramer and Díez, 1972, p. 160, pl. 34, fig. 47.

Type locality. Kentucky (locality 14a:6400), USA.

Type horizon. Estill Shale Member of the Crab Orchard Formation.

Stratigraphic age. Upper Llandovery (Telychian).

Original diagnosis (Cramer and Díez de Cramer 1972, p. 160). ‘Vesicle hollow, elongately fusiform in outline not appreciably compressed dorsoventrally. At each pole of the vesicle there is a hollow, drawn-out needle-like process that is differentiated from the body of the vesicle by the absence of sculptural elements on it. The length of the process is about ten percent of the body length proper. The vesicle wall is about one micron thick and wrinkles easily, thus forming folds that are oriented roughly in a longitudinal direction. The surface of the body is ornamented with small, solid, spinose protrusions. These sculptural elements are arranged in rows that coincide with, or [are] the cause of, the longitudinal folds mentioned before. The elements are flat, their widest direction being parallel with the longitudinal axis of the vesicle. The elements show no appreciable differentiation in size according to their location on the vesicle. The sculptural elements are approximately one to two microns wide and three to five microns high. Total length of vesicle up to 250 µm (commonly 100 µm)’.

Remarks. Ornamentation is simple rather than complex, acuminate or needle-like, without distal branches, knobs, or other features. Hence, this species is placed in *Poikilofusa* rather than *Dactylofusa*. Previously synonymized by Martin (1968) with *P. spinata*, but (Cramer and Díez de Cramer 1972) comb. nov. has longitudinal folds.

Poikilofusa fastidiona (Cramer 1964) comb. nov.

Synonyms.

1964 *Leiofusa fastidiona* Cramer, p. 324, pl. 6, fig. 6; pl. 19, fig. 5; text-fig. 33 no. 9.

1967 *Dactylofusa fastidiona* (Cramer 1964) Cramer et al., p. 297 (invalid combination, full basionym not given).

Basionym. 1990 *Dactylofusa fastidiona* (Cramer 1964) Fensome et al. 1990.

Holotype. Cramer 1964, 324, pl. 6 fig. 6.

Type locality. Geras de Gordón, León, northwest Spain.

Type horizon. La Vid Shale Member.

Stratigraphic range. Middle Siegenian (Pragian) to Emsian.

Original diagnosis (Cramer 1964, p. 324). ‘Body dorsoventrally compressed, hollow, very elongated fusiform. The wall is psilate at 1200× magnification, except for a great number of small echinae (smaller than 1 µm), that are irregularly distributed over the body. The echinae occur in a relatively greater number at the poles. Length is 70 µm or more’.

Remarks. The presence of short, simple echinae suggests the species belongs to *Poikilofusa* rather than *Dactylofusa*, as the latter genus is characterized by complex ornamentation (e.g. processes having distal branches).

Poikilofusa horrida (Le Hérisse et al. 1995) comb. nov.

Basionym. 1995 *Dactylofusa horrida* Le Hérisse et al., p. 65, pl. 2, fig. 7.

Synonym.

2000 *Disparifusa horrida* (Le Hérisse et al. 1995) Le Hérisse, 64 (invalid combination, no basionym given).

Holotype. Le Hérisse et al. 1995, pl. II, fig. 7, p. 66.

Type locality. NYYM-2 well (between 11,060 and 11,022.6 ft or 3371 and 3359.5m), Saudi Arabia.

Type horizon. Qusaiba Member of the Qalibah Formation.

Stratigraphic range. Rhuddanian (equivalent to the graptolite *acinaces* zone).

Original diagnosis (Le Hérisse et al. 1995, 65). ‘Vesicle fusiform in outline, elongated, continuing in one short, pointed process at each pole. The vesicle wall is thin, less than 1 µm in thickness, and ornamented with simple spines which are filiform. The ornamentation dies out toward the poles and the processes are smooth. No excystment opening observed. Vesicle 60 to 90 µm in length, process length 17 to 22 µm’.

Remarks. The ornamentation consists of simple, filose elements irregularly distributed on the surface of the vesicle. Although the arrangement of ornamentation is similar to *P. spinata*, this species has acuminate processes, rather than filose ones. The type of ornamentation suggests an assignment to *Poikilofusa* rather than *Dactylofusa*.

Genus ***Disparifusa*** Loeblich 1970

Type species. *Disparifusa hystricosa* Loeblich 1970, p. 716–717, pl. 10, figs. A–B; pl. 11, figs. B–C.

Original diagnosis (Loeblich 1970, p. 716). 'Asymmetrically fusiform central body, inflated on one side in a broad curve, straight or concave on the other side, each end produced into a sharp to bluntly pointed polar spine of variable length, wall thin, 0.5 μ or less in thickness, ornamented by numerous short conical spines having no apparent regular arrangement; excystment probably by a longitudinal splitting of the wall on the straight or concave side'.

Remarks. As mentioned above (for *Poikilofusa*), *Disparifusa* is grouped into a *Poikilofusa*–*Disparifusa* complex because of similarities in their shape (both being fusiform, with *Disparifusa* commonly having distinct appendages) and ornamentation types. There is a slight difference in their original diagnoses with *Disparifusa* having a more asymmetrical fusiform shape, but some specimens of *Poikilofusa estillis* (Martin 1968) comb. nov. exhibit the same asymmetry stated for *Disparifusa*. It is possible that the asymmetrical fusiform shape is a minor natural variation on the outline, and future morphometric studies can shed light on whether some *Disparifusa* species represent ecophenotypes of *Poikilofusa*.

Informal morphotype groups of the *Poikilofusa*–*Disparifusa* complex.

Remarks. Species under the two respective genera fall under two types of ornamentation. One morphotype group is characterized by the presence of processes (*P. spinata* group), while the other has granulations and tubercles (*P. oblancana* group).

Poikilofusa spinata group

Description. This group includes species ornamented with processes, which can be filiform (cylindrical) or acuminate. The arrangement can be random, or in longitudinal rows.

Remarks. The specific epithet of *Disparifusa quasibernesgae* Le Hérisse 2002 is derived from similarities in the form and opening to *Leiofusa berneseae* Cramer 1964. However, the epithet *berneseae* appears to be derived from the Bernesga River in the Cantabric mountains of Spain, where the type locality of *L. berneseae* is situated (Eisenack et al. 1976). Thus, we correct the epithet to *quasibernesgana*, based on Recommendation 60D for geographic names.

Silurian and Devonian species.

Disparifusa quasibernesgana Le Hérisse 2002

Poikilofusa estillis (Cramer and Díez de Cramer 1972) comb. nov.

Poikilofusa horrida (Le Hérisse et al. 1995) comb. nov.

Poikilofusa spinata Staplin et al. 1965

Poikilofusa oblancana group

Description. The *P. oblancana* group is made up of species with ornamentation (or sculptural elements) consisting of echinae, granules or tubercles. They can have random or regular arrangement in longitudinal rows.

Remarks. We correct the specific epithet from *oblancae* to *oblancana* following Recommendation 60.D of the ICN for algae, fungi and plants (Turland et al. 2018), as the name was derived from the type locality of Oblanca de Luna, Spain (Eisenack et al. 1976).

Silurian and Devonian species.

Disparifusa psakadoria Loeblich and Tappan 1978

Poikilofusa ampulliformis (Martin 1966) comb. nov.

Poikilofusa cucumis (Le Hérisse et al. 1995) comb. nov.

Poikilofusa fastidiosa (Cramer 1964) comb. nov.

Poikilofusa granulata Pöthe de Baldi 1997

Poikilofusa oblancana Cramer and Díez 1968 ex Eisenack et al. 1976

Genus ***Dactylofusa*** Brito and Santos 1965 emend. Cramer (1970) emend. nov.

Type species. *Dactylofusa maranhensis* Brito and Santos 1965, p. 12–13, 20; pl. 1, fig. 7; pl. 2, fig. 5.

Original diagnosis (Brito and Santos 1965, p. 12, 20). 'Navicular shaped organisms covered with claviform processes which are regularly distributed in longitudinal rows. At the end of the clavae are five or more digitiform appendages in regular ornament'.

Emended diagnosis. Outline is generally fusiform, with the vesicle wall ornamented by processes that can be capitate, furcate or clavate, in contrast to simple acuminate or cylindrical spines, granules and tubercles. The processes can be variable in length, randomly distributed or arranged in rows parallel to the longitudinal axis. Prominent appendages may or may not be present. The longitudinal axis is typically straight but may be curved in some species. A straight, longitudinal split may be present at the equatorial region.

Remarks. Cramer (1970) emended the original definition by including the presence of appendages, the length of which can vary within a species. Cramer also introduced an arbitrary limit of 1 μ m in height for the ornamentation, which is not retained in our emendation.

The genus is differentiated from the *Poikilofusa*–*Disparifusa* complex and *Eupoikilofusa* by the type of its ornamentation (see emended diagnosis above). *Poikilofusa*–*Disparifusa* has simple processes, tubercles or granules, while *Eupoikilofusa* is striated. *Holothuriadeigma* also features processes, but the ornamentation remains simple and has a characteristic reniform outline.

Silurian and Devonian species.

Dactylofusa aff. *neahgae* Cramer 1970 ex Eisenack et al. 1976 sensu Le Hérisse et al. 2001

Dactylofusa hispidusa Le Hérisse 2002

Dactylofusa maranhensis Brito and Santos 1965 emend. Combaz et al. 1967

Genus ***Eupoikilofusa*** Cramer 1970

Type species.

1964 *Leiofusa striatifera* Cramer, p. 35–36, pl. 2, fig. 9, 13.

1968 *Poikilofusa striatifera* (Cramer 1964) Martin, p. 118–120, pl. 4, figs. 172–173, pl. 8, fig. 393.

1970 *Eupoikilofusa striatifera* (Cramer 1964) Cramer, p. 35–36, pl. 2, figs. 9, 13.

Original diagnosis (Cramer 1970, p. 83). 'Vesicles fusiform, elongated and with pointed poles. At each pole there may be a simple, equivalent process. Within the same species the length of the polar processes may vary greatly. The vesicle wall is unilayered, and the sculpture distribution symmetry is holomorphic with elements arranged in a pattern parallel to the

longitudinal axis, and with a decreasing size, number and complexity of elements towards the poles. The ectoderm surface is ornamented with elements of the striate kind: rugulae, striae, fossulae, or microechinate elements in longitudinally oriented rows. The vesicle may open by splitting along the axis at approximately an equatorial position. The vesicle axis may be straight or curved, even in the same species'.

Emended diagnosis. Fusiform outline, with or without prominent appendages; the surface of the thin, unilayered, organic vesicle wall is marked by continuous longitudinal or helicoidal striations. These striations are produced by folds, ridges, muri, or thickening of the vesicle wall. Granulations or processes may occasionally be present as minor ornamentation on the main vesicle or appendages.

Remarks. We restrict the genus to fusiform morphotypes with striations. Forms with longitudinally arranged microechinate elements are instead assigned to *Poikilofusa*, specifically in the *P. oblancana* group (see genus *Poikilofusa*). Curved *Eupoikilofusa* morphotypes are essentially identical to *Baiomeniscus*; further studies of specimens from both genera are needed to determine whether they represent ecophenotypes or different taxa. Similar striated morphotypes, albeit with an elongate outline, rounded polar ends and no appendages, are classified as *Deusilites*.

The presence of striations, which dominate the ornamentation of the vesicle, distinguishes this genus from *Dactylofusa* and *Poikilofusa*. Furthermore, *Dactylofusa* has complex ornamentation while *Poikilofusa* has simple ornamentation.

Eupoikilofusa johnii (Le Hérisse et al. 1995) comb. nov.

Basionym. *Anomaloplaesium johnsium* Le Hérisse et al. 1995, p. 63, pl. 1, figs. 1–2.

Holotype. Le Hérisse et al. 1995, p. 63, pl. 1, fig. 1.

Type locality. KAHF-1 well (4921.2 ft depth), northwest Saudi Arabia.

Type horizon. Qusaibah Member of the Qalibah Formation.

Stratigraphic age. Early Wenlock.

Original diagnosis (Le Hérisse et al. 1995, p. 63). 'Based on three specimens; vesicle fusiform in outline, elongated with one pointed process at each pole; vesicle wall thin and finely ornamented with longitudinal striae; polar processes communicating freely with vesicle cavity and sculptured with delicate spines with varied length; no excystment structure observed. Vesicle length 112–134 µm long; spines 5–9 µm long'.

Remarks. We correct the specific epithet from *johnsium* to *johnii*, because the species was dedicated to Dr. John Richardson (Le Hérisse 1995), following the rules for personal names stated in Sec. 60.8(b) of the Shenzhen Code (Turland et al. 2018).

Le Hérisse et al. (1995) assigned this species to *Anomaloplaesium* based on the presence of sculptural elements on the poles. However, the vesicle is also striated which is typical for *Eupoikilofusa*. This species appears to be a transitional form between the two genera. Nevertheless, the presence of the striations is the more dominant feature; thus, we reassign the species to *Eupoikilofusa*.

Eupoikilofusa punctalirella (Loeblich 1970) comb. nov.

Basionym. *Leiofusa punctalirella* Loeblich 1970, p. 725, fig. 19A–D.

Holotype. Loeblich 1970, p. 725, fig. 19A.

Type locality. Access road to Rochester Gas and Electric Corporation plant on the right bank of Genesee River.

Type horizon. Maplewood Shale.

Stratigraphic age. Middle Silurian.

Original diagnosis (Loeblich 1970, 725). 'Rigid fusiform central body merging imperceptibly into hollow polar spines; wall thin, less than 1 µm in thickness, surface ornamented by broad low ridges separated by narrower troughs, 7–8 visible on a side, ridges ornamented with numerous scattered pits with no apparent alignment, ridging dies out abruptly at the polar ends of the central body, processes smooth; no pylome observed. Maximum length of complete specimens ranges from 191 to 235 µm: maximum diameter of central body ranges from 29 to 32 µm'.

Remarks. The spindle-shaped outline and presence of striations observed in these species are diagnostic features of *Eupoikilofusa*; hence, *L. punctalirella* is assigned to this genus.

Informal morphotype groups.

Remarks. Species of *Eupoikilofusa* can be classified under two morphotype groups based on shape, and orientation of striations. Members of the *Eupoikilofusa cantabrica* group are smaller, and has distinct appendages compared to those from the *E. striatifera* group. The *E. rhomba* group is unique among other groups in having diamond-shaped instead of longitudinally aligned striations.

Eupoikilofusa cantabrica group

Description. Members of the *E. cantabrica* group are distinguished by their spindle-shaped outline, with prominent appendages. They are also smaller in size compared to the *E. striatifera* group.

Silurian and Devonian species.

Eupoikilofusa cantabrica (Cramer 1964) Cramer 1970

Eupoikilofusa striatospinata Le Hérisse et al. 2001

Eupoikilofusa tenuistriata (Pöthe de Baldi 1975) Pöthe de Baldi 1981

Eupoikilofusa tenuistriata var. *aperturata* Pöthe de Baldi 1997

Eupoikilofusa striatifera group

Description. The *E. striatifera* group is distinguished by its spindle shaped outline, with prominent appendages.

Silurian and Devonian species.

Eupoikilofusa argentina (Pöthe de Baldi 1971) Pöthe de Baldi 1981

Eupoikilofusa filifera (Downie 1959) Dornig 1981a

Eupoikilofusa johnii (Le Hérisse et al. 1995) comb. nov.

Eupoikilofusa punctalirella (Loeblich 1970a) comb. nov.

Eupoikilofusa rhikne (Loeblich 1970a) Al-Ruwaili 2000

Eupoikilofusa rochesterensis Cramer 1970 ex Eisenack et al. 1976

Eupoikilofusa striata (Staplin et al. 1965) Eisenack et al. 1976

Eupoikilofusa striatifera (Cramer 1964) Martin 1968

Eupoikilofusa rhomba group

Description. This group consists of one species with helical striations around the longitudinal axis, instead of parallel to it. The outline is spindle-shaped with no appendages.

Remarks. This group can be distinguished from *Moyeria* Thusu 1973, which also has helical striations but has a variable, rectangular-like shape.

Silurian and Devonian species.

Eupoikilofusa rhomba Miller and Eames 1982

Genus *Baiomeniscus* Loeblich 1970

Type species. *Baiomeniscus granulatus* Loeblich 1970, p. 712–713, fig. 5A–E.

Original diagnosis (Loeblich 1970, p. 711–712). ‘Small cysts, crescent-shaped to nearly semi-circular in outline with extremities rounded to bluntly pointed; wall thin, surface ornamented by striae and commonly with grana, either scattered or aligned in rows; no pylome observed’.

Remarks. This genus is essentially identical to the curved morphotypes of *Eupoikilofusa*. Further analysis of specimens attributed to either genus is necessary to determine whether these morphotypes are indeed variants of each other.

Silurian and Devonian species.

Baiomeniscus camurus Loeblich 1970a

Eupoikilofusa striatifer (Cramer 1964) Cramer 1970 sensu Martin 1973

Eupoikilofusa striatifer (Cramer 1964) Cramer 1970 sensu Thusu 1973

Genus *Lunulidia* Eisenack 1958

Type species. *Lunulidia lunula* (Eisenack 1951) Eisenack 1958, p. 193–194, pl. 4, fig. 1.

Original diagnosis (from Eisenack 1958, p. 391). ‘Hüllen von der Gestalt einer Mondsichel, aus der für silurische Hystrichosphären charakteristischen Substanz bestechend’.

Original diagnosis (translation from Eisenack et al. 1976, p. 863). ‘Crescent-shaped vesicles, consisting of the material that is characteristic of Silurian hystrichospheres’.

Remarks. The genus strongly resembles *Navifusa bacilla* but with a curved longitudinal axis. It is possible that species of *Lunulidia* are actually subspecies, variants or ecophenotypes of *N. bacilla* rather than a separate genus, and this warrants a further morphological study of specimens of this morphotype.

Silurian and Devonian species.

Lunulidia micropunctata Pöthe de Baldi 1979

Pseudolunulidia laevigata Brito and Quadros 1985b

Informal Subgroup **Diacromorphitae** Downie et al. 1963

Original diagnosis (Downie et al. 1963, p. 10). ‘Acritarchs having a spherical to ellipsoidal test, without an inner body. Equatorial zone smooth or slightly wrinkled, polar areas ornamented with punctae, tubercles or spines. No openings observed’.

Remarks. We accept the definition of the subgroup as given in the diagnosis of Downie et al. (1963) and subsequent emendations (see below), and consider the two genera *Deunffia* and *Domasia* to be diacromorphs.

Genus *Deunffia* Downie 1960 emend. Thusu 1973

Type species. *Deunffia monospinosa* Downie 1960 (p. 198, pl. 1, fig. 8)

Original diagnosis (Downie 1960, 198). ‘Shell hollow, elongate ellipsoidal, more or less smooth, less than 100 μ in length. Body composed of thin, pale yellow to brown, organic membrane. Ornament consisting of a single hollow spine situated at one end. Spine terminates in a point or branches in various ways’.

Remarks. Thusu (1973) emended the genus to include forms with a short spine (1–2 μ m) at one polar end and removed the 100 μ m length limit.

The genus is similar to some morphotypes of *Dicrodiacrodium* with a single apical process; however, *Deunffia* does not possess parallel ribs on the other pole. *Hemideunffia* has a more elongated outline, and *Polydeunffia* is also ellipsoidal in shape. The latter two genera differ from *Deunffia* in having more than one long process on one pole.

Informal morphotype groups.

Remarks. The morphotypes in this species can be broadly divided into two, those with only one appendage, and those with two (the second appendage is significantly smaller than the other on the opposite pole). The former includes the *Deunffia monospinosa*, *D. furcata* and *D. ramusculosa* groups while the second includes varieties of *D. monospinosa* and *D. ramusculosa*; these are the *D. monospinosa* var. *tonowadensis* and *D. ramusculosa* var. *rochesterensis* groups.

Deunffia monospinosa group

Description. The *Deunffia monospinosa* group consists of *Deunffia* species with a single appendage at one end having no distal branches. This appendage can have varying lengths.

Remarks. The various species listed in this group have essentially the same elliptical main vesicle shape and a single appendage. The size of the vesicle and the length of the appendage varies in size between the reported species.

Silurian and Devonian species.

Deunffia brevispinosa Downie 1960

Deunffia monocantha (Deunff 1951) Downie 1960

Deunffia monospinosa Downie 1960

Deunffia monospinosa var. *robusta* Le Hérisse 1989

Deunffia furcata group

Description. This morphotype group is characterized by the presence of a single, bifurcated appendage.

Remarks. *Deunffia furcata* var. *dorothyensis* is differentiated from *D. furcata* by the presence of a small, insignificant process at the juncture of the bifurcation (Thusu 1973). However, it has been included in this group as it not clear whether the third process is a normal or teratological feature. Another variety, *D. furcata* var. *niagarensis*, is placed in the *D. amphora* group because of the presence of a smaller appendage at the opposite pole.

Silurian and Devonian species.

Deunffia furcata Downie 1960

Deunffia furcata var. *dorothyensis* Thusu 1973

Deunffia ramusculosa group

Description. *Deunffia ramusculosa* has one appendage which can have three to six distal branches of roughly the same size.

Remarks. *Deunffia furcata* var. *dorothyensis* is excluded from this group as its 'third process' is small and insignificant.

Silurian and Devonian species.

Deunffia ramusculosa Downie 1960

***Deunffia monospinosa* var. *tonowadensis* group**

Description. This variety has two appendages, one shorter than the other, on either pole.

Remarks. The presence of a second short appendage is typically characteristic of species from *Domasia*; however, *Domasia* has two or more appendages on the opposite pole.

Silurian and Devonian species.

Deunffia monospina var. *tonawadensis* Thusu 1973b

***Deunffia ramusculosa* var. *rochesterensis* group**

Description. This group also consists of morphotypes with two appendages, one significantly shorter than on the opposite pole. The longer appendage can be multifurcated, or may have numerous branching processes arising from the appendicular surface.

Remarks. The presence of a short appendage on one pole is characteristic of *Domasia*; however, this genus has two or more appendages on the other pole.

Silurian and Devonian species.

Deunffia eisenackii Cramer 1970a

Deunffia ramusculosa var. *rochesterensis* Thusu 1973b

Genus ***Polydeunffia*** Cramer 1970 ex Eisenack et al. 1973

Type species. *Polydeunffia eisenackii* Cramer 1970 (p. 60–61; pl. 1, fig. 23) ex Eisenack et al. 1973 (p. 945).

Original diagnosis (from Eisenack et al. 1973, p. 943).

'Vesicle symmetry bipolar, hemimorphic; a longitudinal symmetry axis is present. Ectoderm sculpture absent to minor. If present, it is mostly microscabrate (elements less than 0.5 μ high). One pole is without ornamentation, the other bears several simple, slender processes or spines'.

Description. As with *Hemideunffia*, this genus also contains only one species, *P. eisenackii*. It is ellipsoidal in shape, with one pole unornamented while the other bears 3–10 processes.

Remarks. The genus differs from *Deunffia* in having three or more processes.

Silurian and Devonian species.

Polydeunffia sp. Mabillard and Aldridge 1985

Genus ***Domasia*** Downie 1960 emend. Hill 1974 emend. nov.

Type species. *Domasia trispinosa* Downie 1960, 199–200, pl. 1, fig. 7.

Original diagnosis (Downie 1960, p. 199). 'Shell hollow, elongate, ellipsoidal more or less smooth, about 20 μ in length. Body composed of pale yellow to brown organic membrane. Ornament consisting of two relatively long hollow spines arising near one pole and a single spine of variable length at the opposing pole'.

Emended diagnosis. Ellipsoidal in outline with heteropolar symmetry and thin organic vesicle wall; both poles are ornamented with appendages which differ in number and appearance. One side always has the shorter or no appendage, while the other can have a short, bifurcated appendage or two to four appendages.

Remarks. Cramer (1970) removed the 20 μ m vesicle length limit, as many specimens exceeding this length were found. Hill (1974) further emended the genus to include forms with more than two processes on one pole. However, some morphotypes included in the genus (e.g. *Domasia amphora*) differ from the original definition and subsequent emendations in having a base compressed into a very short neck that distally furcates into two relatively long processes. Furthermore, *Domasia bispinosa* does not possess the shorter appendage on one pole, similar to many *Deunffia* species. We thus emend *Domasia* to officially include these morphotypes.

The genus is heteromorphic, with one pole having one or no process and the other at least two, in contrast to *Deunffia*, which always has only one long polar process. It has a more compact outline to *Hemideunffia*. Additionally, in *Hemideunffia*, the processes radiate from a single point on one pole, whereas similar forms of *Domasia* have three processes on one side.

Informal morphotype groups.

Remarks. Four morphotype groups are recognized within *Domasia*, differentiated based on the number of appendages. One pole typically has the smaller appendage (except for *D. bispinosa* where the appendages only occur on one pole), while the other pole has longer ones, which can vary in number from one to five.

***Domasia amphora* group**

Description. For this group the longer appendage is always distally bifurcated.

Remarks. Within this group the length of the bifurcated appendage varies from short (resembles a neck) in *Domasia amphora* to very long in *Domasia intermedia*. *Deunffia furcata* var. *niagarensis* is included here as it has essentially the same characters, with the length of its longer appendage falling somewhere within the *D. amphora*–*D. intermedia* spectrum.

Silurian and Devonian species.

Deunffia furcata var. *niagarensis* Thusu 1973b

Domasia amphora Martin 1969 emend. Hill 1974

Domasia canadensis Thusu 1973b

Domasia elongata Downie 1960

Domasia intermedia Kiryanov 1978

***Domasia bispinosa* group**

Description. Two long appendages are present on one pole, and none on the opposite side.

Remarks. The absence of appendages on one side is notable from the rest of the morphotype groups in this genus. However, *D. bispinosa* is differentiated from *Deunffia* species, with the latter never having multiple appendages at a pole.

Silurian and Devonian species.

Domasia bispinosa Downie 1960

***Domasia trispinosa* group**

Description. The presence of three appendages characterizes this group. One pole has one appendage while the other side has two; small processes may arise from the latter appendages.

Remarks. The species reported in this group vary mainly in their outline, from having a rounded appearance (*D.*

trispinosa) to more elongated and triangular outlines (*D. elongata*).

Silurian and Devonian species.

Domasia elongata Downie 1960

Domasia limaciformis (Stockmans and Willièrè 1963) Cramer 1970a emend. Hill 1974

Domasia rochesterensis Thusu 1973b

Domasia trispinosa Downie 1960 emend. Hill 1974

Domasia trispinosa var. *bohémica* Dufka and Pacltová 1988

Domasia quadrispinosa group

Description. This group contains one species, characterized by the presence of four appendages (three on one pole and one on the other).

Silurian and Devonian species.

Domasia quadrispinosa Hill 1974

Genus *Hemideunffia* Thusu 1973

Type species. *Hemideunffia trifurcata* Thusu 1973, 810, pl. 104, figs. 10, 16.

Original diagnosis (Thusu 1973, p. 810). 'Vesicle highly elongate, tapering, pale yellow, thin, smooth-walled; one pole simple; opposite pole terminates into three processes, processes may be closed or open at the distal end, septate processes may be present'.

Remarks. The genus contains only one species. It differs from *Domasia* in that its three appendages radiate from a single point on one pole, whereas in *Domasia*, the appendages originate from several loci. It is distinct from *Leiofusa* in having heteromorphic symmetry.

Silurian and Devonian species.

Hemideunffia trifurcata Thusu 1973

Genus *Metaleiofusa* Wall 1965

Type species. *Metaleiofusa arcuata* Wall 1965, p. 161, pl. 5, figs. 18–20, pl. 9, figs. 1–2.

Original diagnosis (Wall 1965, p. 161). 'Test small, about 20 μ in length, fusiform, ornamented by an apical spine at each pole and a small number of additional sub-apical or lateral equatorial processes of a simple nature'.

Remarks. The presence of lateral appendages distinguish the genus from *Deunffia* and *Domasia*.

Silurian and Devonian species.

Metaleiofusa arcuata Wall 1965 emend. Rubinstein and Vajda 2023

5. Stratigraphy, paleoecology and paleogeography

5.1. Stratigraphic distribution in the middle Paleozoic

The earliest netromorph taxa were reported from middle to late Proterozoic strata in India, China and the former Soviet Union. These include some species of *Leiofusa*, *Leiovalia* and *Navifusa* (Fensome et al. 1990). Netromorphs were very scarce in the Cambrian, with only two species of *Leiovalia*, but underwent a sudden radiation during the Ordovician with the appearance of *Dactylofusa*, the *Poikilofusa*–*Disparifusa* complex and *Eupoikilofusa* (Fensome et al. 1990). The highest diversity occurred during the Silurian before

tapering off reducing sharply in the later part of the Devonian (Downie 1963). Some *Leiofusa* species were reported in the Triassic and Jurassic, and some *Leiovalia* sp. were reported from the Paleogene of China (Jiabo 1978).

Netromorphs and related morphotypes reached the peak of their diversity in the Silurian (Figure 5), particularly during the Wenlock. Almost all netromorphs were reported from the Silurian, except for *Lunulidia*, which was reported from Middle to Upper Devonian sediments, strata, respectively. Category 1 netromorphs, including the genus *Leiofusa*, have the longest ranges. Within these groupings *Navifusa* and the *Leiofusa tumida* group range from the Llandovery to the Late Devonian. The genus *Dactylofusa* is restricted to the Silurian (Llandovery to Pridoli). The *Poikilofusa spinata* group appears in Llandoveryan strata, while the *P. oblancana* group has a longer range from the Llandovery to the Early Devonian. The genus *Eupoikilofusa* is present from the Llandovery to the Early Devonian, with the *E. striatifera* group having a longer range (lower part of the Llandovery to upper part of the Lower Early Devonian) than the *E. cantabrica* group. *Baiomeniscus* has a longer range than *Eupoikilofusa*, from the Llandovery to the Middle Devonian.

The *Deunffia*–*Domasia* complex is largely confined to the Silurian, from the Llandovery to Wenlock, except for the *Deunffia monospinosa* group and *Domasia trispinosa* group occurrences in the Lower Early Devonian. *Metaleiofusa* occurs within the Llandovery.

5.2. Paleoecology

Netromorph acritarchs have been recorded in various sedimentary facies, but they appear to prefer shallow marine environments. Branch 3 morphotypes of Vavrdová (1978) were recovered from the Ordovician Šárka Formation, which was deposited in a lagoonal environment. In the Ludlovian shelf along the Welsh Borderland, *Eupoikilofusa striatifera* and the *Leiofusa estrecha* complex are found inshore, while smaller leiofusids such as *Leiofusa parvitatensis* are found abundantly onshore (reported as 'offshore' by Dorning 1981). Dorning and Bell (1987) also reported a *Leiofusa tumida* assemblage from the Wenlockian shallow carbonate shelf in the same area. At the boundary between the Lower and Middle Ordovician in the Yangtze platform of China, fusiforms were abundant in the nearshore environment at the Kunming section and were not found elsewhere, except for the Guiyang section in the middle of the shelf (Li et al. 2004). Paris et al. (2012) interpret the depositional environment of *Eupoikilofusa*-bearing, Lower Silurian Taneezucht Formation core (CDEG-2a borehole) from the Murzuq Basin (southern Libya) as offshore. Netromorph acritarchs may thus be related to shallower water environments, with a possible post-mortem transport into deeper water environments, although exceptions might be possible.

Fluctuations in sea-level appear to influence netromorph morphology. In one case study, Fatka and Brocke (2008) measured the dimensions of more than 300 *Navifusa* specimens from the Emsian Císařská Rokle section in the Czech Republic that was deposited during the Daleje transgressive

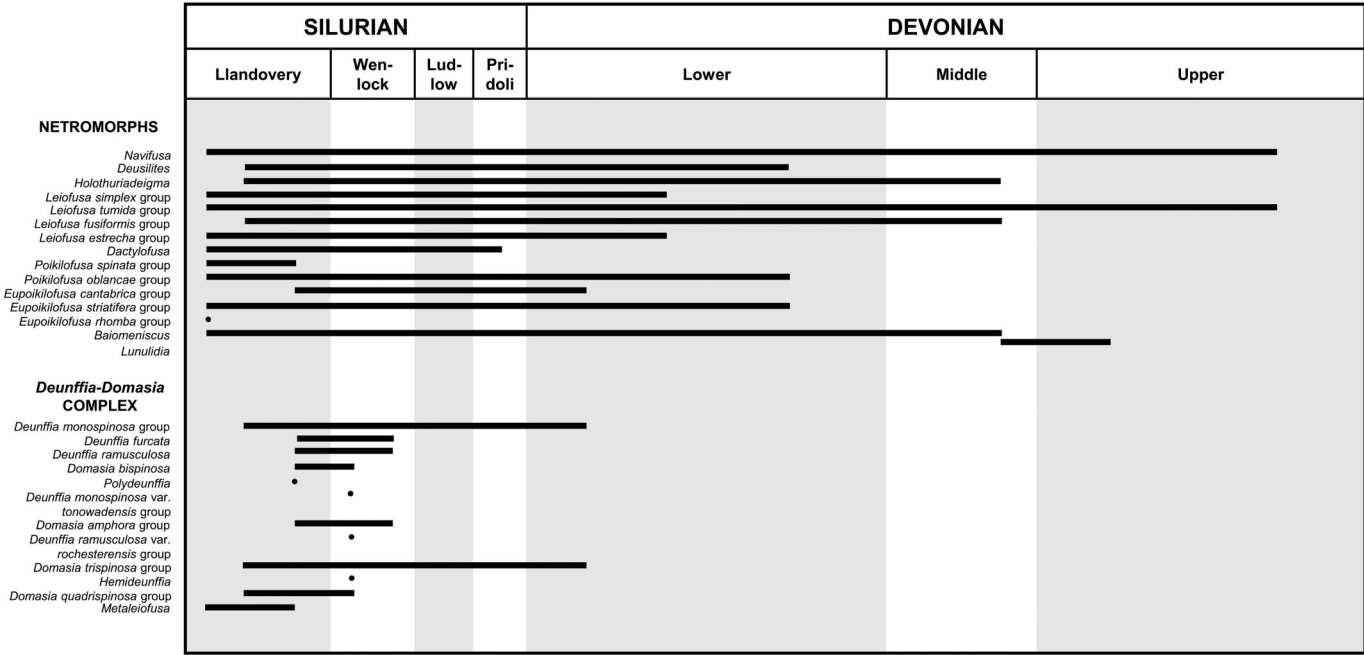


Figure 5. Stratigraphic range of netromorphs and related morphotypes of the *Deunffia*–*Domasia* complex in the Silurian and Devonian. Occurrences from the Phytopal database of Mullins et al. (2022) along with more recent sources (see captions in Figures 6–8).

event. The results show a continuous trend from long and narrow to short and wide forms upward through the section, suggesting ecophenotypic variation. Although the biological affinity of the netromorphs remains unclear (see below), a comparison with the morphological variation of other paly-nomorphs related to phytoplanktonic organisms is straight-forward. Morphometric analysis by Mertens et al. (2009) on dinoflagellate cysts from recent surface sediments showed that process lengths and distribution in *Lingulodinium machaephorum* cysts are affected by water salinity and temperature. Similarly, the presence of numerous transitional forms between genera of the galeate acritarch plexus in the Cambro–Ordovician of the Algerian Sahara (Stricanne and Servais 2002; Servais et al. 2004) may be a case of ecophenotypic variation related to changes in marine environmental conditions. Foerster (1971) observed morphological changes (development of appendages) in the freshwater chlorophyte *Oocystis parva* when subjected to estuarine-like conditions with changing salinities (from 33.8 to 0.03‰), suggesting this species and the marine *O. submarina* are probably ecophenotypes.

Thus, netromorphs can be found in various marine – but generally near- and onshore – environments, and exhibit morphological plasticity in response to changing paleoecological and paleoenvironmental conditions. The morphological variation in *Leiofusa* (Figure 4), associated with changes in the length of appendages and outline, might also be linked to cycles and fluctuations in marine salinity and temperature. Future studies are needed to confirm or refute this correlation.

5.3. Paleogeography

Netromorphs are documented from almost all continents during the Silurian (Figure 6), with the highest morphological

diversity in the well-sampled regions of southern Laurentia and Baltica, between the equator and 15°S paleolatitude. They are also present in eastern Gondwana, on the north-western and eastern sides of the Rheic ocean, respectively. The related morphotypes also exhibit a similar distribution pattern (Figure 7). The genus *Leiofusa* is the most widespread netromorph genus during the Silurian.

During the Devonian, as the Rheic ocean began to close with Laurentia moving southeastward, the center of netromorph diversity shifted from Baltica to northern central Gondwana, situated below the equator at –30° latitude (Figure 8). The related morphotypes were reported from two occurrences in northern central Gondwana. Netromorph acritarchs thus do not appear to be restricted to specific climate zones on the globe.

6. Possible biological affinities

The fusiform acritarchs, attributed to netromorphs, are most probably polyphyletic, with different morphological groups having possibly completely different biological affinities. Clear assignments to biological groups are currently only tentative.

6.1. Fungal spores

The elongated outline of fusiform acritarchs with long appendages, such as those in the *Leiofusa estrecha* group, superficially resembles that of fungal spores. For example, a rare non-septate fungal spore, Type UG-1329 of Gelorini et al. (2011, pl. IV), possibly related to the Xylariaceae and the genus *Rosellinia*, exhibits a fusiform shape. However, it differs from the *L. estrecha* group in having one convex and one flattened side, a thick cell wall, and a longitudinal slit near the flattened side (no preferential splits were identified

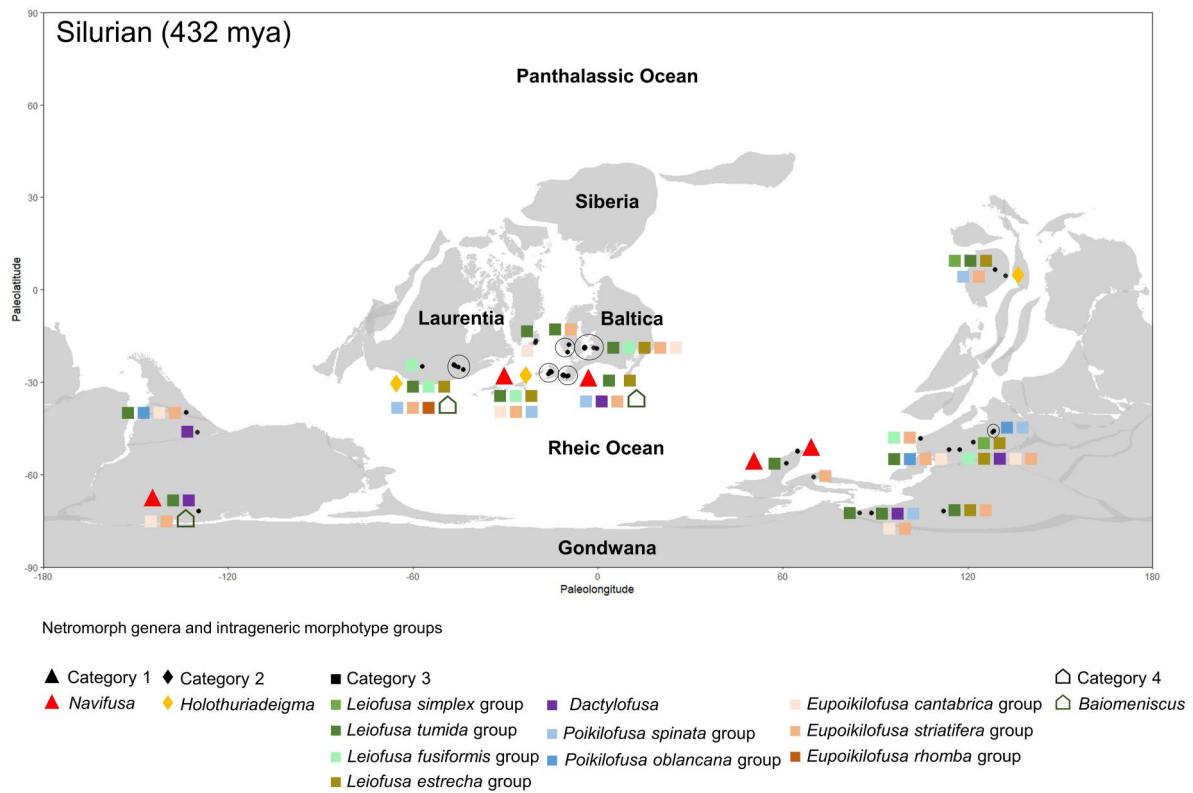


Figure 6. Netromorph occurrences (black dots) in the Silurian. The occurrences are from the Phytopal database of Mullins et al. (2022) along with additional sources: Vecoli et al. (2009), Paris et al. (2012), Le Hérisse et al. (2015), Rubinstein et al. (2016), Venckutė-Aleksienė et al. (2016), Breuer et al. (2017), and Oktay and Wellman (2019). The paleogeographic map used is the reconstruction by Scotese and Wright (2018).

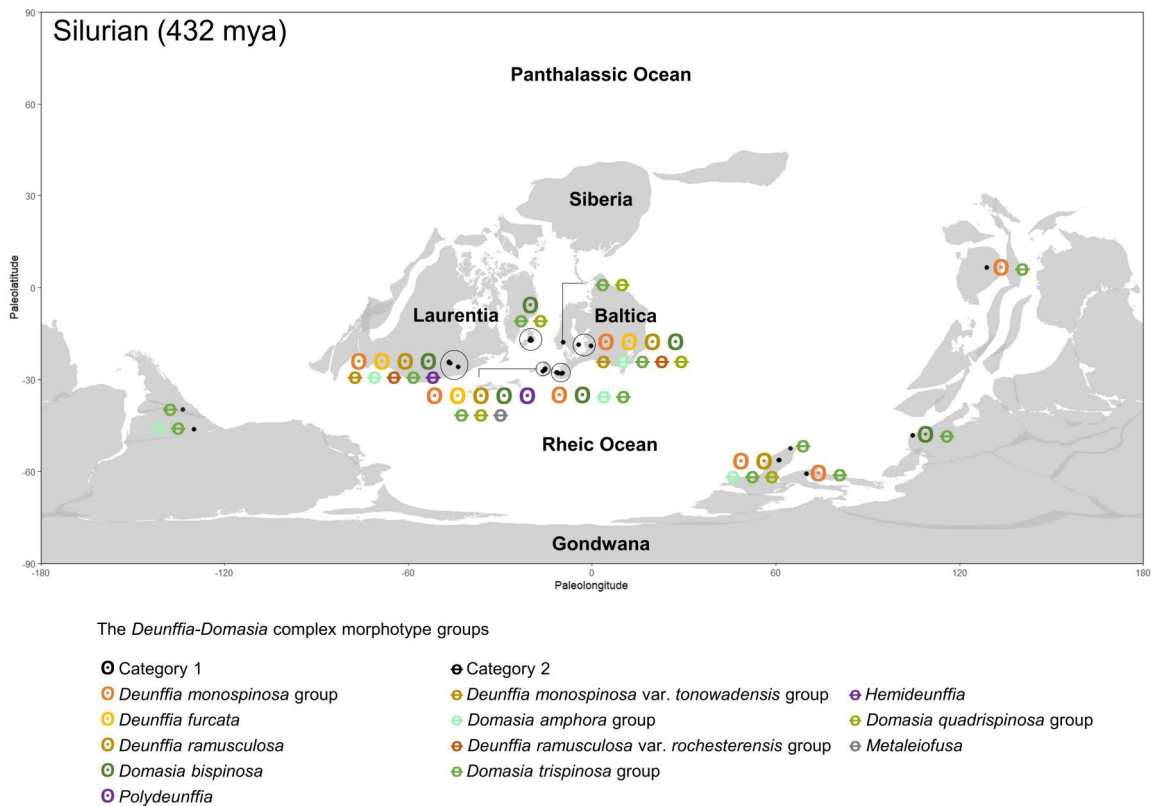


Figure 7. *Deunffia*-*Domasia* complex occurrences (black dots) in the Silurian. The occurrences are from the Phytopal database of Mullins et al. (2022) along with additional sources: Rubinstein et al. (2016) and Oktay and Wellman (2019). The paleogeographic map used is the reconstruction by Scotese and Wright (2018).

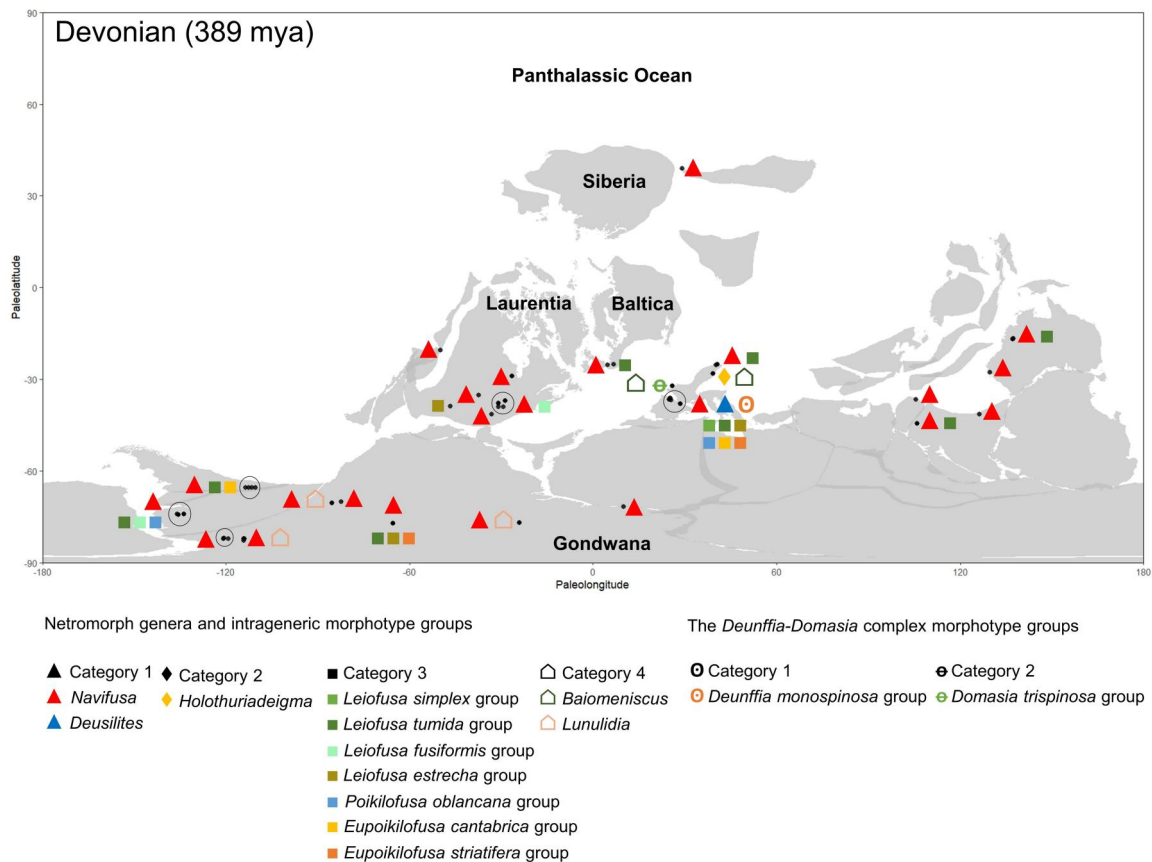


Figure 8. Netromorph and related morphotype occurrences (black dots) in the Devonian. The occurrences are from the Phytopal database of Mullins et al. (2022) along with additional sources: Zhu et al. (2008), Amenábar et al. (2009), Filipiak (2009), Vavrdová and Dašková (2011), Wicander et al. (2011), Bosetti et al. (2012), Grahn et al. (2013), García Muro et al. (2014, 2017, 2018, 2021, 2022), Atta-Peters and Achaegakwo (2017), Daners et al. (2017), di Pasquo et al. (2017), Rubinstein et al. (2017), Askew (2019), de Andrade et al. (2020), Taherian et al. (2021), Kondas and Filipiak (2022), and Wicander and Playford (2017). The paleogeographic map used is the reconstruction by Scotese and Wright (2018).

for the *L. estrecha* group). The spores are also brown in color, whereas *L. estrecha* is transparent. Additionally, the fungal spore is smaller, with a total length of 68 µm, compared to the average length of *L. estrecha* morphotypes, which exceeds 100 µm. Moreover, the fungal spores were deposited in a freshwater lake within the East African rift system of western Uganda, in contrast to the marine origin of *L. estrecha* group specimens. Other netromorphs may also resemble fungal spores, but simple morphological comparisons are not sufficient to conclude a biological affinity.

6.2. Euglenids

The acritarch *Moyeria cabottii* was previously classified under *Eupoikilofusa* due to its bi-helical striations parallel to its longitudinal axis. However, transmission electron microscope (TEM) analysis of *Moyeria* cross-sections from Scotland and the type locality in New York by Strother et al. (2020) revealed an articulated wall microstructure comparable to pellicle frames in modern euglenids. Consequently, Strother et al. (2020) reclassified *M. cabottii* from acritarchs into Euglenida. Despite the superficial similarity between *Eupoikilofusa* and *Moyeria*, further morphological and even spectral analysis (such as Fourier transform infrared spectroscopy) of *Eupoikilofusa*

specimens is needed to establish a possible connection between this netromorph genus and euglenids.

6.3. Turbellarian egg capsules

Some examples of netromorphs and related morphotypes resemble the egg capsules of turbellarians (flatworms). These organisms can be either free-living or parasitic, inhabiting hosts such as sea cucumbers and sea urchins (e.g. Shinn 1985, 1993). Egg capsules are part of the reproductive organs of Neorhabdocoelan turbellarians: they consist of a swollen portion of the vagina where several eggs can be stored and the embryos eventually mature (Matsuoka and Ando 2021). The egg capsules generally consist of a main capsule from which a posterior stalk arises; they change morphology after hatching by splitting at the top to form an operculum and the aperture, with a basal attachment at the end of the stalk to anchor to a substrate (see Matsuoka and Ando 2021, fig. 2).

Two types of turbellarian spindle-shaped egg capsules are reported by Lohmann (1910) from plankton collected by Vanhöffen (1897) from the Karajak fjord in western Greenland. Forma a (fig. 1a in Matsuoka and Ando 2021) also resembles the *L. estrecha* group, described as having a slender, spindle-shaped shell ending in two threads on either side (Kräfft 1908) but can be larger than the *L. estrecha*

group, with lengths reaching 1 mm (60 µm wide). Forma b (fig. 1b in Matsuoka and Ando 2021) is more spherical, like the *L. tumida* group, but with very short pointed ends and a greater total length than *L. tumida* morphotypes, at 200–300 µm (100–170 µm wide). Both turbellarian egg capsule forms are considered to belong to *Neorhabdocoela* (Matsuoka and Ando 2021).

Modern *Gyratrix* turbellarians also produce egg capsules that consist of a capsule, stalk and basal attachment (fig. 2 of Matsuoka and Ando 2021), which are overall similar to Type 1 of the *Deunffia*–*Domasia* complex with single processes. The Cretaceous acritarch *Domasiella discophora* Cookson and Eisenack (1962) was identified by Matsuoka (1994) as a possible stalked turbellarian egg capsule. Single-process morphotype groups from the *Deunffia*–*Domasia* complex may also be egg capsules similar to *Gyratrix*, although the identity of those with two or more antapical processes are uncertain.

Gelorini et al. (2011) also reported the presence of flatworm oocytes in the Ugandan rift valley lakes. The Type UG-1224 morphotype is an oocyte from the flatworm *Neorhabdocoela* (plate VIII in Gelorini et al. 2011), and resembles the Ordovician netromorph species *Dactylofusa velifera* in having longitudinal crests (despite the absence of longitudinal granulations). The Type UG-1224 specimens appear to have an apical excystment structure, which has not been reported from *Dactylofusa*. It is possible that all Type 2 netromorphs also represent some form of invertebrate egg capsules, although it is unclear whether flatworms or another group of animals produced them.

Fossil preservation of parasite and free-living flatworms are extremely rare (De Baets et al. 2015) due to the scarcity of hard parts, and none has been found with intact egg capsules still inside. The problematic Early Cambrian fossil *Vetustovermis planus* has been identified as either an annelid (Glaessner 1979) or an arthropod (Luo et al. 1999) but could be more closely related to turbellarians, among other groups (Chen et al. 2005). Knaust and Desrochers (2019) interpreted some pyritized remains from the Late Upper Ordovician Vauréal Formation of Anticosti Island, Canada, as putative turbellarian body fossils. De Baets et al. (2015) have discussed in detail the fossil record of parasitic flatworms, with potential fossil evidence traceable back to the Devonian.

6.4. Possible other affinities

Many acritarchs are generally interpreted as phytoplankton, with structures such as the pylome or split being considered excystment openings, similar to those found in algal groups like dinoflagellate cysts (which have an excystment opening called the archeopyle). Further studies are needed to determine the biological affinities of netromorphs and related morphotypes. It is possible that some species or genera are phylogenetically distinct. Future research could focus on morphological and biochemical comparisons with extant fungal spores and oocytes of *Neorhabdocoela* turbellarians. Additionally, spectroscopic analysis may be employed to ascertain biological affinities (e.g. Mudie et al. 2024).

7. Conclusions

A new classification for netromorphs and related morphotypes is proposed. The netromorphs are categorized into four groups based on their gross outline: elliptical, reniform, spindle and crescent-shaped forms. The presence and complexity of ornamentation in the main vesicle are then used to further differentiate between genera. Within the genera, differences in outline and type of ornamentation can be used to distinguish between different intrageneric morphotype groups. Several netromorph species are reassigned to other genera or reverted to their original genus based on our classification.

For the *Deunffia*–*Domasia* complex, the various morphotypes are differentiated based on the presence of polar and lateral appendages and the number of posterior appendages. Intrageneric morphotype groups are established based on the number of distal branches of the single posterior appendage types. However, the morphotype groupings do not necessarily correspond to genera, indicating that a redefinition of both *Deunffia* and *Domasia* may be necessary.

Some modern fungal spores and turbellarian egg capsules have a similar gross morphology to spindle-shaped netromorphs and single-process *Deunffia* and *Domasia* morphotype groups. Further studies are necessary to determine a possible biological affinity for the netromorphs and related groups.

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No potential conflict of interest was reported by the authors.

Notes on contributors



EIVER GELAN MANZANO is a PhD student at the Université de Lille in France, mapping the diversity and distribution of acritarchs in the early and middle Paleozoic. For his master's thesis he has worked on identifying various morphotypes of the Cretaceous dinoflagellate genus *Pseudoceratium* Gocht 1957 at the CSTJF of TotalEnergies in Pau, France. He holds a joint MSc from the Université de Lille and the National and Kapodistrian University of Athens (Greece) through the Erasmus PANGAEA program (Applied Palaeontology track), and a BSc in Geology from the University of the Philippines-Diliman. Prior to studying organic microfossils, EGM gained extensive experience in the exploration of various metallic resources in the Philippines.



CLAUDE MONNET is an invertebrate paleontologist and data analyst at the University of Lille, France. He received his M.Sc. (1999) in Paleontology from the University of Lyon (France), his Ph.D. (2005) in Paleontology from the University of Zürich (Switzerland), both with awards, and his 'habilitation' thesis at the University of Lille (France) in 2016. His major research interests focus on macroevolution, biodiversity (taxonomic richness), morphological disparity, and macroecology, as well as quantitative paleontology, in particular quantitative biostratigraphy. Taxonomic strength and field experience are in Triassic and Cretaceous (Mesozoic) ammonoids (cephalopods) from North America, Europe and North Africa.



KENNETH NEIL MERTENS is a researcher at Ifremer, LER BO, Concarneau, France. He received his PhD in 2009 from Ghent University. His research interests are the taxonomy, evolution, phylogeny and biogeography of dinoflagellates, and the paleoceanographic application of dinoflagellate cysts, particularly in the Quaternary and Neogene.



THOMAS SERVAIS is a Research Director at the French Centre of Scientific Research (CNRS). His research is focused on the biostratigraphy, palaeobiogeography and palaeoecology of Paleozoic acritarchs. His current research is mostly dedicated to a better understanding of the Ordovician Plankton Revolution. He is currently Chairman of the Ordovician Subcommittee of Stratigraphy.

ORCID

Eiver Gelan Manzano  <http://orcid.org/0009-0001-3403-6306>
 Claude Monnet  <http://orcid.org/0000-0002-0899-8392>
 Kenneth Neil Mertens  <http://orcid.org/0000-0003-2005-9483>
 Thomas Servais  <http://orcid.org/0000-0002-4089-7874>

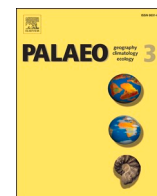
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Acritarch distribution in the Middle Ordovician of Öland, Sweden: Ecostratigraphical or biostratigraphical signal?[☆]

Jaqueline L. Calero Gordon^a, Baptiste Chaigneau^a, Anders Lindskog^b, Mats E. Eriksson^c, Eiver G. Manzano^a, Claude Monnet^a, Axel Munneke^d, Sylvie Régnier^a, Thomas Servais^{e,*}

^a Univ. Lille, CNRS, UMR 8198 Evo-Eco-Paléo, F-59000 Lille, France

^b Department of Environmental Science, Kristianstad University, Sweden

^c Department of Geology, Lund University, Lund, Sweden

^d Geozentrum Nordbayern, Paläobiologie, Friedrich-Alexander Universität Erlangen-Nürnberg, Erlangen, Germany

^e CNRS, Univ. Lille, UMR 8198 Evo-Eco-Paléo, F-59000 Lille, France

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ABSTRACT

The Middle Ordovician of the palaeocontinent Baltica provides some of the best preserved and most diverse acritarch assemblages of the lower Palaeozoic. A great number of widely used acritarch genera and species have been described from this area since the 1960s and many of these taxa are considered as biostratigraphically useful for both regional and international correlation. Here, we document the changing proportion of acritarch morphotypes through two well-documented Darriwilian (Middle Ordovician) sections of Öland, Sweden. Progressive changes of key morphological characters, such as the standard process length, as well as the relative abundance of different morphotypes, are continuous throughout the sections. These changes in the acritarch assemblages parallel the transition from deeper to shallower water environments as deduced from local facies analyses and regional sedimentation patterns. Consequently, the previously suggested biostratigraphical signals in the acritarch assemblages could also be interpreted as ecophenotypic responses to the changing palaeo-environment. Therefore, the morphological plasticity of acritarchs challenges their accuracy and validity for precise correlation if their palaeoecology is not addressed.

1. Introduction

The group Acritarcha was erected by Evitt (1963) to include small organic-walled microfossils of unknown and probably varied biological affinities, with a central body displaying different symmetries, shapes, structure and ornamentation. Evitt (1963) proposed the acritarchs to include the ‘residue’ of hystrichospheres that could not be referred to the Dinophyceae (dinoflagellate cysts), with the main objective to facilitate communication about this widespread group of palynomorphs. In the following decades, several thousands of acritarchs have been described, mostly from the Palaeozoic (Kroeck et al., 2022). The group is clearly polyphyletic (Evitt, 1963; Colbath and Grenfell, 1995; Servais, 1996) with most taxa related to phytoplanktic organisms even if exceptions are known (Navidi-Izad et al., 2022; Shan et al., 2023). The acritarchs showed a rapid increase in diversity during the early Palaeozoic (Kroeck et al., 2022) with a shift from shallow-water environments to the open-

marine water column starting in the late Cambrian (Shan et al., 2022). Regardless of the biological affinities, the group is considered to be linked to the radiation of marine life during the Cambrian–Ordovician biodiversification (Martin and Servais, 2020).

Before being used increasingly in a palaeobiological context during the last decades in order to understand the early Palaeozoic marine biodiversifications, acritarchs were first widely used, and are still mostly described, in a biostratigraphical context (particularly in the lower and middle Palaeozoic; Brocke et al., 1995; Molyneux et al., 1996). As extremely resistant organic-walled microfossils, they are very abundant in fine-grained sedimentary rocks and they can even be found in slightly metamorphosed strata. In this context, acritarchs have sometimes been the only fossils recorded in meta-sedimentary rocks of unknown age. For example, Molyneux (1998) was able to assign an Ordovician age to the Macduff Slate of northeast Scotland based on a single acritarch specimen. Montenari and Servais (2000) found acritarchs in three out of 133

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* Corresponding author.

E-mail address: thomas.servais@univ-lille.fr (T. Servais).

samples of meta-sediments from the Black Forest of Germany, thus providing the first indications of a late Cambrian–Early Ordovician age for a few samples from the Baden–Baden – Gaggenau zone, allowing tectono-stratigraphic considerations for these rock units, the age of which had remained obscure for decades. More recently Benachour et al. (2020) found the first evidence of Ordovician rocks in northwestern Algeria based on the presence of a few age-diagnostic acritarchs. Acritarchs have thus often been used when other macro- and microfossils are unavailable, and they are of great biostratigraphical importance even if a very high resolution might be lacking.

The group has also been used to establish acritarch biozonations (for a summary see Molyneux et al., 1996) and new species are still commonly described for biostratigraphical applications (e.g., Ghavidel-syooki, 2021; Palacios et al., 2022). However, detailed biostratigraphical schemes allowing international correlation of acritarch biozones remain rare (Molyneux et al., 1996, 2007). Until now, acritarchs have never been used as an index fossil to correlate the Global Boundary Stratotype Section and Points (GSSPs) in the Palaeozoic, and their biostratigraphical potential remains (much more) limited compared to that of conodonts, graptolites and even chitinozoans (Servais and Paris, 2000; Goldman et al., 2023).

In comparison with other classical fossil groups described since a few centuries ago, the stratigraphical research on acritarchs appears today to be somewhat outdated. Despite the fact that a number of quantitative biochronological methods have been developed during the last decades (Boulard, 1993; Monnet et al., 2015), acritarchs have still not been used in modern studies of quantitative biochronology. Some of the methods of quantitative biochronology, such as Ranking and Scaling (RASC; Agterberg and Gradstein, 1999), Unitary Associations (UAs; Guex, 1991), or Constrained Optimization (CONOP; Sadler and Cooper, 2003), have been used for the major fossil groups used in biostratigraphy, such as graptolites, conodonts and chitinozoans (Goldman et al., 2013; Fan et al., 2020; Toro et al., 2023). However, such methods have not yet been applied to Palaeozoic acritarchs. This absence of modern biostratigraphical methods in acritarch research is possibly partly based on the taxonomic instability of the group, with no commonly accepted classification schemes among authors.

A major problem of acritarch classification (taxonomy) clearly is their significant morphological plasticity, which has been documented recently for a number of taxa, for example the late Cambrian – Early Ordovician genus *Vulcanisphaera* (Kroeck et al., 2020), the Ordovician genus *Peteinosphaeridium* (Kroeck et al., 2021), and the Cambrian genus *Skiagia* (Waller et al., 2022). These studies, among others, highlighted that it is commonly impossible to precisely distinguish different taxa as many morphotypes clearly intergrade. Therefore, a large amount of acritarch species appear to be junior synonyms of previously described taxa. It also becomes increasingly evident that the morphological plasticity observed among some acritarchs is influenced by environmental factors, similar to the variability observed in modern phytoplankton (e.g., Mertens et al., 2009, 2012). Several investigations have provided insights into the morphological development of dinoflagellate cysts in laboratory cultures (e.g., Kokinos and Anderson, 1995). More recent studies confirm that salinity, temperature and light influence dinoflagellate cyst production and morphology (e.g., Zonneveld and Susek, 2007). It thus appears likely that the morphological plasticity of acritarch taxa also is influenced by such environmental parameters.

Palaeoecology indeed appears to play an important role regarding not only the morphology of individual taxa but also the composition of acritarch assemblages. Jacobson (1979) was one of the first to consider acritarchs as palaeoenvironmental indicators in the Middle and Upper Ordovician of the Cincinnati area, USA. Dornig (1981) provided another landmark study on the onshore–offshore distribution of acritarchs in the Silurian of the UK. Striccanne et al. (2004) subsequently confirmed such distribution patterns in the Silurian of Gotland, Sweden, and also observed that the process length of some taxa increased towards the open shelf. Li et al. (2004) described the onshore–offshore

distribution pattern of the Lower–Middle Ordovician of the Yangtze Platform, China, and noted significant palaeobathymetric differences in assemblage composition. Thus, because both acritarch taxa and communities are distinguishable not only from different time intervals, but also from different palaeoenvironments of a given time, it can be difficult to discern biostratigraphical from palaeoecological signals.

Waterhouse (1976) proposed that, in addition to the lithostratigraphic, biostratigraphic and chronostratigraphic categories, the category ecostratigraphy should be recognized in the International Stratigraphic Guide. Boucot (1984) summarized the concept of ecostratigraphy as a term that intended to find a relationship between ecology and stratigraphy, based on the observation that during all time intervals there are a distinctive, finite number of biofacies. Boucot (1981) investigated in great detail the palaeoecology of the benthic brachiopods, and demonstrated that their distribution patterns are related to different palaeoecologies. Thus, the use of brachiopods for biostratigraphy is considered to be restricted compared to several planktic and nektic groups. Nonetheless, even classical planktic biostratigraphical index fossils, such as the graptolites, show distinct palaeoecological patterns (Cooper et al., 2012) and are thus also facies dependent as has been suggested by some biostratigraphers. Although the term ecostratigraphy is not clearly defined, several paleontologists use the terminology to depict the palaeoenvironmental evolution of fossil assemblages, for example for coccolithophorids (e.g., Giunta et al., 2003), foraminifers (e.g., Nikitenko et al., 2013) or ammonites (Abdelhady et al., 2021), using in addition to biozones also ecozones or eco-biozones in stratigraphical successions. Like all fossil organisms, acritarchs are also linked to both biofacies (ecostratigraphy) and time (biostratigraphy), and it is possible that in some acritarch biozones palaeoenvironmental changes are included.

In order to better understand the biostratigraphical and/or ecostratigraphical patterns of acritarch morphotypes and assemblages, it is necessary to analyze in detail well-preserved material from sections that have good sedimentological and biostratigraphical control. Such sections are available in the Ordovician of Baltica. The Early–Middle Ordovician of Öland, Sweden, is a classical area of acritarch research. In the present study, we revisit some of the sections that were investigated already by pioneering paleontologists in the 1960s and that have been restudied for biostratigraphical purposes during the last 60 years. By applying multiple qualitative and quantitative methods, we attempt to objectively decipher the influence of environmental factors on the morphological variability of acritarchs.

2. Öland: geology and history of palynological studies

2.1. Geological setting and carbonate texture analysis

The palaeocontinent Baltica drifted northwards from high to low southern latitudes during the Ordovician (Torsvik and Cocks, 2017) concomitant with a large increase of biodiversity recorded during the Great Ordovician Biodiversification Event (GOBE; Servais and Harper, 2018; Lindskog et al., 2023). During most of the Ordovician, parts of Baltica were largely covered by an epicontinental sea. A package of well-preserved sediments that remained relatively undisturbed is present in Sweden, the Baltic States and Poland (Fig. 1).

The geological succession of the island of Öland in the Baltic Sea, southeast of the Swedish mainland, contains Cambrian–Ordovician sediments overlying Proterozoic basement rocks (Jaanusson and Mutvei, 1982; Stouge, 2004). The island provides some exceptionally preserved Ordovician sedimentary sequences, and Öland is therefore considered as a classical key area for the study of Ordovician palaeontology and stratigraphy (Nielsen et al., 2023).

The well-preserved fossiliferous Ordovician strata of Öland predominantly consist of reddish and grayish limestone broadly referred to as the ‘orthoceratite limestone’ (e.g., Jaanusson and Mutvei, 1982; Lindskog and Eriksson, 2017). The macrofossils present in the

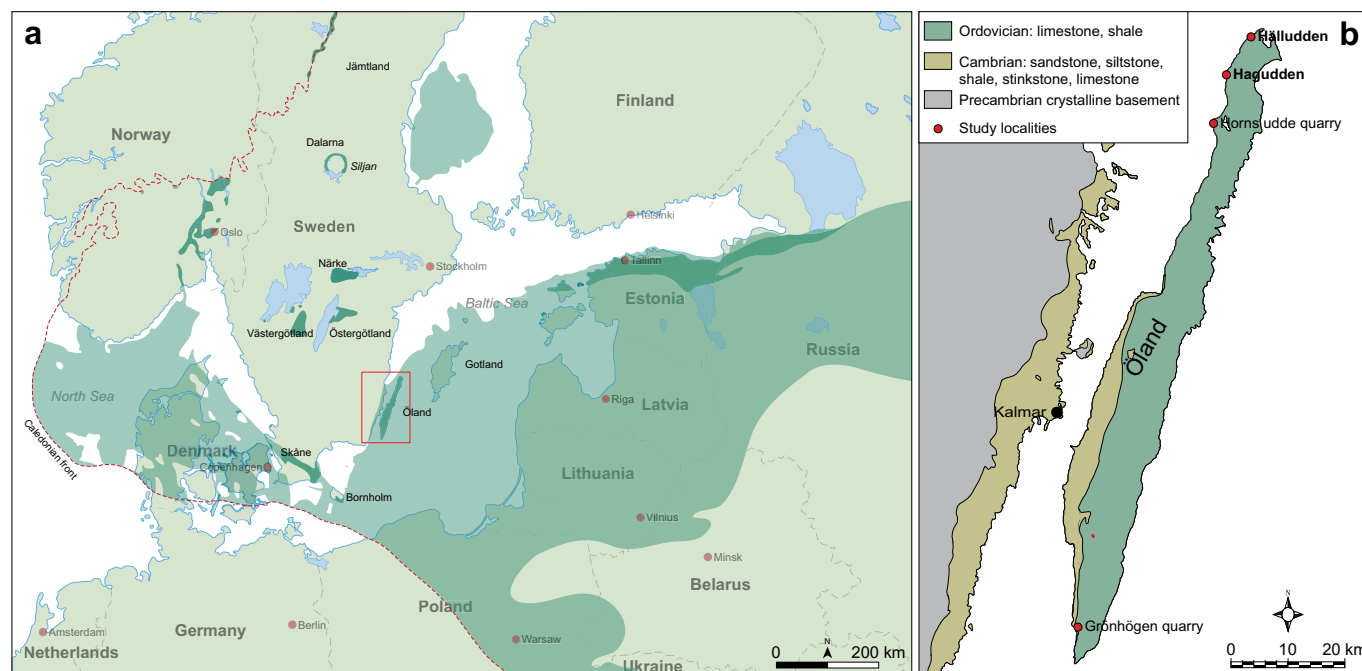


Fig. 1. (a) map of southern Sweden and the surrounding Baltoscandian region, with the distribution of lower Palaeozoic rocks; the red rectangle indicates the location of the island of Öland in the Baltic Sea; (b) map of Öland, with location of studied sections (figure elements modified from Ahlberg et al., 2019). The coastal sections of Hälludden and Hagudden are investigated in the present study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

limestones consist of abundant cephalopod conchs (Grahn, 1986) alongside trilobites and brachiopods, as well as cystoid echinoderms that occur abundantly in some levels (Régnell, 1945). However, microfacies and thin-section analyses reveal that the fossil fauna is much more diverse than what first meets the eye (Hadding, 1958; Jaanusson, 1960; Olgun, 1987; Lindskog and Eriksson, 2017). These studies also show that the 'orthoceratite limestone' contains only a minor siliciclastic component and is mainly characterized by a variable mixture of carbonate mud and skeletal grains. The strata are considered to mainly represent cool-water to temperate deposits (Lindskog and Eriksson, 2017, and references therein). In terms of biostratigraphy, the studied succession is very well dated as Darriwilian, based on detailed studies of conodonts, trilobites and graptolites (Skevington, 1963; Stouge and Bagnoli, 1990; Bagnoli and Stouge, 1997; Pärnaste et al., 2013). Fig. 2 illustrates a combined section, based on the stratigraphy of the two coastal sections of Hälludden and Hagudden.

For the present study, a petrographical-sedimentological study of the Hälludden and Hagudden sections was carried out, describing the constituents and the textural characteristics of the carbonate rocks (mudstones, wackestones and packstones) by counting the relative proportion of grains, cement and matrix of the carbonate sediments. The investigation follows the general approach of Lindskog and Eriksson (2017) and Lindskog et al. (2018), with the study of thin-sections cut perpendicular to bedding in order to undertake studies of grain orientation and packing, grading and other sedimentological properties. Carbonate textures were characterized quantitatively by counting 600 points per thin-section. When considered in relation to hydrodynamic indicators and fossil grain composition, the variations in carbonate texture (abundance of skeletal grains, glauconitic grains and cement versus matrix) allow for an interpretation of the relative sea level (Fig. 2; see Lindskog and Eriksson, 2017, and references therein, for a discussion on the interpretative approach). Both sedimentological and palaeontological data suggest a trend of decreasing sea level through the studied interval, as is generally the case also regionally (and possibly also globally; e.g., Jaanusson and Mutvei, 1982; Nordlund, 1986, 1989; Nielsen, 2004; Lindskog and Eriksson, 2017; Lindskog et al., 2018, 2023;

Nielsen et al., 2023).

Concerning the palaeoecology, it appears that water depth increased, roughly from north(west) to south(east) in the Öland area. This is manifested by coarser carbonate textures in the northern sections, together with more abundant and consistent signs of physical abrasion/erosion and (local) reworking (and vice versa in southern sections). The overall fossil composition also changes with the depth gradient, with 'typical' shallow-water faunal/floral elements being more common northward. Northern Öland typically had higher-energy conditions compared to the south, with the notable exception of some lagoon-like sediments. In those latter beds, *Girvanella* 'balls' (documented in detail by Nordlund, 1986) and peloid-like grains occur, indicating very shallow and relatively warmer-water environments. Overall, southern Öland represents more open marine conditions, with a regular contact with oceanic water masses, whereas the northern areas commonly appear more isolated with more stagnant water. This is also indicated by redox data (Lindskog et al., 2023, and references therein).

The studied time interval appears to record a long-term drop in sea level, upon which some higher-frequency minor (traceable) variations are superimposed (Fig. 2). A distinct sea-level lowstand appears to have been reached slightly below the *Asaphus expansus*–*Asaphus raniceps* trilobite Zone boundary (uppermost Darriwilian stage slice 1, Dw1). The uppermost part of this interval is associated with mass occurrences of *Sphaerionites* cystoids in the 'Täljsten' at the Grönhögen quarry, as it is also the case in many other localities in Sweden (e.g., Lindskog et al., 2023). During the Volkhovian Regional Stage, a major sea-level drop known as the 'Komstad Regressive Event' occurred, extensively depositing limestone facies towards the west in Scandinavia while clayey limestones accumulated eastward in Estonia and Russia. This regression was punctuated by moderate deepening episodes. Near the base of the Kundan regional Stage another major sea-level fall possibly occurred (Nielsen, 2004). Overall, the Kundan recorded upwards in the sequence a long-term coarsening of carbonate textures, which, together with coincident variations among fossil assemblages, can probably be attributed to changes in (relative) sea level. In summary, the Middle Ordovician of Öland represents shallow marine environments, with the

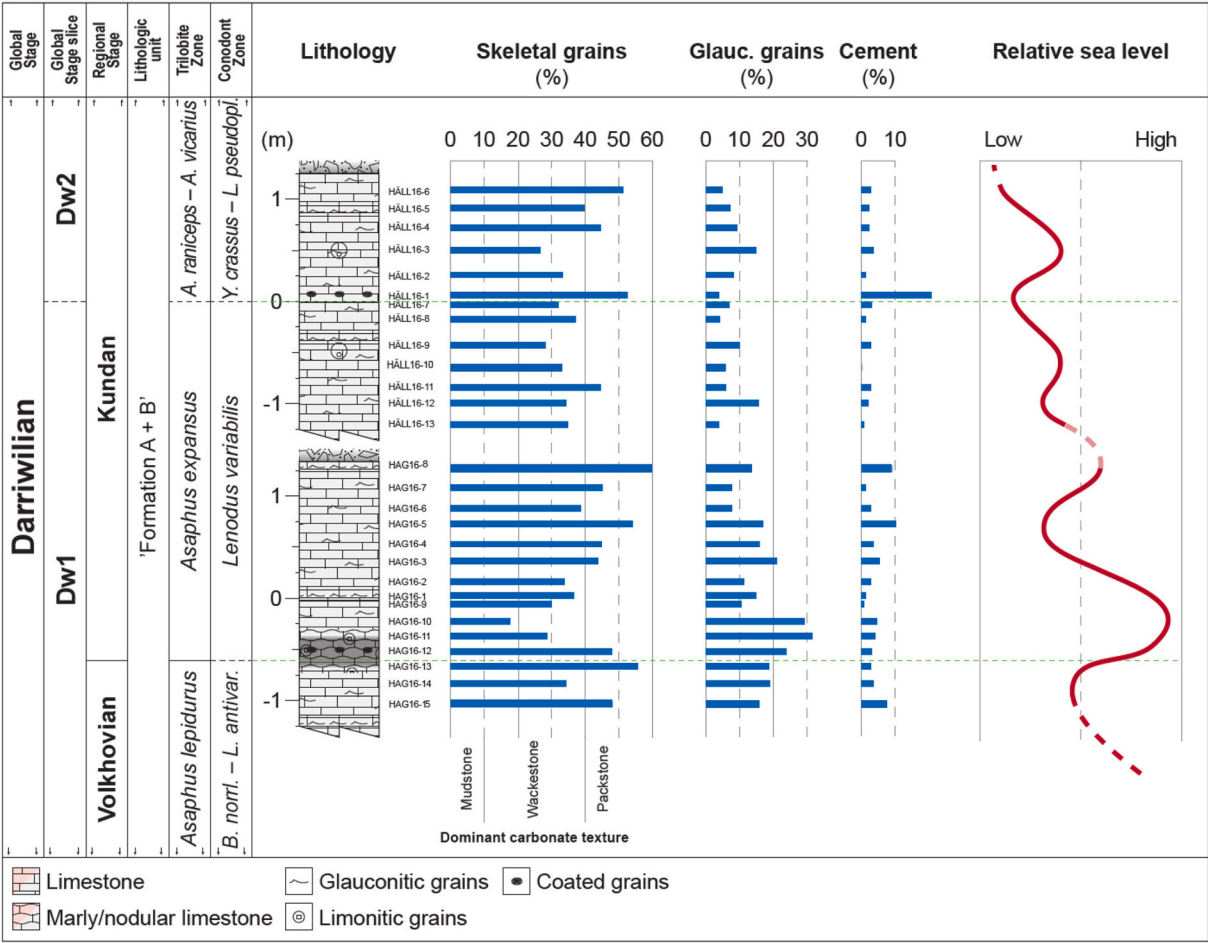


Fig. 2. Combined section illustrating the stratigraphy of the coastal sections of Hälludden and Hagudden, with position of investigated palynological samples. Sea-level curve based on a petrographical-sedimentological study following the approach of Lindskog and Eriksson (2017) and Lindskog et al. (2018).

middle and upper part of the Volkhovian Stage and the lower part of the Kundaan Stage displaying a regressive sequence.

2.2. Öland: a historical center for palynological studies in the Ordovician

Over the last decades, the island of Öland has become a center for reference studies on Ordovician palynology, with numerous studies on acritarchs, but also chitinozoans (e.g. Grahn, 1980, 1981, 1982) and scolecodonts (e.g. Eriksson et al., 2013, 2016).

A number of acritarch taxa have been originally described from the Swedish Ordovician, in particular from Öland. The research started with the pioneering studies in the 1930s by Alfred Eisenack, who collected erratics from the coast of East-Prussia around Königsberg, the present Kaliningrad, Russia (Eisenack, 1938). Some of Eisenack's publications concern Swedish Ordovician acritarchs from those erratics (Eisenack, 1958), but also outcrop material (Eisenack, 1959, 1968) including the Hälludden section of Öland (Eisenack, 1976). More detailed systematic studies were performed in the frame of the rapid development of palynological investigations during the booming petroleum industry in the 1960s and 1970s, which included studies on the Swedish Ordovician, and Öland specifically (Kjellström, 1972). Staplin et al. (1965) also used samples from Öland for the re-evaluation of some important acritarch taxa, such as the genus Baltisphaeridium and some of its most common species, such as Baltisphaeridium brevispinosum, B. longispinosum and B. robustum. Based on Öland material, these authors also erected the important Ordovician acritarch genus Peteinosphaeridium by reconsidering Eisenack's original work.

Subsequent investigations by palynologists from the University of

Pisa (Italy) started in the late 1980s on Cambrian and Tremadocian assemblages of the Furuhall and Degerhamn sections (Bagnoli et al., 1988; Tongiorgi and Ribecai, 1990). The latter were also studied in an unpublished thesis by Ribecai (1996), who also investigated in detail the Middle Ordovician of several sections, including the coastal section of Horns Udde (Ribecai and Tongiorgi, 1995, 1997). The Pisa group also published biozonation schemes, based on acritarch assemblages, and additionally investigated other sections, such as Hagudden and Hälludden (Righi, 1991; Bagnoli and Ribecai, 2000). The latter study is of particular interest because the authors described a number of taxa, including four new species of the Peteinosphaeridium complex, that they considered as biostratigraphically significant. A reinvestigation of the peteinoid acritarchs of Öland by Kroeck et al. (2021), however, showed that most morphotypes intergrade and that the distinction of different peteinoid species and even genera proved to be very difficult to practically impossible.

3. Material and methods

3.1. Material

In the frame of new palynological investigations, which focus on the palaeoecological analysis and interpretation of acritarch distribution, several sections in northwestern Öland were sampled by research teams from the universities of Lund (Sweden), Erlangen (Germany) and Lille (France), including localities that have previously been investigated (Fig. 1). From North to South, the localities include the coastal sections of Hälludden and Hagudden, and the sections of Horns Udde Quarry and

Grönhögen Quarry. The present study is focused on material from Hälludden and Hagudden, corresponding to the upper part of the Ordovician succession in the area. These localities cover the uppermost part of the Volkhovian and the lower part of the Kundan regional stages, corresponding to the global Darriwilian Stage, and more precisely the stage slices Dw1 and Dw2 (Fig. 2). The investigated strata belong to the informal Formation A + B ('Gillberga Formation') of the lower-middle Kundan Stage (Stouge and Bagnoli, 1990; Stouge, 2004), corresponding to the Lanna Limestone (upper part) and the Holen Limestone (lower part) in the traditional 'topostratigraphic' framework (e.g., Lindskog et al., 2018; Nielsen et al., 2023). The biostratigraphy of these units is well-established and mainly based on trilobites and conodonts (Fig. 2; Bohlin, 1949; Grahn, 1982; Jaanusson and Mutvei, 1982; Nordlund, 1989; Stouge and Bagnoli, 1990; Bagnoli and Stouge, 1997).

A total of 13 samples from Hälludden and 15 samples from Hagudden were collected for palynological studies. The stratigraphic position of these samples is shown in Fig. 2. The samples were processed using standard palynological procedures (Riding, 2021), which include the use of HF and HCl and micrometric mesh filters (15 and 51 µm) to extract two fractions of organic-walled microfossils (a first fraction of palynomorphs between 15 and 51 µm and a second fraction of material larger than 51 µm). The investigated palynological slides are stored in the collections of the Palaeontology research team of the Evo-Eco-Paleo CNRS research unit in the University of Lille.

3.2. Methods

In order to evaluate the composition and evolution of the acritarch assemblages throughout the studied sections, two independent counts of palynomorphs have been performed by two of the co-authors (JLCG, BC). During a first count, the acritarch assemblages were separated into 'morphotypes' whereas in the second count, the assemblages were classified into 'groups.' The two independent counts allow a quick view

on the relative proportion of the acritarch morphologies in the different assemblages, independent from previously established classification schemes. Moreover, in order to provide a neutral view on the assemblages present in the palynological slides, the relative proportions of acritarchs were observed by two co-authors (JLCG, BC) outside of the field, with no previous experience in acritarchs. The counts were thus made by voluntarily ignoring previously published data in acritarch literature (i.e., by not counting genera and species published in literature).

In each slide, a minimum of 200 acritarch specimens have been counted. The counts of the newly established categories are presented in Fig. 3. In the first count, the acritarchs present in the slides have been separated into the following five 'acritarch morphotype' categories, essentially based on the key character of process length/type (Fig. 3): acritarchs (1) with long processes, (2) with short processes, (3) with complex processes, (4) with few processes, and (5) with no processes. In the second count, the specimens were separated into six 'acritarch groups' represented by (1) the 'veryhachids' (simple morphologies of triangular or rectangular shape), (2) 'sphaeromorphs' (rounded vesicles without processes), (3) 'polygonomorphs' (polygonal vesicles), (4) 'multiplicisphaerids' (vesicles with complexly branched processes), (5) 'micrhystrids' (very small acritarchs, usually 20 µm in diameter or less), and (6) 'baltisphaerids' (rounded vesicles with simple, long, distally tapering processes). The counts of the six groups were additionally conducted for both fractions of the palynological material, i.e., in the slides with the fraction from 15 to 51 µm, and in the slides with the fraction larger than 51 µm (Fig. 4).

In addition to these aspects, two of the basic morphological parameters of acritarch specimens in all investigated samples were measured in order to detect changing trends in acritarch morphology: the vesicle diameter and the process (appendix) length. These measurements were made in a standard way (see Kroeck et al., 2021, Fig. 3). In order to avoid errors, only complete specimens were measured, displaying a vesicle

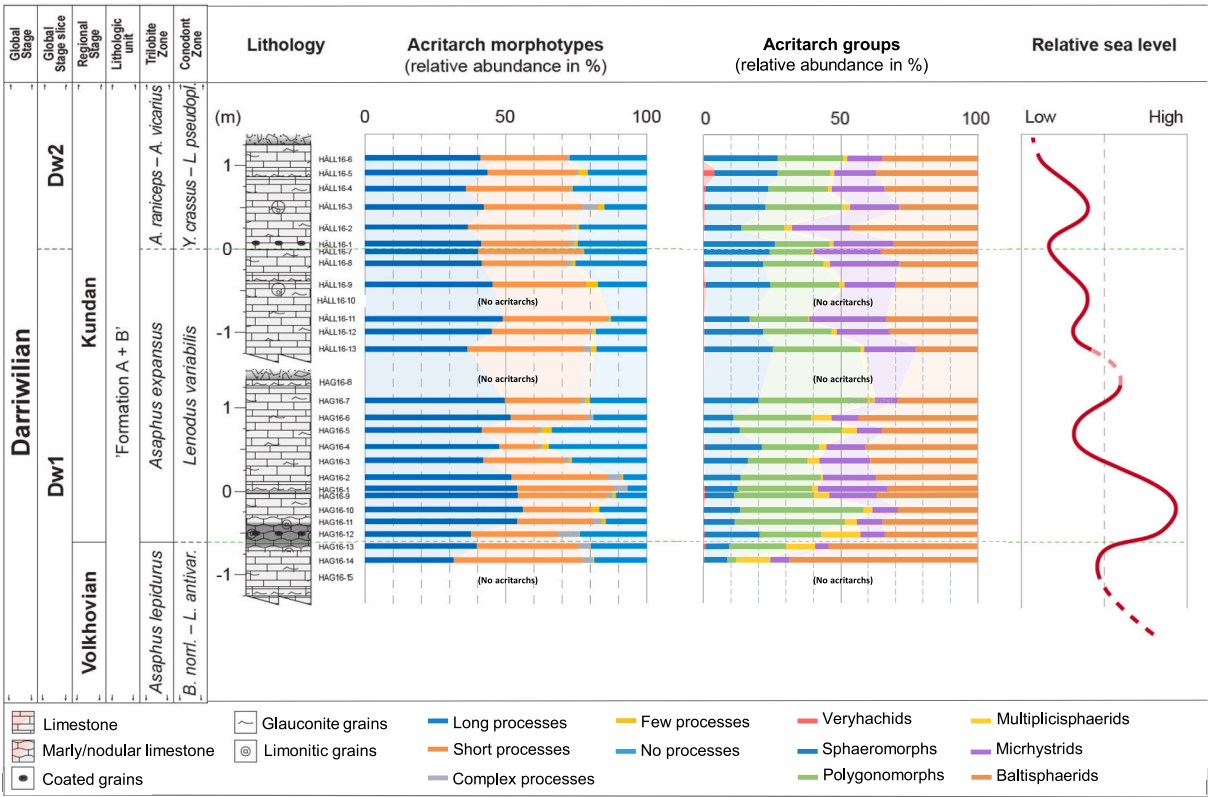


Fig. 3. Relative abundances (in %) of acritarch morphotypes and acritarch groups, as defined in the text, in the intervals sampled from the Hälludden and Hagudden sections.

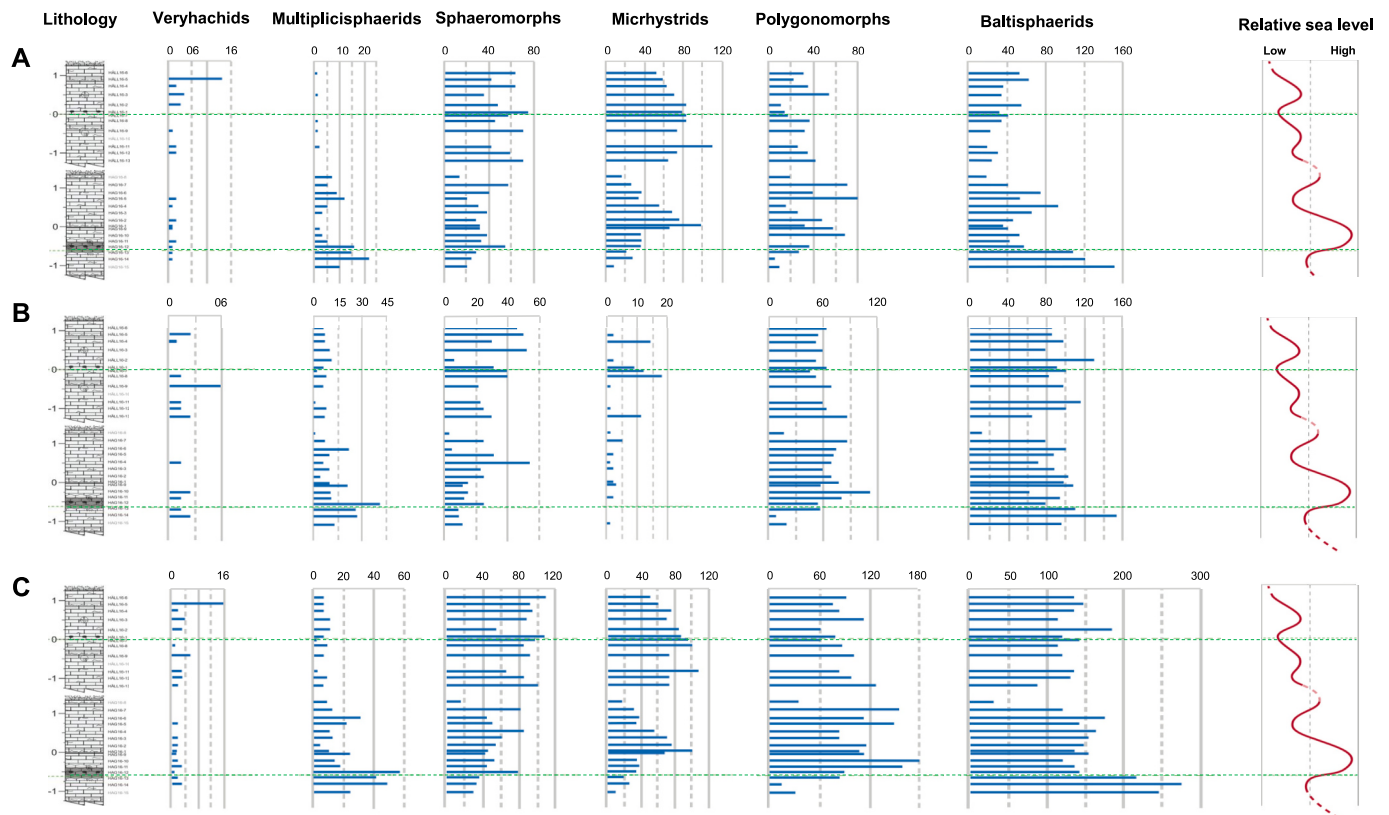


Fig. 4. Relative abundances (in %) of the six acritarch groups, as defined in the text, in the intervals sampled from the Hälludden and Hagudden sections. A: size fraction 15–51 μm ; B: size fraction $> 51 \mu\text{m}$; C: Total.

that was not disrupted and with complete processes that were not broken. The process length was measured by taking into consideration the mean value of the longest processes of a specimen. 200 specimens were measured for each sample of both sections. The evolution of these biometrics (process length, central body diameter, and the ratio central body diameter/process length) throughout the stratigraphic sequence are shown in Fig. 5.

In order to understand the interrelation between sedimentological and palynological parameters through the stratigraphic sequence, the morphological groupings of the acritarchs and their biometrical parameters are quantitatively compared to the sedimentological parameters (abundance of skeletal grains, glauconitic grains and cement). The potential relationship among all combinations of these parameters have been tested by Pearson and Spearman linear correlation tests (Table 1).

In addition, the relative abundance of the six acritarch groups has been ordinated by a correspondence analysis, CA (Fig. 6) with the aim to evaluate a potential gradient of these morphological groups through the stratigraphic sequence characterized by a sea-level shallowing trend through time. The multivariate analyses were performed using the software PAST (version 3.26; Hammer et al., 2001). For further details on these methods see, e.g., Legendre and Legendre (2012) and Hammer and Harper (2006).

4. Results

4.1. Distribution of acritarch morphotypes and acritarch groups

The patterns of proportion of acritarch morphotypes and acritarch groups through the study interval are illustrated in Figs. 3 and 4. Some general tendencies can be identified and a clear distinction of the changing assemblages is discernible. Regarding the proportions of the five acritarch ‘morphotypes’ (with long, short, complex, few, and no

processes), the following patterns are recognized: (1) the largest proportion of acritarchs are those with long processes, i.e., morphotypes with clearly visible long, simple processes (without distal ramification), the length of which is at least one third of the vesicle diameter ($\pm 10 \mu\text{m}$). Specimens belonging to this morphotype are commonly attributed to genera such as *Baltisphaeridium*. In the lower (but not lowermost) part of the section, these morphotypes are very abundant, and represent more than half of all specimens in the slides. Their relative proportion decreases slightly towards the top of the sequence, although it remains high (about 35 to 40 %). (2) The second largest proportion of morphotypes are the acritarchs with short processes. These are specimens with clearly visible, albeit short, processes, usually measuring less than one third of the diameter of the central body, or shorter ($\pm 5 \mu\text{m}$). Such morphotypes are commonly attributed to genera such as *Solisphaeridium* or *Comasphaeridium*. They are abundant in the lowermost part of the sections and they show fluctuating, but slightly decreasing values towards the top of the investigated sequence. (3) The third most abundant morphotype comprises the acritarchs without processes, i.e. simple spherical vesicles, usually attributed to sphaeromorphic genera such as *Leiosphaeridia*. With lower proportions at the base of the succession (about 20 %), their number increases to up to one third of all morphotypes higher in the sequence. (4) The acritarch morphotypes with complex processes, corresponding to taxa such as *Multiplicisphaeridium*, remain overall rare, but with a distinctive presence at the base of the succession, and very low sporadic occurrences at the top. (5) The final category observed herein comprised the morphotypes with few processes. They correspond to triangular or rectangular vesicles, usually attributed to the genus *Veryhachium*. These acritarchs are not very abundant, with no clearly discernible trend visible.

In the second, independent, analysis, another subdivision was used. The six identified groups partly resemble the subdivision of the acritarchs by Downie et al. (1963) and Downie (1973), but also the different

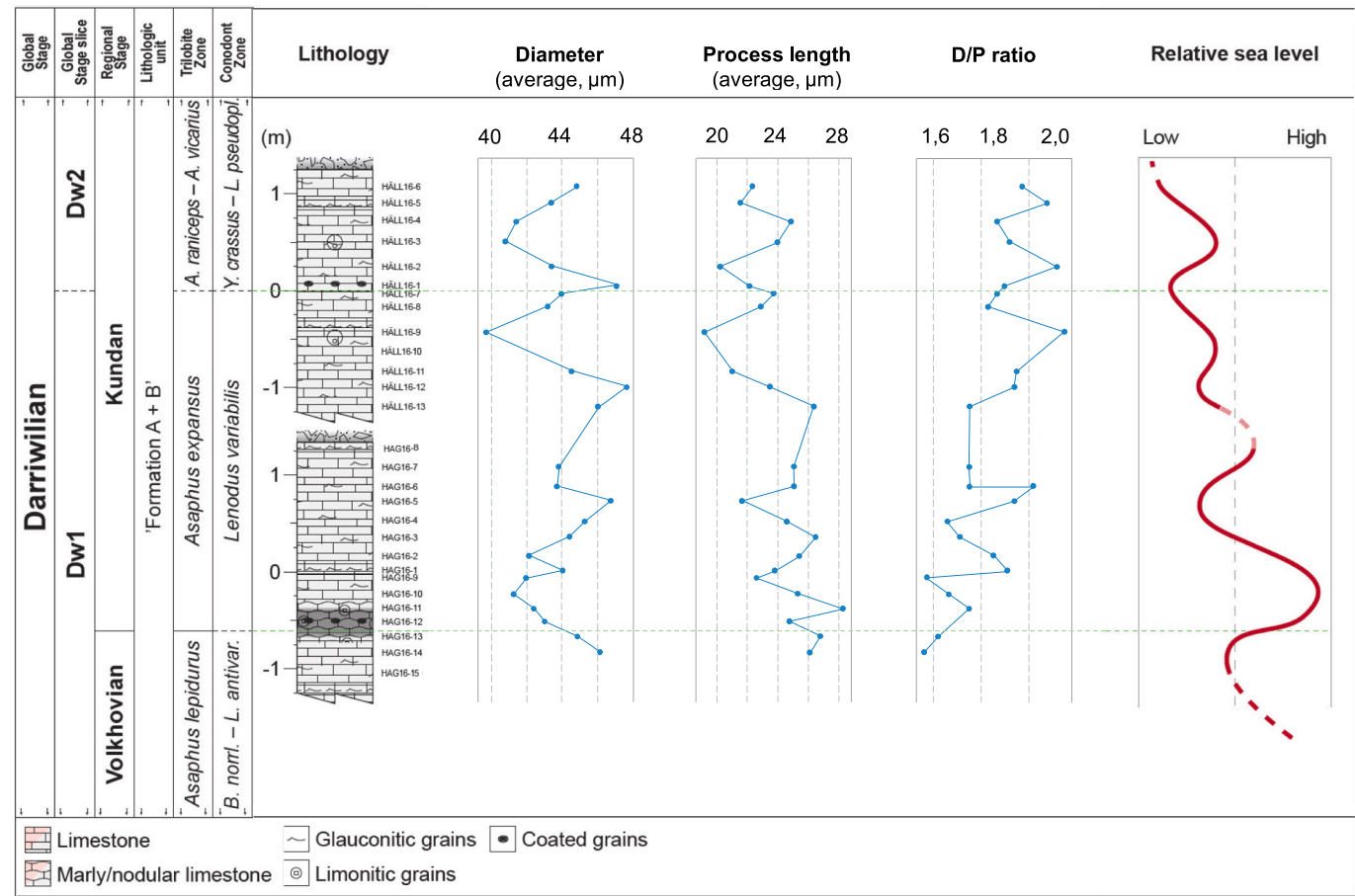


Fig. 5. Evolution of the central body diameter, the process length, and the ratio central body diameter/process length of the acritarch populations in the intervals sampled from the Hälludden and Hagudden sections.

genera used by Staplin et al. (1965, Figs. 1–8). These six groups are the following: veryhachids (including genera such as *Veryhachium*, *Villosacapsula*, etc.), sphaeromorphs (e.g., *Leiosphaeridia*), polygonomorphs (*Goniosphaeridium*, *Polygonium*), multiplicisphaerids (e.g., *Multiplicisphaeridium*, *Peteinosphaeridium*), micrhystrids (e.g., *Micrhystridium*), and baltisphaerids (e.g., *Baltisphaeridium*, *Pachysphaeridium*). Regarding the proportions of these six acritarch ‘groups,’ some clear tendencies also emerge throughout the succession. Clearly dominant, the baltisphaerids are especially abundant in the lowermost part of the section, comprising nearly 70 % of all taxa. This proportion continuously decreases, with about one third of all acritarchs being attributed to the baltisphaerids near the top of the sequence. Another group clearly shows a contrasting evolution: the sphaeromorphs are relatively rare at the base of the succession (less than 10 %) but they become increasingly abundant, representing about one quarter of all morphotypes towards the top of the sequence. Multiplicisphaerids are clearly present at the base (over 10 %) but progressively diminish, with very few specimens counted in the top of the succession. Micrhystrids show fluctuating proportions, with increasing values towards the top. Polygonomorphs also show fluctuating relative abundances, with very low numbers (less than 5 %) present in the lowermost sample. Veryhachids play only a miniscule role, with a single occurrence in the upper part of the succession.

To summarize, both counting techniques show a distinctive trend. Baltisphaerid acritarchs (spherical vesicles with long simple processes) decrease towards the top of the sequence. Multiplicisphaerid acritarchs (with complex processes) are present in low numbers only at the base of the succession. Sphaeromorph acritarchs (without processes) become increasingly abundant towards the top of the succession.

4.2. Distribution of acritarch groups related to sieving fractions

As the standard palynological techniques used in this study separates the investigated material in two sieving fractions, two sets of slides were obtained, a first set with the fraction from 15 to 51 μm, and a second set with the fraction larger than 51 μm. Fig. 4 illustrates the proportions of the six different acritarch groups in the two fractions. Whereas Fig. 4A illustrates the proportion in the finer fraction, Fig. 4B illustrates the larger one, and Fig. 4C shows a combination of the two.

Interestingly, the trends in the proportion of the acritarch groups are clearly visible in the different fractions, but the changing proportions vary from one fraction to another. The micrhystrid group is usually represented by acritarchs with smaller vesicles. Therefore, it is much more abundant in the fine (15–51 μm) fraction, with a clear trend of fluctuating proportions. However, in the larger fraction, this group is very rare and no trend is obvious. Sphaeromorphs are present in similar quantities in both fractions, and show similar trends. In the polygonomorph group, the tendency of diminishing proportion towards the top of the sequence is more evident in the finer fraction. The multiplicisphaerid and baltisphaerid groups are more abundant in the larger fraction. Whereas the trend of changing proportions in the multiplicisphaerid group is similar in both counts, the baltisphaerid group shows almost no tendency of proportional change in the larger fraction. However, in the finer fraction a clear trend is visible, with much higher proportions of both groups in the lower part of the fraction.

The different proportions of the morphotypes in the two different size fractions clearly demonstrates that the mesh size used in palynological laboratories matters and influences the results, in particular for counts with a palaeoecological objective. When interpreting the relative

Table 1

Pearson linear correlation tests between sedimentological (petrographical) data obtained from the analysis of carbonate textures (abundance of skeletal grains, glauconitic grains and cement – the matrix is the remaining part of the sediment), morphometric criteria (central body diameter: DiameterL; process length: ProcessL; and ratio central body diameter versus process length: Diameter/Process), and the six different acritarch groups (sphaeromorphs, veryhachids, micrhystrids, baltisphaerids, polygonomorphs, multiplicisphaerids). Asterisks indicate statistical significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Variable 1	Variable 2	Correlation		Variable 1	Variable 2	Correlation		Variable 1	Variable 2	Correlation	
Matrix	Cement	−0.61	**	Skeleton	Sphaeromorphs	0.08		Multiplicisphaerids	Polygonomorphs	−0.01	
Matrix	Skeleton	−0.72	***	Skeleton	Micrhystrids	−0.19		Multiplicisphaerids	Baltisphaerids	0.74	***
Matrix	Glauconite	−0.43	*	Skeleton	Polygonomorphs	−0.22		Multiplicisphaerids	ProcessL	0.36	
Matrix	Veryhachids	0.12		Skeleton	Baltisphaerids	0.24		Multiplicisphaerids	DiameterL	0.25	
Matrix	Multiplicisphaerids	−0.53	**	Skeleton	ProcessL	−0.05		Multiplicisphaerids	Diameter/Process	−0.48	*
Matrix	Sphaeromorphs	0.2		Skeleton	DiameterL	0.55	**	Sphaeromorphs	Micrhystrids	0.25	
Matrix	Micrhystrids	0.45	*	Skeleton	Diameter/Process	0.09		Sphaeromorphs	Polygonomorphs	−0.24	
Matrix	Polygonomorphs	−0.06		Glauconite	Veryhachids	−0.07		Sphaeromorphs	Baltisphaerids	−0.54	**
Matrix	Baltisphaerids	−0.39		Glauconite	Multiplicisphaerids	0.46	*	Sphaeromorphs	ProcessL	−0.3	
Matrix	ProcessL	−0.25		Glauconite	Sphaeromorphs	−0.51	**	Sphaeromorphs	DiameterL	0.03	
Matrix	DiameterL	−0.45	*	Glauconite	Micrhystrids	−0.49	*	Sphaeromorphs	Diameter/Process	0.31	
Matrix	Diameter/Process	0.24		Glauconite	Polygonomorphs	0.39		Micrhystrids	Polygonomorphs	−0.37	
Cement	Skeleton	0.37		Glauconite	Baltisphaerids	0.35		Micrhystrids	Baltisphaerids	−0.62	***
Cement	Glauconite	0.01		Glauconite	ProcessL	0.54	**	Micrhystrids	ProcessL	−0.5	*
Cement	Veryhachids	−0.11		Glauconite	DiameterL	−0.15		Micrhystrids	DiameterL	−0.06	
Cement	Multiplicisphaerids	0.06		Glauconite	Diameter/Process	−0.52	**	Micrhystrids	Diameter/Process	0.49	*
Cement	Sphaeromorphs	0.15		Veryhachids	Multiplicisphaerids	−0.15		Polygonomorphs	Baltisphaerids	−0.31	
Cement	Micrhystrids	−0.03		Veryhachids	Sphaeromorphs	−0.15		Polygonomorphs	ProcessL	0.25	
Cement	Polygonomorphs	−0.05		Veryhachids	Micrhystrids	0.06		Polygonomorphs	DiameterL	−0.29	
Cement	Baltisphaerids	−0.03		Veryhachids	Polygonomorphs	−0.1		Polygonomorphs	Diameter/Process	−0.2	
Cement	ProcessL	−0.12		Veryhachids	Baltisphaerids	0.04		Baltisphaerids	ProcessL	0.39	
Cement	DiameterL	0.39		Veryhachids	ProcessL	−0.27		Baltisphaerids	DiameterL	0.24	
Cement	Diameter/Process	0.04		Veryhachids	DiameterL	−0.13		Baltisphaerids	Diameter/Process	−0.42	*
Skeleton	Glauconite	−0.25		Veryhachids	Diameter/Process	0.41	*	ProcessL	DiameterL	0.08	
Skeleton	Veryhachids	−0.05		Multiplicisphaerids	Sphaeromorphs	−0.45	*	ProcessL	Diameter/Process	−0.88	***
Skeleton	Multiplicisphaerids	0.31		Multiplicisphaerids	Micrhystrids	−0.72	***	DiameterL	Diameter/Process	−0.05	

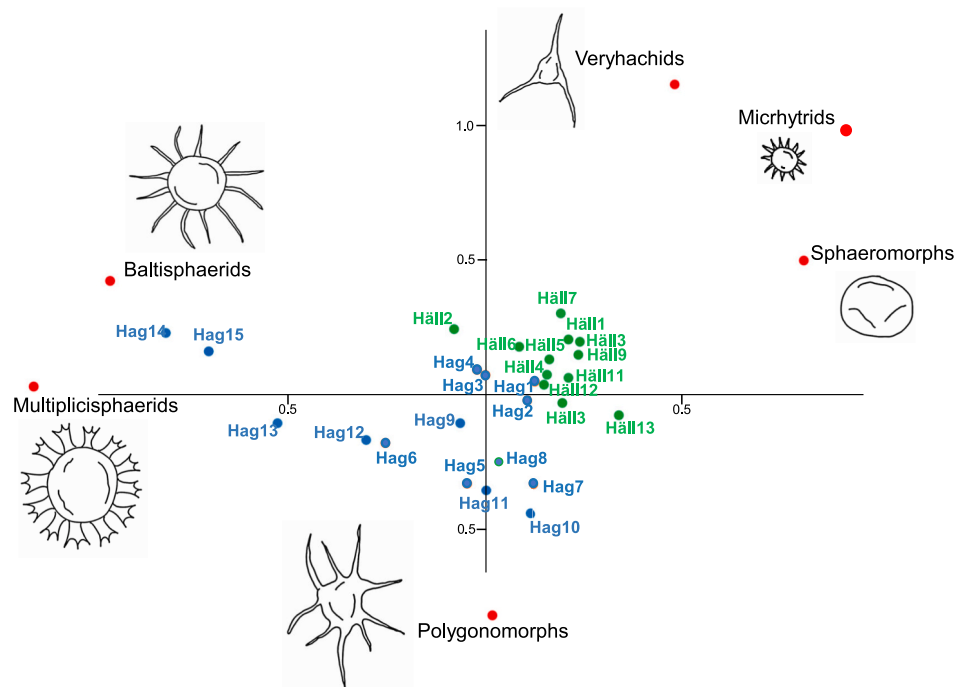


Fig. 6. Relative abundance of the six acritarch groups ordinated by a correspondence analysis (CA) indicating a gradient of the morphological groups through the stratigraphic sequence.

abundances of palynomorphs, it is therefore important to consider what size fraction is used, in particular when considering that different palynological laboratories use different mesh sizes for filtering.

4.3. Central body diameter and process length

Fig. 5 shows the results of the measurement of two classical biometric parameters in acritarch morphology: the diameter of the vesicle, and the length of the processes. The vesicle diameter in the study samples show values between 40 and 48 μm , with no clear trends. The process length, however, overall varies from longer processes (mean length up to 28 μm) in the lower part of the section, to slightly shorter processes higher in the succession (19 to 25 μm). Therefore, despite minor fluctuations, a clear trend can be observed, with processes becoming shorter towards the top of the investigated succession. This trend becomes even more obvious when the ratio of the vesicle diameter (D) versus process length (P) is analyzed. The D/P ratio displays values of about 1.6 in the lower part of the section, and over 2.0 in the upper part.

4.4. Comparison between acritarch morphologies and sedimentology

Table 1 illustrates the comparison between results of sedimentological (petrographical) data, obtained from the analysis of the carbonate textures, consisting of proportions of sediment matrix (%), cement (%), skeletal grains (%) and glauconite grains (%), and morphological acritarch criteria (process length, central body diameter, and the ratio central body diameter/process length), together with the proportions of the six acritarch groups outlined above (veryhachids, sphaeromorphs, polygonomorphs, multiplicisphaerids, micrhytrids, and baltisphaerids).

These correlations provide useful insights to some of the assumptions above. Spearman and Pearson correlation tests were run, providing very similar results. The analyses show several significant correlations among the three data sets (sedimentological data, morphological criteria, and the proportion of the acritarch groups). Asterisks indicate statistical significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ (Table 1).

Regarding the acritarch groups, only some of them show strong correlations. Multiplicisphaerid and baltisphaerid acritarchs have a strong positive correlation, with both groups commonly occurring together, which may suggest a similar life habitat. By contrast, there is a strong negative correlation between multiplicisphaerid and micrhytrid acritarchs, and, to a lesser extent, between micrhytrid and baltisphaerid acritarchs, that possibly indicates that these groups had different habitats. Similarly, there are negative correlations between multiplicisphaerid and sphaeromorph acritarchs, and between baltisphaerid and sphaeromorph acritarchs.

The Pearson correlation test (Table 1) indicates no relation between process length and central body diameter ($R = 0.08$). However, there is a strong negative correlation between process length and the ratio diameter/process length. Importantly, the process length shows a clear and significant correlation ($R = 0.54$; $p < 0.01$) with the percentage of glauconite grains, and, thus, with sea level (via, e.g., hydrodynamic effects such as winnowing). A correlation between the percentage of skeletal grains and the diameter of the acritarch vesicles also exists ($R = 0.55$; $p < 0.01$). This suggests that morphological data are related to the observed trend of a progressive shallowing of the water depth, recognized in the shortening of acritarch processes towards the top of the sequence (and increasing grain amounts compared to fine-grained matrix). However, for the vesicle diameter there seems to be no distinct pattern. Furthermore, not all acritarch groups are correlated with the percentage of glauconite grains, which is assumed to reflect sea-level depth: veryhachids are not correlated ($R = -0.07$); multiplicisphaerids are positively correlated ($R = 0.46$) whereas sphaeromorphs and micrhytrids are negatively correlated ($R = -0.51$ and $R = -0.49$, respectively).

Finally, the correspondence analysis (CA) provides insights into the distribution of the six acritarch groups (Fig. 6). The samples from Hälludden and Hagudden show a gradient in the ordination space that matches the stratigraphic sequence and, thus, the shallowing sea-level trend. The biplot also clearly shows that this gradient is related to the relative abundance of baltisphaerids, multiplicisphaerids and polygonomorphs on the one side, and veryhachids, micrhytrids and sphaeromorphs on the other side. This pattern fully corroborates the

results of those identified by the significance tests.

Therefore, the results highlight that acritarch assemblages not only reflect evolution through time, but also changing palaeoenvironments such as palaeobathymetry. In this context, it appears that baltisphaerids and multiplicisphaerids tend to be more abundant in deeper-water environments whereas they are replaced by micrhystrids and sphaeromorphs in shallower waters. It is worthwhile to note that the two other acritarch groups, veryhachids and polygonomorphs, are neither correlated with the previously discussed groups nor to the perceived sea-level gradient, and therefore their primary influential factor remains uncertain.

5. Discussion – ecostratigraphy rather than biostratigraphy?

In recent years, acritarchs have very often, and mostly, been used as biostratigraphical tools. Taxa were and are typically described from vertical sedimentary sequences, with the interpretation that the succession of different acritarch morphologies reflects a biostratigraphical change. However, studies of coeval sedimentary sequences from different palaeoenvironmental settings (or different parts of a sedimentary basin) are almost lacking in acritarch research, in particular in recent years. The comparison of samples of the same age, but from different parts of a sedimentary basin remains the exception in acritarch research (e.g., Li et al., 2004; Stricanne et al., 2004).

The Ordovician of Öland has been the subject of many palynological studies (see Section 2.2). Several of the most commonly found acritarch taxa have been described from the island by some of the pioneers in acritarch research. On the one hand, some of these taxa have become ‘waste-basket’ taxa, such as several species of *Baltisphaeridium* and *Multiplicisphaeridium* that were established with a wide original diagnosis allowing the inclusion of many different morphotypes. On the other hand, some authors described very narrowly diagnosed new ‘species’ with the objective to create biostratigraphical markers. In addition, many acritarch taxa have proven to represent species plexuses leading to taxonomic dilemmas. For example, the peteinoid acritarchs with the three genera *Peteinosphaeridium* (a genus described and erected from the Ordovician of Öland by Staplin et al., 1965), *Cycloposphaeridium* and *Liliosphaeridium*, illustrate well this dilemma because the various peteinoid taxa can hardly be discerned (see Kroeck et al., 2021). Considering this, can peteinoid acritarchs actually be used as stratigraphical or even palaeobiogeographical markers (Tongiorgi et al., 1995), or are they all cysts of a single dinoflagellate-like organism that produced a wide range of morphotypes (see Mertens et al., 2009)?

Therefore, many palynologists working on rich, well-preserved, and highly diverse acritarch assemblages encounter a number of problems, because it appears difficult to identify clearly stratigraphical markers within the morphotypes displaying a large variability. Another question arises about the classification of genera that include too many species of which most are probably synonyms. The morphological plasticity makes it difficult to distinguish individual taxa, because morphotypes integrate not only at the species level, but sometimes also between genera.

In the present study, the analyses span a portion of the Middle Ordovician (Darriwilian) of Öland, and the regional Kundan Stage. This interval has been investigated numerous times, and contains a very high microfossil diversity and abundance, with specimens in outstanding preservation. Therefore, it is possible to pose the question if an ecological signal is present in the acritarch communities of Öland.

Our results can be interpreted in comparison with previous studies. The presence of specific morphological characteristics that may function as a proxy for sea level was analyzed from the Silurian of Gotland, Sweden, by Stricanne et al. (2004). The Gotland succession allows for the observation of an onshore-offshore transect, as the sediments from different palaeoenvironmental settings are excellently preserved on the island. The presence of acritarchs with larger and more complex processes was found on the carbonate shelf formed under relatively deeper-water conditions (Stricanne et al., 2004). In contrast, the occurrence of

smaller acritarchs lacking processes indicates shallower marine and more nearshore settings of the Silurian of Gotland. The Öland sections compare well with the Gotland example, with the upper part of the Hälludden succession providing a greater number of sphaeromorphs, inferring relatively shallower palaeoenvironments. By contrast, the lower parts of the Hagudden section, which yields a greater proportion of specimens with long and complex processes (corresponding to the baltisphaerids and multiplicisphaerids) infer more open marine conditions. Stricanne et al. (2004) also observed changing tendencies in process lengths. They noted that morphotypes with shorter processes are mainly present in proximal environments, whereas longer and ramified processes occur more distally on the shelf. For the sections studied herein, the aforementioned acritarch characteristics suggest that the lower part of the studied interval (Hagudden section) was further offshore, with acritarch specimen displaying longer processes. However, in the upper part (Hälludden section), the processes are relatively shorter, further corroborating the interpreted sea-level trends.

In a study from the Cambrian–Ordovician boundary interval of the Algerian Sahara, Servais et al. (2004) observed the morphological changes in the galeate acritarch plexus, and identified more complex processes and an increasing process length in the samples deriving from deeper water palaeoenvironments, which again is comparable to the trends observed in Öland.

With respect to their relative abundance, the acritarch biofacies of the Öland sections can also be compared to the inshore–offshore trend observed by Li et al. (2004) from a similar time interval (Early–Middle Ordovician boundary interval) from Yangtze Platform sections in South China. Similarly to Gotland and Öland, the Chinese transect documents inshore and onshore settings, but probably no slope and clearly no deep-water (basin) environments. Li et al. (2004) noted higher proportions of baltisphaerid acritarchs and specimens with complex branching (*Rhopaliophora* and *Peteinosphaeridium*) on the more distal shelf, and less abundant proportions of these acritarchs in nearshore settings. On the other hand, sphaeromorphs (‘leiosphaerids’) and micrhystrids were comparably abundant in nearshore environments of the Yangtze Platform transect (Li et al., 2004, Fig. 6). The cool-/temperate-water acritarch assemblages from the Öland sections show similar gradients in characteristics to those observed on the Yangtze Platform shelf platforms, with more abundant *Peteinosphaeridium* (multiplicisphaerid group) in the Chinese sections reflecting more onshore settings, similar to what is observed on Öland.

These studies echo some of the historical scenarios that were described by palynologists who were not merely focused on biostratigraphy, but who also studied the acritarch assemblages from a more palaeobiological or palaeoecological point of view. For example, already Staplin (1961) observed that thin-spined acritarchs occur close to the reef areas in the Devonian of Alberta, Canada, whereas the taxa with longer and thicker processes are more abundant at a greater distance from the reefs. Riegel (1974) investigated the Lower and Middle Devonian of the Eifel area in western Germany and described low-diversity assemblages from ‘neritic’ facies and high diversity acritarch microfloras from more ‘pelagic’ facies. Already at that time, some five decades ago now, Riegel (1974) declared that the composition of the acritarch assemblages of the Devonian of the Eifel area was probably controlled more by facies than by climatic or phylogenetic changes.

Another set of instructive studies is that of the Silurian of Wales and the Welsh Borderland by Dorning (1981, 1987) who divided the acritarch assemblages into three ‘classes’ (nearshore, offshore, deep water) based on semi-quantitative analyses. Similarly, Dorning and Bell (1987) distinguished four assemblages typical of reef limestone environments, shallow shelf carbonates, open shelf carbonates, and deeper shelf environments, respectively. Subsequently, Richardson and Rasul (1990) described the palynological distribution in a vertical succession as a regressive sequence present in the upper Silurian of that same area. They distinguished different ‘palynofacies’ in which specific associations correspond to different depositional environments.

Similar studies on the extremely rich, highly diversified, and well-preserved acritarch assemblages from the Ordovician of Sweden have never before been carried out. The acritarchs of the Ordovician of Öland have until now never been analyzed from a palaeoecological framework, but were mostly the focus of the research related to biostratigraphical markers (Tongiorgi and Ribecai, 1990; Ribecai and Tongiorgi, 1995; Bagnoli and Ribecai, 2000).

The present study is a first attempt to investigate the Öland acritarchs with the objective to understand if and how their distribution is regulated by a palaeoecological signal. The multivariate analyses (Fig. 6; Table 1) succinctly illustrate the challenges concerning acritarch associations, showing that the Hälludden and Hagudden sections have co-developed within similar environmental conditions (i.e., relatively shallow-water environments on a carbonate platform/ramp) but documenting a continuous, long-term trend, that allows a distinction between the two localities in terms of progressively changing palaeoenvironments (Fig. 6). The multivariate analyses document a palaeoecological signal, suggesting the possibility that the control on the distribution and relative abundance of different acritarch taxa is related to the palaeoenvironment (notably, relative sea level). There are possibly no biostratigraphical signals (no new incoming species). However, it seems likely that the acritarch assemblages from Öland simply follow eustatic cycles (transgression–regression) that have a direct influence on the marine microphytoplankton communities, but also on the morphology of the acritarch morphotypes (historically attributed to different genera and species), with possibly a high ecophenotypism.

Moreover, it is so far difficult to correlate the local Öland trend at a larger scale, with for example sections from the United Kingdom or China, that have also been investigated in great detail. In addition, the sea-level change recorded on Öland does not necessarily follow a global trend (e.g. Haq and Schutter, 2008). It would therefore be premature to extrapolate the results from this part of the Baltic area at a larger (global) scale.

Similar re-investigations of the acritarch communities from other areas with good biostratigraphical and sedimentological control would be interesting, and would allow for testing of our hypothesis. Hälludden and Hagudden show important changes occurring in the local depositional environment, and the overall sedimentological/petrographical patterns and trends are remarkably similar to those seen elsewhere in Baltoscandia (and, possibly, abroad). For example, Lindskog et al. (2018) investigated an interval including coeval strata at Lanna, southcentral Sweden, showing similar variations in carbonate textures and fossil grain assemblages, making the interpretation of the relative sea level possible. It would be interesting to investigate the palynomorphs of those strata and compare the results with those of Öland. It would also be valuable to extend the studies on Öland to investigating sections that expose the lower part of the succession covered herein, which was deposited further offshore.

To conclude, if the hypothesis that acritarch morphologies partly are controlled by environmental factors is corroborated by our further analyses, this may, at first glance, seriously question the biostratigraphical reliability and/or significance of acritarchs. However, it is obvious that acritarchs do have a great biostratigraphical potential and that it is very easy to distinguish, for example, Cambrian, Ordovician and Silurian rocks. But acritarchs can not only be used at a large scale, with low stratigraphical resolution. It is clear that among the large amount of morphotypes in the highly diverse acritarch communities, a few taxa have short stratigraphical ranges, that can be depicted by the palynologists for biostratigraphical applications, as it is done on a daily basis in the petroleum industry. Thus, not all acritarch taxa are biostratigraphical markers, but a few are.

Servais et al. (2018), for example, selected a number of Early–Middle Ordovician acritarch taxa that clearly provide biostratigraphical signals. The morphological plasticity of the taxa was analyzed in detail, so that the ecophenotypic signal could be distinguished from genotypical

characters. The first appearance data (FAD) of the selected morphotypes can be used, with accuracy, to precisely date the stratigraphical levels where these taxa occur, allowing precise international correlations. The iconic acritarch genus *Veryhachium* (with several hundreds of species described) is a perfect example. Although numerous species have been observed, essentially based on varying process lengths, the simple morphology of *Veryhachium* first appears in the Tremadocian (Servais et al., 2007), making the genus of great biostratigraphical use (as a marker of Tremadocian or younger rocks), despite the confusing taxonomic situation at the species level. Most interestingly, the *Peteinosphaeridium* plexus was shown to have a very high biostratigraphical value: the peteinoid acritarchs first appear in the Early Ordovician Tremadocian Tr3 Stage Slice. This first occurrence can be correlated and is therefore a useful biostratigraphical tool. On the other hand, the significant morphological changes within the peteinoid plexus (*Peteinosphaeridium*, *Cycloposphaeridium* and *Liliosphaeridium*), as visible in Öland, most probably reflect local or regional ecological conditions, which makes the different taxa potentially of high ecostratigraphical use, i.e. they indicate specific palaeoecologies, but not time.

Attempts at discriminating time and ecological components in the stratigraphic distribution of taxa represent an old dilemma (Gradstein et al., 1985; Guex, 1991; Holland and Patzkowsky, 2002). For acritarchs, this could be resolved by quantitative biochronological studies at regional and global scales, as has been done for other fossil groups (Cody et al., 2008; Sadler et al., 2009, 2011; Goldman et al., 2013; Paluvere et al., 2014; Monnet et al., 2015; Fan et al., 2020), and by clearly accounting for various palaeoenvironments in an ‘eco-biostratigraphical’ approach (Abdelhady et al., 2021). To strengthen the (bio-)stratigraphical potential of the acritarchs, it will be necessary, in the future, to adopt the modern computing methods that have become standard for other fossil groups.

Although it is highly probable that the observed local sea-level fluctuations are responsible for the compositional distribution in the acritarch assemblages, additional studies are needed, also from other areas of the Baltic shelf area, to confirm the trends observed in the present study.

6. Conclusions

A palynological re-investigation of ‘classical’ sections of the Middle Ordovician from Öland, Sweden, provides new insights to acritarch communities that have been studied for several decades. Our study indicates gradual changes in assemblage compositions, following a dominantly regressive trend during the lower Darriwilian. This is reflected by: (1) decreasing numbers of acritarchs with complex processes (baltisphaerid and multiplicisphaerid acritarchs), (2) increasing numbers of simple morphotypes, including sphaeromorph acritarchs, (3) decreasing process lengths.

As underlined by taxonomic studies published during the last few decades, it appears increasingly difficult to recognize and distinguish separate acritarch taxa (species and genera), in particular in the well-preserved assemblages from Öland. However, the assemblages can be integrated into a wider context, as communities in larger populations clearly interact with the environment, and reflect palaeoecological changes. For example, water depth, which is most probably related to other parameters, such as salinity or turbulence, can be tracked through the morphological changes in acritarch morphotypes (changing process lengths) and communities (relative proportions).

Following the principle of ecostratigraphy, most fossil groups show not only differences with time, but also space. As such, the acritarch taxa and communities from Öland can be interpreted in an ecostratigraphical context. The composition of the acritarch assemblages from the different samples does not necessarily reflect phylogenetic changes with time, but clearly the changing palaeoenvironment. The acritarchs from the investigated sections of Öland obviously conform to a palaeoecological pattern.

This study reinforces the fact that acritarchs are clearly not facies independent, and that their stratigraphical distributions are to some extent controlled by the palaeoenvironment. This also means that successive occurrences of species described from the Öland succession may have less biostratigraphical significance than previously thought. Nevertheless, despite a clearly visible morphological plasticity (usually at the species level), some innovative morphological parameters in selected taxa (usually at the generic level) appear to be clearly controlled by the genotype and make these taxa thus biostratigraphically useful.

Therefore, in the future, the accuracy of acritarchs as biostratigraphic markers must be evaluated in a palaeoecological frame, by taking into account the various sediment facies where they occur. The use of computer-based quantitative biochronological techniques appears necessary to achieve these goals.

Declaration of competing interest

We declare that we have no conflict of interest regarding our manuscript.

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Data availability

Data will be made available on request.

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Complete List of Authors:	CAILLAUD, Virgile; Université de Lille, Sciences de la Terre Birolini, Enzo; Université Claude Bernard Lyon 1 Faculté des Sciences et Technologies, Laboratoire de Géologie de Lyon Lefebvre, Bertrand; UMR CNRS 5276, LGLTPE Manzano, Eiver Michel, Soline; Université Claude Bernard Lyon 1, École Normale Supérieure de Lyon, CNRS, UMR5276, LGL-TPE Régner, Sylvie Vaucher, Romain; James Cook University, Earth and Environmental Science Servais, Thomas; University of Lille, CNRS UMR 8198
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Acritarchs from the Floian (Early Ordovician) of the Montagne Noire, France: biostratigraphical and palaeobiogeographical implications

Virgile CAILLAUD, Enzo BIROLINI, Bertrand LEFEBVRE, Eiver Gelan MANZANO, Soline MICHEL, Sylvie REGNIER, Romain VAUCHER, Thomas SERVAIS

Virgile CAILLAUD [virgile.caillaud.etu@univ-lille.fr], *Univ. Lille, CNRS, UMR 8198 Evo-Eco-Paléo, F-59000 Lille, France.* **Enzo BIROLINI** [enzo.biolini@etu.univ-lyon1.fr], Université Claude Bernard Lyon 1, École Normale Supérieure de Lyon, CNRS, UMR5276, LGL-TPE, Villeurbanne, France. **Bertrand LEFEBVRE** [bertrand.lefebvre@univ-lyon1.fr], Université Claude Bernard Lyon 1, École Normale Supérieure de Lyon, CNRS, UMR5276, LGL-TPE, Villeurbanne, France. **Eiver Gelan MANZANO** [eivergelan.manzano@univ-lille.fr], *Univ. Lille, CNRS, UMR 8198 Evo-Eco-Paléo, F-59000 Lille, France.* **Soline MICHEL** [michel.soline@gmail.com], Université Claude Bernard Lyon 1, École Normale Supérieure de Lyon, CNRS, UMR5276, LGL-TPE, Villeurbanne, France. **Sylvie REGNIER** [sylvie.regnier@univ-lille.fr], *Univ. Lille, CNRS, UMR 8198 Evo-Eco-Paléo, F-59000 Lille, France.* **Romain VAUCHER** [romain.vaucher@jcu.edu.au], Department of Earth Sciences, University of Geneva, Geneva, Switzerland and College of Science and Engineering, James Cook University, Townsville, QLD, 4811, Australia., **Thomas SERVAIS** [thomas.servais@univ-lille.fr], *Univ. Lille, UMR 8198 Evo-Eco-Paléo, F-59000 Lille, France.*

ORCID

Virgile Caillaud : <https://orcid.org/0009-0002-9100-9141>
Enzo Birolini <https://orcid.org/0009-0008-4122-7865>
Bertrand Lefebvre <https://orcid.org/0000-0002-3803-9176>
Eiver Gelan Manzano <https://orcid.org/0009-0001-3403-6306>
Soline Michel
Sylvie Régnier
Romain Vaucher <https://orcid.org/0000-0003-3051-4128>
Thomas Servais <https://orcid.org/0000-0002-4089-7874>

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Abstract

The Early Ordovician Cabrières Biota was recently discovered in the southern Montagne Noire (southern France). The present study describes the acritarch assemblages from the siltstone and claystone of the Landeyran Formation from several localities displaying the Cabrières Biota, and from the Landeyran section that is coeval with the fossil-bearing unit. The moderately to well-preserved organic-walled microfossils allow the identification of a rich and diverse palynoflora bearing different important biostratigraphical and palaeobiogeographical markers. The presence of typical Early Ordovician index species, such as *Coryphidium bohemicum*, *Ampullula* spp., *Barakella* spp., together with the absence of the genera *Arkonia*, *Frankea*, *Orthosphaeridium* and *Dicrodiacrodium*, allow an assignment to the late-middle to early-late Floian (transition FI2 to FI3), confirming biostratigraphical data from trilobite and graptolite biozonations. The presence of the genera *Acanthodiacrodium*, *Arbusculidium*, *Coryphidium* and *Striatotheca* enables the attribution of the southern Montagne Noire area to the peri-Gondwana acritarch province in high southern latitudes. The presence of the genus *Ampullula* in the late Floian in the southern peri-Gondwana province allows a modification of its First Appearance Datum in this province where it was previously only recorded from the early Darriwilian.

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Keywords

Cabrières Biota, Landeyran Formation, palynology, phytoplankton, early Palaeozoic, peri-Gondwana

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Introduction

The southern part of the Montagne Noire, located in the South of France, is a well-studied area displaying an almost complete geological succession from the early and middle Palaeozoic (Cambrian–Devonian). Since almost a century, the different paleontological studies in this area have allowed to identify the presence of trilobites, mollusks, brachiopods, conodonts, echinoderms, conulariids, graptolites, hyoliths and other groups (Thoral, 1935; Ubaghs 1969, 1987, 1998; Courtessole 1973; Capéra *et al.* 1978; Babin *et al.* 1982; Courtessole *et al.* 1983; Vidal 1996; Vizcaïno & Lefebvre 1999; Shergold *et al.* 2000; Vizcaïno *et al.* 2001, 2004; Tortello *et al.* 2006 ; Štorch and Feist 2008; Kröger and Evans 2011; Devaere *et al.* 2014; Ebbestad *et al.* 2020 ; Van Iten and Lefebvre, 2020; Dupichaud *et al.* 2023). A specific biota, recently discovered in the area of the village of Cabrières, was named the Cabrières Biota. Featuring groups already known from either Cambrian or Ordovician Lagerstätten, the Cabrières Biota bears a unique taxonomic composition for the Early Ordovician, dominated by algae and sponges. In a first study of the new Lagerstätte, Saleh *et al.* (2024b) mentioned the presence of many others marine fossils (arthropods (trilobites, ostracods), brachiopods, cnidarians (conulariids), graptolites, hyolithids, molluscs (cephalopods, gastropods, rostroconchus) and vermiforms organisms that are currently studied in more detail (Harper *et al.* this volume; Polechová *et al.* this volume; Van Iten *et al.* this volume). Among the different fossil groups, the Cabrières Biota is characterized by a majority of non-biomineralized organisms preserving soft tissues, like algae, bivalved arthropods, chelicerates, hemichordates, lobopodians, and sponges. Although, biomineralized remains without soft-tissue preservation including brachiopods, echinoderms, mollusks, and trilobites are also present in lower proportion, the exceptional preservation indicates that the biota corresponds to a Konservat-Lagerstätte (Seilacher 1970; Kimmig & Schiffbauer 2024). Corresponding to the late Early Ordovician (Floian), the Cabrières Biota is present in the lower part of the regional Landeyran Formation, for which different sedimentological studies were conducted in the last decades (Noffke & Nitsch 1994; Vizcaïno *et al.* 2001; Vaucher *et al.* this volume). Located around 67-68°S according to palaeomagnetic data (Nysaether *et al.* 2002), the Montagne Noire was located on the southern margin of Gondwana during the Middle Ordovician. However, the palaeobiogeographical information provided by different groups in the Cabrières Biota suggest even higher latitude settings (Saleh *et al.* 2024b). These very high latitudes are corroborated by palaeogeographical and palaeontological studies, making the Cabrières Biota one of the very few Lagerstätten typically characteristic of polar ecosystems of the Early Ordovician, similar to the Fezouata (Anti-Atlas, Morocco) and Klabava (Czech Republic) biotas (Saleh *et al.* 2024a). This almost unique Lagerstätte of the Montagne Noire underlines that the Early Ordovician, bearing the Cabrières Biota, should be considered as essential for the understanding of the composition and operation mode of marine ecosystems between the Cambrian 'explosion' and the Ordovician radiations.

Defined by Evitt (1963), the group "Acritarchs" includes organic-walled microfossils of uncertain origin characterized by a vesicle, displaying variable shapes, with or without different kinds of processes (appendages). Acritarchs of the Early Ordovician are well

described in diverse areas of the world, in particular from Bohemia, Czech Republic (e.g. Vavrdová 1965, 1973, 1977, 1979, 1986, 1990), Sweden (e.g. Gorká 1987; Tongiorgi & Ribecai 1990; Kroeck *et al.* 2021; Rubinstein & Vajda 2023), the British Isles (e.g. Booth 1979; Turner 1985, Molyneux & Dorning 1989; Molyneux 2009), North Africa (e.g. Cramer & Díez 1977; Vecoli & Le Hérissé 2004; Nowak *et al.* 2015, 2016), South America (e.g. Kroeck *et al.* 2020) and China (e.g. Brocke *et al.* 2000, Li *et al.* 2004, 2006; Yan & Li 2010; Yan *et al.*, 2011, 2013, 2023).

Ordovician acritarchs have also been described from southern France (e.g. Deflandre 1942, 1945; Martin 1973; Rauscher 1971, 1974; Baudelot & Bessière 1975, 1977; Fournier-Vinas & Donnot 1977; Fournier-Vinas 1978) and to a lesser extend from western France (e.g. Paris & Le Hérissé 1992). However, the area of the Montagne Noire has not been re-investigated after the early 1980s. The study of palynomorphs within this area remains rather complicated because of the strong deformation, recrystallization and metamorphism affecting the rocks of the early Palaeozoic. Different localities have provided variable preservation degrees of palynomorphs, including acritarchs and chitinozoans. Over five decades ago, moderately well-preserved organic microfossils were described from rocks from the Landeyran Valley, La Roquemaillère (Monts de Cabrières) and the Monts de Pardailhan by several authors. While Rauscher (1971) mainly discussed the general characteristics of the assemblages (sub-groups and main genera) assigning the microfloras to the Early Ordovician (Tremadocian and Arenigian), Martin (1973) provided a more detailed taxonomical investigation based on samples from the Mont de Cabrières and Mont de Pardailhan areas, describing 17 genera and 56 species, including 15 new species and one new sub-species, from levels attributed to the Early and Middle Ordovician (Tremadocian and Arenigian/Llanvirnian).

The present work is a part of a broader concerted effort to holistically evaluate the Cabrières Biota using palaeontology, sedimentology, biostratigraphy, geochemistry, and palaeoecology. Here, we present a palynological study based on acritarchs, collected from the Carbières Biota Lagerstätte, as well as from another location (Landeyran section), displaying a complete succession of the Landeyran Formation in the Landeyran Valley, approximately 25 km West-South-West of the village of Cabrières, that can be considered as coeval with the levels including the fossil-bearing horizons of the Cabrières Biota. The main objective of this study is to analyze the biostratigraphical signal present in the acritarch assemblages. In addition, the palaeobiogeographical signature of the assemblage is documented.

Geological Setting

The Montagne Noire is a complex tectonostratigraphic unit, formed during the Variscan Orogeny, located in the southern part of the French Massif Central (Fig. 1). Its formation has long been debated, however, the latest studies agreed on a complex process of fold and thrust belts in an important sinistral East-North-East transpressive context linked to the axis of the Cévennes Fault (e.g. Demange 1999; Chardon *et al.* 2020). The presence of sedimentary and metamorphic rocks, and the strong

deformation that affected both of them, allowed a distinction of the Montagne Noire in three main parts: a northern and a southern deformed sedimentary flank, separated by an axial zone (Fig. 1) (Gèze 1949; Arthaud 1970; Montmartin *et al.* 2021; Lefebvre *et al.* 2023). This axial zone is mainly characterized by an elongated dome formed by an association of migmatized orthogneiss, paragneiss and other rocks that experienced a partial melting, and whose protoliths were parautochthonous units of Ordovician age (from 472 Ma to 416 Ma) (Roger *et al.* 2004; Montmartin *et al.* 2021; Lefebvre *et al.* 2023). The southern part of the Montagne Noire is mainly composed of an almost-complete inverted stratigraphic succession of sedimentary layers from the Cambrian to the Devonian, organized in nappes or units that suffered strong deformation (recumbent folds, sheath folds...) during the Carboniferous. Among those different units, the Ecailles de Cabrières correspond to very dispersed Ordovician to Carboniferous layers, transported over a wildflysch succession (Gèze 1949). They clearly differ from the other nappes from the southern part from the Montagne Noire (Minervois, Monts de Pardailhan, Mont de Faugères, Mont Peyroux...) (Fig.1) by bearing different Ordovician successions and faunas (de Rouville & Delage 1892; Miquel 1894; Thorat 1941; Colmenar *et al.* 2013 Álvaro *et al.* 2016, 2018; Lefebvre *et al.* 2023).

The main palaeogeographical and part of the sedimentological settings of the southern Montagne Noire during the Ordovician have already been investigated since the 19th century. Different studies have shown a high to very-high latitude setting of the Montagne Noire during the Ordovician. Mainly based on the analysis of Middle Ordovician olistolithic blocks from the Ecailles de Cabrières, Nysaether *et al.* (2002) already assigned very high latitudes (67/68°S) to the Montagne Noire. More recently, the faunal assemblage of the Cabrières Biota dominated by sponges and algae provide a significant signal of polar ecosystems (Saleh *et al.* 2024b) and suggest even higher latitudes than those presented for the Middle Ordovician.

Considering the sedimentological setting of the Ordovician, only the Ecailles de Cabrières have shown a preservation of Middle and Late Ordovician sediments. However, their tectonic and sedimentological characteristics are making them very different from the other units of the Montagne Noire, suggesting another geological context (Colmenar *et al.* 2013; Álvaro *et al.* 2016, 2018; Lefebvre *et al.* 2023). The sedimentology of the Lower Ordovician of the other nappes, including the Minervois, Mont de Pardailhan, Mont de Faugères, Mont Peyroux and the Pic de Vissou-Montpeyroux units, has been investigated in several studies that allowed to identify different sedimentary formations from the Cambrian to the Early Ordovician (e.g. Noffke & Nitsch 1994; Vizcaïno *et al.* 2001; Álvaro *et al.* 2003, Vaucher *et al.* in press), from bottom to top: the La Gardie (upper Cambrian), Val d'Horns (Cambrian-Ordovician transition), La Dentelle (Tremadocian), Saint Chinian (upper Tremadocian/lower Floian), La Maurerie (Floian), Cluse de l'Orb (Floian), Foulon (Floian) and finally the Landeyran (Floian) Formation. The facies succession shows different transgressive and regressive phases between the late Cambrian and the end of the Early Ordovician (Noffke & Nitsch 1994; Vizcaïno *et al.* 2001).

Known for bearing a major faunal transition with a diversification of echinoderms, trilobites, brachiopods, etc., and the re-occurrence of several groups of the underlying

Saint Chinian and La Maurerie formations (Vizcaino *et al.* 2001), the Landeyran Formation corresponds to the upper part of the Lower Ordovician sedimentological succession that is present in most of the Montagne Noire outcrops. Conformably overlying the Foulon Formation, the Landeyran Formation carries the levels from the Cabrières Biota. The section displaying the Landeyran Formation studied in this work corresponds to the Landeyran section, located nearby the Landeyran river (Fig. 2). The examination, in this section, of silty to clayey laminated siltstones, characteristic of the Landeyran Formation in different sections across the southern part of the Montagne Noire, allowed to assign a rather distal prodelta to offshore or typical-shelf depositional setting to the sediments (Vaucher *et al.* in press).

Materials and Methods

For this palynological study a total of 18 samples from two different localities were analyzed; 16 samples come from a continuous section in the Landeyran Valley (Landeyran section), located in the Mont Peyroux unit and more precisely within the municipality of Saint-Nazaire-de-Ladarez (Fig. 2). The Landeyran valley section (called Landeyran section in this work) provides continuous insights of the uppermost part of the Foulon Formation, the transition to the Landeyran Formation and the lower part of the Landeyran Formation (Vaucher *et al.* in this volume).

Two additional samples were collected from the small Pic de Vissou-Montpeyroux nappe (Fig. 1). In this small unit, where the Cabrières Biota was described, the samples were more precisely collected from “La Brouette” and “La Sangle” sites, nearby the East of Valmascle, in the Bois de Boutoury, in the North-West of the village of Cabrières (Fig. 2). The exposure and complexity of these outcrops did not allow any logging of the sections, however their belonging to the lower part of the Landeyran Formation is supported by the associated benthic faunas (Saleh *et al.* 2024b).

The continuity of the outcrops in the Landeyran valley enabled a precise localization of the palynological samples along the Landeyran section (GPS coordinates: 43°29'46.1" 03°04'38.5"). This allows to study the distribution of the different acritarch assemblages with the aim to understand the biostratigraphical evolution of the acritarchs across the Floian succession and to understand their palaeobiogeographical position in relation to the global distribution of late Early Ordovician acritarchs (Fig. 3).

All samples were prepared according to a standard procedure of palynological preparation techniques (e.g. Riding 2021). The sediments collected were first treated with hydrochloric acid in order to eliminate all carbonates. After several rinses, the samples were then treated with hydrofluoric acid to dissolve the siliciclastic matrix from which the different palynomorphs were extracted. Because this step in the preparation can engender the formation of some fluorosilicate crystals, a final treatment was performed with boiled hydrochloric acid to eliminate a maximum of the newly formed mineral phases. The palynological preparation was sieved with 51µm and 15µm filter meshes in order to separate the biggest fragments and the main palynological material, respectively. Some of the slides analyzed were also re-oxidized in order to reduce the

opacity of the palynological material. All slides were observed under a Zeiss Axio Imager A2 transmitted light microscope (with oil immersion objectives and digital interference contrast), on which was mounted a Zeiss AxioCam ERc5s camera. All pictures were reworked with the software Zeiss 3.11. All studied samples, preparations and slides are stored in the collections of the Evo-Eco-Paleo department of the University of Lille, France.

Results

Distribution of Acritarchs

Landeyran section

From the 16 samples collected from the Landeyran section, only the sample "SILT1" in the collections of Lille University (named "LPS1.2" below), located around 25 meters above the base of the Landeyran Formation, shows very few unidentifiable fragments of palynomorphs (Fig. 3). All the samples labelled "LPS" and "Point Sup" (named "LPS10.2" below), and the "Landeyran Inf" sample in the collections of Lille University (named "LPS0" below), as well as the samples "Landeyran" (called "LPS2.2" below) and "Landeyran Sup" (called "LPS11.2" below) bear acritarchs in varying abundance and with different qualities of preservation in the $15\text{ }\mu\text{m} < x < 51\text{ }\mu\text{m}$ fraction. The upper fraction with larger palynomorphs ($x > 51\text{ }\mu\text{m}$) mostly contains organic debris and chitinozoans larger than $51\text{ }\mu\text{m}$, but bears only up to a maximum of 20 acritarchs per palynological slide. On the other hand, the smaller fraction ($15\text{ }\mu\text{m} < x < 51\text{ }\mu\text{m}$) allows the identification of at least 150 (and up to more than a thousand) specimens per slide, depending on the preservation and the abundance of palynomorphs in the sample. An evolution of the preservation of the organic-walled microfossils and their abundance, from the bottom to the top of the section can be observed. The samples from the top of the section provide usually more abundant specimens, while those being closer to the base of the section, including the samples "LPS0" and "LPS1," show a less diversified and abundant palynoflora. Furthermore, between the base and the top of the Landeyran section, a slight difference in terms of colors of palynomorphs and of their preservation can be observed. At the base of the section, the palynomorphs are in general poorly preserved, often bearing dark central bodies and appearing to be more degraded, with commonly broken processes (appendages) and vesicles, making the identification more difficult and sometimes impossible. At the top of the Landeyran section, the samples are clearly better preserved, being less fragmented (especially the processes) and displaying lighter colors making the identification of palynomorphs easier. This difference in abundance and preservation of the palynomorphs of the Landeyran section is also found between the two samples collected from the Cabrières Biota locality.

Cabrières area

Concerning the samples from the Cabrières Biota Lagerstätte, both samples (labelled “Cabrières 166.1-166.5” and “Cabrières 173.3”) bear a relatively abundant acritarch microflora. However, the latter sample, displaying darker colors and more fragmented palynomorphs in the slides, seems to be more degraded than the first one. This leads to a difference in the abundance of identified specimens between both samples. While in the sample “Cabrières 173.3” around 200 specimens were identified in the smaller fraction ($15\text{ }\mu\text{m} < x < 51\text{ }\mu\text{m}$), the sample “Cabrières 166.1-166.5” bears almost four times more identifiable acritarchs in this same fraction. As for the Landeyran section, the upper fraction ($x > 51\text{ }\mu\text{m}$) contains only very few acritarchs while bearing more chitinozoans and other bigger organic debris.

Composition of the acritarch assemblages

Although some abundance and preservation differences have been identified between the samples, the composition of the palynomorph assemblages from the Floian of the Montagne Noire remains very similar in all investigated levels. The taxa observed include galeate acritarchs (*Caldariola* (Molyneux in Molyneux and Rushton (1988), *Cymatiogalea* (Deunff, 1961), *Stelliferidium* (Deunff et al., 1974, *Priscogalea* Deunff, 1961), diacromorphs (e.g. *Acanthodiacrodium* (Timofeev, 1958 emend. Deflandre and Deflandre-Rigaud, 1962), *Barakella* (Cramer and Diez, 1977), *Arbusculidium* (Deunff, 1968 emend. Welsch, 1986), few sphaeromorphs, very rare netromorphs, and other genera, such as *Adorfia* (Burmman, 1970), *Ampullula* (Righi, 1991 emend. Yan et al., 2010), *Aureotesta* (Vavrdová, 1972), *Baltisphaeridium* (Eisenack, 1958 emend. Eiserhardt, 1989), *Coryphidium* (Vavrdová, 1972), *Dasydorus* (Playford and Martin, 1984), *Micrhystridium* (Deflandre, 1937), *Petaloferidium* (Jacobson, 1978), *Peteinosphaeridium* (Staplin et al., 1965 emend. Playford et al., 1995), *Pirea* (Vavrdová, 1972), *Polygonium* (Vavrdová, 1966 emend. Le Hérissé, 1989), *Rhopaliophora* (Tappan and Loeblich, 1971 emend. Li et al., 2014), *Stellechinatum* (Turner, 1984), *Striatotheca* (Burmman, 1970), *Tectitheca* (Burmman, 1968), the *Veryhachium lairdii* and *Veryhachium trispinosum* groups of the genus *Veryhachium* Deunff, 1954 emend. Sarjeant and Stancliffe, 1994; but see Servais et al. 2009) and *Vogtlandia* (Burmman, 1970).

A selection of the taxa present in the assemblages are illustrated in Figs. 4-5. For some taxa the identification at the species level is possible due to detailed taxonomical revisions made in recent years (e.g. Servais 1993, 1997; Servais et al. 1996, 2003, 2007, 2008, 2014; Brocke et al. 1998; Fatka & Brocke 1999; Stricane & Servais 2002; Yan et al. 2010, 2017; Li et al. 2014). For others the taxonomy remains unclear, and the identification is made at the genus level only, with either one (sp.) or several (spp.) species of the genus being present.

The different acritarch taxa show variations in their abundance and relative proportions, between the site of the Cabrières Biota and the Landeyran section, but

also within the latter one. These variations will be discussed in the frame of palaeoecological interpretations in a separate paper focusing on the palaeoecology of the Cabrières Biota (Michel *et al.* this volume). On the other hand, even the rare or very rare presence of specimens of particular taxa can be of great significance, because some index taxa, although very rare, can be biostratigraphically or palaeobiogeographically useful.

Across the whole section, one of the predominant acritarch sub-groups is the polygonomorph group representing around 30% of the specimens in the assemblages. Mainly represented by different species of the genus *Polygonium*, such as *P. gracile* Vavrdová, 1966 *emend.* Jacobson & Achab, 1985 (Fig. 4R), the group comprises also extremely rare occurrences of *Petaloferidium*, with *P. florigerum* (Vavrdová, 1977) Fensome *et al.*, 1990, and rare to common occurrences of *Tectitheca*, including *T. additionalis* Burmann, 1968, and of *Stellechinatum*, including *S. uncinatum* (Downie, 1958) (Fig. 4S) and *S. sicaforme* Molyneux *in* Molyneux & Rushton, 1988.

The galeate group is also predominant at the base of the Landeyran section. However, their proportion tends to diminish towards the top of this section. This trend is observable in all four genera (*Caldariola*, *Priscogalea*, *Cymatiogalea* and *Stelliferidium*). The two latter genera are the most abundant representatives of the galeate group, with *Cymatiogalea* (Fig. 5D-H) being slightly more present than *Stelliferidium* (Fig. 5I-K). Among the galeate acritarchs the species *Cymatiogalea messaoudensis* Jardiné *et al.*, 1974 (Fig. 5G) and *C. deunffii* Jardiné *et al.*, 1974 are extremely rare, whereas other species like *C. cuvillieri* (Deunff, 1961) Deunff, 1964 (Fig. 5E) and *C. granulata* Vavrdová, 1966 (Fig. 5H) are rare to very rare. On the contrary to the polygonomorph group, that appears only in the small fraction, some galeate taxa (*Stelliferidium* and *Cymatiogalea*) are also observable within the larger fraction of well-preserved samples from the middle or top of the section.

The dominance of the galeate group progressively diminishes as other genera are appearing, like the spinose *Baltisphaeridium* and the veryhachid group, that includes the genus *Veryhachium* as well as the striated rectangular-shaped acritarchs attributed to *Striatotheca*. Two different subgroups of *Veryhachium* have been identified within the sediments of the Montagne Noire: the *Veryhachium lairdii* group (Fig. 4N), and the *V. trispinosum* group (Fig. 4O). Represented by different forms, the genus *Striatotheca* (Fig. 4L-M) is almost absent in the first 27m of the section. However, the genus becomes more and more abundant towards the top of the section. Finally, baltisphaerids, present in all fractions ($x > 51 \mu\text{m}$ and $15 \mu\text{m} < x < 51 \mu\text{m}$) and represented by different species, such as *Baltisphaeridium klavabense* (Vavrdová, 1965) Kjellström, 1971 (Fig. 5B), are common throughout the section.

Diacromorphs are also rare to common across the whole section. Although their proportion slightly varies (from 4 to 9%) from one sample to another, no clear trend in these changes has been observed across the section. Although rare, this group is, however, represented by a diversity of genera and species, some of which are biostratigraphically useful. The diacromorphs present in the samples include *Arbusculidium filamentosum* (Vavrdová, 1965) Vavrdová, 1972 *emend.* Fatka and Brocke, 1999 (Fig. 4A-B), *Barakella felix* Cramer and Díez, 1977 (Fig. 4E) and different species of *Acanthodiacrodium* (Fig. 4 F-I), such as *A. angustizonale* Rauscher, 1974

(*non* Burmann, 1968) (Fig. 4G) and *A. angustum* (Downie, 1958) Combaz, 1967 (Fig. 4I).

The sphaeromorphs, mostly represented by specimens of *Leiosphaerida*, display also a more or less constant proportion across the section with only slight variations depending on the samples.

Following the same evolution of proportions as the galeate group, the genus *Michrystidium*, usually represented by small specimens (< 20 µm), shows approximately the same proportions (~5%) as the sphaeromorphs at the bottom of the section, becoming less and less present and being almost absent at the top of the studied section. Following the complete opposite trend of *Michrystidium*, the biostratigraphically significant genus *Coryphidium* is represented by different species, including rare to common *C. bohemicum* Vavrdová, 1972 *sensu strictu* (Fig. 4J), and very rare *C. minutum* Cramer & Díez, 1976 (Fig. 4K) and *C. elegans* Cramer & Díez, 1976.

Other forms are rare to very rare in the Landeyran section, as well as in the Cabrières Biota samples, like the genus *Pireia* (mean ~1.9%) (Fig. 4T and 4V), represented by different species, including *P. ornata* (Burmann, 1970) Eisenack *et al.*, 1976 (Fig. 4T), and the genus *Dasydorus* (mean ~0.1%) (Fig. 4U). Other rare taxa include some of the genera showing complex process structures, such as *Peteinosphaeridium* (with low proportions, mean ~1,2%) (Fig. 5M-N), *Rhopaliophora* (mean ~0,2%) (Fig. 5O-P), including possible representatives of the species *Rhopaliophora palmata* (Combaz and Péniguel, 1972) Playford and Martin 1984 (Fig. 5P), *Ampullula* (mean ~0.2%), *Vogtlandia* (mean ~0.9%), with as the main representatives *V. multiradialis* Burmann, 1970 (Fig. 5 Q-R) and *V. flosmaris* (Deunff 1977) Molyneux, 1987 (Fig. 5S), and *Adorfia* (mean ~0.1%).

Finally, both varieties of the biostratigraphically useful species *Aureotesta clathrata*, i.e., *A. clathrata* var. *clathrata* Vavrdová, 1972 *emend.* Brocke *et al.*, 1998 (mean ~0.1%) and *A. clathrata* var. *simplex* (Cramer *et al.*, 1974) Brocke *et al.*, 1998 (mean ~0.1%) (Fig. 4 P-Q), have also been observed very rarely across the Landeyran section.

It can be concluded that there is only a single assemblage present in the Landeyran section, displaying varying proportions of the different acritarch taxa present. Both samples from the Cabrières Biota bear the same assemblage with similar proportions than in the Landeyran Section. Although small differences in the abundance of the main groups from the Landeyran section have been observed in the samples of the Cabrières Biota, a correlation of both of these samples with levels within the Landeyran section is possible. While the abundance of *Baltisphaeridium* in the Cabrières samples is close to the samples found at the top of the Landeyran section, the proportion of the galeates and of the *Veryhachium lairdii* group is closer to the proportions from the middle part of the Landeyran section. The sample “Cabrières 166.1-166.5” from the “La Brouette” site shows similarities to the samples “LPS4,” “LPS2,” “LPS1” and “LPS0,” suggesting that it could be correlated with the levels of the Landeyran section between 25 m and 40 m from the base of the section. On the other hand, the sample “Cabrières 173.3” from the “La Sangle” site bears more affinities with the samples

“Landeyran” and “LPS5.” Thus, this sample could be tentatively correlated a little bit higher in the Landeyran section, between 35 m and 46 m above the base of the measured section.

Discussion

Biostratigraphy

Age of the palynomorph assemblages

Although acritarchs are not yet used as standard index fossils in Palaeozoic biostratigraphy to define global series and stage boundaries, a few clearly established biozonation schemes, correlating different palaeobasins across the globe, have been published, allowing for some early Palaeozoic time intervals precise age assignments. In addition, the group has often been used by palaeontologists and stratigraphers to attempt to provide a first age identification for sediment successions, in particular when the investigated areas do not provide some of the classical stratigraphical index fossils, like graptolites, conodonts and chitinozoans, or when the rocks are very poorly preserved, with the acritarchs being the only fossil remains preserved (e.g. Benachour *et al.* 2020).

For the Early-Middle Ordovician, acritarchs currently display a high correlation potential, following detailed reviews of the biostratigraphy of several easily recognizable acritarch taxa. Servais *et al.* (2018) established a first basis of a possible biozonation scheme for the Early and Middle Ordovician of the Gondwana area by pointing out the First Appearance Data (FADs) of selected acritarch taxa. Among the 19 different taxa selected by Servais *et al.* (2018), 12 have been identified in the samples from the southern Montagne Noire (Fig. 6). The presence of these biostratigraphically useful index taxa allows to provide precise information concerning the stratigraphical position of the studied section from the lower part of the Landeyran Formation and from the Cabrières Biota.

As indicated above, the composition of the acritarch associations is approximately the same across the whole Landeyran section, with no clear first appearance being identified, and no indication of a succession of biozones in the investigated section. Some taxa are only present higher in the section, but this is rather an indication of palaeoenvironmental changes (with higher diversities towards the top of the section) than the result of biostratigraphical changes with first occurrences of species within the section, because all taxa identified belong to a same time interval.

Besides some long-ranging taxa, several acritarch taxa present provide stratigraphic information, allowing to place relatively precisely the samples from the southern Montagne Noire in terms of biostratigraphy and international correlation. The abundance of taxa belonging to the genera *Acanthodiacrodium*, *Stelliferidium*, and *Cymatiogalea*, which all appear around the Cambrian-Ordovician transition (e.g. Vecoli

& Le Hérissé 2004), is a first indication that the Landeyran Formation displays a typical Early Ordovician palynoflora. Other more common taxa in the Ordovician are also present, such as the long-ranging species *Polygonium gracile* and *Stellechinatum uncinatum*, that are commonly present in sediments between the late Cambrian and the Late Ordovician, and that display large morphological variability.

In addition, the occurrence in the assemblages of the Montagne Noire of easily identifiable taxa with clearly distinguishable morphologies and well-known FADs provides a more precise age of the investigated samples (Fig. 6). The presence of the *Veryhachium lairdii* and *V. trispinosum* groups, as well as that of the genera *Rhopaliophora* (including the species *R. palmata*), *Peteinosphaeridium*, *Striatotheca*, and *Coryphidium* allows to conclude that the lower boundary of the Landeyran section must be of late Tremadocian/early Floian or younger age. Furthermore, the presence of age-diagnostic taxa, such as *Ampullula*, *Arbusculidium filamentosum*, *Aureotesta clathrata* var. *simplex*, *Barakella*, *Coryphidium bohemicum*, and *Dasydorus*, implies a middle Floian or younger age according to the first FADs identified by Servais *et al.* (2018) at a global scale, because these taxa have never been recorded in older rocks (Fig. 6). Among these taxa, most of them are commonly found in localities of the southern Gondwana margin, with *Arbusculidium filamentosum*, *Coryphidium bohemicum*, and *Striatotheca* being diagnostic for the peri-Gondwana province during the Arenigian (Floian–early Darriwilian) (see below). In addition, the presence of *Vogtlandia flosmaris*, previously recorded from the Arenig (Floian) to late Darriwilian, and *Adorfia hoffmanensis*, so far only known from the late Arenig (Floian) to early Darriwilian, also implies at least a Floian age (or younger) for the sediments. Although the first appearance data of these two species have not yet been clarified, most of their occurrences have been recorded from the middle-late Arenig, which corresponds to a late Floian to an early Dapingian age.

Of particular importance is the fact that typically younger acritarch taxa are missing in the investigated sedimentary succession. This constitutes a further indication, although not a proof, for a middle Floian age. Some of the younger age-diagnostic taxa that appear later elsewhere, such as *Arkonia*, *Dicrodiacrodium*, *Frankea*, *Orthosphaeridium* and *Sacculidium*, have not been recorded in the present study. All these taxa appear typically during the latest Floian or the Middle Ordovician (Dapingian and Darriwilian). Even if their absence in our samples does not provide clear evidence in biostratigraphical terms, the fact that they are all missing in all the samples from the Montagne Noire is in indication that helps to constrain the age of the Landeyran Formation in both the Landeyran section and the Cabrières Biota to an interval that most probably corresponds to the middle-late Floian (Top of FI2- Base FI3) (Fig. 6).

Comparison of the age of the palynomorph assemblages with other established biozonations in the Montagne Noire

In the lower Palaeozoic sedimentary successions from the southern Montagne Noire different studies based on trilobites (Vizcaïno & Álvaro 2002) have assigned to the Landeyran Formation two different trilobites biozones: the *Apatokephalus incisus*

497 Biozone for its lower part and the *Hangchungolithus primitivus* Biozone for its upper
 498 part. Both of these biozones allowed the assignment of a late Floian age to the
 499 Landeyran Formation.

500 Moreover, in an ongoing study based on graptolites the biozones of this group are
 501 correlated with Floian biozonations all around the world, allowing a suggestion of a
 502 more precise age thanks to the graptolite content (Gutierrez Marco, paper in prep).
 503 The results indicate the assignment of the levels from the Cabrières Biota, and by
 504 extension the probable age of the samples studied in our study, to the *Baltograptus*
 505 *minutus* graptolite Biozone, which can be correlated to the late Floian of southern
 506 Scandinavia by Maletz (2023).

507 Both studies on trilobites and graptolites seem to be roughly in concordance with the
 508 age assigned to the Landeyran section and the Cabrières Biota by the palynomorphs
 509 recorded in the present study. However, slight differences have to be noted. While the
 510 graptolite study seems to show clearly a late Floian age, the age range by the
 511 palynomorphs assigned to the Cabrières Biota is clearly wider, englobing the middle
 512 part of the Floian and the earliest part of the late Floian. Indeed, the absence of genera
 513 as *Arkonia*, *Frankea*, and *Dicrodiacrodium* suggests a maximum age from the samples
 514 corresponding to the early part of the FI3 time slice, although this does not provide
 515 strong evidence. The biozonations based on acritarchs still being very rare in literature,
 516 the remaining problems in the classification of many taxa and the current knowledge
 517 on acritarch biostratigraphy do not allow us for the moment to provide more precise
 518 age indications of the sediments, based on the palynomorph association alone. In
 519 addition to the acritarchs, a biostratigraphical investigation of the chitinozoans would
 520 therefore be useful in the future.

521

522 A new FAD of *Ampullula* in southern peri-Gondwana

523

524 The work from Servais *et al.* (2018) is a first basis for a biostratigraphical scheme,
 525 based on the FAD of different genera. However this database remains incomplete, and
 526 the analysis of newly discovered assemblages might change some First Appearance
 527 Data in the future. In the present study, the presence of *Ampullula* in the samples from
 528 the Cabrières Biota and the Landeyran section, from levels that can be attributed to
 529 the middle-late Floian, would change the First Appearance Datum of this genus in the
 530 southern part of the Gondwana. Although *Ampullula* is already known since the middle
 531 Floian elsewhere in the world, its earliest occurrence in the southern part of Gondwana
 532 is so far only from the Dapingian from Mýto near Rokycany in Bohemia, Czech
 533 Republic (Vavrdová 1990).

534 The genus *Ampullula*, Righi 1991, was revised by Yan *et al.* (2010), allowing the
 535 distinction of six species, including some new combinations: *A. calix* (Quintavalle and
 536 Playford, 2008) Yan *et al.*, 2010, *A. composita* (Yin *et al.*, 1998) Yan *et al.*, 2010, *A.*
 537 *crassula* (Vavrdová, 1990) Yan *et al.*, 2010, *A. erchunensis* (Fang, 1986) Brocke, 1997
 538 *emend. nov.* Yan *et al.*, 2010, *A. princeps* (Brocke, 1997) Yan *et al.*, 2010 and *A.*
 539 *sueticus* Righi, 1991. Found in Baltica and all around the peri-Gondwana province, the
 540 genus is present in a wide range of climatic zones from tropical zones, warm-temperate

and even cold-temperate water environments during the late-Early and Middle Ordovician. Its palaeoenvironmental range along the continental margin is also wide, making it a eurytopic microfossil (Yan *et al.* 2010). The records of the genus remain rare in the Mediterranean subprovince ("southern" Gondwana), being only represented by the species *A. crassula* in the Dapingian of Bohemia. The lack of descriptions of the genus from other localities is surprising, because this would suggest that the genus is present in the southernmost part of the Gondwanan margin for the first time only around 6 to 7 Myrs after its appearance in all other palaeobiogeographical provinces (Eastern and Western Gondwana, South China and Baltica). Indeed, the first peri-Gondwana appearance of the genus is recorded from the middle Floian in the Yangtze Platform, while in Argentina, Pakistan, Russia, Poland and even Turkey this taxon appeared in the late Floian. The presence of the genus in the assemblages of the Montagne Noire in this study is thus significant for biostratigraphical considerations.

Ampullula crassula has been recovered from the Yangtze Platform in South-China, the Leba area in Poland (Baltica), Pakistan (East Gondwana), Argentina (West Gondwana), but also from southern Gondwana in the Mýto area (Bohemia, Czech Republic). In all areas where it has been discovered the species appeared during the late Floian in the *deflexus* or *suecicus* graptolite biozones and even earlier (FI2) in South China. Thus, the observation of the species *A. crassula* in the middle to late Floian of the southern Montagne Noire is conform to its global FAD (middle Floian) and its already demonstrated occurrence in the South Peri-Gondwana province (in Bohemia) slightly later on. In conclusion, the presence of *Ampullula* in southern France in the middle to late Floian, and thus in the southern part of Gondwana, clearly provides an important palaeogeographic implication, strengthening the biostratigraphical significance of the genus with a high potential for global correlation.

Comparison with previous palynomorphs studies in the Montagne Noire

Although the acritarchs from the Montagne Noire are known since the late 1940's with the first studies by Deflandre (1942, 1945), several papers about palynomorph assemblages from the (southern and northern) Montagne Noire were published during the 1970s and early 1980s (Martin 1973; Rauscher 1971, 1974; Fournier-Vinas & Donnot 1977; Fournier-Vinas 1978), identifying and describing different assemblages from the Cambrian-Ordovician boundary to the Middle Ordovician.

Among the samples studied by Martin (1973), those from Col de Sainte Colombe in the Mont de Pardailhan Unit helped to locate the Cambrian-Ordovician boundary. Despite being highly degraded and poorly diverse, with only 13 species identified, these Cambrian-Ordovician assemblages from the Montagne Noire were dominated by *Micrhystridium*, *Priscogalea* and *Acanthodiacrodium*. The sedimentary layers from this period are characterized by an important transition from slope deposits to sandy shoals in the southern Montagne Noire (Álvaro *et al.* 2003). However, the Mont de Pardailhan Unit is considered to be at that time rather in a distal setting (Álvaro *et al.* 2003, 2008). The high degradation might be a reason for a loss of many acritarch data

because they are either too opaque or too degraded. To date, the description of Cambrian-Ordovician palynomorphs remain rare in the southern Montagne Noire.

Most of the other assemblages described from the southern Montagne Noire were collected from the Ecailles de Cabrières (Roquemaillère, Roque de Bandies, Mougno, etc...) by Martin (1973) and Rauscher (1971, 1974) and were assigned to the Tremadocian. Despite the presence of long-ranging taxa in the previously described Tremadocian assemblages and in the newly studied Floian samples, significant differences have been identified between Tremadocian and Floian associations by these authors in the 1970's. The Tremadocian palynoflora are characterized by a strong domination of diacromorphs with an important abundance and diversity of representatives of the genus *Acanthodiacrodium*, such as *A. angustum*, *A. simplex*, *A. hamatum*, and *A. ubui*. This observation is characteristic for the Tremadocian in France in general (Rauscher 1974). Abundant *Michrystidium*, *Priscogalea*, common *Cymatiogalea*, *Stelliferidium*, very rare to absent *Veryhachium*, and rare *Baltisphaeridium*, *Goniosphaeridium*, *Cymatiosphaera*, *Dasydiacrodium*, sphaeromorphs were also identified. Rauscher (1974) characterized the Tremadocian Stage thanks to a palynoflora from the Montagne Noire with genera either found later in the Floian, like *Acanthodiacrodium*, *Cymatiogalea*, *Stelliferidium*, or with genera not found in the samples from the present study, such as *Vulcanisphaera* and *Impluviculus*. Although the Ecailles de Cabrières are known for bearing different fossil assemblages from the other units of the Montagne Noire (Colmenar *et al.* 2013, Álvaro *et al.* 2016, 2018; Lefebvre *et al.* 2023), suggesting a different geological context, the presence of *Acanthodiacrodium* specimens in the samples from the Tremadocian of the Ecailles de Cabrières and the Floian of the Mont Peyroux and Pic de Vissou units implies that both of them have been part of the Peri-Gondwana province during the Early Ordovician (see palaeobiogeography section below).

In the present study, the Floian samples are collected from the section bearing the Cabrières Biota, and from the Landeyran section, that was already partly studied by Rauscher (1971, 1974). Therefore, our work can be considered as an update to the knowledge of the acritarch assemblages from the Floian (corresponding more or less to the earlier parts of the Arenigian) in the southern part of the Montagne Noire. The common occurrence of *Striatotheca*, rectangular and triangular *Veryhachium*, *Polygonium gracile*, *Baltisphaeridium* (*Baltisphaeridium klavabense*), the presence of *Peteinosphaeridium* and diacromorphs like *Arbusculidium*, the identification of *Coryphidium* (*Coryphidium bohemicum*), and the rarity of netromorphs and galeates are the most important features identified by Rauscher (1971, 1974) to characterize the 'Arenigian' of the southern Montagne Noire. All these main features have been identified in the samples investigated in the present study, thus confirming the observations made by Rauscher (1971, 1974). Furthermore, Rauscher (1971, 1974) already noted in the 1970's the strong similarities between the Floian assemblages from the Montagne Noire and those described in Bohemia (Vavrdová 1965). Our study also confirms these affinities with the Bohemian assemblages described by Vavrdová in numerous papers.

However, in his description of the section within the Landeyran Valley, Rauscher (1971) described only a single assemblage without showing any evolution of acritarch

associations as highlighted in the present study. The reason is possibly that Rauscher's (1971) material was not very well preserved and did not allow countings of hundreds of specimens per slide. It is not clear where the samples from Rauscher (1971) were exactly collected in the formation. The present work shows that the polygonomorphs and the galeates are especially abundant at the base of the lower part of the Landeyran Formation, with rare *Baltisphaeridium* and *Veryhachium*, which is not consistent with the observation of Rauscher (1971). Nevertheless, the common presence of *Baltisphaeridium*, *Veryhachium*, as well as the rarity of galeates and netromorphs, noted by Rauscher (1971), are characteristic from the samples of the upper part of the Landeyran section. As a consequence, the samples described by Rauscher (1971) possibly come from the upper part of the Landeyran section as investigated here, or from even higher levels not studied in the present work (uppermost part of the *A. incisus* zone or *H. primitivus* zone).

Although some samples from the Ecailles de Cabrières were assigned to a late Arenigian to Llanvirnian age by Martin (1973), their composition are different from those of our study, with occurrences of the genus *Dicrodiacrodium*, absent from all the samples of the present study. The First Appearance Datum of this genus being in the latest part of the Floian (Servais *et al.* 2018) suggesting that the samples from the Cabrières area described by Martin (1973) are of slightly younger than those studied in the present work, probably coming from another tectonic unit.

Palaeobiogeography

The study of acritarch diversity during the early Palaeozoic allowed the identification of different phases within the evolution of organic-walled phytoplankton. The Ordovician is today identified as the period with the highest acritarch diversities of the entire Palaeozoic, following an especially strong diversification between the late Cambrian and the Middle Ordovician (Kroek *et al.* 2022; Shan *et al.* 2022). However, the assemblages from this period did not only reveal a high diversity but also a strong provincialism of the microfloras that seems to be at its maximum during the Early–Middle Ordovician. Acritarch provincialism and the spreading into different palaeobiogeographical units appears indeed less pronounced during the Cambrian and decreased again during the Late Ordovician (Servais *et al.* 2003; Molyneux *et al.* 2013). Different palaeogeographical and palaeoenvironmental factors, like oceanic currents, water chemistry, nutrient availability, sea-level change, the distribution of the different continental masses, etc., have been identified as possible drivers for the distribution of acritarch assemblages and taxa (Molyneux *et al.* 2013).

Because palaeobiogeographical provinces, as all palaeobiogeographical units, are based on the degree of endemism of the taxa present, the different acritarch assemblages from the Early–Middle Ordovician allowed the distinction of two (Vecoli & Le Hérissé 2004; Molyneux *et al.* 2013) to three (discussion in Servais *et al.* 2003) main palaeobiogeographical provinces. The Baltic province has been defined as a province of mixed cold and warm-water environments located in medium to high southern latitudes (between 30°S and 60°S). The peri-Gondwana province is currently

considered as a very large palaeoprovince extending around the margin of Gondwana from Argentina to South-China, including many localities from Colombia, eastern Newfoundland, North Africa, central and southern Europe, southern Turkey, Jordan, Iran, Pakistan, and others (Servais *et al.* 2003, fig. 2; Molyneux *et al.* 2013, fig. 23.5; Kroeck *et al.* 2020, fig. 5). A debated third main palaeobiogeographical province from the Early Ordovician concerns the “warm-water” province identified by Playford *et al.* (1995) and Volkova (1997), regrouping North-America, North-China and Australia.

The latter “warm-water” province was defined on the basis of the presence of genera like *Aryballomorpha*, *Athabascaella*, *Corollasphaeridium*, *Goniomorpha*, and *Lua* during the latest Tremadocian (Volkova 1997) or on the recognition of particular *Peteinosphaeridium* species (Playford *et al.* 1995). The existence of this Tremadocian province is currently questioned, as it was actually based on the occurrence of taxa of which the distribution remains poorly known. *Corollasphaeridium* is actually not phytoplanktonic, but can now be related to the Small Carbonaceous Fossils (SCFs), being possibly a loricate protist (Green *et al.* 2025). *Goniomorpha* is also clearly related to the SCFs, representing the teeth of priapulid worms (Shan *et al.* 2023). Both *Corollasphaeridium* and *Goniomorpha* are thus not phytoplanktonic. They remain rarely described and were often ignored by acritarch workers, but it now appears that they are much more abundant than previously thought, and they are not just present in areas related to the warm-water environments of the Tremadocian, but appear to be much more cosmopolitan (Shan *et al.* 2023; Green *et al.* 2025). Similarly, *Aryballomorpha* is currently under revision (Navidi-Izad, pers. comm), and this genus appears also to be more pandemic than previously thought, with occurrences in high latitudes. The main characteristic features of *Aryballomorpha* are similar to the ones of *Athabascaella*. This latter genus has been found in southern Gondwana and thus in high latitudes by Vecoli & Le Hérissé (2004), after being considered typical of warm-water environments, following the definition of the “warm-water” province by Volkova (1997). The peteinoid acritarchs also need a complete revision. It is difficult to discern the different species and subspecies, that possibly cannot serve as palaeobiogeographical markers (Kroeck *et al.* 2021) and the recognition of species of *Peteinosphaeridium* considered as diagnostic for a warm-water province, as suggested by Playford *et al.* (1995) is today questionable.

The Baltic (Baltica) province, first defined by Vavrdová (1974) and then redefined by Tongiorgi and Di Milia (1999), can be identified more easily. This province seems to be lacking clear typical (endemic) acritarch taxa. Bearing many cosmopolitan species and genera, the Baltic province was considered to contain no diacromorph acritarchs and to display specific taxa of the genus *Peteinosphaeridium*, such as *P. bergstroemii* and *P. hymeniferum* (but see above for the limited use of peteinoid acritarchs for palaeobiogeography), as well as species of the genus *Pachysphaeridium*, as possible marker species (Vecoli & Le Hérissé 2004). However, the lack of clarity in the classification of peteinoid acritarchs makes the identification of such markers easily confusing (Servais *et al.* 2003; Kroeck *et al.* 2021).

Finally, the peri-Gondwana province, originally described as the ‘Mediterranean Province’ (limited to only southern and central Europe) by Vavrdová (1974), bears as major palaeobiogeographic markers the genera *Arbusculidium*, *Coryphidium*, and

Striatotheca (Li 1989), and large abundances of diacromophs, such as *Acanthodiacrodium* and *Dasydiacrodium* (Albani 1989). This province was long considered as being of ‘cold-water’ environments in high latitudes (but see discussion in Li & Servais 2002).

The presence of different species of *Acanthodiacrodium*, *Arbusculidium*, *Coryphidium* and *Striatotheca* is a very clear indicator for an attribution of the Montagne Noire samples to the palaeobiogeographical peri-Gondwana province (Albani 1989; Li 1989; Servais *et al.* 2003, Molyneux *et al.* 2013). The plotting of the province on a palaeogeographic reconstruction of the Floian clearly confirms that the Montagne Noire belongs to this palaeobiogeographical unit (Fig. 7).

Most interestingly, Playford *et al.* (1995) proposed a subdivision of the peri-Gondwana province into three subprovinces: the ‘Mediterranean’ (corresponding to the primary definition of the province by Vavrdová 1974), the ‘South America,’ and the ‘South China’ subprovinces. In order to define precisely this ‘Mediterranean’ subprovince, Vavrdová (1997) subsequently identified 16 diagnostic taxa from an assemblage from the ‘Arenigian’ of Bohemia, called the ‘*Coryphidium bohemicum* assemblage.’ Among these 16 taxa, most are identified within the samples from the Montagne Noire, such as: *Adorfia hoffmanensis*, *Arbusculidium filamentosum*, *Aureotesta clathrata* var. *clathrata*, *A. clathrata* var. *simplex* (formerly *Marrocanium simplex*), *Coryphidium bohemicum*, *Cymatiogalea granulata*, *Pireia*, *Striatotheca principalis*, and *Vogtlandia multiradialis*. These findings clearly allow to assign the palynoflora from the late Early Ordovician from the Cabrières Biota and the base of the Landeyran Formation to the Mediterranean subprovince within the peri-Gondwana acritarch palaeoprovince. However, most of these taxa, like *Coryphidium bohemicum*, *Cymatiogalea granulata*, *Aureotesta clathrata* var. *clathrata* and var. *simplex* (Brocke *et al.* 1998), have now also been found all around peri-Gondwana (from Argentina to South China) reducing the relevance of the identification of such an assemblage to identify specifically the very high palaeolatitudes of the peri-Gondwana province. Among the different subprovinces from the peri-Gondwana province, the South-America and South China subprovinces are also known to bear a mix of acritarchs from different palaeobiogeographical affinities. Although the peri-Gondwana acritarchs are the main representant of these subprovinces, Baltic and Australian influences have been identified in rather significative proportions (Molyneux *et al.* 2013). The main representatives of the influences listed by Molyneux *et al.* (2013) have, however, for most of them, not been identified in the samples from the Montagne Noire. In conclusion, the Montagne Noire assemblage investigated in this study seems to be typical for the high palaeolatitude “Mediterranean” subprovince, (central and southern Europe, Turkey, but also Belgium, Germany and southern Britain).

In addition, although the occurrences of genera such as *Ampullula* and *Rhopaliophora*, found in the Montagne Noire, were during a long time considered to be more typical for warm-water environments and therefore lower latitudes (Li & Servais 2002; Achab *et al.* 2006), the subsequent revisions of both taxa, respectively made by Yan *et al.* (2010) and Li *et al.* (2014), have highlighted their presence in a very wide area, including the “Mediterranean” subprovince. Therefore, the presence of the two species *Rhopaliophora palmata* and *Ampullula crassula* is not that surprising. *Rhopaliophora*

palmata was so far known from Baltica, South China, Australia and in a wide range of localities from the peri-Gondwana province, including Bohemia and North Africa. *Ampullula crassula*, on the other hand, was recorded so far from South China, South-America (Argentina) and the Mediterranean (Bohemia) subprovinces, but also from Baltica (Poland). The presence in the samples from the Landeyran section and from the Cabrières Biota of these taxa does thus not necessarily imply a warm-water environment or a low-latitude setting for the assemblage of the Montagne Noire.

Conclusions

Our study of the palynomorphs from the Landeyran section and the Cabrières Biota in the southern Montagne Noire (France) has allowed to identify different characteristics of the assemblages present.

Firstly, the diverse, abundant and fairly well-preserved acritarch microflora described provide important biostratigraphical information. The presence of typically Lower-Middle Ordovician taxa like *Arbusculidium filamentosum*, *Barakella felix*, *Coryphidium bohemicum*, *Peteinosphaeridium*, *Rhopaliophora*, *Striatotheca*, the *Veryhachium lairdii* and *trispinosum* groups, associated with the absence of genera such as *Arkonina*, *Frankea* and *Orthosphaeridium*, allows to assign a middle to late Floian age (transition FI2-FI3) to the levels studied, which is rather conform to the age given by graptolites and trilobites analyses.

Moreover, the presence of *Ampullula* in the samples suggests a new First Appearance Datum of this genus in the southern Gondwana area (central and southern Europe).

In terms of palaeobiogeography, the diverse assemblages bear a signal typical of the peri-Gondwana acritarch province, with the presence of different diagnostic taxa, such as *Arbusculidium*, *Coryphidium*, *Striatotheca* and abundant *Acanthodiacrodium*. More precisely, the samples are showing the presence of almost all the typical taxa from the “Mediterranean” subprovince. Indeed, the present study has shown that the assemblages from Bohemia and Montagne Noire are very similar.

Not studied since over four decades, the palynomorph assemblages from southern France also allow to complete the acritarch data from this time interval and as a consequence a better understanding of the evolution of this palynoflora in this area.

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Figure Captions:

Figure 1: Geological context of the study area. (A) Localization of the Montagne Noire within the different Variscan massifs (modified from Demange, 1999; Faure *et al.* 2010; Montmartin *et al.* 2021); (B) Area of the southern slope part of the Montagne Noire including the Pic de Vissou-Montpeyrroux Unit, yielding the Cabrières Biota.

Figure 2: Location of the investigated outcrops on a map (Google Earth). Red Star = Landeyran section; Blue Star: Cabrières Biota locality.

Figure 3: Stratigraphic column of the Landeyran section recording the uppermost part of the Foulon Formation and the base of the lower part of the Landeyran Formation. The log and the main sedimentary facies are from Vaucher *et al.* (in press). The position of palynological samples and distribution of acritarch taxa in the section and in the samples from the Cabrières Biota area are shown.

Figure 4: Specimens of selected taxa from the Ordovician of the Landeyran Valley and Cabrières Biota, Montagne Noire, France. For each illustrated specimen, the following information is given: slide label, England Finder coordinates. For example, LPS11, R48/3 refers to slide LPS11, England Finder coordinates R48/3. Scale bar = 10 μ m. A) *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972 *emend.* Fatka and Brocke 1999, LPS3, 15<x<51, E64; B) *Arbusculidium filamentosum*, (Vavrdová 1965) Vavrdová 1972 *emend.* Fatka and Brocke 1999, LPS6, 15<x<51, H66-2; C) *Arbusculidium* sp., LPS11.2 15<x<51, S64; D) *Barakella* sp., Cabrières 166,1-166,5, 15<x<51, J53; E) *Barakella felix* Cramer and Díez 1977, LPS8, 15<x<51, X53; F) *Acanthodiacrodium* sp., LPS11.2, 15<x<51, E57-4; G) *Acanthodiacrodium* cf. *angustizonale*, Rauscher 1974 (non Burmann 1968), LPS10, 15<x<51, W54-2; H) *Acanthodiacrodium* sp., LPS11.2 15<x<51, S60; I) *Acanthodiacrodium angustum*, (Downie, 1958) Combaz 1967, LPS10, 15<x<51, L48; J) *Coryphidium bohemicum*, Vavrdová 1972 *sensu strictu*, LPS11.2, 15<x<51, S52-2; K) *Coryphidium minutum*, Cramer and Díez, 1976, LPS10, 15<x<51, F64-4; L) *Striatotheca* sp., LPS6, 15<x<51, G64-2; M) *Striatotheca* sp., LPS2, 15<x<51, M64-2; N) *Veryhachium laiirdii* group, LPS11.2, 15<x<51, R55-1; O) *Veryhachium trispinosum* group, LPS10, 15<x<51, H67-1; P) *Aureotesta clathrata* var. *simplex*, (Cramer *et al.* 1974) Brocke *et al.* 1998, LPS11.2, 15<x<51, F64; Q) *Aureotesta clathrata* var. *simplex*, (Cramer *et al.* 1974) Brocke *et al.* 1998, LPS3, 15<x<51, U71-3; R) *Polygonium gracile*, Vavrdová 1966, LPS11, 15<x<51, O60-3; S) *Stellechinatum uncinatum*, (Downie, 1958) Molyneux, 1987, LPS8, 15<x<51, M71-2; ; T) *Pirea ornata* (Burmann 1970) Eisenack *et al.* 1976, LPS8, 15<x<51, N72; U) *Dasydorus* sp., LPS10, 15<x<51, Y72-1; V) *Pirea* sp., LPS11.2, 15<x<51, R62-1

Figure 5: Specimens of selected taxa from the Ordovician of the Landeyran Valley and Cabrières Biota, Montagne Noire, France. For each illustrated specimen, the following information is given: slide label, England Finder coordinates. For example, LPS11, R48/3 refers to slide LPS11, England Finder coordinates R48/3. Scale bar = 10 μ m. A) *Cymatiosphaera* sp., LPS11.2 15<x<51, T64; B) *Baltisphaeridium klabavense* (Vavrdová 1965) Kjellström 1971, LPS5, 15<x<51, O57; C) *Baltisphaeridium* sp., LPS11, >51, V73-1; D) *Cymatiogalea* sp., LPS4, 15<x<51, X51-3; E) *Cymatiogalea cuviellieri* (Deunff, 1961) Deunff 1964, LPS10, 15<x<51, Q58-3; F) *Cymatiogalea* sp., LPS11.2, 15<x<51, G50-3; G) *Cymatiogalea messaoudensis* (Jardiné *et al.*, 1974) LPS10.2, 15<x<51, M63-4; H) *Cymatiogalea* cf. *granulata* Vavrdová 1966 Cabrières 166,1-166,5, 15<x<51, K48-2; I) *Stelliferidium* cf. *trifidum*, LPS4, 15<x<51, T56-3 ; J) *Stelliferidium* sp., LPS4, 15<x<51, L51; K) *Stelliferidium* sp., Cabrières 166,1-166,5 15<x<51, R69 ; L) *Ampullula* cf. *crassula* (Vavrdová 1990) *comb. et emend.* Kui *et al.*, 2010, LPS8, 15<x<51, X68-1; M) *Peteinosphaeridium* sp., LPS9, 15<x<51,

1306 L59-1; N) *Peteinosphaeridium* sp., LPS11, >51, K70-1; O) *Rhopaliophora* sp., LPS10.2, 15<x<51,
1307 P51; P) *Rhopaliophora* cf. *palmata* (Combaz and Péniguel, 1972) emend. Playford and Martin, 1984,
1308 LPS11.2, 15<x<51, F49-4; Q) *Vogtlandia* cf. *multiradialis* (Burmman, 1970) LPS10.2, 15<x<51, M72-4;
1309 R) *Vogtlandia multiradialis* (Burmman, 1970) LPS11.2, 15<x<51, U52-3; S) *Vogtlandia* cf. *flosmaris*
1310 (Deunff 1977) Molyneux 1987 LPS11.2, 15<x<51, Q59

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1312 *Figure 6: Age of the samples from the Landeyran section and the Cabrières Biota based on the*
1313 *acritarchs content and the First Appearance Datum (FAD) of selected taxa (Figure based and modified*
1314 *from Servais et al. 2018).*

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1316 *Figure 7: Floian (475 Ma) palaeogeographical reconstruction with the location of the Baltica Province*
1317 *(Nord.: Norway, Denmark, Sweden; Bal.-W. Russia: Estonia, St. Petersburg area, Finland; N. Pol.;*
1318 *northern Poland), and the Peri-Gondwana Province, including Eastern Gondwana (Arg.-Bol.:*
1319 *Argentina, Bolivia, Columbia), Western Gondwana (S. China: southern China), Northern Gondwana*
1320 *(Aus.: Australia), and the “southern peri-Gondwana subprovince” (Newfound.: Newfoundland; Eng.:*
1321 *England, Wales, Ireland; Fra.-Ita.: southern France, Sardinia, etc.; SE Ger.-Cze: south-eastern*
1322 *Germany and the Czech Republic; Mor.: Morocco; Alg.: Algeria) Reconstruction based on the*
1323 *PALAEOMAP project (Scotese 2016).*

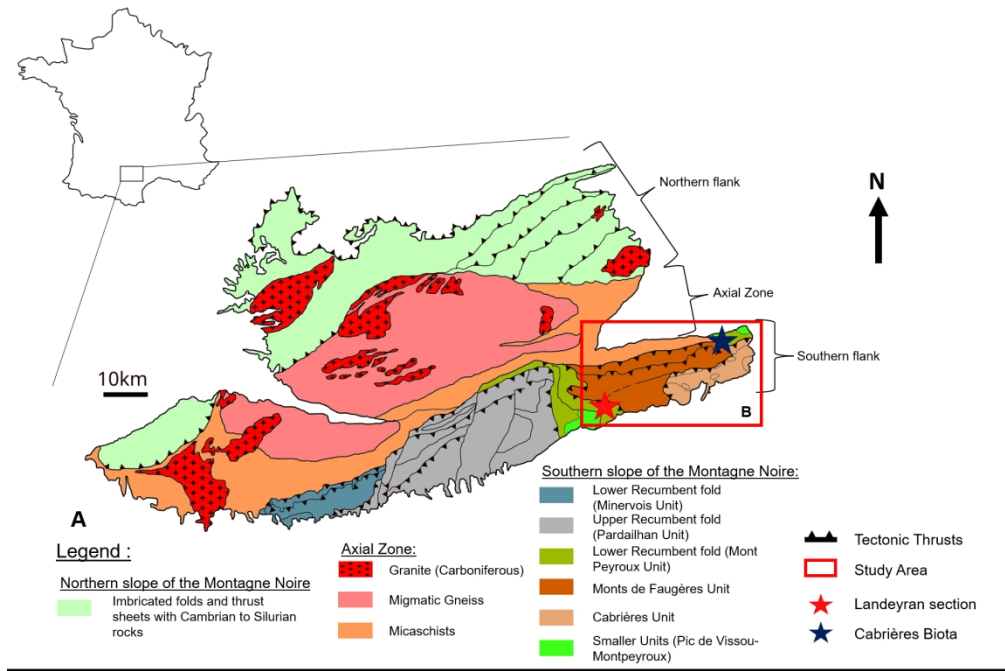


Figure 1: Geological context of the study area. (A) Localization of the Montagne Noire within the different Variscan massifs (modified from Demange, 1999; Faure et al. 2010; Montmartin et al. 2021); (B) Area of the southern slope part of the Montage Noire including the Pic de Vissou-Montpeyroux Unit, yielding the Cabrières Biota.

836x555mm (59 x 59 DPI)

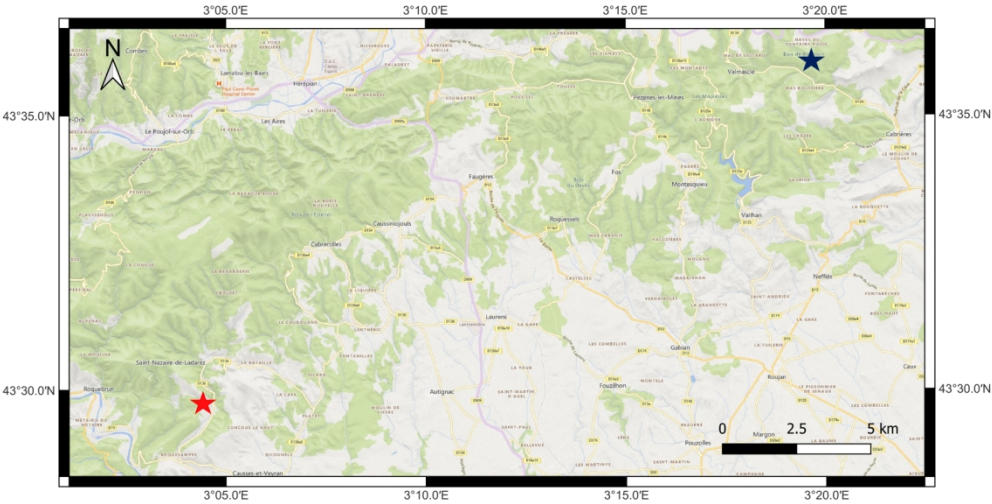


Figure 2: Location of the investigated outcrops on a map (Google Earth). Red Star = Landeyran section; Blue Star: Cabrières Biota locality.

749x431mm (59 x 59 DPI)

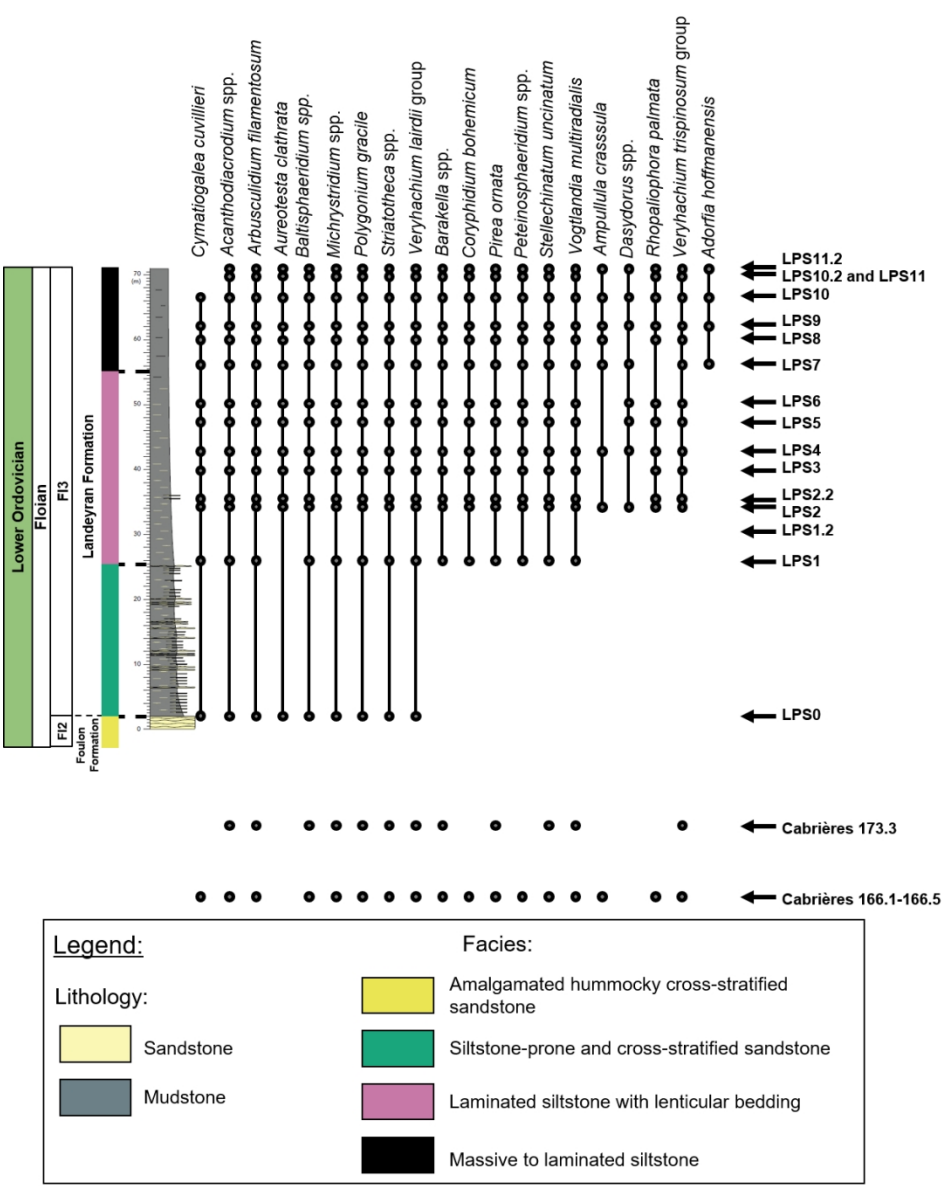


Figure 3: Stratigraphic column of the Landeyran section recording the uppermost part of the Foulon Formation and the base of the lower part of the Landeyran Formation. The log and the main sedimentary facies are from Vaucher et al. (in press). The position of palynological samples and distribution of acritarch taxa in the section and in the samples from the Cabrières Biota area are shown.

551x686mm (59 x 59 DPI)

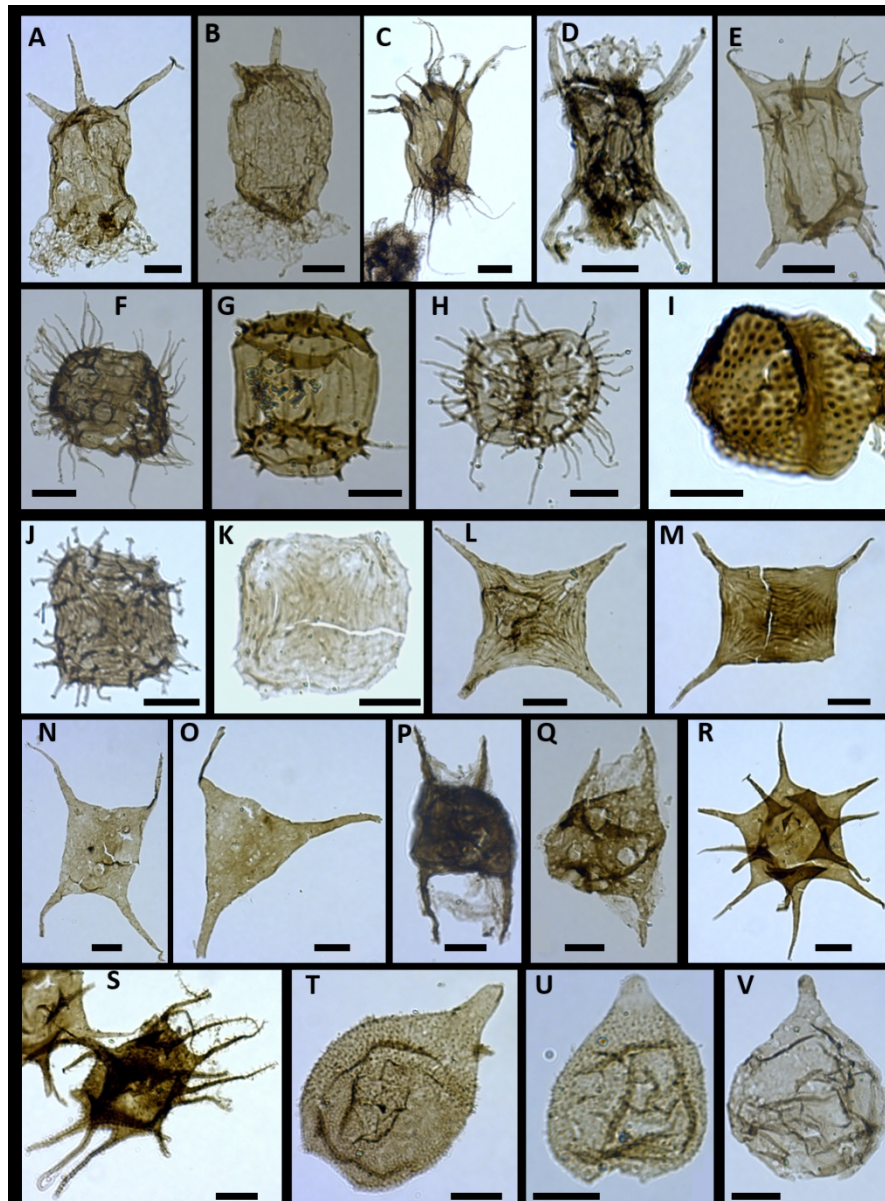


Figure 4: Specimens of selected taxa from the Ordovician of the Landeyran Valley and Cabrières Biota, Montagne Noire, France. For each illustrated specimen, the following information is given: slide label, England Finder coordinates. For example, LPS11, R48/3 refers to slide LPS11, England Finder coordinates R48/3. Scale bar = 10 μ m. A) *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972 emend. Fatka and Brocke 1999, LPS3, 15<x<51, E64; B) *Arbusculidium filamentosum*, (Vavrdová 1965) Vavrdová 1972 emend. Fatka and Brocke 1999, LPS6, 15<x<51, H66-2; C) *Arbusculidium* sp., LPS11.2 15<x<51, S64; D) *Barakella* sp., Cabrières 166,1-166,5, 15<x<51, J53; E) *Barakella felix* Cramer and Díez 1977, LPS8, 15<x<51, X53; F) *Acanthodiacrodium* sp., LPS11.2, 15<x<51, E57-4; G) *Acanthodiacrodium* cf. *angustizonale*, Rauscher 1974 (non Burmann 1968), LPS10, 15<x<51, W54-2; H) *Acanthodiacrodium* sp., LPS11.2 15<x<51, S60; I) *Acanthodiacrodium angustum*, (Downie, 1958) Combaz 1967, LPS10, 15<x<51, L48; J) *Coryphidium bohemicum*, Vavrdová 1972 sensu strictu, LPS11.2, 15<x<51, S52-2; K) *Coryphidium minutum*, Cramer and Díez, 1976, LPS10, 15<x<51, F64-4; L) *Striatotheca* sp., LPS6, 15<x<51, G64-2; M) *Striatotheca* sp., LPS2, 15<x<51, M64-2; N) *Veryhachium laiirdii* group, LPS11.2, 15<x<51, R55-1; O) *Veryhachium trispinosum* group, LPS10, 15<x<51, H67-1; P) *Aureotesta clathrata* var. *simplex*, (Cramer

et al. 1974) Brocke et al. 1998, LPS11.2, 15<x<51,F64; Q) Aureotesta clathrata var. simplex, (Cramer et al. 1974) Brocke et al. 1998, LPS3, 15<x<51, U71-3; R) Polygonium gracile, Vavrdová 1966, LPS11, 15<x<51, O60-3; S) Stellechinatum uncinatum, (Downie, 1958) Molyneux, 1987, LPS8, 15<x<51, M71-2; ; T) Pirea ornata (Burmenn 1970) Eisenack et al. 1976, LPS8, 15<x<51,N72; U) Dasydorus sp., LPS10, 15<x<51,Y72-1; V) Pirea sp., LPS11.2, 15<x<51,R62-1

492x665mm (59 x 59 DPI)

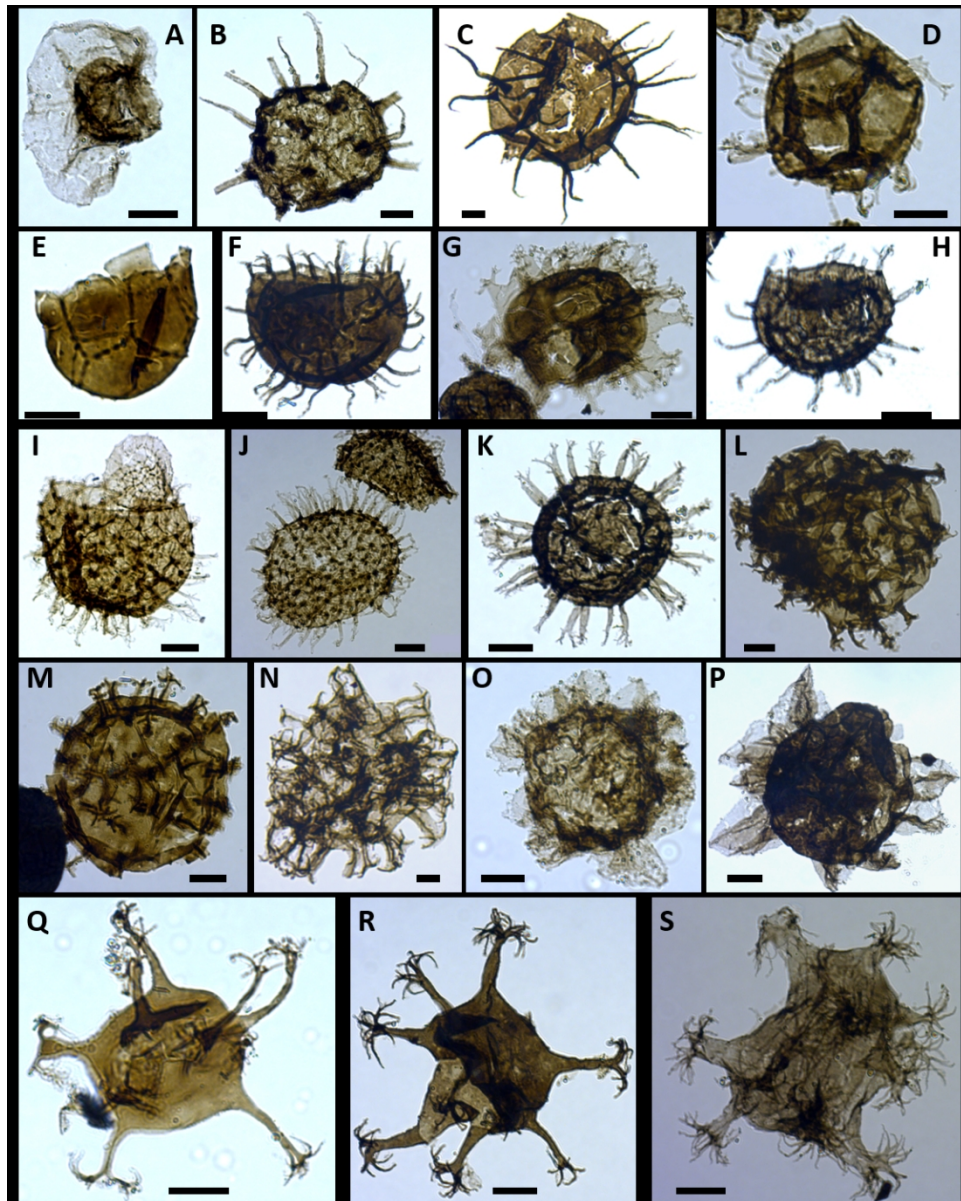


Figure 5: Specimens of selected taxa from the Ordovician of the Landeyran Valley and Cabrières Biota, Montagne Noire, France. For each illustrated specimen, the following information is given: slide label, England Finder coordinates. For example, LPS11, R48/3 refers to slide LPS11, England Finder coordinates R48/3. Scale bar = 10 μ m. A) *Cymatiosphaera* sp., LPS11.2 15<x<51, T64; B) *Baltisphaeridium* klabavense (Vavrdová 1965) Kjellström 1971, LPS5, 15<x<51, O57; C) *Baltisphaeridium* sp., LPS11, >51, V73-1; D) *Cymatiogalea* sp., LPS4, 15<x<51, X51-3; E) *Cymatiogalea cuviellieri* (Deunff, 1961) Deunff 1964, LPS10, 15<x<51, Q58-3; F) *Cymatiogalea* sp., LPS11.2, 15<x<51, G50-3; G) *Cymatiogalea messauoudensis* (Jardiné et al., 1974) LPS10.2, 15<x<51, M63-4; H) *Cymatiogalea* cf. *granulata* Vavrdová 1966 Cabrières 166,1-166,5, 15<x<51, K48-2; I) *Stelliferidium* cf. *trifidum*, LPS4, 15<x<51, T56-3; J) *Stelliferidium* sp., LPS4, 15<x<51, L51; K) *Stelliferidium* sp., Cabrières 166,1-166,5 15<x<51, R69; L) *Ampullula* cf. *crassula* (Vavrdová 1990) comb. et emend. Kui et al., 2010, LPS8, 15<x<51, X68-1; M) *Peteinosphaeridium* sp., LPS9, 15<x<51, L59-1; N) *Peteinosphaeridium* sp., LPS11, >51, K70-1; O) *Rhopaliophora* sp., LPS10.2, 15<x<51, P51; P) *Rhopaliophora* cf. *palmata* (Combaz and Péniguel, 1972) emend. Playford and Martin, 1984, LPS11.2, 15<x<51, F49-4; Q) *Vogtlandia* cf. *multiradialis* (Burmman, 1970) LPS10.2, 15<x<51, M72-

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4; R) *Vogtlandia multiradialis* (Burmman, 1970) LPS11.2, 15<x<51, U52-3; S) *Vogtlandia* cf. *flosmaris*
(Deunff 1977) Molyneux 1987 LPS11.2, 15<x<51, Q59

495x616mm (59 x 59 DPI)

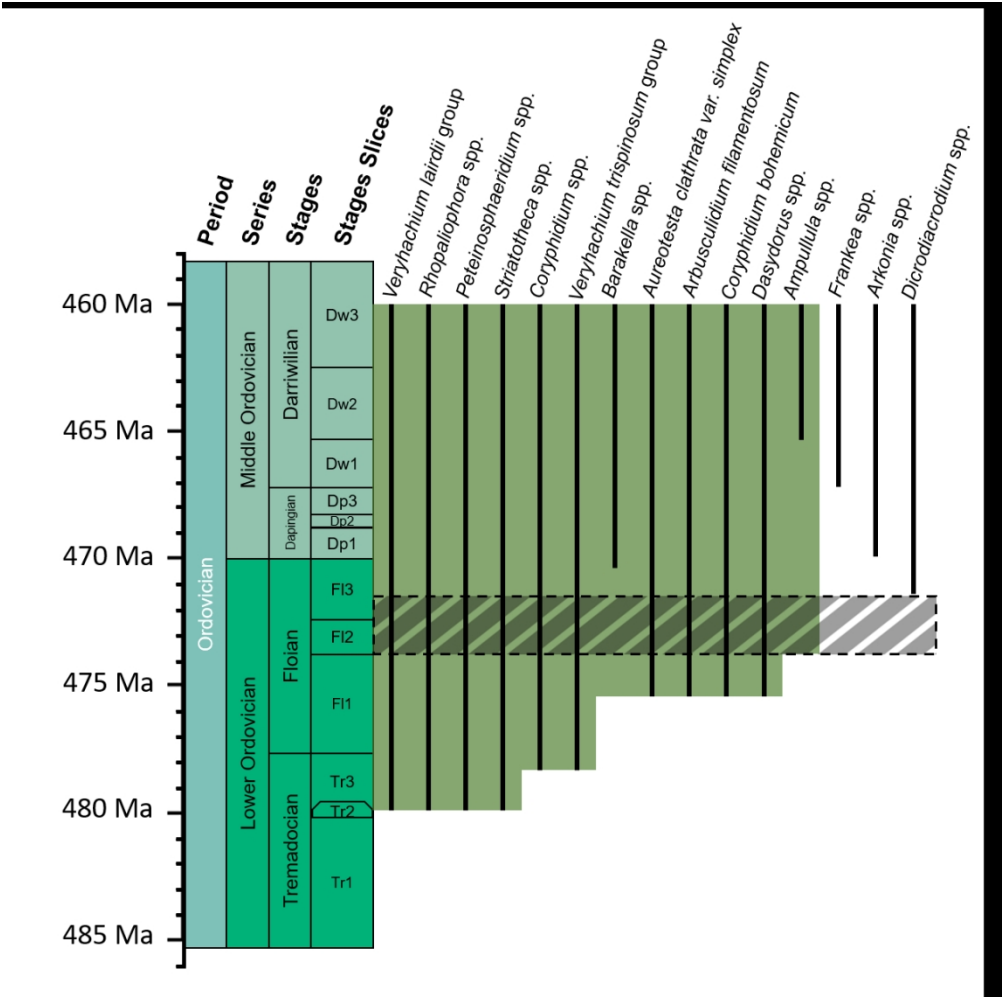


Figure 6: Age of the samples from the Landeyran section and the Cabrières Biota based on the acritarchs content and the First Appearance Datum (FAD) of selected taxa (Figure based and modified from Servais et al. 2018).

545x541mm (59 x 59 DPI)

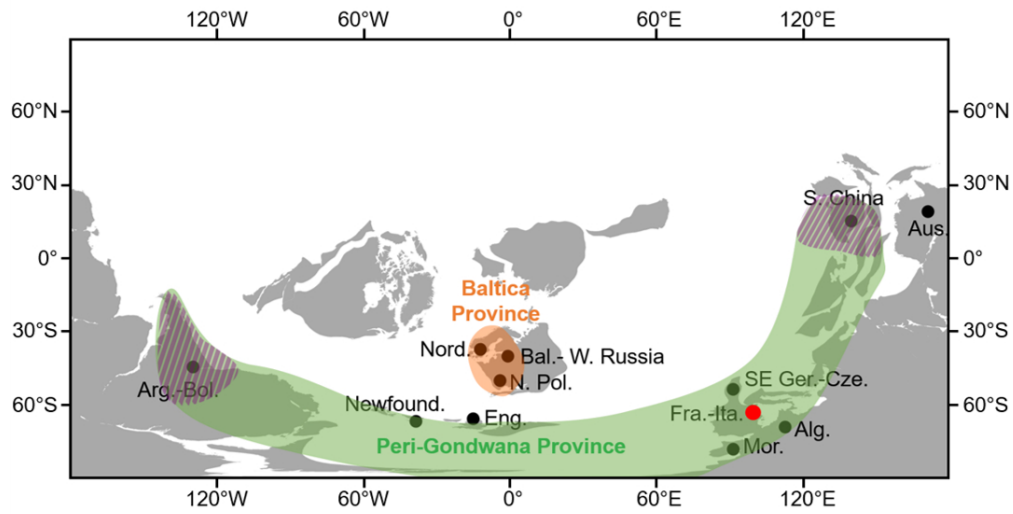


Figure 7: Floian (475 Ma) palaeogeographical reconstruction with the location of the Baltica Province (Nord.: Norway, Denmark, Sweden; Bal.-W. Russia: Estonia, St. Petersburg area, Finland; N. Pol.: northern Poland), and the Peri-Gondwana Province, including Eastern Gondwana (Arg.-Bol.: Argentina, Bolivia, Columbia), Western Gondwana (S. China: southern China), Northern Gondwana (Aus.: Australia), and the “southern peri-Gondwana subprovince” (Newfound.: Newfoundland; Eng.: England, Wales, Ireland; Fra.-Ita.: southern France, Sardinia, etc.; SE Ger.-Cze: south-eastern Germany and the Czech Republic; Mor.: Morocco; Alg.: Algeria) Reconstruction based on the PALAEOMAP project (Scotese 2016).

461x245mm (59 x 59 DPI)

Alternative texts for figures :

Figure 1: Simplified geological map of the Montagne Noire, oriented North-South, showing its different parts. The northern flank of the Montagne is colored in light green and affected in its eastern part by different NW-SE tectonic thrusts and in some areas by intrusion of carboniferous granite. The axial zone is mainly composed of granite (in red with black crosses) formed during the Carboniferous, magmatic gneiss (in light red) and micaschists (light orange). Finally, the southern flank is composed of different sedimentary units affected by different tectonic thrust faults. From the West to the East, the southern flank is composed of the Minervois unit (Blue), the Pardailhan unit (Grey). The easternmost part of the southern flank corresponds to the study area, highlighted by a red frame, and comprise the Mont Peyroux unit (dark green), bearing the Landeyran section, the Mont Faugères Unit (brown), the Cabrières unit (beige) and finally the small Pic de Vissous-Montpeyroux unit (neon green), housing the Cabrières Biota.

Figure 2 : Satellite map of the study area illustrating the precise location of the investigated outcrops modified from Google Earth on the software QGIS. Red Star = Landeyran section, nearby the D136; Blue star: Cabrières Biota levels within the Bois de Boutoury, North East from the village of Cabrières.

Figure 3: Stratigraphic distribution of key acritarchs taxa across Lower Ordovician lithostratigraphic units and facies in the Landeyran Section (uppermost part of the Foulon Formation and lower part of the Landeyran Formation) and the Cabrières Biota (Cabrières, France). The left column illustrates lithologic and facies variations, within the Landeyran section colors denoting an amalgamated hummocky cross-stratified sandstone facies in yellow (0-2m) from the Foulon Formation. Then the Siltstone-prone and cross-stratified sandstone (2m to 23m) marking the base of the Landeyran Formation is in green. The laminated siltstone with lenticular bedding (23m to 55m) is represented in pink while finally the massive to laminated siltstone facies corresponding to the end of the section from 55 to 71m is represented in dark. On the right, different arrows are representing the position of the different

samples within the Landeyran section and below it, 2 arrows indicate the samples from the Cabrières biota. In the middle, the occurrences of selected acritarchs taxa in each samples are represented by dots. The lowermost and uppermost occurrences from each taxa within the section define the stratigraphic range of the acritarch taxa within the Landeyran section. The taxa are organized from the left to the right depending on their first occurrence within the section, with the one on the left appearing earlier than the one represented on the right. Taxa include species from *Cymatogalea*, *Acanthodiacrodium*, *Arbusculidium*, *Aureotesta clathrata*, *Baltisphaeridium*...

Figure 4 :

Panel A : Picture of *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972 *emend.* Fatka and Brocke 1999, on the slide LPS3, 15 μm $\times$ 51 μm , E64, with a scale bar of 10 μm .

Panel B : Picture of *Arbusculidium filamentosum*, (Vavrdová 1965) Vavrdová 1972 *emend.* Fatka and Brocke 1999, on the slide LPS6, 15 μm $\times$ 51 μm , H66-2, with a scale bar of 10 μm .

Panel C : Picture of *Arbusculidium* sp., on the slide Landeyran Sup 15 μm $\times$ 51 μm , S64, with a scale bar of 10 μm .

Panel D : Picture of *Barakella* sp., on the slide Cabrières 166,1-166,5, 15 μm $\times$ 51 μm , J53, with a scale bar of 10 μm .

Panel E : Picture of *Barakella felix* Cramer and Díez 1977, on the slide LPS8, 15 μm $\times$ 51 μm , X53, with a scale bar of 10 μm .

Panel F : Picture of *Acanthodiacrodium* sp., on the slide Landeyran Sup, 15 μm $\times$ 51 μm ,E57-4, with a scale bar of 10 μm .

Panel G : Picture of *Acanthodiacrodium* cf. *angustizonale*, Rauscher 1974 (non Burmann 1968), on the slide LPS10, 15 μm $\times$ 51 μm , W54-2, with a scale bar of 10 μm .

Panel H : Picture of *Acanthodiacrodium* sp., on the slide Landeyran Sup 15 μm $\times$ 51 μm , S60, with a scale bar of 10 μm .

Panel I : Picture of *Acanthodiacrodium angustum*, (Downie, 1958) Combaz 1967, on the slide LPS10, 15 μm $\times$ 51 μm , L48, with a scale bar of 10 μm .

Panel J : Picture of *Coryphidium bohemicum*, Vavrdová 1972 *sensu strictu*, on the slide Landeyran Sup, 15 μm $\times$ 51 μm ,S52-2, with a scale bar of 10 μm .

Panel K : Picture of *Coryphidium minutum*, Cramer and Díez, 1976 , on the slide LPS10, 15 μm $\times$ 51 μm , F64-4, with a scale bar of 10 μm .

Panel L : Picture of *Striatotheca* sp., on the slide LPS6, 15 μm $\times$ 51 μm , G64-2, with a scale bar of 10 μm .

Panel M : Picture of *Striatotheca* sp., on the slide LPS2, 15 μm $\times$ 51 μm , M64-2, with a scale bar of 10 μm .

Panel N : Picture of *Veryhachium laiirdii* group, on the slide Landeyran Sup, 15 μm $\times$ 51 μm , R55-1, with a scale bar of 10 μm .

Panel O : Picture of *Veryhachium trispinosum* group, on the slide LPS10, 15 μm $\times$ 51 μm , H67-1, with a scale bar of 10 μm .

Panel P : Picture of *Aureotesta clathrata* var. *simplex*, (Cramer *et al.* 1974) Brocke *et al.* 1998, on the slide Landeyran Sup, 15 μm $\times$ 51 μm , F64, with a scale bar of 10 μm .

Panel Q : Picture of *Aureotesta clathrata* var. *simplex*, (Cramer *et al.* 1974) Brocke *et al.* 1998, on the slide LPS3, 15 μm $\times$ 51 μm , U71-3, with a scale bar of 10 μm .

Panel R : Picture of *Polygonium gracile*, Vavrdová 1966, on the slide LPS11, 15 μm $\times$ 51 μm , O60-3, with a scale bar of 10 μm .

Panel S : Picture of *Stellechinatum uncinatum*, (Downie, 1958) Molyneux, 1987, on the slide LPS8, 15 μm $\times$ 51 μm , M71-2, with a scale bar of 10 μm .

Panel T : Picture of *Pireia ornata* (Burmann 1970) Eisenack *et al.* 1976, on the slide LPS8, 15 μm $\times$ 51 μm , N72, with a scale bar of 10 μm .

Panel U : Picture of *Dasydorus* sp., on the slide LPS10, 15 μm $\times$ 51 μm , Y72-1, with a scale bar of 10 μm .

Panel V : Picture of *Pireia* sp., on the slide Landeyran Sup, 15 μm $\times$ 51 μm , R62-1, with a scale bar of 10 μm .

Figure 5 :

Panel A : Picture of *Cymatiosphaera* sp., on the slide Landeyran Sup 15 μm $\times$ 51 μm , T64, with a scale bar of 10 μm .

Panel B : Picture of *Baltisphaeridium klabavense* (Vavrdová 1965) Kjellström 1971, on the slide LPS5, 15 μm $\times$ 51 μm , O57, with a scale bar of 10 μm .

Panel C : Picture of *Baltisphaeridium* sp., on the slide LPS11, >51 μm , V73-1, with a scale bar of 10 μm .

Panel D : Picture of *Cymatiogalea* sp., on the slide LPS4, 15 μm $\times$ 51 μm , X51 μm -3, with a scale bar of 10 μm .

Panel E : Picture of *Cymatiogalea cuviellieri* (Deunff, 1961) Deunff 1964, on the slide LPS10, 15 μm $<x<51 \mu\text{m}$, Q58-3, with a scale bar of 10 μm .

Panel F : Picture of *Cymatiogalea* sp., on the slide Landeyran Sup, 15 μm $<x<51 \mu\text{m}$, G50-3, with a scale bar of 10 μm .

Panel G : Picture of *Cymatiogalea messaoudensis* (Jardiné et al., 1974), on the slide Point Sup, 15 μm $<x<51 \mu\text{m}$, M63-4, with a scale bar of 10 μm .

Panel H : Picture of *Cymatiogalea* cf. *granulata* Vavrdová 1966, on the slide Cabrières 166,1-166,5, 15 μm $<x<51 \mu\text{m}$, K48-2, with a scale bar of 10 μm .

Panel I : Picture of *Stelliferidium* cf. *trifidum*, on the slide LPS4, 15 μm $<x<51 \mu\text{m}$, T56-3, with a scale bar of 10 μm .

Panel J : Picture of *Stelliferidium* sp., on the slide LPS4, 15 μm $<x<51 \mu\text{m}$, L51 μm , with a scale bar of 10 μm .

Panel K : Picture of *Stelliferidium* sp., on the slide Cabrières 166,1-166,5 15 μm $<x<51 \mu\text{m}$, R69, with a scale bar of 10 μm .

Panel L : Picture of *Ampullula* cf. *crassula* (Vavrdová 1990) *comb. et emend.* Kui et al., 2010, on the slide LPS8, 15 μm $<x<51 \mu\text{m}$, X68-1, with a scale bar of 10 μm .

Panel M : Picture of *Peteinosphaeridium* sp., on the slide LPS9, 15 μm $<x<51 \mu\text{m}$, L59-1, with a scale bar of 10 μm .

Panel N: Picture of *Peteinosphaeridium* sp., on the slide LPS11, $>51 \mu\text{m}$, K70-1; P51 μm , with a scale bar of 10 μm .

Panel O : Picture of *Rhopaliophora* sp., on the slide Point Sup, 15 μm $<x<51 \mu\text{m}$, with a scale bar of 10 μm .

Panel P : Picture of *Rhopaliophora* cf. *palmata* (Combaz and Péniguel, 1972) *emend.* Playford and Martin, 1984, on the slide Landeyran Sup, 15 μm $<x<51 \mu\text{m}$, F49-4, with a scale bar of 10 μm .

Panel Q : Picture of *Vogtlandia* cf. *multiradialis* (Burmann, 1970), on the slide Point Sup, 15 μm $<x<51 \mu\text{m}$, M72-4, with a scale bar of 10 μm .

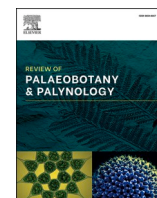
Panel R : Picture of *Vogtlandia multiradialis* (Burmann, 1970), on the slide Landeyran Sup, 15 μm $<x<51 \mu\text{m}$, U52-3, with a scale bar of 10 μm .

Panel S : Picture of *Vogtlandia* cf. *flosmaris* (Deunff 1977) Molyneux 1987, on the slide Landeyran Sup, 15 μm $<x<51 \mu\text{m}$, Q59, with a scale bar of 10 μm .

Figure 6 : Along a stratigraphic column of the Early and Middle Ordovician, going from 486 Ma to 458 Ma, illustrating the subdivision in series, stages and stages

slices, the First Appearance Datum (FAD from Servais *et al.*, 2018) of different selected genera (*Veryhachium lairdii* group, *Rhopaliophora* spp., *Peteinosphaeridium* spp, *Striatotheca* spp, *Coryphidium* spp., *Veryhachium trispinosum* group, *Barakella* spp., *Aureotesta clathrata* var. *simplex*, *Arbusculidium filamentosum*, *Coryphidium bohemicum*, *Dasydorus* spp., *Ampullula* spp., *Frankea* spp., *Arkonian* spp., *Dicrodiacrodium* spp.) has been represented in order to allow the identification of the time interval corresponding to the samples from the Cabrières Biota and the Landeyran section. The age range of all taxa is represented by a black line. The presence and First Appearance Data of *Veryhachium lairdii* group, *Rhopaliophora* spp., *Peteinosphaeridium* spp, *Striatotheca* spp, *Coryphidium* spp., *Veryhachium trispinosum* group, *Barakella* spp., *Aureotesta clathrata* var. *simplex*, *Arbusculidium filamentosum*, *Coryphidium bohemicum*, *Dasydorus* spp., *Ampullula* spp. highlighted by a green background and the absence of *Frankea* spp., *Arkonian* spp., *Dicrodiacrodium* spp., without any colored background allowed to assign a middle to early-late Floian age to the assemblage (Stages slices FI2 and beginning of FI3), represented by a dark hatched rectangle.

Figure 7 : Paleogeographical reconstruction of the world during the Floian (475 Myrs) illustrating the distribution of the different acritarch provinces at that time : the Baltica province regroups the area of the current Scandinavia, West-Russia, North of Poland, represented in orange. The Peri-Gondwana province, forms a very important arc-shaped province, highlighted in light green, ranging from the coast of the Gondwana palaeocontinent from South America (Argentina and Bolivia) to South China passing by Newfoundland, the British Isles, Western Europe, and the Middle East. The South-China and Argentinian subprovinces are also identified with purple hatching because of their typical composition differing from the rest of the Peri-Gondwana provinces. The localization of the Cabrières Biota from South of France is indicated by a red dot, above 60°S and around 100°E, in the southern part of this province, being part of the Peri-Gondwana Province in the same area as the South-Easter Germany, Czech Republic, Morocco and Algeria.



Research papers

Famennian phytoplankton from the Hongguleleng Formation of Western Junggar, NW China

Zhen Shen^{a,*}, Claude Monnet^b, Eiver Gelan Manzano^b, Yiming Gong^{c,*}, Thomas Servais^d^a College of Resources and Environment, Shanxi University of Finance and Economics, Taiyuan 030006, China^b Université de Lille, CNRS, UMR 8198 Evo-Eco-Paleo, F-59000 Lille, France^c State Key Laboratory of Geomicrobiology and Environmental Changes, School of Earth Sciences, China University of Geosciences, Wuhan 430074, China^d CNRS, Université de Lille, UMR 8198 Evo-Eco-Paleo, F-59000 Lille, France

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ABSTRACT

The Hongguleleng Formation is a stratigraphical unit in proximity to the Frasnian/Famennian and Devonian/Carboniferous boundaries within the Kazakhstan Palaeoplate. Nonetheless, the absence of conodont, ammonoid, and brachiopod assemblages in some significant stratigraphical horizons limits the precise subdivision of the formation. To address this issue, a new palynostratigraphical analysis was conducted at the Gennaren section, in order to provide additional data that would facilitate the delineation of biostratigraphical zones within the Hongguleleng Formation. In this study, a total of forty-one phytoplankton species belonging to 20 genera have been identified, including some in open nomenclature. The phytoplankton taxa can be separated into three assemblages. Of particular interest is the species *Ammonidium levigatum*, which exhibits potential as an index acritarch species for equivalents of the VCo miospore Zone in eastern Europe. The phytoplankton assemblage described here has its taxonomic composition closest to northeastern Europe (Poland) and belongs to the Laurussia Realm at a time of high cosmopolitanism. According to the percentage of marine and terrestrial palynomorphs observed in the Gennaren section, the sedimentary environment of the lower member of the Hongguleleng Formation is interpreted to have undergone a dynamic transformation, shifting initially from a coastal environment to a neritic one, subsequently shifting to a deep-water setting, and ultimately reverting back to a neritic environment.

1. Introduction

The Frasnian–Famennian (F–F) biotic crisis, occurring approximately at 372 Ma, is postulated to have been triggered by the expansion of marine anoxia and climatic cooling (Murphy et al., 2000; Bond et al., 2004; Marynowski et al., 2011; Whalen et al., 2015; White et al., 2018; Huang et al., 2018; Song et al., 2017; Zhang et al., 2024; Zhao et al., 2024). This event resulted in the extinction of approximately 80% of marine fauna, making it one of the ‘Big Five’ Phanerozoic extinction events (Joachimski and Buggisch, 1993; Hallam and Wignall, 1997; Formolo et al., 2014; Sim et al., 2015; Song et al., 2017). A contributing factor to this marine diversity decline may have been the expansion of forests during the Late Devonian, which led to increased chemical weathering and nutrient influx into the oceans due to vascular land plants (Zhao et al., 2024; Algeo and Scheckler, 1998). The long-term consequences included algal blooms, heightened carbon burial, and

global cooling (Algeo et al., 1995). Despite these blooms, there was a substantial reduction in phytoplankton diversity, a phenomenon termed the “Phytoplankton Blackout” by Riegel (2008), although the applicability of this term and the causes of the decline remain debated (Servais et al., 2006, 2016; Strother et al., 2010).

Acritarchs are organic-walled microfossils of uncertain affinity or origin, but often considered to primarily represent cysts of marine phytoplankton. Despite there being problems in classification, the growing literature, characterized by well-known stratigraphy and well-preserved assemblages, highlights the potential of acritarch and prasinophyte groups in resolving Paleozoic biostratigraphical, palaeogeographic, and palaeoenvironmental problems. This is particularly significant as these palynomorphs are in some cases the only or most frequently occurring fossils present in sediments (e.g., Molyneux et al., 1996; Le Hérisse et al., 2000).

Within the Devonian, the Upper Devonian phytoplankton have

* Corresponding author.

E-mail addresses: zshen@sxufe.edu.cn (Z. Shen), ymgong@cug.edu.cn (Y. Gong).<https://doi.org/10.1016/j.revpalbo.2025.105332>

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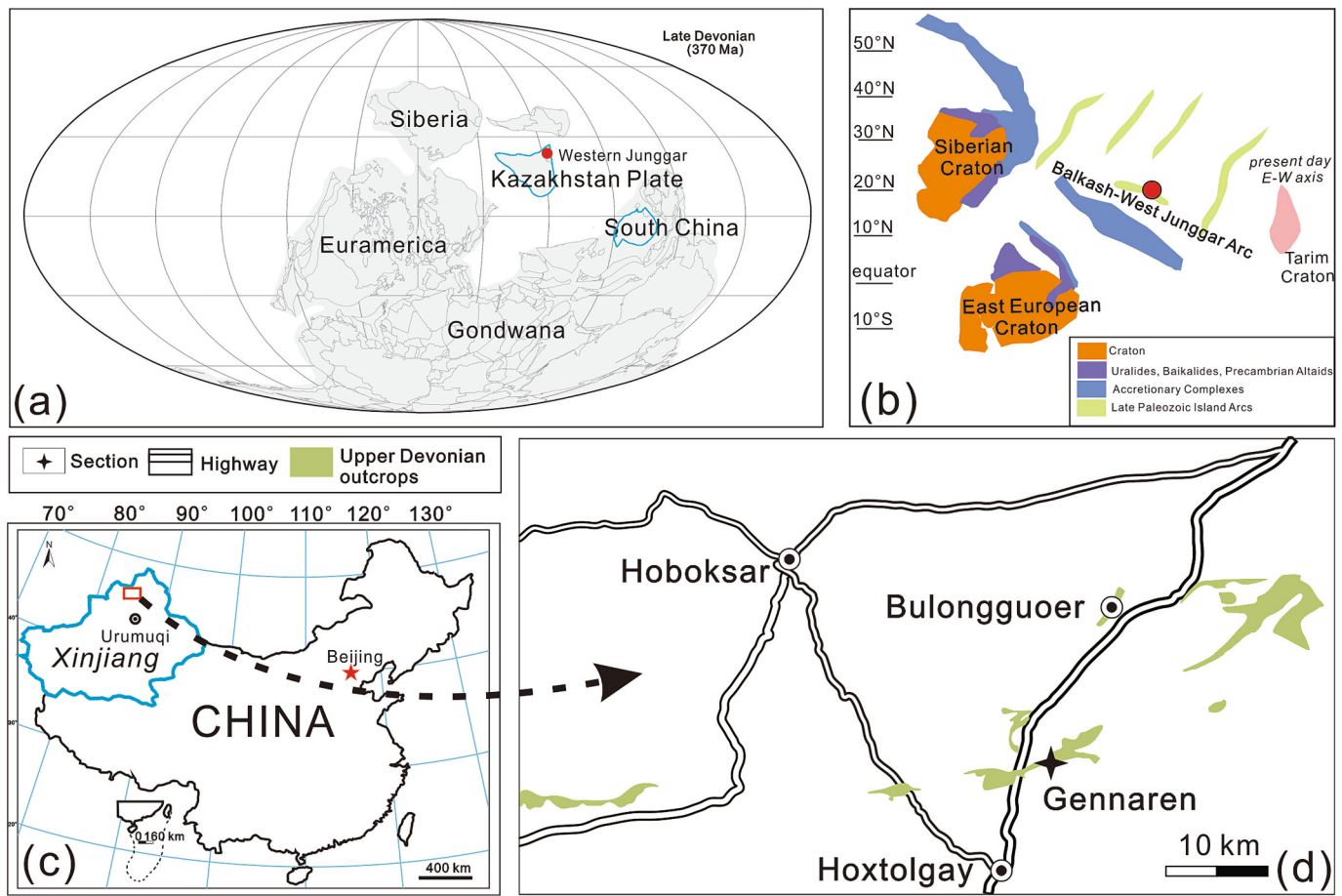


Fig. 1. (a): A revised palaeogeographic map of the Late Devonian period (modified from [Boucot et al., 2013](#)), showing the precise location of the Kazakhstan Plate, where palynological samples have been collected; (b): An interpretive tectonic model of the study area during the Late Devonian (shown by red circle), indicating a complex amalgamation of island arcs and accretionary complexes characteristic of the period. Figure modified from [Xiao et al. \(2010\)](#); (c): The geographic location of the study site within Xinjiang, NW China; (d): Location of the studied section and the distribution of Upper Devonian outcrops in Western Junggar.

received the greatest attention, with numerous well-preserved palynological assemblages being discovered in well-defined outcrops and subsurface sections across North America, Europe, South America, Africa, Asia, Australia, and China (e.g., [Jardiné et al., 1974](#); [Ghavidel-Syooki, 2001](#); [Molyneux et al., 1984](#); [Wicander and Playford, 2013](#); [Pereira et al., 2008](#); [Playford and McGregor, 1993](#); [Vavrdová et al., 1996](#); [Martin, 1981, 1984](#)). However, compared to miospore research, studies on Upper Devonian phytoplankton remain very scarce. To date, only three reports exist on Famennian acritarchs from northern Xinjiang, NW China. [Lu and Wicander \(1988\)](#) conducted a pioneering study on acritarch and miospore assemblages from the Hongguleleng Formation at the Bulongguoer section. More recently, [Stachacz et al. \(2021\)](#) provided a detailed palynological and ichnological investigation of the Hongguleleng Formation (from the Bulongguoer and Haer sections) and the overlying Heishantou Formation. [Shen et al. \(2021\)](#) reported on miospore and phytoplankton assemblages from the lower part of the lower member of the Hongguleleng Formation at the Bulongguoer section, indicating similarities in palynostratigraphy and sedimentary sequences between this section in Western Junggar and certain regions of western and eastern Europe.

The miospore content of the section and its biostratigraphical implications are detailed in a separate publication ([Shen et al., 2024](#)). The present study focuses mainly on the phytoplankton of this interval. Here, we present the palynological characteristics of the lower and middle Famennian phytoplankton assemblage from the Gennaren section in NW China. Additionally, we discuss the palaeobiogeographical significance of the phytoplanktonic assemblages and depositional environment of the

lower member of the Hongguleleng Formation.

2. Regional setting and the stratigraphical section investigated

The Western Junggar region constitutes a significant Paleozoic volcanic arc within the Central Asian Orogenic Belt (CAOB) ([Windley et al., 2007](#); [Xiao et al., 2008](#)). It played a crucial role in the Kazakhstan Plate, especially during the Devonian and early Carboniferous periods ([Xiao et al., 2010](#); [Ma et al., 2017](#); [Fig. 1](#)).

The Hongguleleng Formation is situated at the northwestern margin of the Junggar Basin and is a typical Upper Devonian sedimentary unit in NW China. The Devonian and Carboniferous strata, derived from the volcanic arc, are extensively distributed and well-exposed ([Buckman and Aitchison, 2004](#); [Gong and Zong, 2015](#)). These strata consist of a series of fossiliferous, shallow-water facies, clastic, and carbonate deposits (e.g., [Hou et al., 1979, 1993](#); [Ma et al., 2017](#)).

The materials investigated in the present study were collected from the Gennaren section within the well-exposed Hongguleleng Formation, located approximately 17 km north of Hoxtolgay town, Hoboksar County, Xinjiang, NW China ([Fig. 1](#)). This section comprises, in ascending order, the Frasnian Zhulumute Formation, the Famennian Hongguleleng Formation, and the lower Carboniferous Heishantou Formation. Lithostratigraphically, the three-member division scheme for the Hongguleleng Formation has been adopted and widely used in previous studies (e.g., [Hou et al., 1993](#); [Fan and Gong, 2016](#); [Ma et al., 2017](#); [Zong and Ma, 2018](#); [Zong et al., 2020](#)). Regarding the contact relationships, there is a consensus on the sequence continuity between

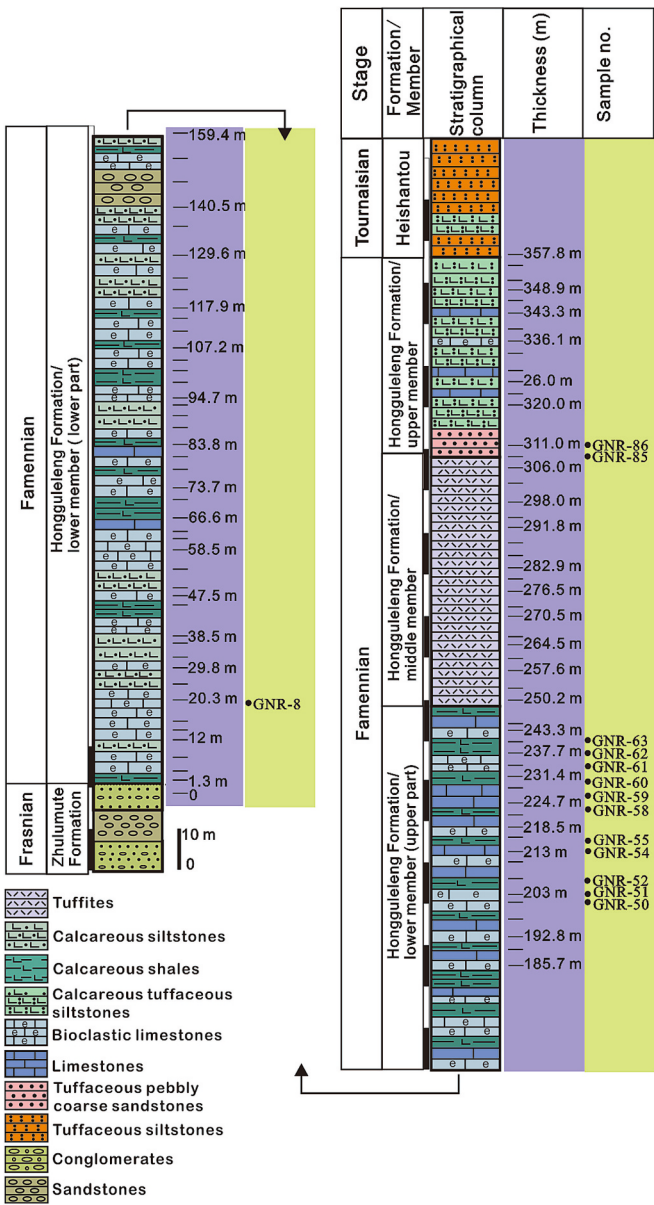


Fig. 2. Detailed stratigraphy of the Gennaren section within the Hongguleleng Formation. This log indicates the precise locations where samples containing palynomorphs were collected. The palynoflora samples are designated with the prefix “GNR-”. The short line “—” in front of the meter mark indicates the location where palynological sample was collected.

the Hongguleleng Formation and the overlying Heishantou Formation. However, the contact relationship between the Hongguleleng Formation and the underlying Zhulumute Formation has long been considered a conformity, partly due to issues of stratigraphical coverage. Recent work at the Gennaren section has revealed a layer of mud debris approximately 2.5 cm thick at the boundary between these two formations, suggesting that the relationship between them should be considered as a disconformity (Shen et al., 2024).

Despite recent advancements in palaeontological (including ammonoids, brachiopods, trilobites, palynomorphs, and conodonts), stratigraphical, and palaeogeographic research (Zhao and Wang, 1990; Xia, 1996; Chen et al., 2009; Ma et al., 2011; Zong and Ma, 2012, 2018; Wang et al., 2016; Zong et al., 2020; Zheng et al., 2020; Stachacz et al., 2021; Shen et al., 2021; Zhang et al., 2021), the precise location and existence of the F–F and Devonian–Carboniferous (D–C) boundaries in the section remains highly controversial. Several issues, such as the

establishment of a detailed biostratigraphy and an understanding of bioenvironmental events during this time interval, are still not adequately addressed.

3. Palynological preparation

Ninety-nine samples were collected for palynological analysis from the Gennaren section. The detailed stratigraphical levels from which these samples were obtained are illustrated in Fig. 2. Among these, only 14 samples yielded useful palynological data for phytoplankton research (Fig. 2). Each sample underwent a standardized processing protocol, which involved acid maceration using HCl–HF–HCl, as described by Wood et al. (1996). Subsequently, the samples were separated using a heavy liquid produced via a chemical reaction involving potassium iodide, hydriodic acid, and zinc particles, and then sieved through 15 µm and 50 µm meshes to isolate the palynological components. The

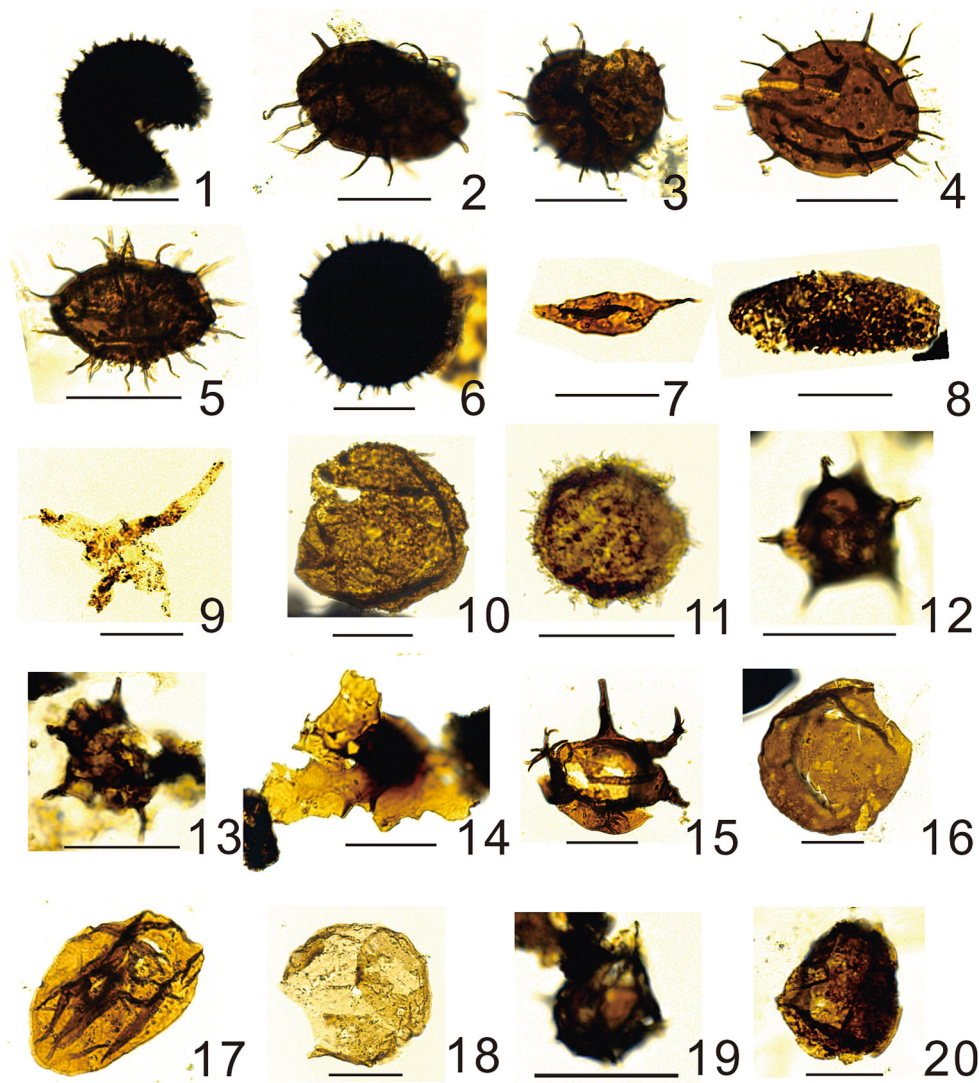


Fig. 3. Famennian phytoplankton from the Hongguleleng Formation in the Gennaren section. Scale bar = 20 μm . 1, 6: *Gorgonisphaeridium plerispinosum* Wicander, 1974, samples GNR8–17, and GNR8–61; 2: *Gorgonisphaeridium savertonense* Wicander and Playford, 2013, sample GNR50–7; 3: *Gorgonisphaeridium* sp., sample GNR50–12; 4: *Gorgonisphaeridium ohioense* (Winslow, 1962) Wicander, 1974, sample GNR50–9; 5: *Gorgonisphaeridium elongatum* Wicander, 1974, sample GNR50–11; 7: *Leiofusa* sp., sample GNR61–4; 8: *Somphophragma miscella* Playford in Playford and Dring, 1981, sample GNR8–5; 9: *Exochoderma* cf. *irregulare* Wicander, 1974, sample GNR85–1; 10: *Lophosphaeridium segregum* Playford, 1981, sample GNR62–6; 11: *Dasyphilula storea* Wicander and Loeblich, 1977, sample GNR50–2; 12–13: *Michrhystridium pentagonale* Stockmans and Willière, 1963, samples GNR8–13 and GNR8–18; 14: *Pterospermella* sp., sample GNR8–6; 15: *Multiplicisphaeridium* sp., sample GNR52–1; 16–18: *Leiosphaeridia* spp., samples GNR54–41, GNR50–21, GNR50–14; 19: *Dailyidium pentaster* (Staplin, 1961) Playford in Playford and Dring, 1981, sample GNR8–383; 20: *Divietipellis robusta* Wicander, 1974, sample GNR54–26.

palynomorphs were photographed with a Zeiss Axio Imager microscope equipped with oil immersion objectives. During the numbering stage, “GNR” represents the section name “Gennaren”. The following number indicates the sample number, and the number following the hyphen “-” represents the specimen number within the sample. For example, the 15th specimen found in the 55th sample under the microscope is denoted as “GNR55–15”. (See Fig. 3.)

The resulting organic residues were mounted on microscope slides and examined under a light microscope. Approximately half of the samples contained identifiable palynomorphs. All illustrated specimens from this study are housed in the collections of the Department of Resources and Environment at Shanxi University of Finance and Economics.

4. Phytoplankton assemblages

A total of forty-one phytoplankton species (Fig. 5) belonging to 20

genera have been identified across the samples. These species can be categorized into three assemblages (Fig. 4). The first assemblage is established within the lower part of the lower member of the Hongguleleng Formation, while the second assemblage is found in the upper part of the same member.

4.1. Phytoplankton assemblage I

Phytoplankton Assemblage I is observed in sample GNR8 (Fig. 5). Sample GNR8 exhibits a high degree of diversification and abundance of specimens. In terms of biostratigraphy, this assemblage corresponds to the *Cyrtospora cristifer* – *Diaphanospora zadonica* (CZ) to *Lagenosporites immensus* (Im) miopore zones of eastern Europe, as delineated by Shen et al. (2024) (Fig. 4).

The assemblage comprises the following species: *Gorgonisphaeridium plerispinosum*, *Somphophragma miscella*, *Michrhystridium pentagonale*, *Pterospermella* sp., *Cymatiosphaera perimembrana*, *Cymatiosphaera*

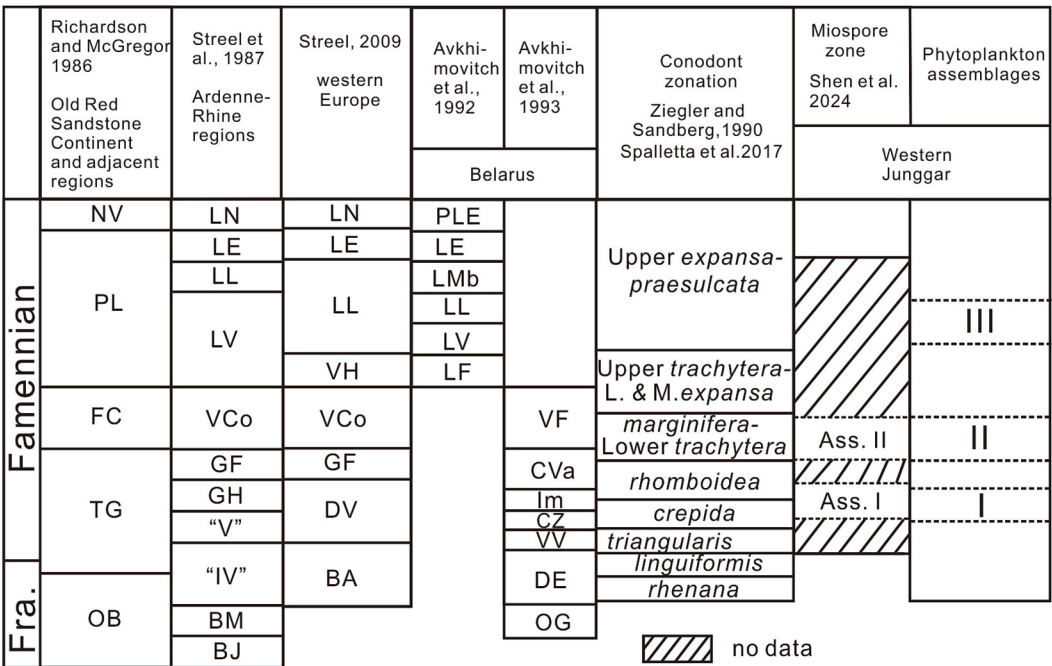


Fig. 4. Correlation of Famennian spore and phytoplankton zonal schemes in Western Junggar, with reference to established miospore zonal schemes from the Old Red Sandstone Continent (ORSC) and adjacent areas (Richardson and McGregor, 1986), western Europe (Stree et al., 1987; Stree, 2009) and eastern Europe (Avkhimovitch et al., 1992, 1993). Additionally, conodont zonal schemes from Ziegler and Sandberg (1990) and Spalletta et al. (2017) are incorporated for comparison. Abbreviations: Fra. = Frasnian; Ass. I = Assemblage I; Ass. II = Assemblage II. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

rhacoamba, *Cymatiosphaera daioariochora*, *Daillydium pentaster*, *Michrystidium* spp., *Solisphaeridium* sp., *Solisphaeridium clavum*, along with *Unellium piriforme*, cf. *Centrasphaeridium armarium*, *Michrystidium flexibile*, *Unellium winslowiae*, *Michrystidium stellatum*, *Cymatiosphaera* cf. *melikera*, and *Veryhachium trispinosum* “group”. *Daillydium pentaster* and *Veryhachium trispinosum* are also present in the succeeding Assemblage II.

4.2. Phytoplankton assemblage II

This assemblage is present in samples GNR50 through GNR63 (Fig. 5), which correspond to the miospore zones of *Grandispora gracilis* – *Grandispora famenensis* (GF) to *Rugospora versabilis* – *Grandispora cornuta* (CVO), as defined for western Europe (Shen et al., 2024). The assemblage is distinguished by the appearance of several species, including *Gorgonisphaeridium savertonense*, *Gorgonisphaeridium tabasense*, *Gorgonisphaeridium ohioense*, *Gorgonisphaeridium elongatum*, *Dasypylula storea*, *Leiosphaeridia* sp., *Ammonidium sprucegrovense*, *Ammonidium loriferum*, and *Ammonidium levigatum* (Fig. 6). Additionally, *Perissolagonella* cf. *amsdenii*, *Pterospermella capitata*, and *Pterospermella solis* (Fig. 7) are also notable members. Other species present include *Multiplicisphaeridium* sp., *Lophosphaeridium* sp., *Divietipellis robusta*, *Veryhachium trispinosum* “group”, *Saharidia lusca*, *Leiofusa* sp., cf. *Veryhachium polyester*, *Lophosphaeridium segregum*, *Gorgonisphaeridium amplum*, *Gorgonisphaeridium absitum*, and *Cymatiosphaera* sp.

This zone is characterized by the frequent occurrence of *Pterospermella* spp., *Gorgonisphaeridium* spp., and the initial appearance of *Ammonidium* spp.

4.3. Phytoplankton assemblage III

This assemblage is present in samples 85 and 86. Although this assemblage does not exhibit a rich association of palynomorphs, it is established as an independent assemblage due to the fact that the samples originate from the top of the middle member of the

Hongguleleng Formation, and the known phytoplankton assemblage and miospore taxa in this zone are distinct from those from the Assemblage II. The assemblage predominantly contains *Exochoderma* spp. (Fig. 6).

Due to the deep-water depositional environment of the middle member of the Hongguleleng Formation, only one possible specimen of *Retispora lepidophyta* was discovered by Shen et al. (2024), from sample GNR83 (recorded as cf. *Retispora* sp.). If *R. lepidophyta* appears at the top of the middle member of the Hongguleleng Formation, the Assemblage III may correspond to the LL miospore Zone, and also to part of the *expansa* conodont Zone.

5. Palynostratigraphical correlation

In contrast to the Early–Middle Devonian, the Late Devonian phytoplankton has received important attention, with many research papers published in recent decades from various regions including North America, Europe, North Africa, and Asia (e.g., Górká, 1974; Wicander and Loeblich, 1977; Martin, 1981, 1984; Playford and Dring, 1981; Molyneux et al., 1984; Wicander and Playford, 1985, 2013; Gao, 1986; Turner, 1986; Hashemi and Playford, 1998; Le Hérisse and Deunff, 1988; Lu and Wicander, 1988; McNestry, 1988; Ghavidel-Syooki, 1994, 2001; González et al., 2005; Filipiak, 2005, 2009; Noetinger, 2010; Stachacz et al., 2021; Wicander, 1974; Wicander et al., 2011).

Jardiné et al. (1974) delineated four acritarch zones (Zones L4 to L7; Fig. 8) within the Late Devonian of Algeria, characterized by taxa such as *Crassianguilina*, *Horologinella*, and *Umbellaspheeridium*, which are infrequently recorded from outside Gondwana. Wicander (1975) established five acritarch biostratigraphical zones spanning the upper Famennian to the lower Mississippian in Ohio (USA). These zones (Fig. 8), in ascending order, are: the *Gorgonisphaeridium ohioense* Assemblage Zone, the *Acriora petala* Assemblage Zone, the *Muraticavea enteichia* Range Zone, the *Cymatiosphaera labyrinthica* Range Zone, and the *Navifusa drosera* Assemblage Zone. Nevertheless, the lack of precise correlations between these biostratigraphical zones and miospore or conodont biozones

Acritarch and Prasinophyte taxa	SAMPLES													
	Ass. I	Assemblage II											Assemblage III	
	GNR8	GNR50	GNR51	GNR52	GNR54	GNR55	GNR58	GNR59	GNR60	GNR61	GNR62	GNR63	GNR85	GNR86
<i>Gorgonisphaeridium plerispinosum</i>	●													
<i>Somphophragma miscella</i>	●													
<i>Michrystidium pentagonale</i>	●													
<i>Pterospermella</i> sp.	●													
<i>Daillydium pentaster</i>	●									●				
<i>Cymatiosphaera rhacoamba</i>	●													
<i>Cymatiosphaera daioariochora</i>	●													
<i>Cymatiosphaera perimembrana</i>	●													
<i>Michrystidium</i> spp.	●													
<i>Solisphaeridium</i> sp.	●													
<i>Solisphaeridium clavum</i>	●													
<i>Unellium piriforme</i>	●													
<i>Michrystidium stellatum</i>	●													
<i>Michrystidium flexibile</i>	●													
<i>Unellium winslowiae</i>	●													
? <i>Centrasphaeridium</i> sp.	●													
<i>Cymatiosphaera</i> cf. <i>melikera</i>	●													
<i>Gorgonisphaeridium savertonense</i>								●			●		●	
<i>Gorgonisphaeridium</i> sp.		●												
<i>Gorgonisphaeridium ohioense</i>		●	●	●	●	●	●	●		●	●	●		
<i>Gorgonisphaeridium elongatum</i>		●						●	●					
<i>Dasyplula storea</i>		●												
<i>Leiosphaeridia</i> sp.		●			●	●	●				●			
<i>Ammonidium loriferum</i>		●			●	●				●	●			
<i>Perissolagonella</i> cf. <i>amsdenii</i>		●												
<i>Pterospermella capitata</i>		●								●	●			
<i>Pterospermella solis</i>			●											
<i>Multiplicisphaeridium</i> sp.				●										
<i>Lophosphaeridium</i> sp.				●	●						●			
<i>Divietipellis robusta</i>					●									
<i>Ammonidium sprucegrovense</i>						●								
<i>Ammonidium levigatum</i>					●	●	●			●	●	●		
<i>Veryhachium trispinosum</i> group	●		●				●	●		●	●			
<i>Saharidia lusca</i>									●					
<i>Leiofusa</i> sp.										●				
<i>Lophosphaeridium segregum</i>											●			
<i>Gorgonisphaeridium amplum</i>											●			
<i>Gorgonisphaeridium absitum</i>					●		●				●			
<i>Cymatiosphaera</i> sp. B											●			
<i>Exochoderma</i> cf. <i>irregulare</i>													●	
<i>Exochoderma</i> sp.														●

Fig. 5. Distribution of prasinophyte and acritarch species in the Gennaren section.

complicates their direct application to a global biostratigraphical correlation framework. Similar phytoplankton zonations for the upper Frasnian to lower Famennian (*linguiformis* to *crepida* conodont zones) in Belgium were proposed by Vanguetaine et al. (1983) (Fig. 8), encompassing the *Visbysphaera* (?) *fecunda*, *Villosacapsula globosa*, *Baltisphaeridium medium*, *Baltisphaeridium basiconstrictum*, *Puteoscortum williereae* (Vf, Vg, Bm, Bb, and Pw) interval zones, and by Martin (1984) (Fig. 8), who defined Zones I to V (I = Vf, II = Vg, III = Bm + Bb, and IV + V = Pw). Subsequently, Vanguetaine (1986) proposed a generalized Upper Devonian acritarch succession for Belgium, based on five species (in ascending order: *Visbysphaera* (?) *fecunda*, *Baltisphaeridium medium*, *Puteoscortum williereae*, *Tornacia sarjeantii*, and *Gorgonisphaeridium winslowae*). Le Hérissé et al. (2000) summarized the biostratigraphy, palaeoecology, and paleogeography of Devonian phytoplankton, mapping the biostratigraphical range and geographical distribution of over 180 phytoplankton species. Filipiak (2005, 2009) distinguished the phytoplankton assemblages of the Holy Cross Mountains (HCM) in central Poland, encompassing deposits from the lower Famennian, upper Famennian, and Lower Carboniferous (Tournaisian and Viséan).

Although numerous local phytoplankton zonations have been established in the Upper Devonian, it is noteworthy that discussions on the stratigraphical-correlative and chronological significance of palynomorph assemblages have predominantly focused on miospore

components, rather than organic-walled phytoplankton. The establishment of a robust, global zonal scheme for phytoplankton biostratigraphy, comparable to those for miospores and conodont biozones (Tyson, 1995; Le Hérissé et al., 1997; Playford, 2003; Shen et al., 2019), remains unattained due to a multitude of influencing factors, including latitude- and current-driven palaeotemperature, water chemistry, fertility, physical barriers, and proximity to coastlines. Although species like *Michrystidium stellatum*, *Daillydium pentaster*, *Unellium winslowiae*, and *Unellium piriforme* exhibit a global distribution, their long biostratigraphical ranges render them of limited biostratigraphical value (Fig. 9).

Based on chronostratigraphical evidence from miospores (Shen et al., 2021), conodonts (e.g., Zhao and Wang, 1990), brachiopods (Ma et al., 2011), and ammonoids (Zong et al., 2014, 2021), reported from the Hongguleleng Formation at the Bulongguoer section, combined with recently recovered miospore assemblages from the Gennaren section (Shen et al., 2024), the phytoplankton Assemblage I correlates approximately with the Old Red Sandstone Continent *Teichertospira torquata* – *Grandispora gracilis* (TG) miospore Zone and the western European *Knoxisporites dedaleus* – *Diducites versabilis* (DV) miospore Zone, and can be compared with the *crepida* conodont Zone (Fig. 4).

The comparison of the taxonomic lists produced by Martin (1984) in her palynoflora IV and V Zones (stratigraphically equivalent to the Pw

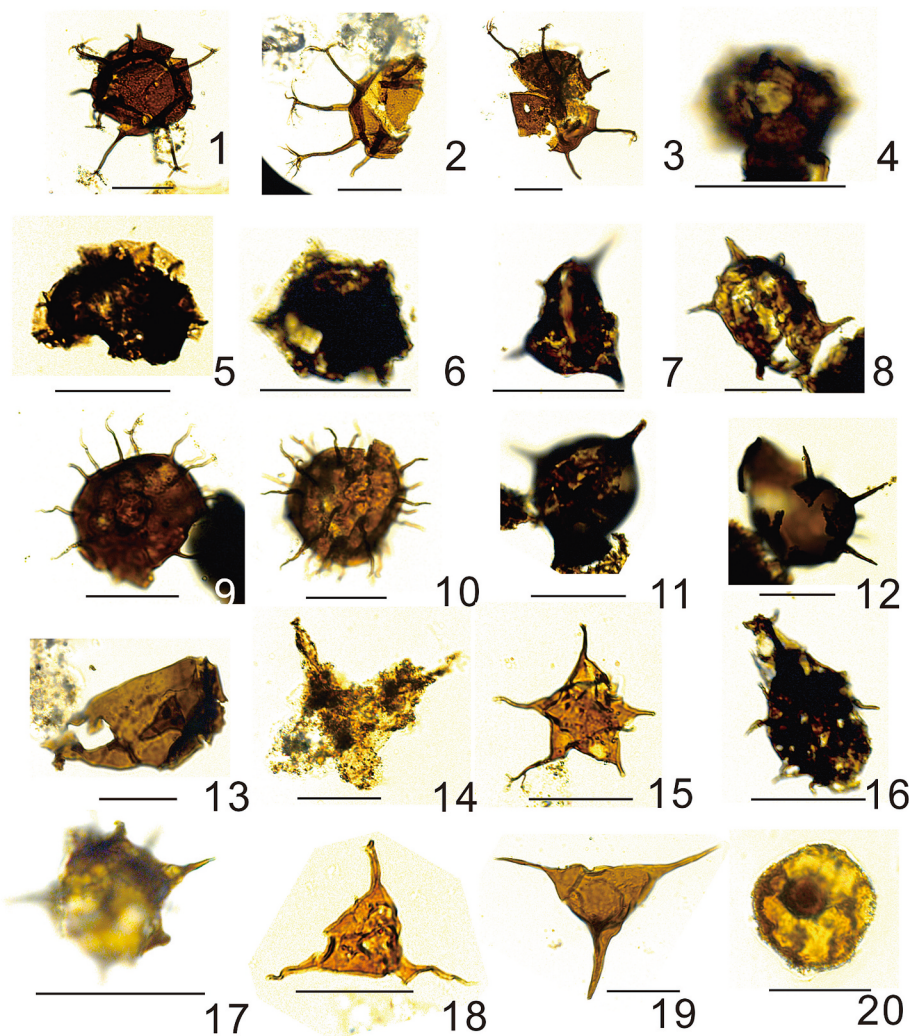


Fig. 6. Famennian phytoplankton from the Hongguleleng Formation in the Gennaren section. Scale bar = 20 μ m. 1: *Ammonidium loriferum* (Deunff, 1965) Hashemi and Playford, 1998, sample GNR50–85; 2: *Ammonidium sprucegroense* (Staplin, 1961) Lister, 1970, sample GNR55–8; 3: *Ammonidium levigatum* Shen et al., 2022, sample GNR55–5; 4: *Cymatiosphaera rhacoamba* Wicander, 1974, sample GNR8–14; 5: *Cymatiosphaera daioariochora* Wicander, 1974, sample GNR8–16; 6: *Cymatiosphaera perimembrana* Staplin, 1961, sample GNR8–7; 7–8: *Michrystidium* spp., samples GNR8–9 and GNR8–3; 9: *Gorgonisphaeridium savertonense* Wicander and Playford, 2013, sample GNR62–48; 10: *Gorgonisphaeridium elongatum* Wicander, 1974, sample GNR50–13; 11: *Solisphaeridium* sp., sample GNR8–4; 12: *Solisphaeridium clavum* Wicander, 1974, sample GNR8–2; 13: *Exochoderma* sp., sample GNR86–1; 14: *Daillydium pentaster* (Staplin, 1961) emend. Playford in Playford and Dring, 1981, sample GNR61–2; 15: *Perissolagonella* cf. *P. amsdenii* Loeblich and Wicander, 1976, sample GNR50–6; 16: *Unellium piriforme* Rauscher, 1969, sample GNR8–8; 17: *Michrystidium stellatum* Deflandre, 1945, sample GNR8–11; 18–19: *Veryhachium trispinosum* (Eisenack, 1938) Stockmans and Willièrè, 1962 “group”, samples GNR58–4 and GNR59–1; 20: *Saharidia lusca* Playford in Playford and Dring, 1981, sample GNR60–1.

zone of Vanguetaine et al., 1983) with the list of taxa from Western Junggar revealed that only *Pterospermella capitata*, a characteristic species of Martin (1984)’s V Zones corresponding to the lower Famennian of Belgium, was identified in samples GNR50, GNR61, and GNR62 from Western Junggar. Other Belgian lower Famennian species such as *Visbysphaera impetuosa*, *Puteoscutum williereae*, *Horologinella wicanderi*, *Palacanthus tipus*, *Cymatiosphaera limbatisphaera*, *Riculusphaera* cf. *fissa*, and *Pterospermella eruption*, are absent in the present study. Not only do the assemblages from Belgium differ from those of China, but they also differ from other assemblages of the same period from other regions. Some contemporaneously important index taxa, including *Baltisphaeridium medium*, *Villosacapsula globosa*, *Palacanthus tripus*, *Ephelopalla media*, and *Visbysphaera? fecunda*, were also absent from Western Junggar, despite being frequently reported from other areas such as the Holy Cross Mountains (central Poland) and the USA (Wicander, 1974; Wicander and Playford, 1985; Filipiak, 2009).

In northeastern Iran (Ghavidel-syooki and Owens, 2007), the appearance of the miospores *Auroraspora torquata* and *Grandispora*

gracilis in acritarch/spore zone IV suggests an assignment to Richardson and McGregor’s (1986) *Auroraspora torquata*–*Grandispora gracilis* (TG) assemblage zone, recognized in the uppermost Frasnian and lower Famennian strata of Europe, Australia, and Canada (Richardson and McGregor, 1986; McGregor and Playford, 1992). The marine phytoplankton assemblage of northeastern Iran (Ghavidel-syooki and Owens, 2007) bears similarities to that of the Western Junggar of the Kazakhstan Plate, sharing species such as *Daillydium pentaster*, *Gorgonisphaeridium ohioensis*, *Ammonidium loriferum*, *Crassiangulina tessellata*, *Cymatiosphaera melikera*, and *Polyedryxium pharaonis*.

In the Iberian Pyrite Belt of Spain, 23 organic-walled microphytoplankton species belonging to 14 genera were recorded by González et al. (2005) from the Phyllite-Quartzite Group (PQ) and the lower part of the overlying Volcano-Sedimentary Complex (VSC). These units are correlated with the *Diducites versabilis*–*Grandispora cornuta* (VCo) miospore Biozone of late Famennian age and the *Retispora lepidophyta*–*Verrucosisorites nitidus* (LN) zone of latest Famennian age, respectively (Fig. 4; Streel, 2009). Notably, the phytoplankton

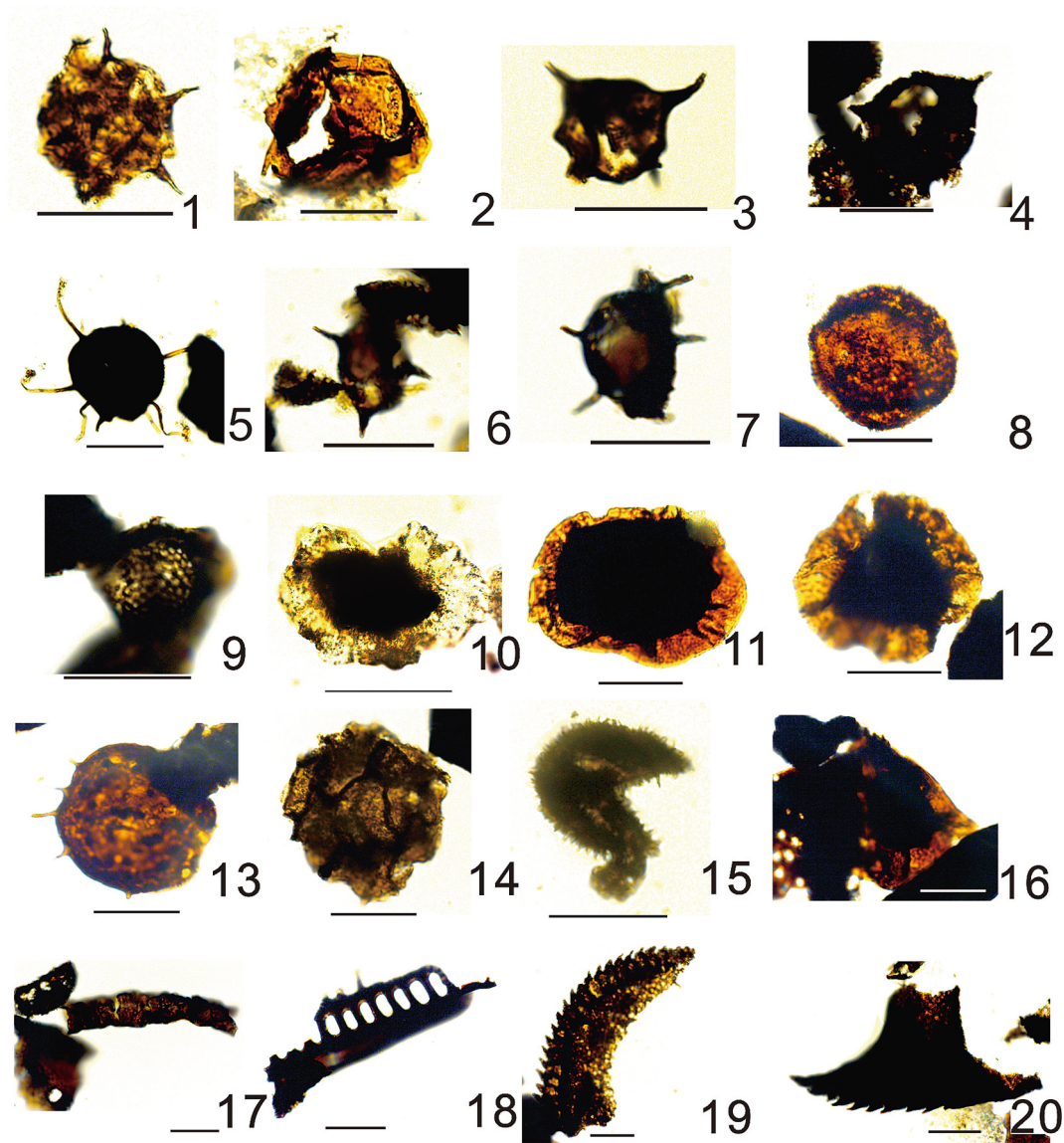


Fig. 7. Phytoclasts, scolecodonts, and phytoclasts from the Hongguleleng section. Scale bar = 20 μm . 1: *Michrystidium flexibile* Wicander, 1974, sample GNR8-50; 2: *Leiosphaeridia* sp., sample GNR50-101; 3: *Unellium winslowiae* Rauscher, 1969, sample GNR8-122; 4: *Centrasphaeridium* sp., sample GNR8-94; 5: *Gorgonisphaeridium amplum* Wicander and Loeblich, 1977, sample GNR62-108; 6–7: *Michrystidium* spp., samples GNR8-164 and GNR8-167; 8: *Lophosphaeridium* sp., sample GNR52-12; 9: *Cymatiosphaera* cf. *melikera* Wicander and Loeblich, 1977, sample GNR8-314; 10: *Pterospermella solis* Wicander, 1974, sample GNR51-4; 11–12: *Pterospermella capitata* Wicander, 1974, samples GNR50-93 and GNR62-109; 13: *Gorgonisphaeridium absitum* Wicander, 1974, sample GNR62-110; 14: *Cymatiosphaera* sp. B, sample GNR62-1; 15: *Gorgonisphaeridium plerispinosum* Wicander, 1974, sample GNR8-428; 16: *Duvernaysphaera radiata* Brito, 1967, sample GNR59-3; 17: tubular phytoclast, sample GNR8-231; 18: Plant remain, sample GNR2-4; 19–20: Scolecodont, samples GNR8-68 and GNR8-69.

assemblage that corresponds to the VCo miospore zone in southwestern Spain exhibits significant differences from that observed in Western Junggar, sharing only six species in common: *Gorgonisphaeridium ohioensis*, *Dalldorfium pentaster*, *Ammonidium sprucegrovense*, *Ammonidium levigatum*, *Michrystidium stellatum*, and the *Veryhachium trispinosum* “group”.

Shen et al. (2022) revised the diagnosis of *Ammonidium* Lister, 1970, leading to the reclassification of several genera, such as *Caicorymbifer* Tappan and Loeblich, 1971, *Gracilisphaeridium* Eisenack and Cramer, 1973, *Puteoscortum* Wicander and Loeblich, 1977, and *Craterisphaeridium* Deunff, 1981, as junior synonyms of *Ammonidium*. Based on morphological distinctions from *A. loriferum* and *A. sprucegrovense*, a new species, *Ammonidium levigatum*, was proposed, characterized by its laevigate wall. The specimens previously reported as *Craterisphaeridium sprucegrovense* by González et al., 2005 (pl. 4, fig. 7, 10; Fig. 10) from the VCo and LN miospore biozones in southwestern Spain, which differs

markedly from *A. sprucegrovense* (González et al., 2005, pl. 4, fig. 8–9; Fig. 10), is here reassigned to *Ammonidium levigatum*.

Due to the lack of high-quality photographs in early publications concerning the species *A. loriferum* and *A. sprucegrovense*, species-level identification of these taxa has been challenging in subsequent studies. Considering the biostratigraphical occurrence of *Ammonidium levigatum* in Iran and Portugal, this species may serve as an index species for the VCo miospore Zone. However, given the paucity of research material, further investigation with a larger sample of palynological specimens is required to confirm this designation.

In the Holy Cross Mountains (Poland), Racka et al. (2010) recorded the presence of miospore and acritarchs belonging to the *Diducites versabilis* – *Grandispora famenensis* (VF) miospore Biozone (Avkhimovitch et al., 1993). Notably, Assemblage II from the Western Junggar shares several acritarch species, namely *Ammonidium loriferum*, *Gorgonisphaeridium ohioense*, and the *Veryhachium trispinosum* “group”, with this

	Conodont zonation	Vanguetaine et al., 1983	Martin, 1984	Jardiné et al., 1974	Wicander, 1975
M. Famennien-Strunian				L7	<i>Navifusa drosera</i> Assemblage Zone
					<i>Cymatiosphaera labyrinthica</i> Range Zone
L. Famennien	crepida	Pw	V	L6	<i>Muraticavea enteichia</i> Range Zone
			IV		
	triangularis	Bb	III	L5	<i>Acriora petala</i> Assemblage Zone
		Bm			<i>Gorgonisphaeridium ohioense</i> Assemblage Zone
U. Frasnian	gigas	Vg	II	L4	
		Vf	I		

Fig. 8. Correlation of the Belgian Vf–Pw Zone (Vanguetaine et al., 1983) I–V Zones (Martin, 1984), acritarch zones within the Upper Devonian of Algeria (Jardiné et al., 1974), the acritarch zones spanning the upper Famennian to the lower Mississippian in Ohio (USA) (Wicander, 1975) with the standard conodont zonation at the Frasnian–Famennian boundary.

Polish locality.

Palynological samples collected from Western Junggar reveal that Assemblage II is not solely composed of acritarch taxa; it also comprises miospores such as *Grandispora microseta*, cf. *Rugospora radiata*, cf. *Terogobulasporites immensus*, *Grandispora famenensis* var. *famenensis*, *Grandispora* cf. *famenensis* var. *minuta*, and *Grandispora cornuta*. The occurrence of these index miospore taxa suggests a middle to late Famennian age for the corresponding strata. This age assignment aligns with the GF through VCo zones in western Europe, as outlined by Streel (2009), and the VCa (for *Cornispora varicornata* Zone) through VF zones in eastern Europe, as described by Avkhimovitch et al. (1993).

Additionally, the appearance of these miospore taxa, coupled with the discovery of a ‘trachytera Biozone’ conodont assemblage by Chen et al. (2009) from the middle member of the Hongguleleng Formation, 113.9 m above the base of the formation in the Bulongguoer section, provides further evidence for the correlation of the lower member of the Hongguleleng Formation with the *crepida* to *trachytera* conodont biozones. Consequently, the phytoplankton assemblage II can be confidently correlated with the middle Famennian *marginifera* to *trachytera* conodont zones (Fig. 4).

6. Palaeobiogeography of Famennian phytoplankton

To characterize the palaeobiogeographical structuring of the Famennian (Late Devonian) phytoplankton and identify the biogeographical affinities of the acritarch assemblage of the Gennaren section (Western Junggar) described here, a global occurrence dataset at the genus level was compiled from the literature. The references used to construct the dataset are listed in Table 1. From these data sources, we built a strictly Famennian phytoplankton database that consists of 88 genera (Table S1) and 13 geographical unit (GUs) (Table 1). Some sampling sites located within the same country/block/belt have been combined into a single geographical unit based on recent palaeogeographic reconstructions (e.g., Boucot et al., 2013). During the construction of the database, all phytoplankton genera have been revised in light of the latest developments in phytoplankton systematics. For example, *Craterisphaeridium* and *Puteoscutum* (Wicander and Playford, 2013) are considered here as junior synonyms of *Ammonidium* (Shen et al., 2022). Also, *Pterospermopsis heol* (Gorka, 1974, pl. XIII, fig. 1) is reassigned to *Pterospermella heol* (Table S2).

Characterization of Famennian phytoplankton palaeobiogeography

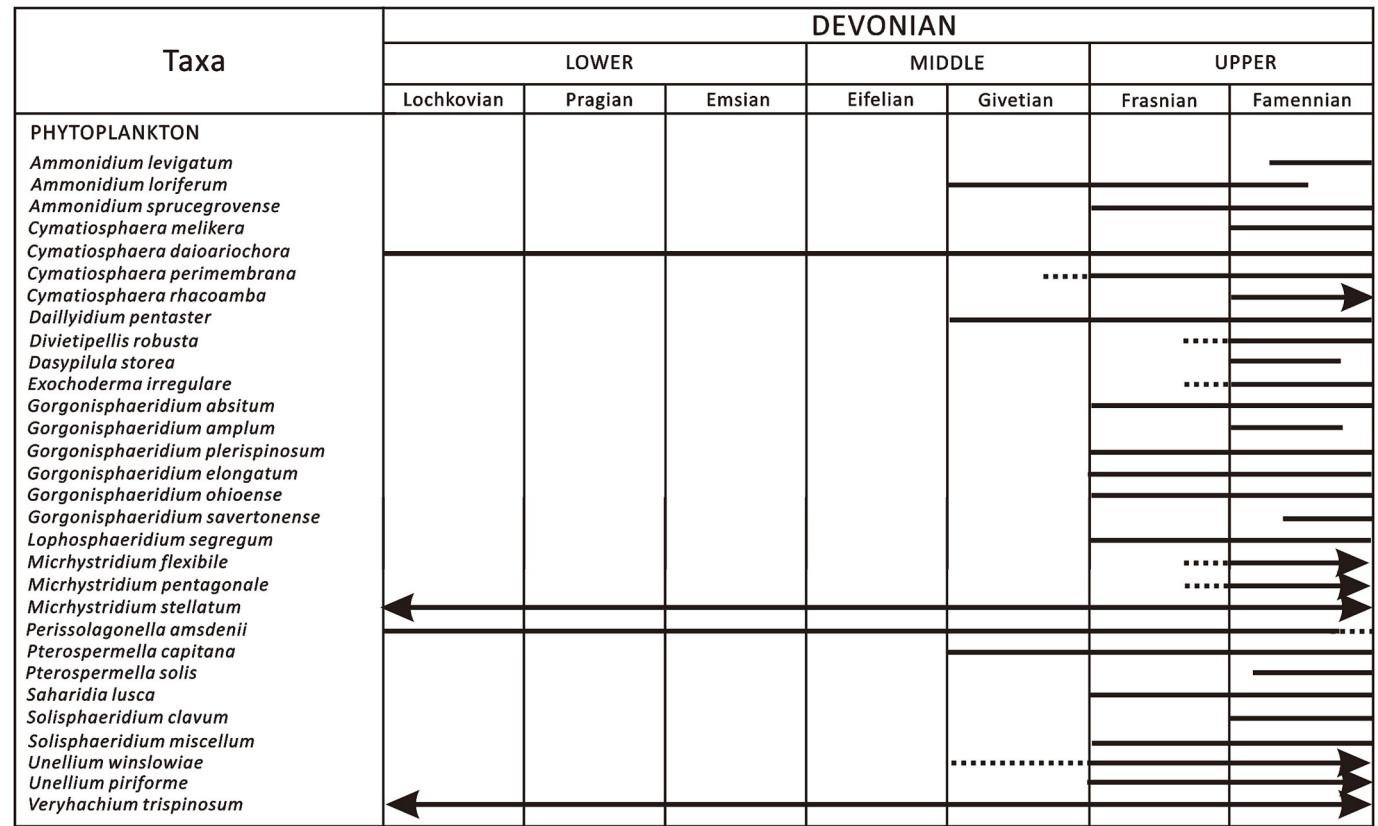


Fig. 9. Stratigraphical ranges of selected phytoplankton species. Dashes indicate uncertainty of range limits; arrows denote ranges extending into the Silurian and Mississippian. The stratigraphical range of species are compiled from the literature (for further details, see text).

is achieved through complementary multivariate techniques applied on this compiled dataset: (1) classical hierarchical cluster analysis (HCA with UPGMA linkage; Legendre and Legendre, 2012) using three similarity indices (Dice/Sørensen, Simpson, and Raup–Crick); (2) neighbor-joining cluster analysis (NJ; Saitou and Nei, 1987); (3) 2D non-metric multidimensional scaling (NMDS; Legendre and Legendre, 2012); and one-way analysis of similarity (ANOSIM; Clarke, 1993). For a description and discussion on these techniques in paleontology, see Shi (1993), Hammer and Harper (2006), Brayard et al. (2015), and Vörös and Escarguel (2020), among others, and references therein. Following Vörös and Escarguel (2020), results of the Dice index are here given priority due to its attractive properties with respect to other classical binary similarity indices (i.e., the double weight attributed to shared presences that underweights absence and unique occurrences as an indication of differences), and results of the Simpson index as potential indication of spurious effects due to genus richness differences between assemblages. The major results of these analyses are reported on Fig. 11 and genus richness of each GU is reported on Table 1. Finally, the GUs considered here are reported on a palaeogeographic map (Fig. 12; modified after Scotese and Wright, 2018) in order to assess consistency of detected patterns. Also, the distribution of the non-singleton taxa among the GUs considered is reported on Fig. 13.

These multivariate analyses (Fig. 11) clearly show that during the Famennian the phytoplankton genus assemblage from Western Junggar has the highest similarity with northeastern Europe (Poland), as can be expected from its closest palaeogeographic distance (Fig. 12). Indeed, during the Famennian, Western Junggar shared a number of phytoplankton species with the Holy Cross Mountains in Central Poland (Filipiak, 2009), such as *Centrasphaeridium lecythium*, *Micrhystridium stellatum*, *Dictyotidium craticulum*, *Gorgonisphaeridium evexispinosum*, *Maranhites stockmansii*, *Polyedryxium embudum*, *Stellinium comptum*, *Stellinium micropolygonale*, *Unellium piriforme*, and *Unellium winslowiae*.

Notably, several of those species demonstrate wide geographical and temporal distributions, such as *Centrasphaeridium lecythium*, *Unellium piriforme*, *Stellinium comptum*, *Maranhites stockmansii*, *Stellinium micropolygonale*, *Micrhystridium stellatum*, *Gorgonisphaeridium evexispinosum*, and *Daillyidium pentaster*. Furthermore, the Famennian phytoplankton assemblages in Western Junggar exhibit a high degree of similarity with those from localities of USA and Canada.

At a global scale, the various cluster analyses show rather consistent patterns with some minor discrepancies (Fig. 11). Two major biogeographical realms can be clearly distinguished: (1) a Laurussia Realm encompassing Western Junggar, Poland, Belgium, South Wales, USA, and Canada; and (2) a North Gondwana Realm covering Portugal, Spain, Morocco, Algeria, Turkey, and Iran.

Although the existence of these two realms is consistent, a few GUs are located at variance among the different cluster analyses. Especially Wales, Canada, and Morocco are often clustered in the opposite realm compared to their actual palaeogeographic position (compare Figs. 11 and 12). The discrepancies in the position of these countries are probably biased by the relative completeness of their fossil record: for example, South Wales (13) and Canada (16) are the GUs with the lowest taxonomic richness (the mean richness among studied GUs being ca. 25), suggesting that their fossil record is too incomplete to recover their actual biogeographical affinity. The biogeographical affinity of Morocco is more questionable: it shows affinity with the Laurussia Realm whereas it has a palaeogeographic position in the North Gondwana Realm; this discrepancy most probably results from a taxonomic composition composed almost exclusively of cosmopolitan taxa (Fig. 13). Finally, one GU stands in contrast: Bolivia shows an affinity with the Laurussia Realm despite having an isolated southward high-latitude palaeogeographic position. Nevertheless, the genus composition of Famennian acritarchs can be partitioned into these two palaeobiogeographical realms, which are characterized mainly by (Fig. 13): (1) *Exochoderma*,

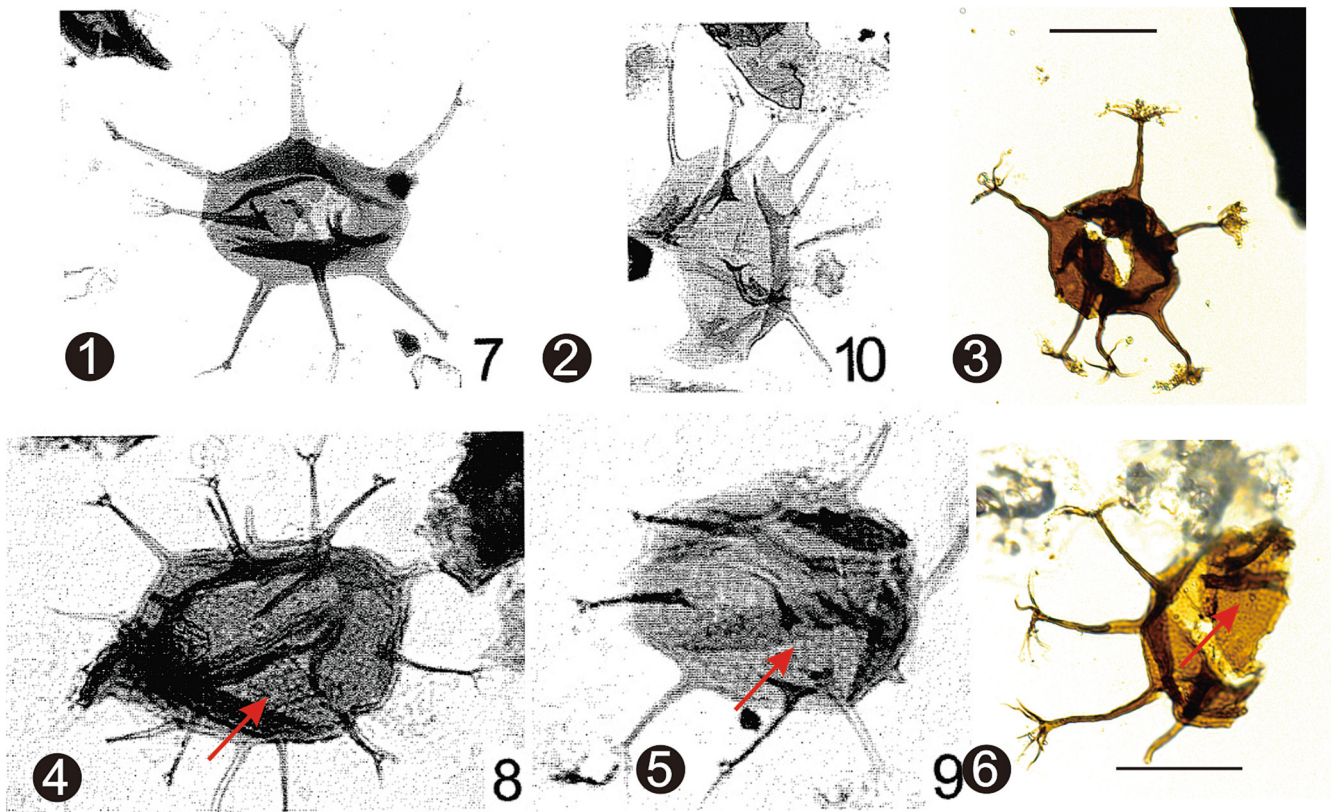


Fig. 10. Comparison of *Ammonidium sprucegroense* and *Ammonidium levigatum*. Figs. 1, 2, 4, and 5 are adapted from [González et al. \(2005\)](#), with permission from the authors. 1: *Ammonidium levigatum* (*Craterisphaeridium spucegroense*, from [González et al., 2005](#), pl. 4, fig. 7); 2: *Ammonidium levigatum* (*Craterisphaeridium spucegroense*, from [González et al., 2005](#), pl. 4, fig. 10); 3: *Ammonidium levigatum*, sample GNR62–92, collected from the upper part of the lower member of the Hongguleleng Formation from the Gennaren section; 4: *Ammonidium sprucegroense* (*Craterisphaeridium spucegroense*, from [González et al., 2005](#), pl. 4, fig. 8); 5: *Ammonidium sprucegroense* (*Craterisphaeridium spucegroense*, from [González et al., 2005](#), pl. 4, fig. 9); 6: *Ammonidium sprucegroense*, sample GNR55–8, collected from the upper part of the lower member of the Hongguleleng Formation from the Gennaren section.

Table 1
Contextual information of the 13 geographical units of global Famennian phytoplankton used in the palaeobiogeographical analysis.

Geographical units (GUs)	Phytoplankton localities	No. of genera	Stratigraphical units/ intervals	Tectonic units	References
Belgium	Dinant Basin	31	Upper Frasnian–Famennian	European block	Martin, 1981, 1984
South Wales	Ewenny, Cwry-yr-ala	13	Famennian–lower Carboniferous		McNestry, 1988 ; Davies et al., 1991
USA	Illinois	47	Bedford Shale, Berea Sandstone Formation	North America block	Molyneux et al., 1984 ; Wicander, 1974 ; Wicander and Loeblich, 1977 ; Wicander and Playford, 2013 ; Playford and McGregor, 1993
Canada	Central Ohio	16	Bakken Formation	North America block	
	Antrim Shale, Indiana				
	Southern Saskatchewan				
Poland	Holy Cross Mountains	34	Famennian–lower Carboniferous	European block	Górka, 1974 ; Filipiak, 2005, 2009 ; Racka et al., 2010
Iran	Esfahan; Shahrud city; Alborz Range	27	Khoshyeilagh Formation	Cimmeria Belt	Ghavidel-Syooki, 1994, 2001 ; Ghavidel-Syooki and Owens, 2007 ; Ghavidel Syooki and Taherian, 2012 ; Taherian et al., 2021
			Padeha and Khoshyeilagh Formations		
			Geirud Formation		
Turkey	Hakkari Province	13	Yiginli Formation	Cimmeria Belt	Higgs et al., 2002
Portugal	South Portuguese Zone	23	Tercenas Formation; Phyllite–Quartzite Group; Volcano Sedimentary Complex; Represa Formation	Iberian Pyrite Belt	Pereira et al. (2008)
Spain	Iberian Pyrite Belt, southwest Spain	19	Phyllite–Quartzite Group, Volcano–Sedimentary Complex	Iberian Pyrite Belt	González et al., 2005, 2006 ; González, 2009
Bolivia	Bermejo	31	Lquiri and Itacua Formation	South America block	Vavrdová et al., 1996 ; Wicander et al., 2011
Algeria	Algerian Sahara	13	Gazelle Formation (Upper Devonian)	Northern Africa block	Jardiné et al., 1974
Morocco	Well DOT1, Doukkala Basin, Central-West Morocco	20	Depth interval of 2800–3134 m	Northern Africa block	Rahmani-Antari, 1990
Western Junggar	Hefeng	33	Hongguleleng Formation	Kazakstan block	Lu and Wicander, 1988 ; Shen et al., 2021 ; Stachacz et al., 2021

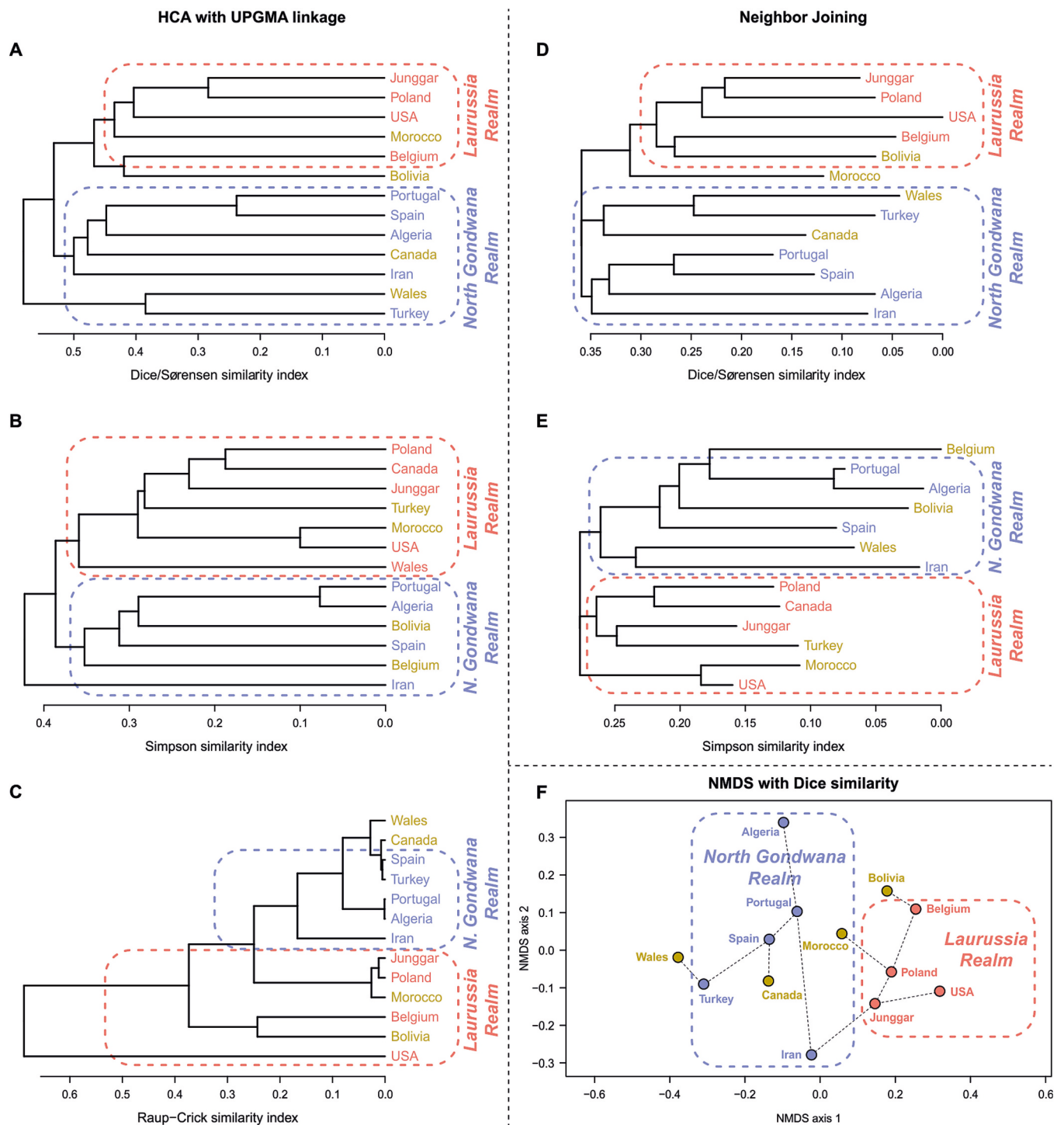


Fig. 11. A–C, the results of cluster analysis with ultrametric hierarchical trees (HCA with Dice/Sørensen, Simpson, and Raup-Crick similarity index); D–E, the results of cluster analysis with metric additive trees (NJ with Dice/Sørensen and Simpson similarity index); F, the result of the NMDS ordination analysis (Dice/Sørensen similarity index) of the phytoplankton dataset are connected by the minimum spanning tree. For explanation see text.

Ephelopalla, *Muraticavea* and *Dasypilula* for the Laurussia Realm; and (2) *Chomotriletes*, *Crassiangulina* and *Navifusa* for the North Gondwana Realm. Interestingly, these results are similar to those published by Shen et al. (2019), for instance, with Poland, Western Junggar, the USA, and Canada being clustered together. On the basis of this biogeographical clustering scheme, the one-way ANOSIM tests (based on the Dice similarity) indicate that the genus composition of the two realms differs weakly ($R = 0.16$, $p = 0.102$).

Additionally, the Famennian acritarch flora can be characterized as

having had a large cosmopolitan component, as indicated by the wide palaeogeographic distribution of many genera (ca. 20% of the 52 non-singleton taxa), such as *Cymatiosphaera*, *Daillydium*, *Gorgonispheeridium*, *Maranhites*, *Michrystidium*, *Multiplicisphaeridium*, *PterospERMella*, *Stellinium*, *Unellium*, and *Veryhachium*, which are documented in two-thirds of the countries studied (Fig. 13). Noteworthy, this high proportion of cosmopolitan taxa explains the discrimination of the two large Laurussia and North Gondwana realms without finer subdivisions; further it partly causes the weak clustering of

Famennian (ca. 365 Ma) (Late Devonian)



Fig. 12. Famennian (Late Devonian) palaeogeographic map (modified after [Scotese and Wright, 2018](#)) showing the geographical units considered, which can be clustered in a Laurussia Realm and a North Gondwana Realm.

poorly sampled GUs. This high proportion of cosmopolitan acritarch flora during the Late Devonian was also pointed out by [Molyneux et al. \(2013\)](#).

7. Palaeoenvironment of the lower member of the Hongguleleng Formation

Numerous studies have indicated that the diversity, abundance, and variations in morphological combinations of phytoplankton assemblages, along with the proportion of marine phytoplankton to terrestrial miospores, commonly associated with significant amounts of amorphous organic matter, are indicative of a normal marine, somewhat offshore shelf environment (e.g., [Li et al., 2004](#); [Wicander and Wood, 1997](#); [Wicander and Playford, 2013](#)).

[Li et al. \(2004\)](#) investigated the ecological spatial distribution of acritarch taxa during the Early to Middle Ordovician. Their findings showed that: (i) the generic and specific diversity of acritarchs increases continuously from nearshore environments towards the shelf area; (ii), the composition of assemblages varies along the nearshore-to-offshore transect; (iii), acanthomorph genera, such as *Baltisphaeridium*, dominate shelf environments; and (iv) further towards the open sea, the process length increases and its appearance becomes more complex.

In the Illinois Basin of the United States, [Wicander and Playford \(2013\)](#) analyzed the relative proportions of phytoplankton and miospores. They concluded that changes in the relative abundance of marine phytoplankton and terrestrial palynomorphs reflect transitions from nearshore to offshore sedimentary environments. A high proportion of acritarchs is indicative of a low-energy, somewhat offshore, normal marine depositional environment, whereas a high proportion of terrestrial palynomorphs suggests a shallow nearshore sedimentary setting.

According to the terrestrial and marine phytoplankton assemblage percentages in the Gennaren section ([Fig. 14](#)), the sedimentary environment of the lower member of the Hongguleleng Formation has experienced a dynamic transition from coastal-shallow water environments to deeper water environments, followed by a reversion to shallow water conditions. This environmental succession is evident in the following observations: initially, samples collected from the base of the Hongguleleng Formation were devoid of marine phytoplankton, containing only terrestrial organic matter and miospores ([Fig. 14](#)). At the

20.3 m level of the Hongguleleng Formation, there is a notable increase in the diversity and abundance of the marine phytoplankton, with the phytoplankton and scolecodonts constituting approximately 52% of the marine/terrestrial assemblage in sample GNR8. The presence of numerous acanthomorph acritarchs and prasinophytes, together with scolecodonts, indicates a low energy, normal marine depositional environment for the lower part of the lower member of the Hongguleleng Formation.

As the sequence progresses upwards, a decline from GNR9 to GNR49 in the abundance of both marine and terrestrial organic material is observed, which suggests a gradual increase in water depth. This deepening water column likely exceeded the optimal habitat range for marine phytoplankton, while also resulting in a reduced proportion of terrestrial palynomorphs and indicating a more distant location from the shoreline.

In the upper part of the lower member of the Hongguleleng Formation, between the samples GNR50 and 61, the percentage of marine to terrestrial assemblages underwent a cyclic pattern, starting low, rising to a high, and then declining again. This vertical succession pattern records a complete transgressive-regressive cycle, reflecting sea-level fluctuations that drove depositional environment changes from initial nearshore conditions through offshore, followed by shallowing regression back to nearshore settings. Particularly noteworthy is the interval between 224 m and roughly 236 m, from GNR58 to 61, at the top of the lower member. Here terrestrial phytoclasts gradually reemerge alongside marine phytoplankton, with the latter predominating the assemblage with miospores being occasionally present. This shift reflects a normal marine, somewhat offshore shelf environment, creating conditions favorable for the proliferation of phytoplankton. Throughout the sedimentary period of the middle member of the Hongguleleng Formation, sea level continued to rise ([Zong et al., 2014](#); [Fan and Gong, 2016](#)). However, by the end of this sedimentary phase, sea level began to decline, leading to the increased appearance of terrestrial phytoclasts and marine phytoplankton, with terrestrial phytoclasts now dominating the assemblage. The above inference of the depositional environment is basically consistent with the depositional environment inferred from the trace fossils in the Wulankeshun section of the coeval sediment in the Western Junggar, which was reported by [Fan and Gong \(2016\)](#). However, more accurate conclusions about the depositional environment

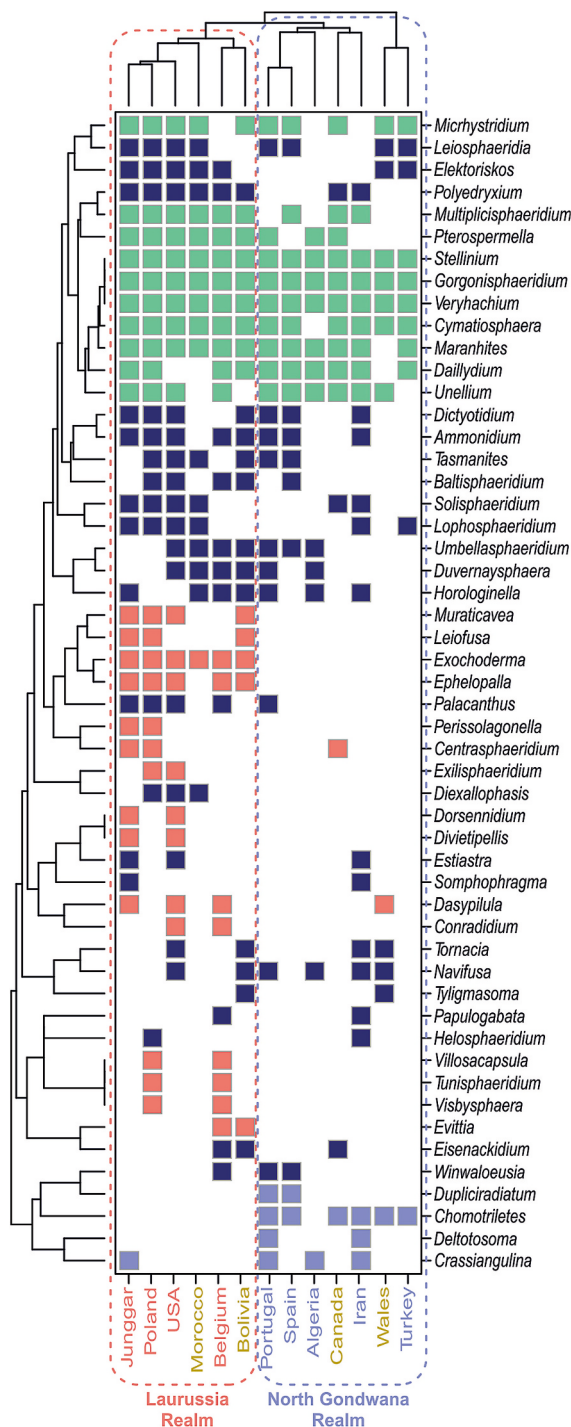


Fig. 13. Distribution of the 52 non-singleton acritarch genera among geographical units considered. (Taxa and countries are ordered by a two-way cluster analysis (UPGMA linkage, Dice similarity).

should be drawn in conjunction with sedimentology and sequence stratigraphy studies in the future.

8. Conclusions

This paper is the first systematic examination of phytoplankton from the Gennaren section in the Western Junggar. Based on the analyzed data, several key conclusions can be drawn:

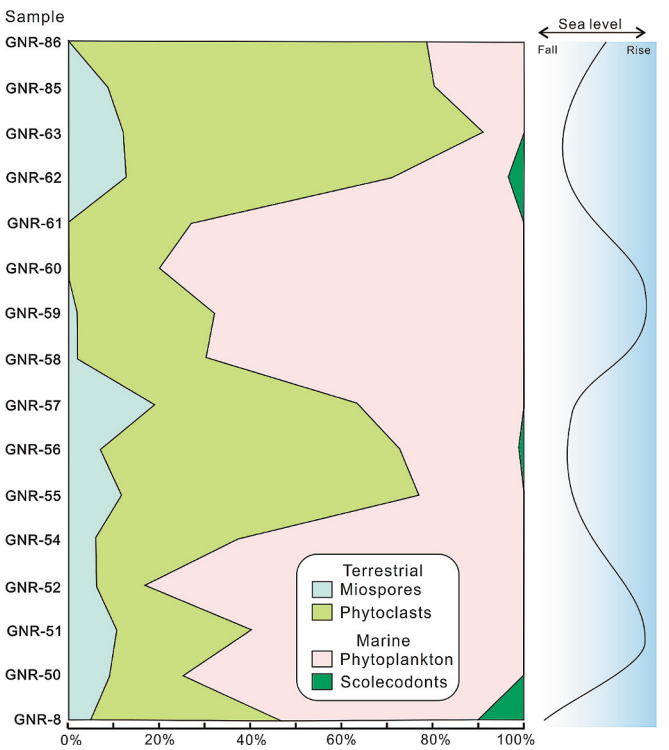


Fig. 14. Palynomorph percentage abundance in the Hongguleleng Formation samples from the Gennaren section.

1. Within the Hongguleleng Formation of the Gennaren section, three distinct assemblages have been recognized, namely Assemblage I, Assemblage II, and Assemblage III. These three identified assemblages correspond to the CZ–LL miospore Zone in eastern Europe, the DV–LL miospore Zone in western Europe, and possibly to the standard conodont *crepida–expansa* Zone.
2. At a global level, two phytoplankton palaeobiogeographical realms are distinguished: the Laurussia Realm and the North Gondwana Realm. Several assemblages identified in the Western Junggar indicate that they belong to the Laurussia Realm. They exhibit similarities with those found in Poland, USA, Canada, and Belgium, suggesting existence of a natural biogeographical relationship during the Famennian period.
3. According to the percentage data of marine and terrestrial palynomorphs observed in the Gennaren section, the sedimentary environment of the lower member of the Hongguleleng Formation has experienced a dynamic transition. Initially, it was characterized by coastal conditions, followed by a shift to neritic water environments. Subsequently, the environment deepened to a deeper water setting, before ultimately reverting to neritic environmental conditions.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2025.105332>.

Data availability

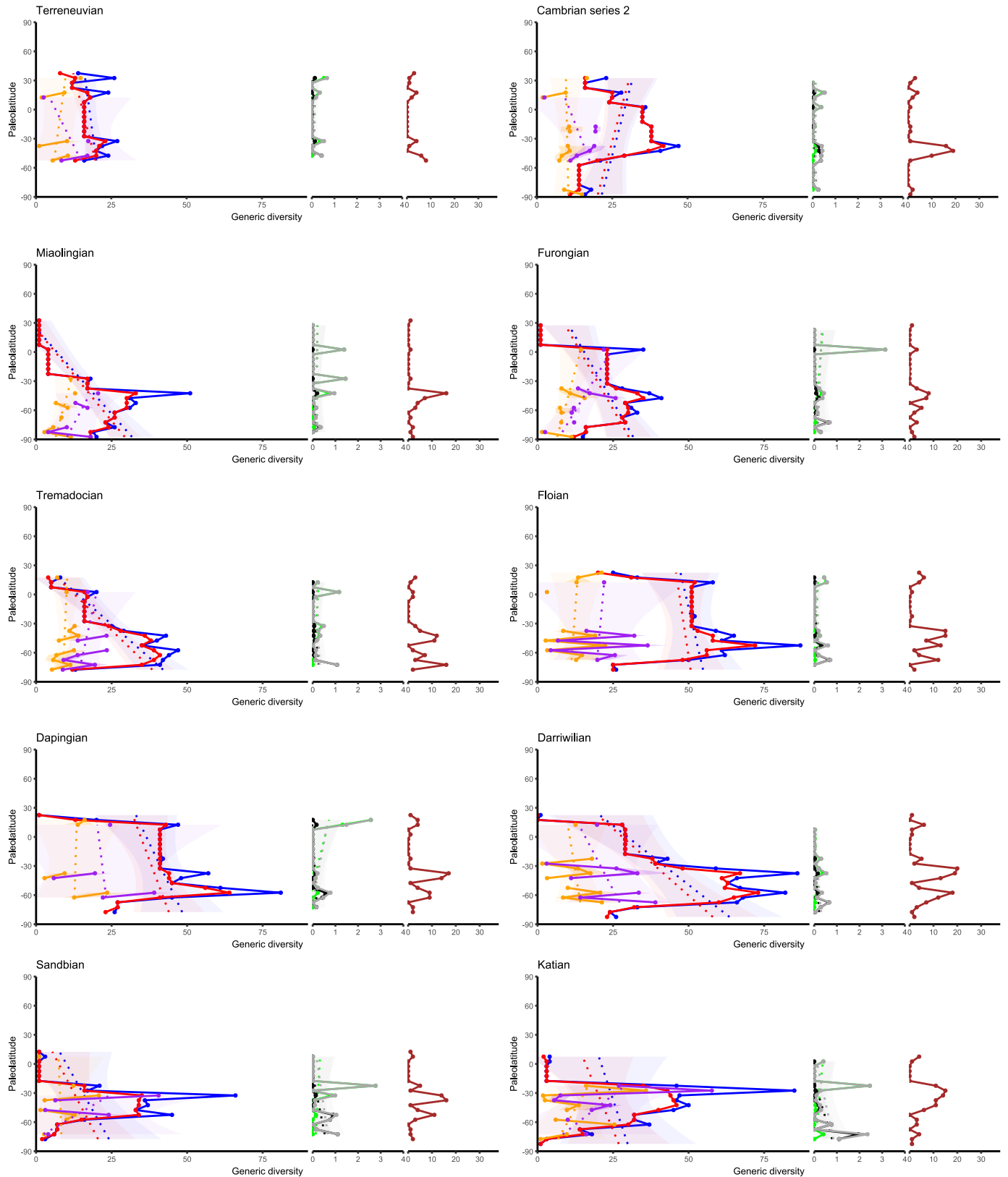
Data will be made available on request.

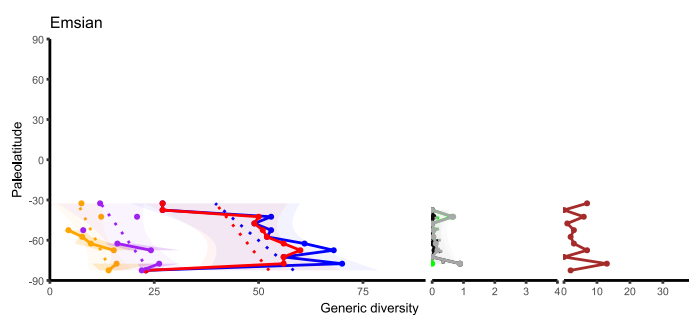
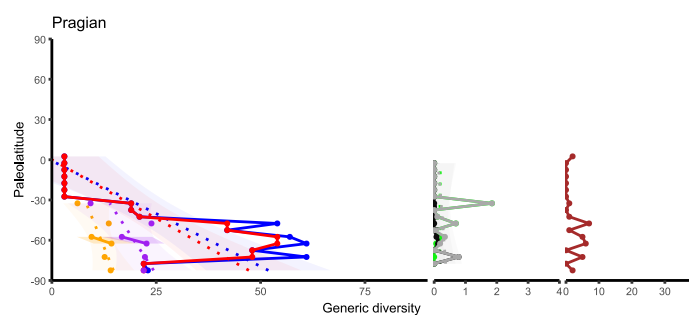
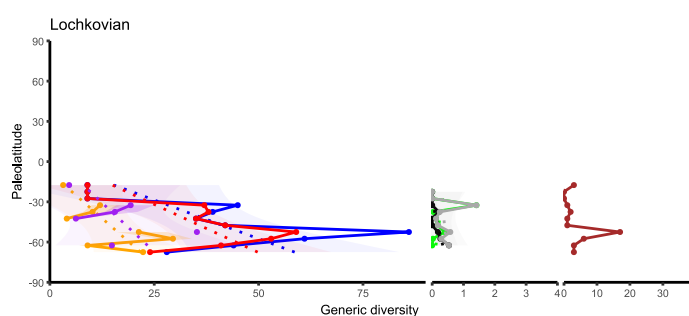
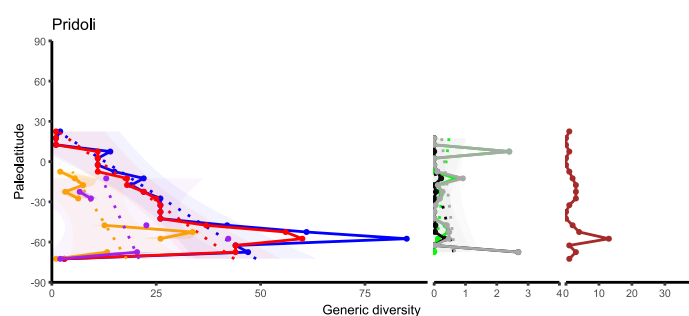
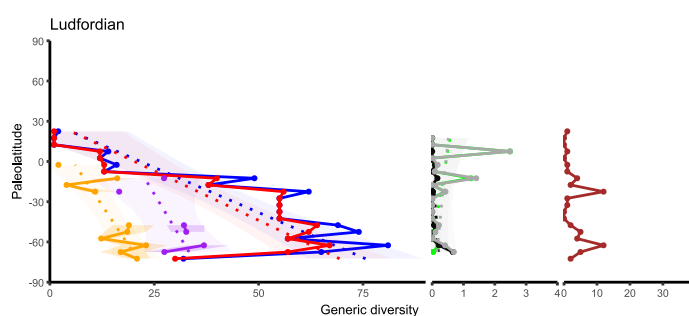
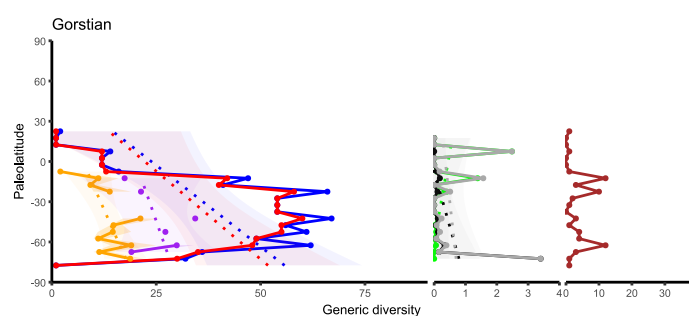
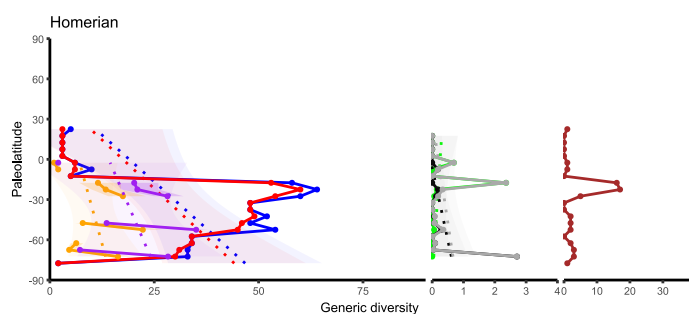
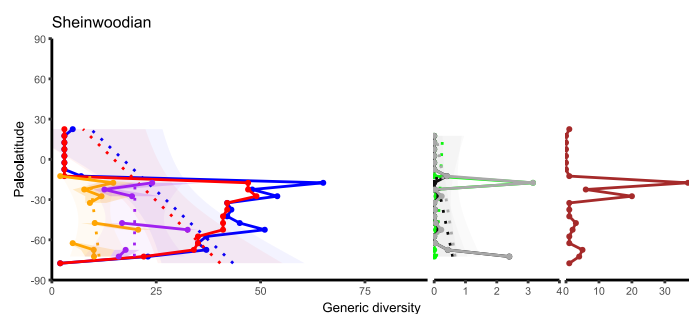
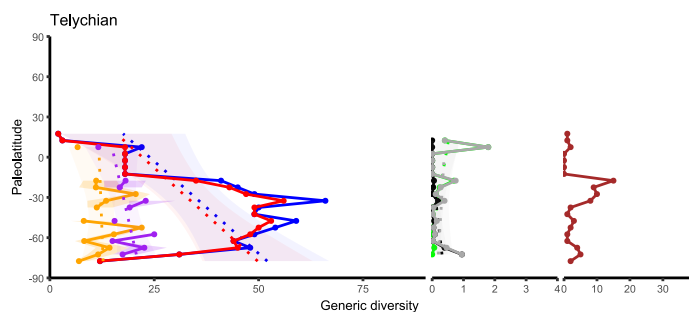
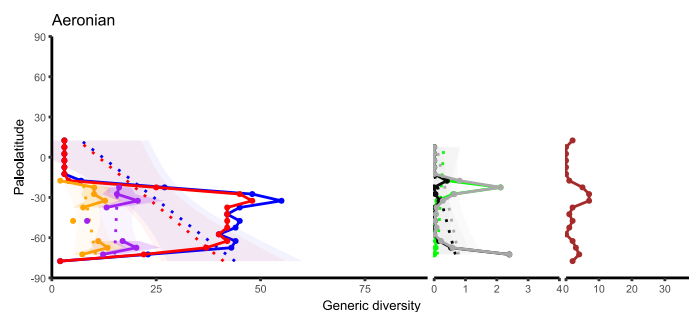
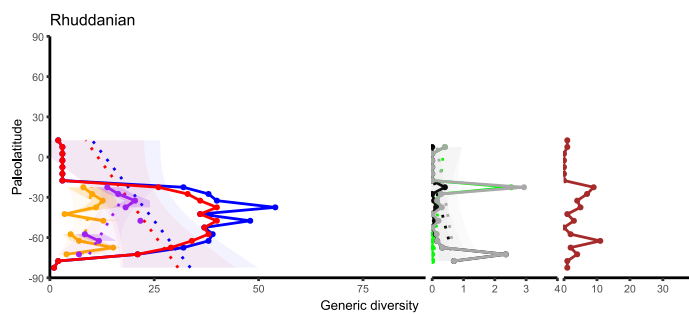
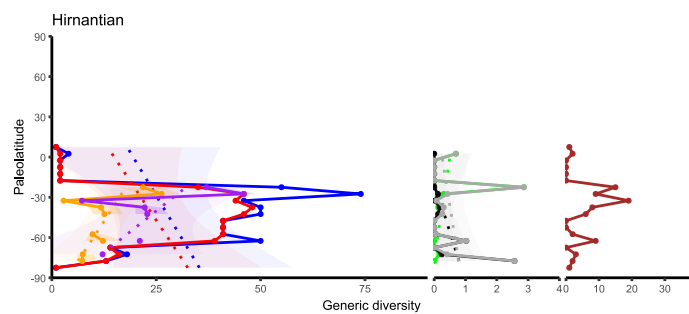
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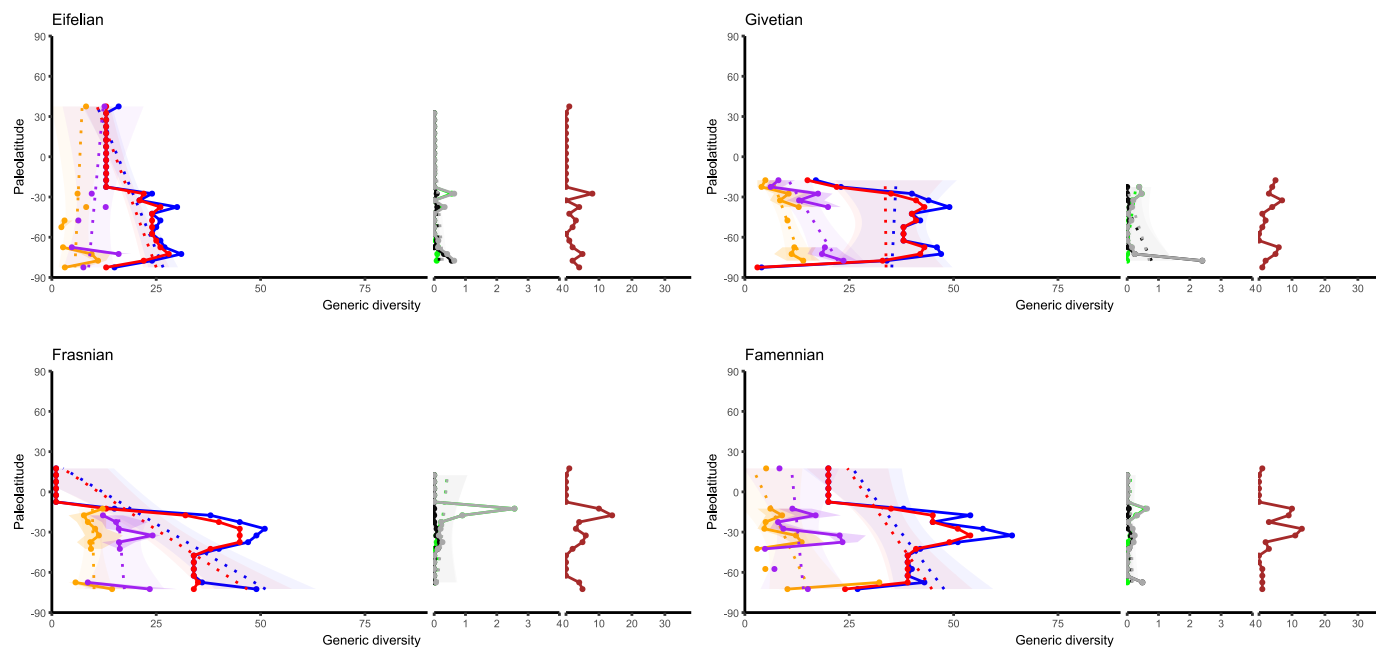
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Appendix 5. Latitudinal gradients of diversity and turnover. The number of localities sampled per latitudinal bin (5°) is also shown. The diversity metrics include range-through (RT), range-through excluding singletons (RTex), and shareholder quorum sampling with quorum of 0.5 (SQS50) and 0.7 (SQS70). Turnover includes origination and extinction rates per capita using Foote (2000) and total turnover. The slope of each diversity and turnover metric is also shown, with the 95% confidence ranges.







Legend:

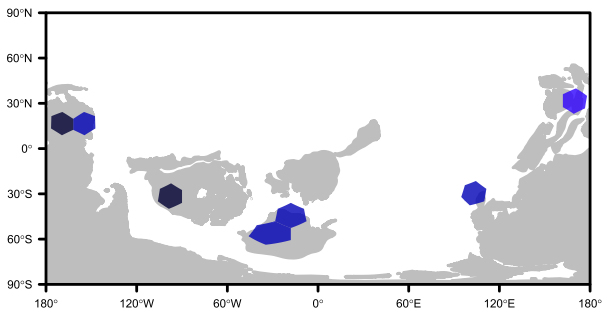
- extPC
- oriPC
- RTextS
- SQS70
- Localities
- RT
- SQS50
- turnover

Slope w/ 95% confidence intervals:

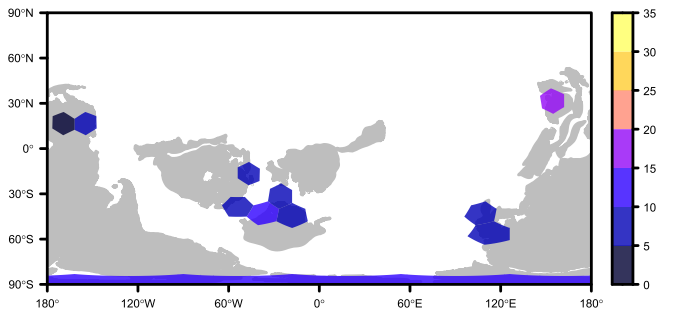
extPC	RT	SQS50
oriPC	RTextS	SQS70

Appendix 6. Grid-cell diversity calculated using shareholder quorum sampling at $q = 0.5$. The color bar represents the number of genera.

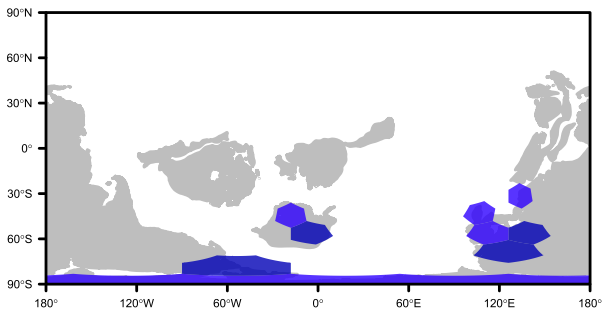
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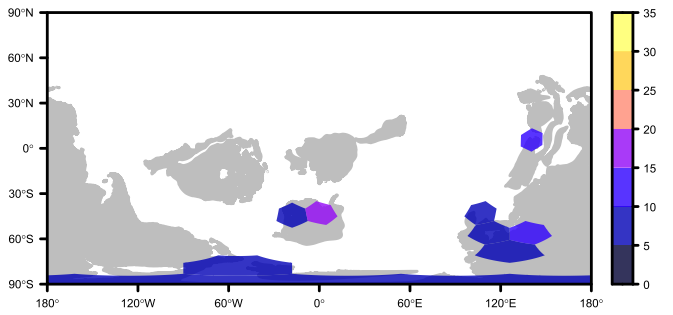
Cambrian series 2



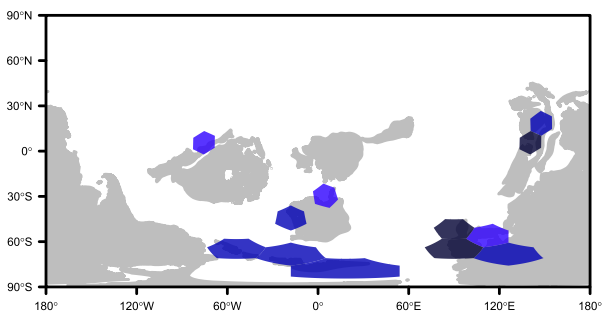
Miaolingian



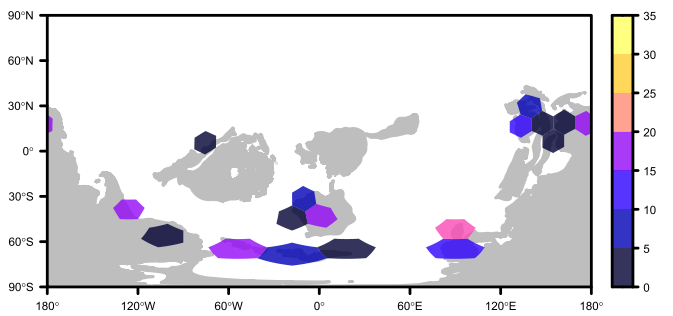
Furongian



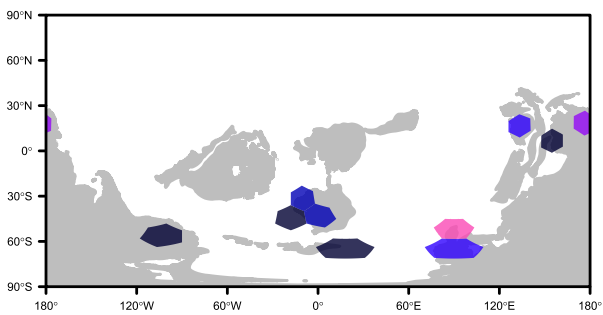
Tremadocian



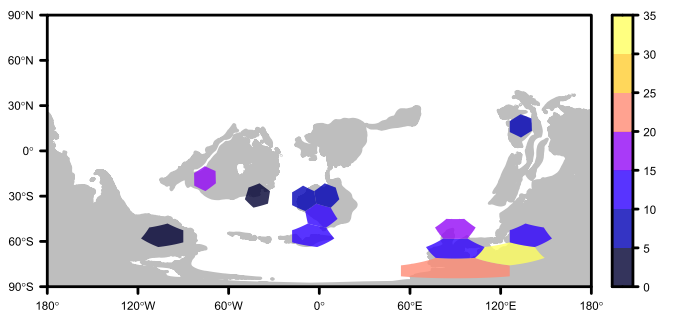
Floian



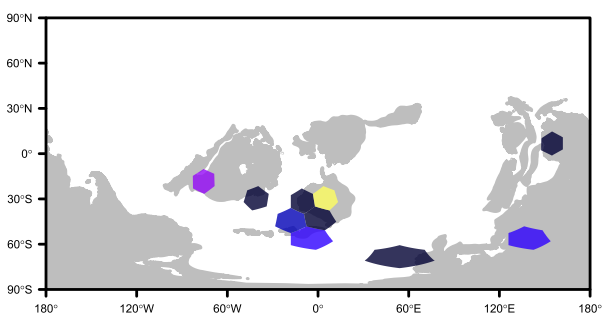
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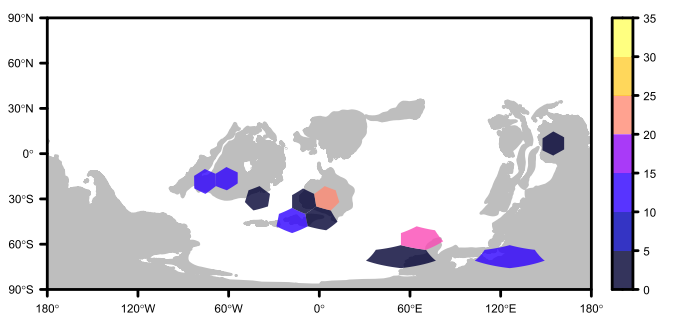
Darriwilian



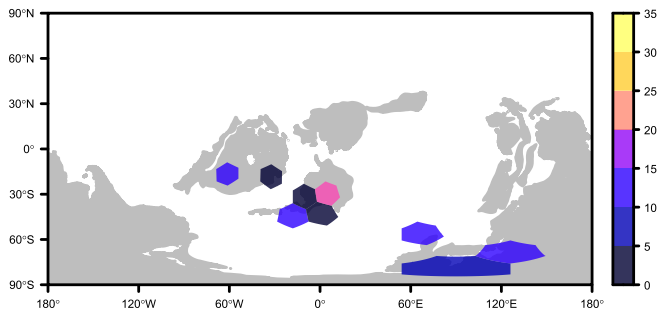
Sandbian



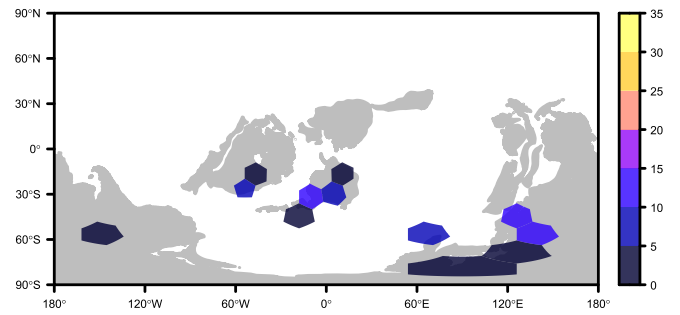
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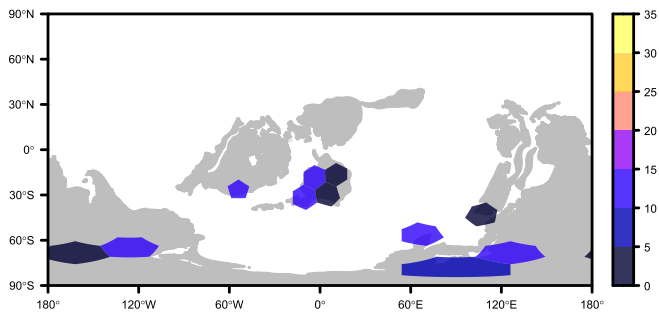
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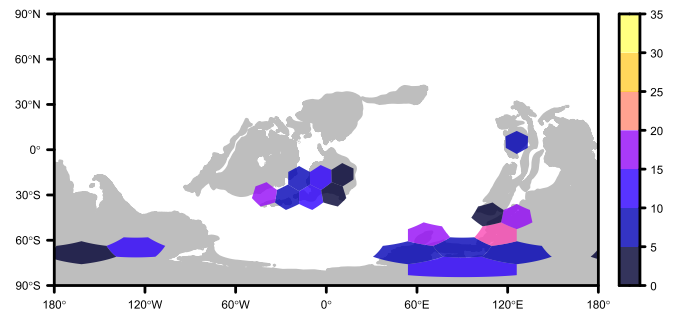
Rhuddanian



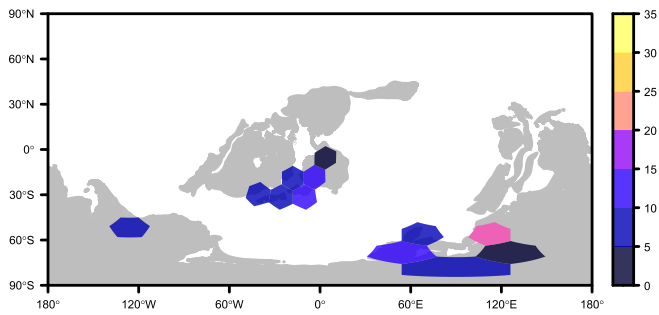
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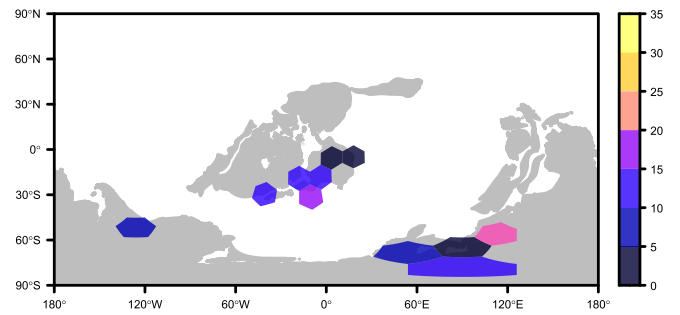
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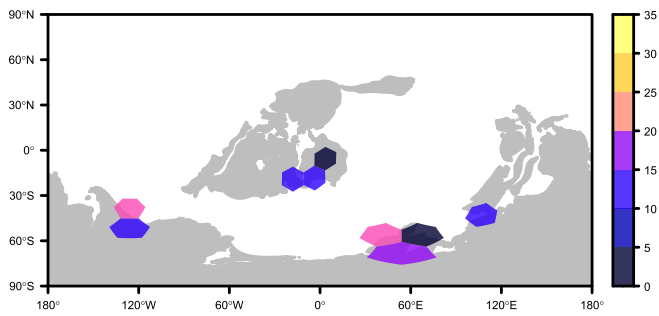
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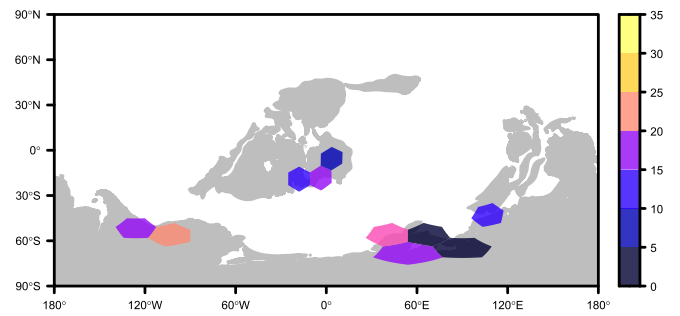
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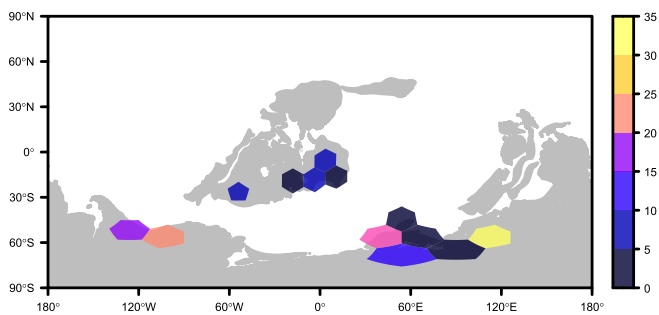
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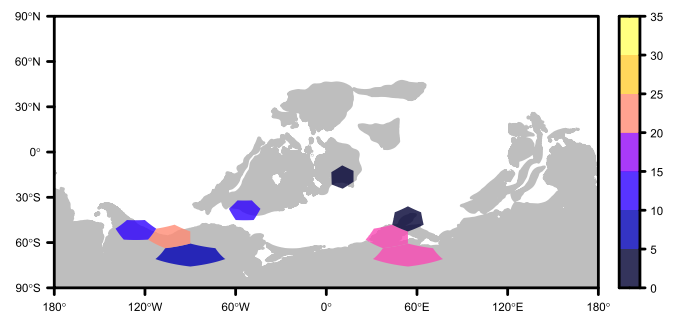
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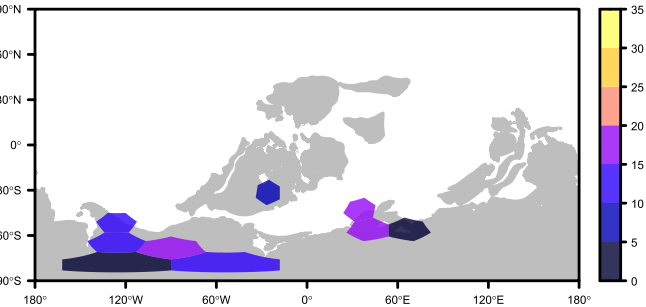
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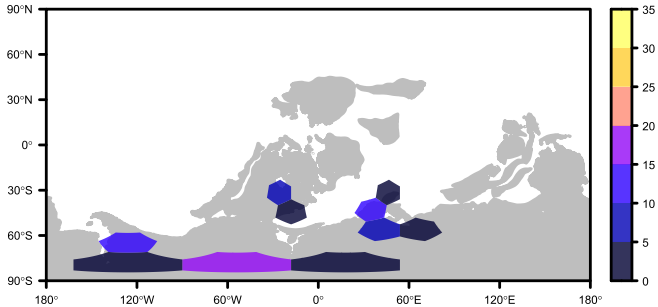
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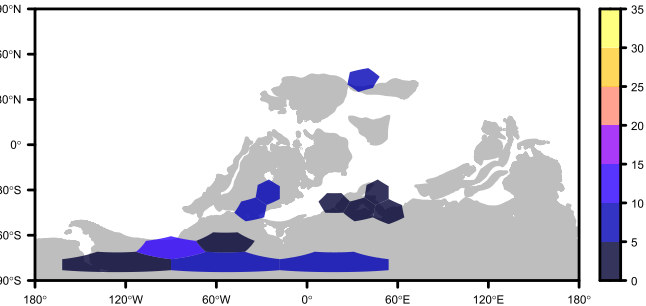
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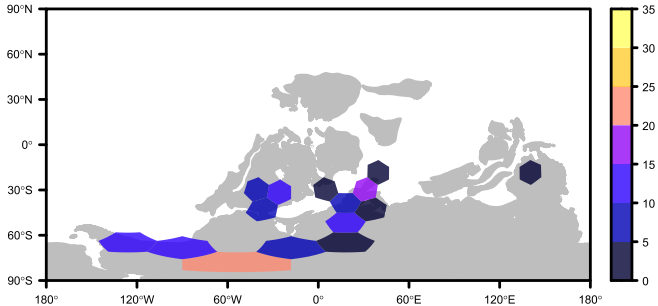
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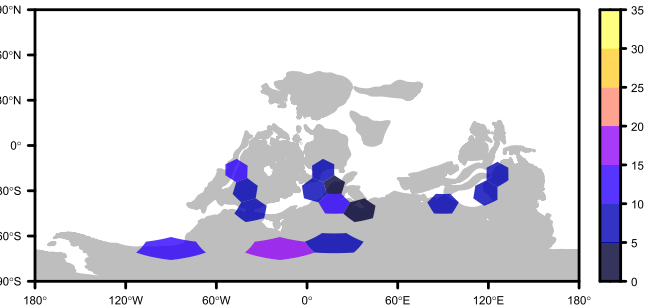
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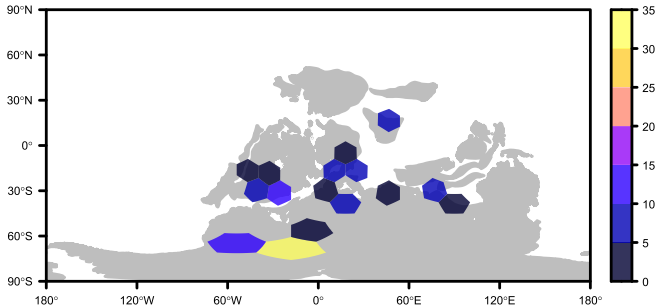
Givetian



Frasnian

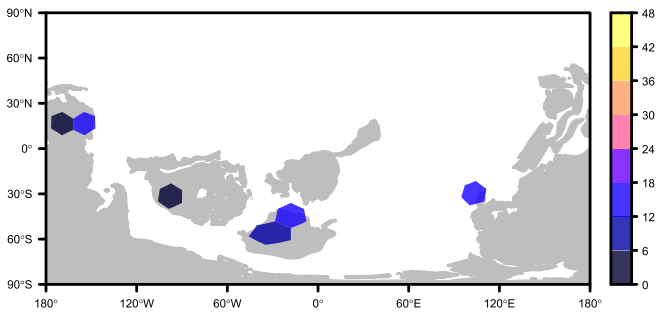


Famennian

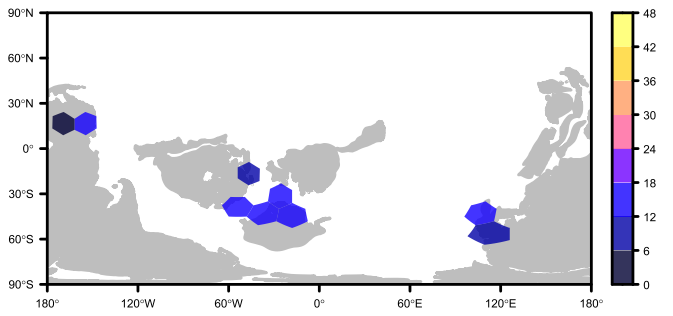


Appendix 7. Grid-cell diversity calculated using shareholder quorum sampling at $q = 0.7$. The color bar represents the number of genera.

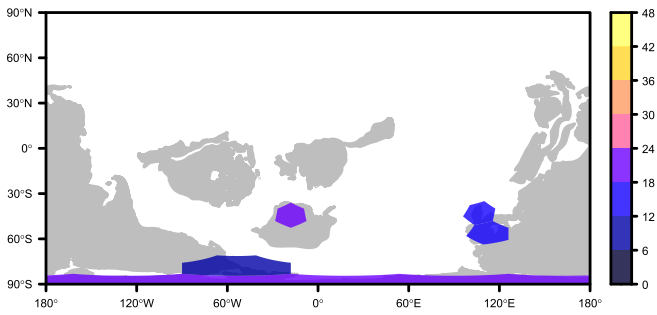
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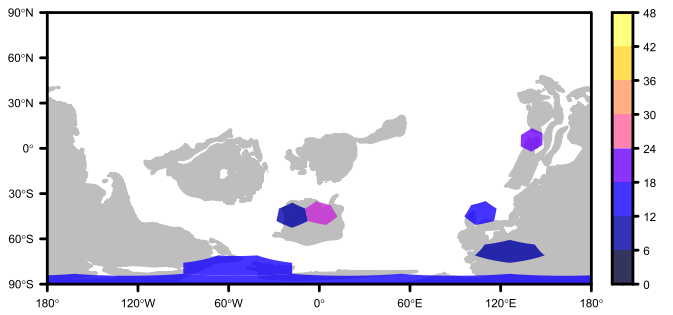
Cambrian series 2



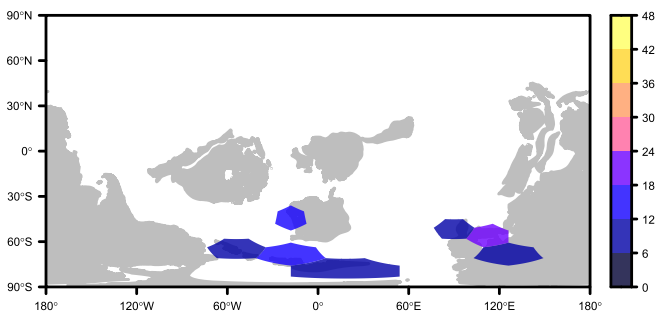
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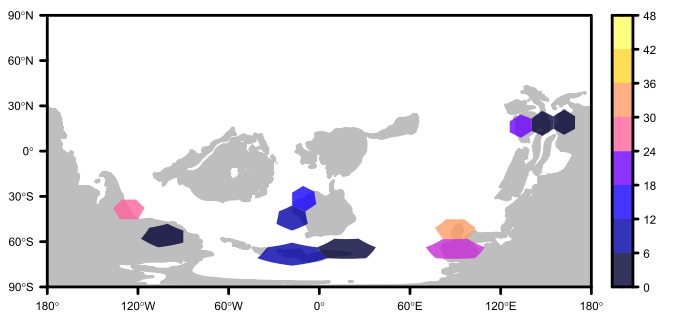
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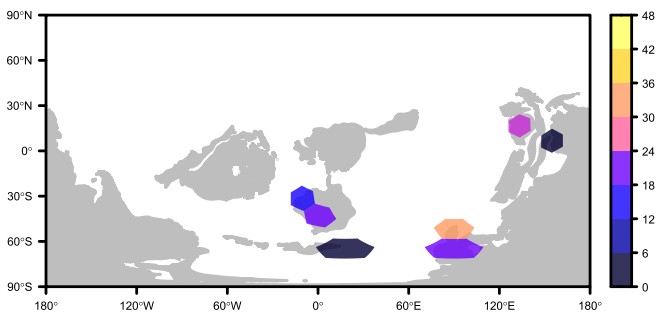
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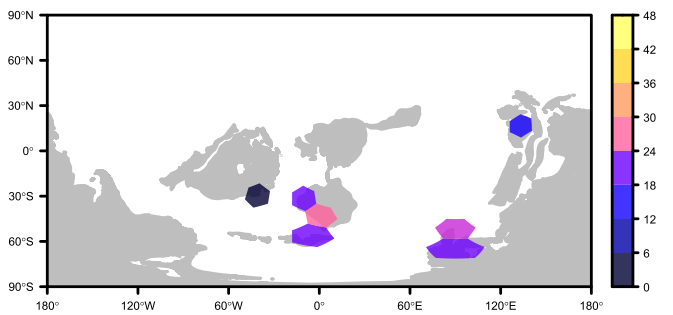
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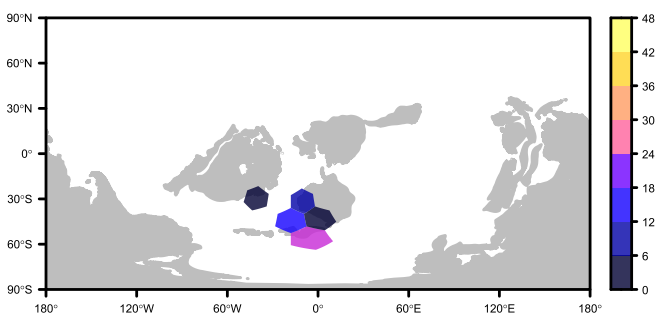
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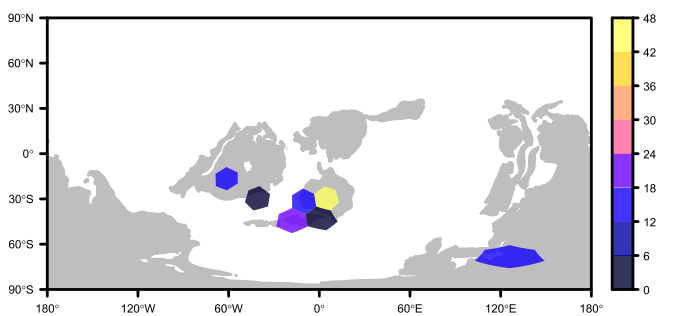
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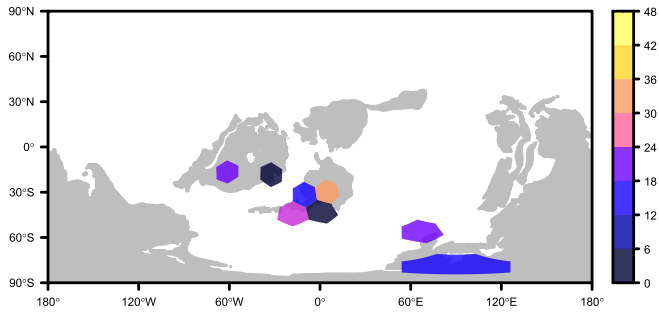
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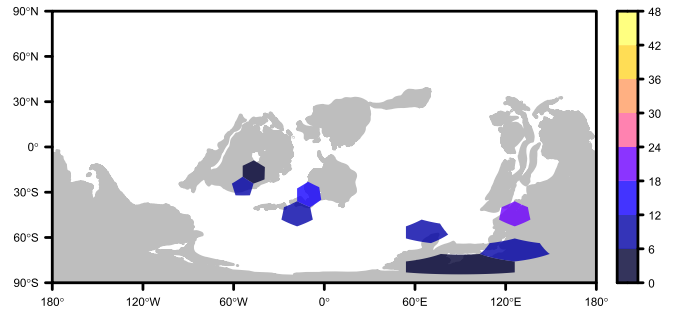
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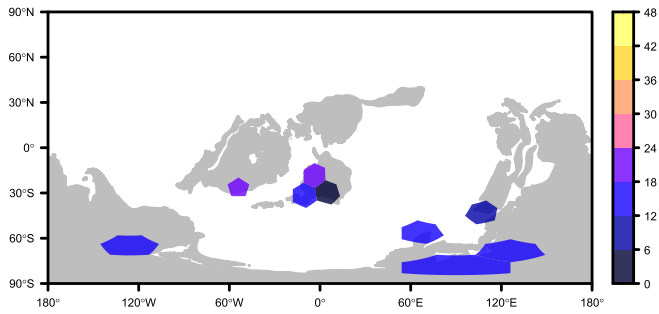
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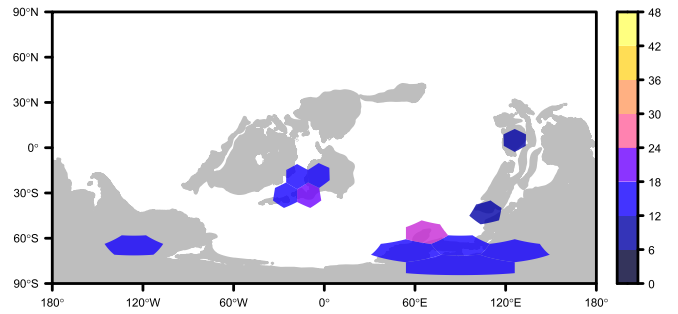
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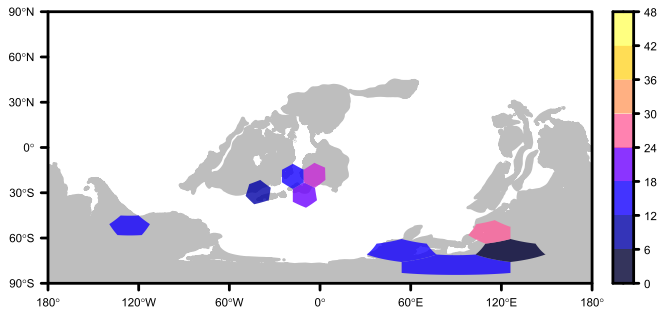
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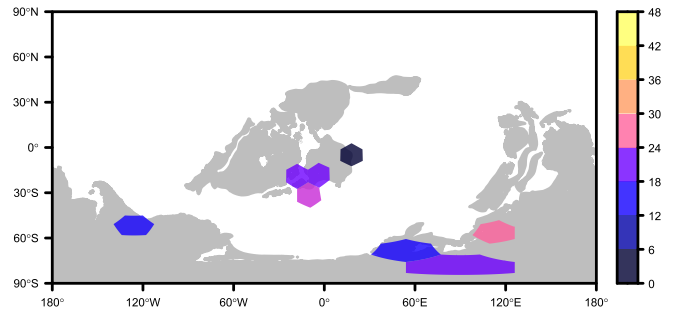
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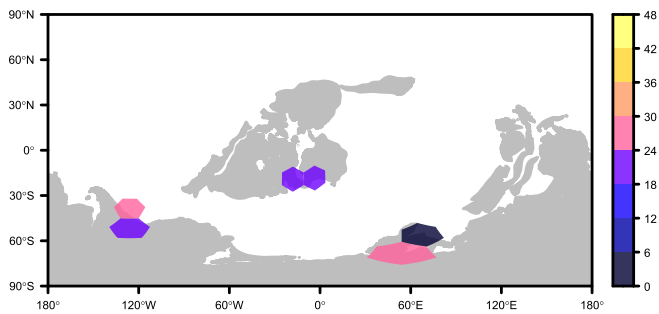
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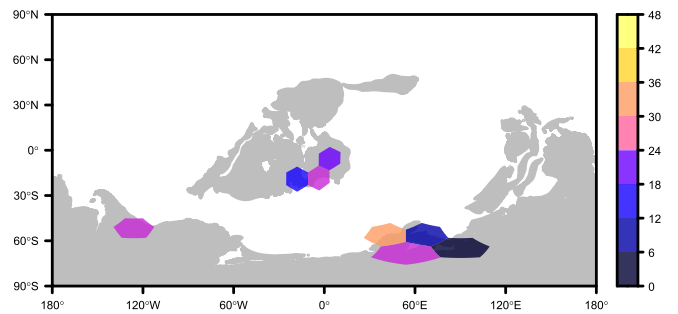
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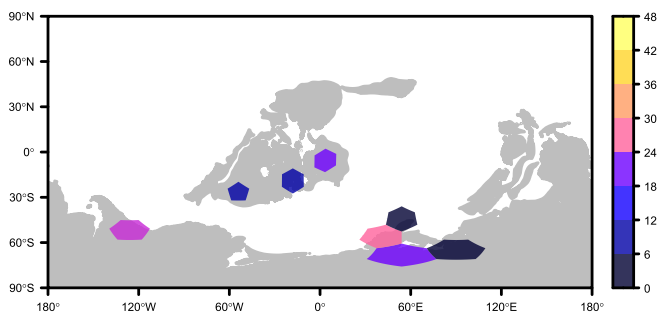
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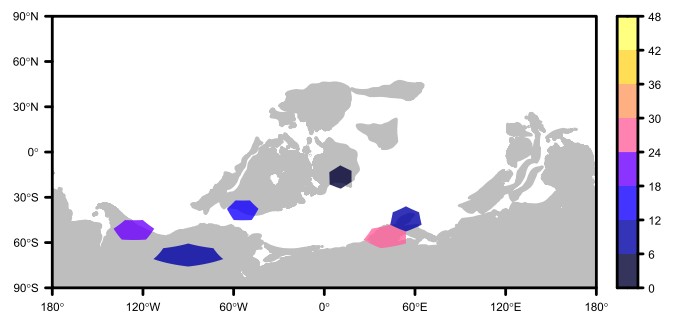
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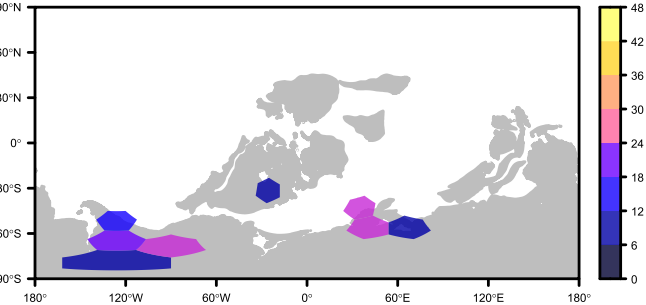
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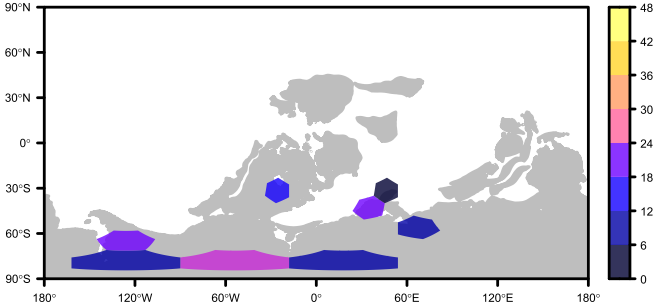
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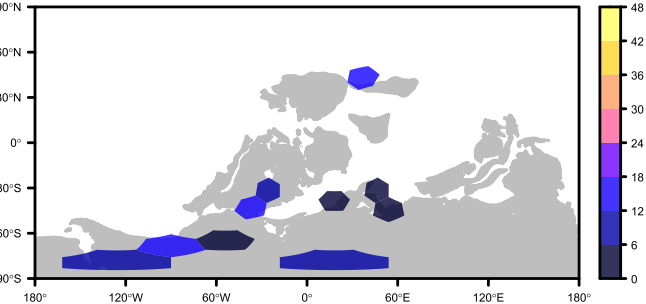
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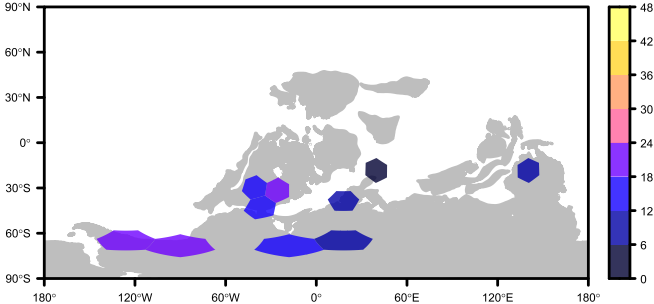
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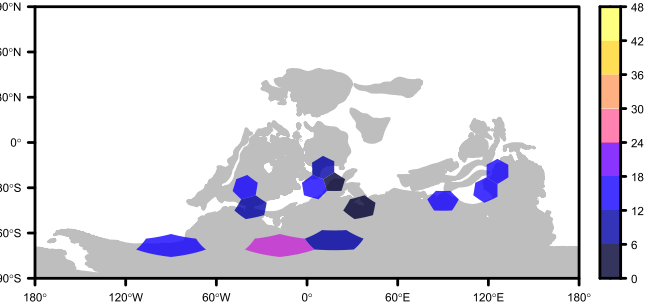
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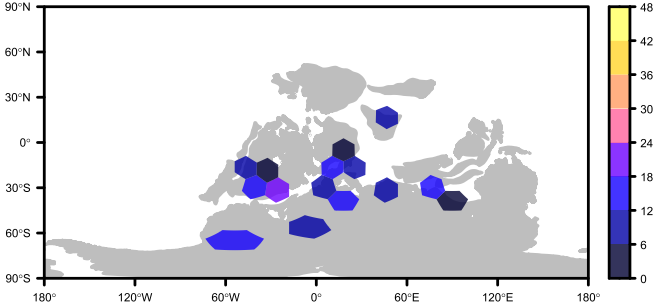
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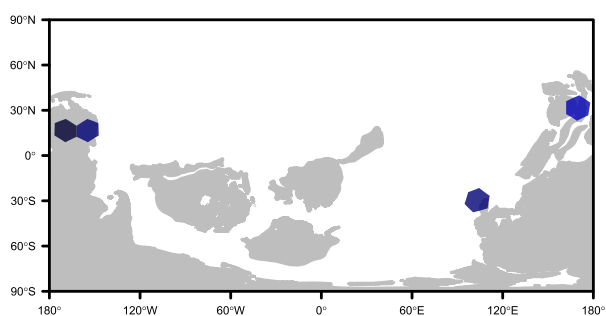


Famennian

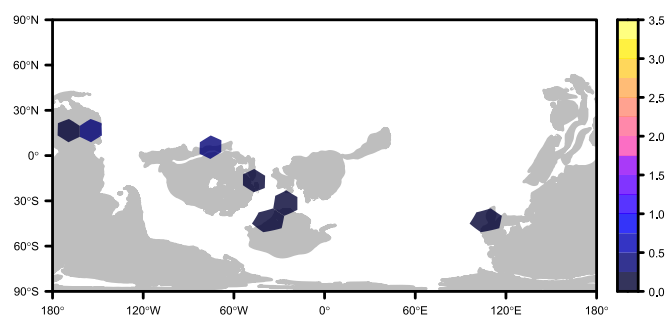


Appendix 8. Origination rates per grid cell, calculated using per capita Foote. Color bar represents per capita rate.

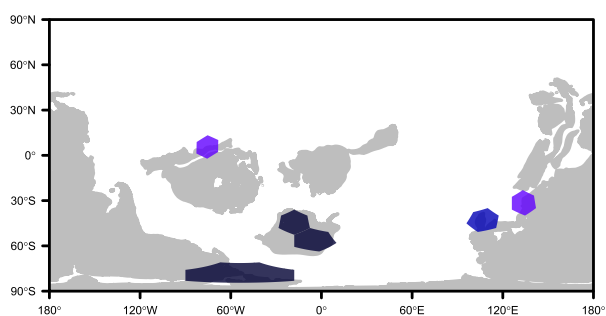
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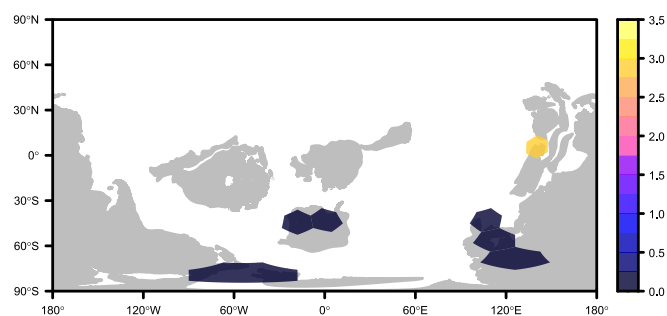
Cambrian series 2



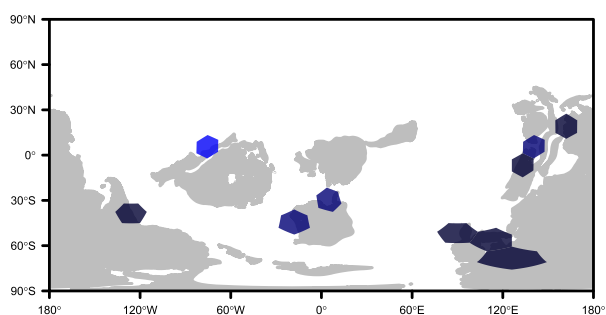
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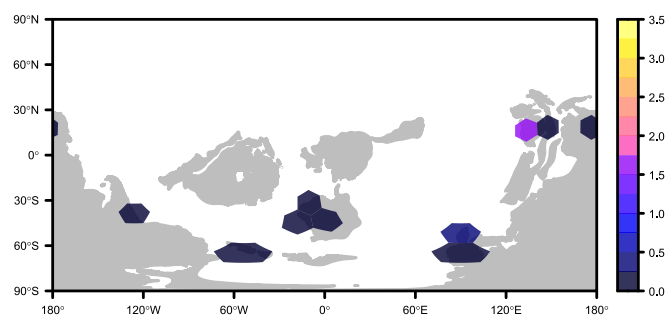
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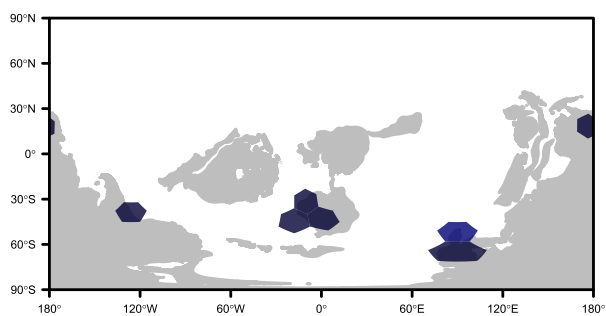
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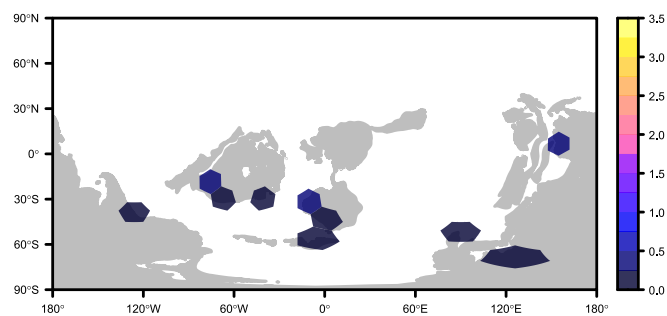
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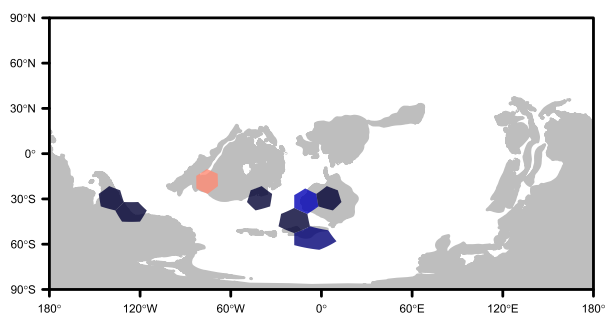
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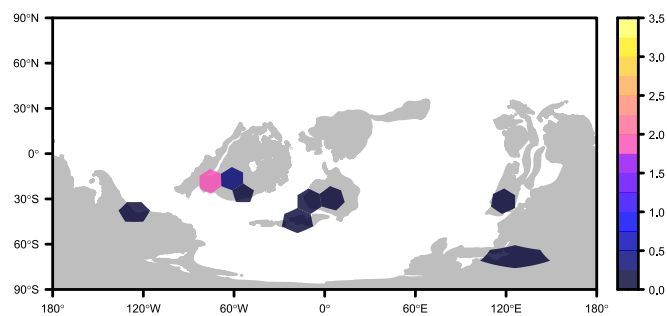
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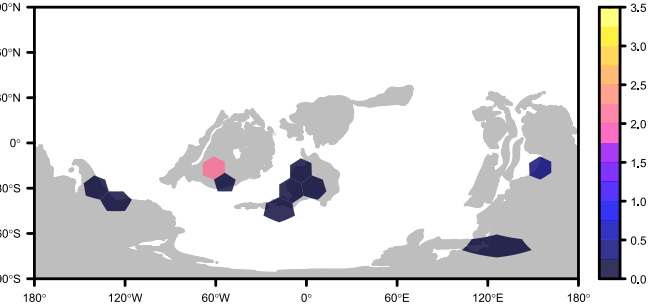
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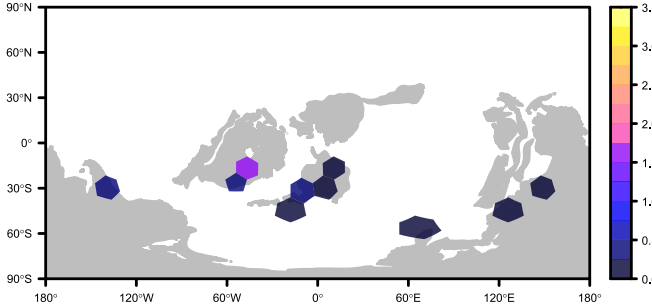
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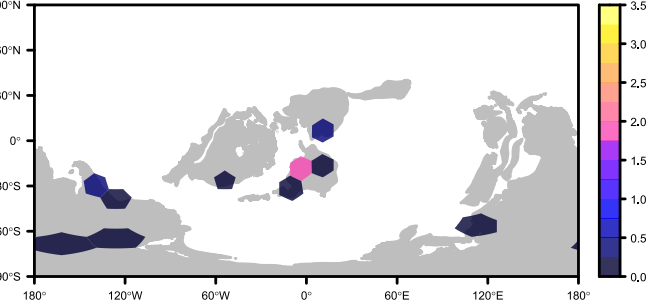
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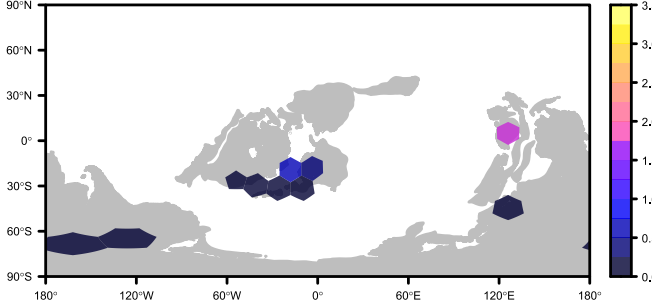
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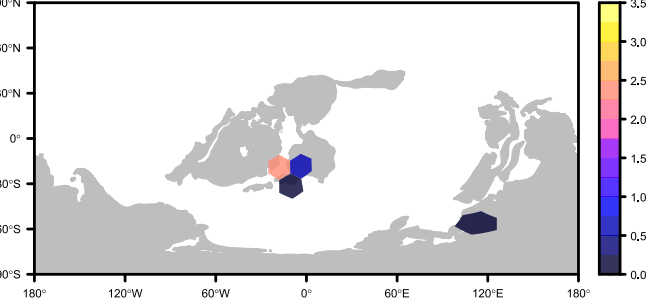
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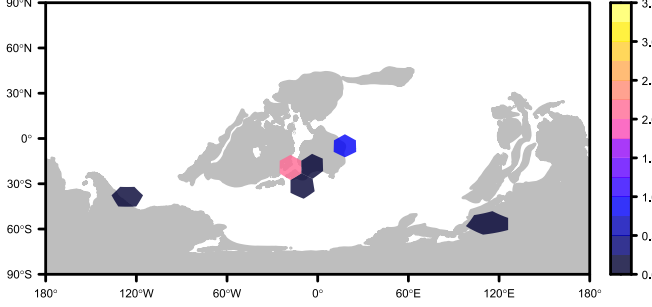
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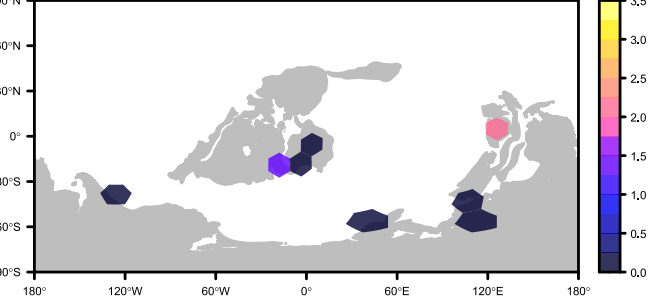
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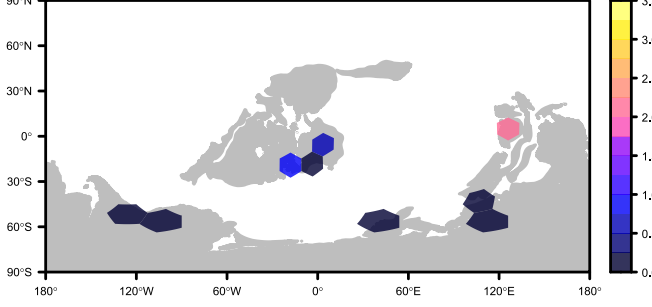
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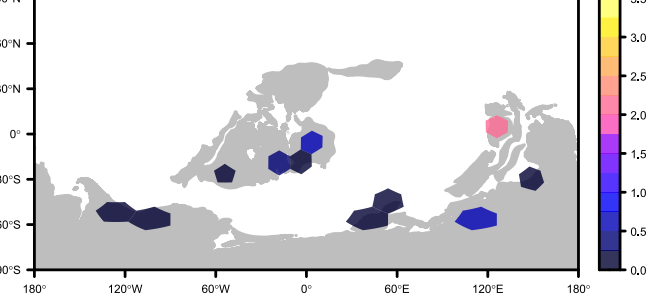
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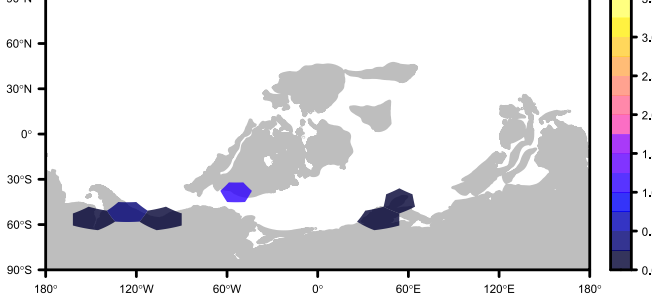
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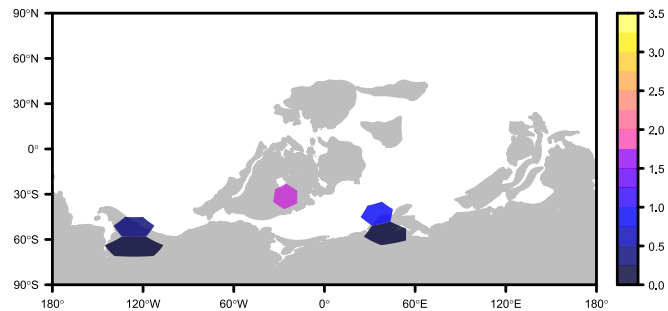
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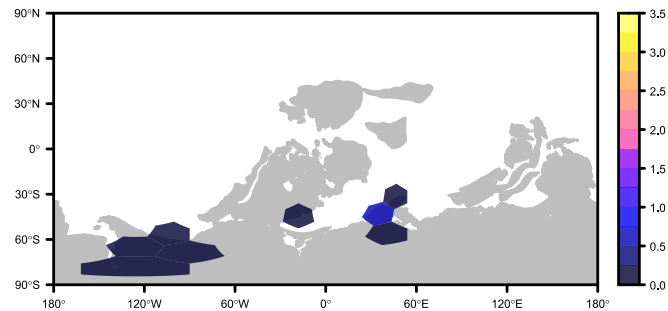
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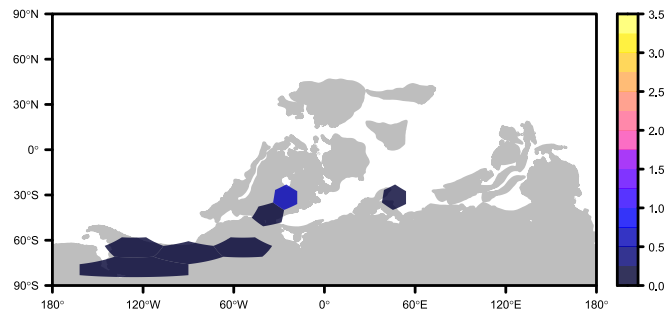
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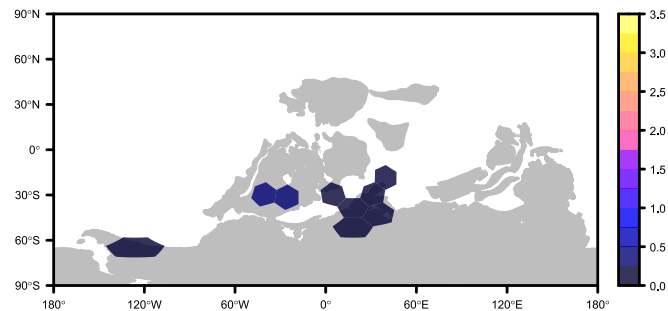
Emsian



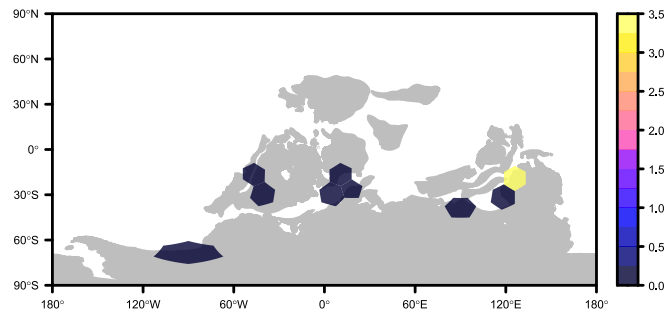
Eifelian



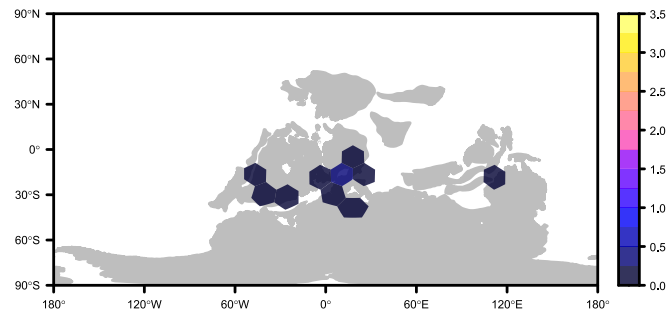
Givetian



Frasnian

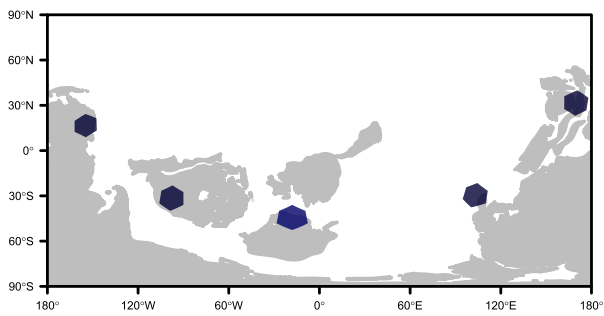


Famennian

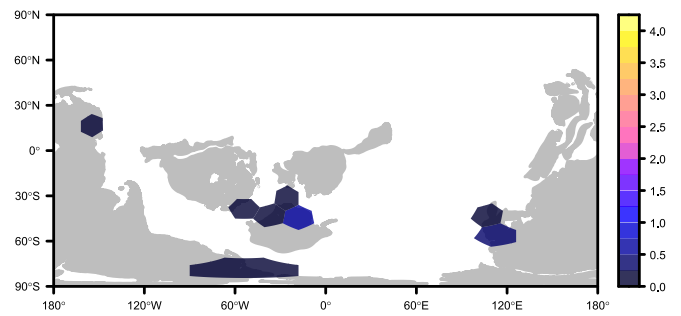


Appendix 9. Extinction rates per grid cell, calculated using per capita Foote. Color bar represents per capita rate.

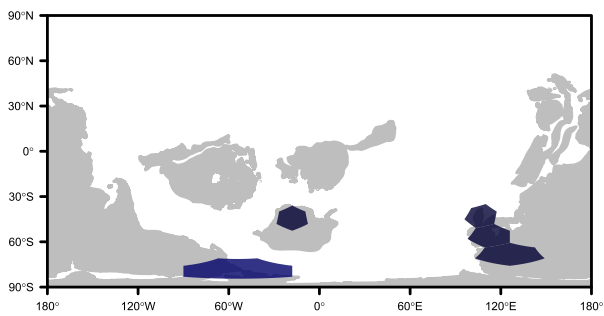
Terreneuvian



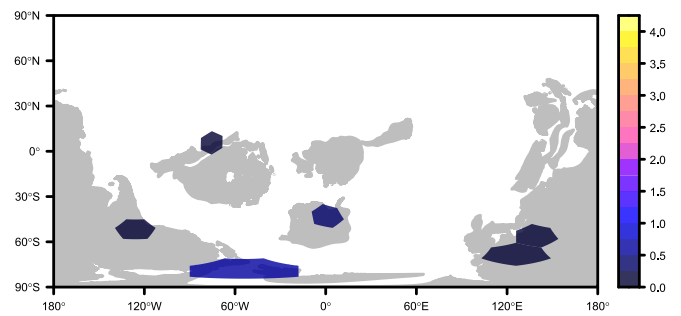
Cambrian series 2



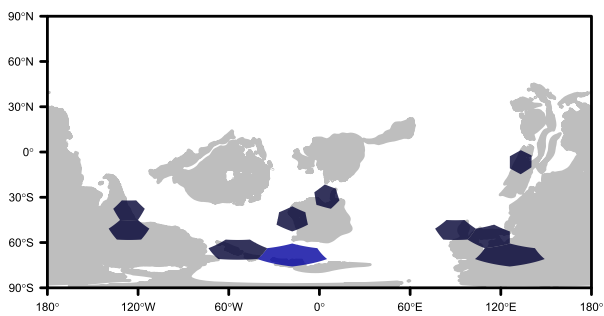
Miaolingian



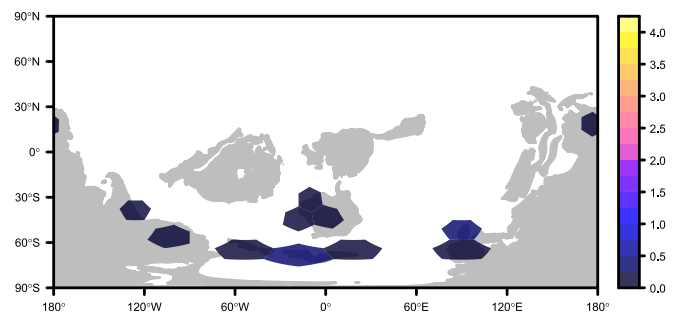
Furongian



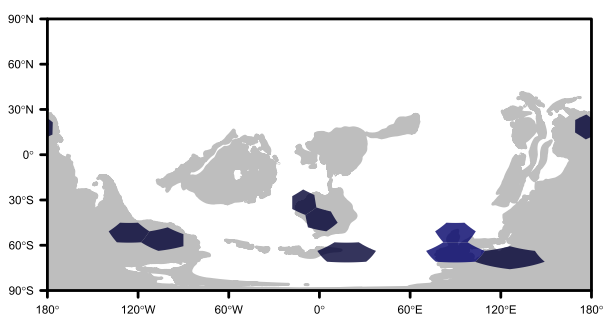
Tremadocian



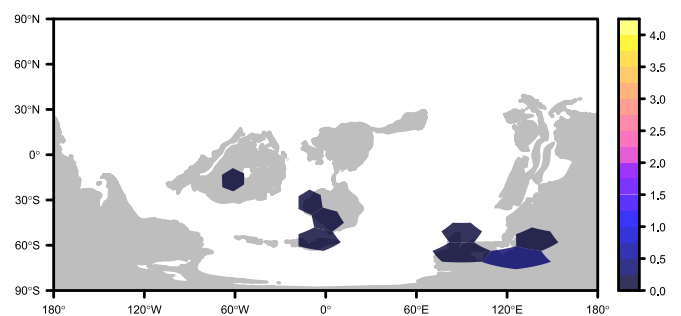
Floian



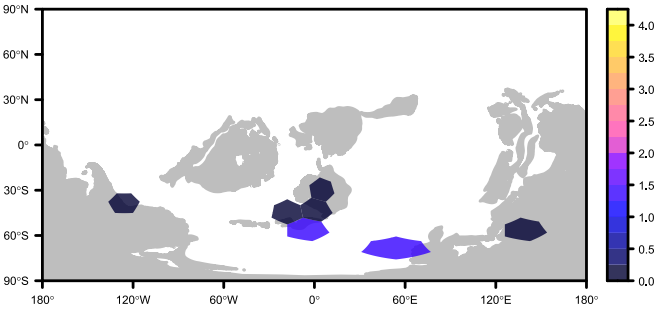
Dapingian



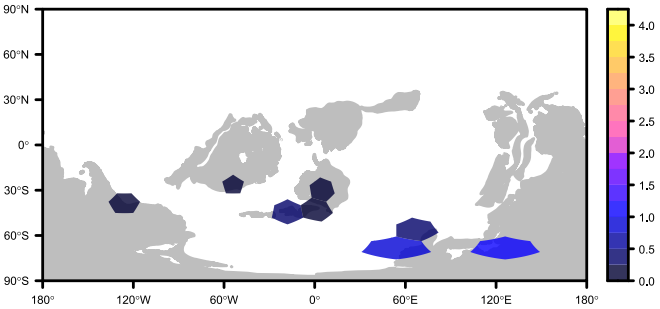
Darriwilian



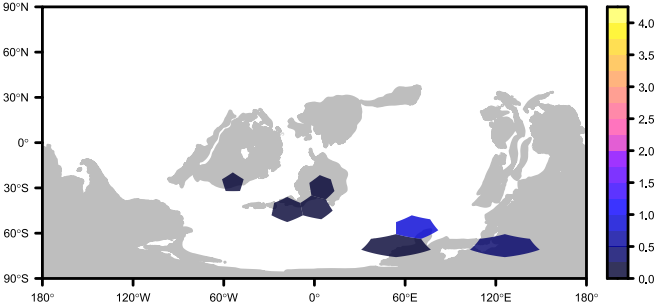
Sandbian



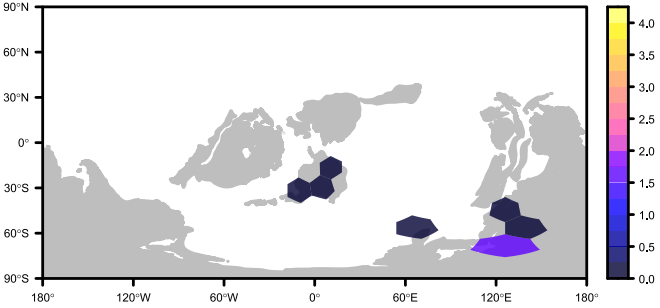
Katian



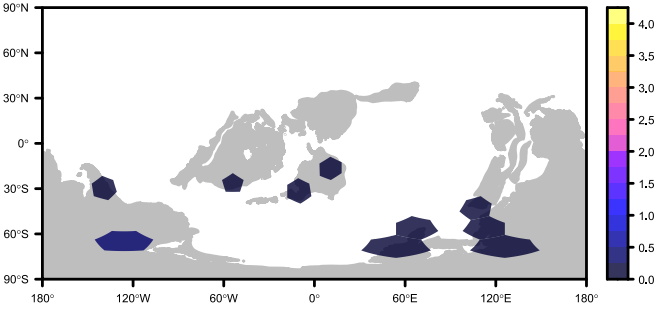
Hirnantian



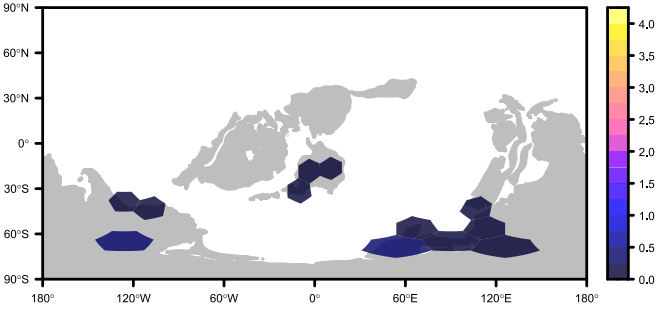
Rhuddanian



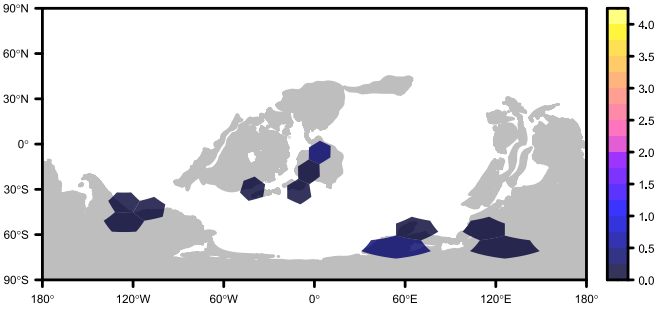
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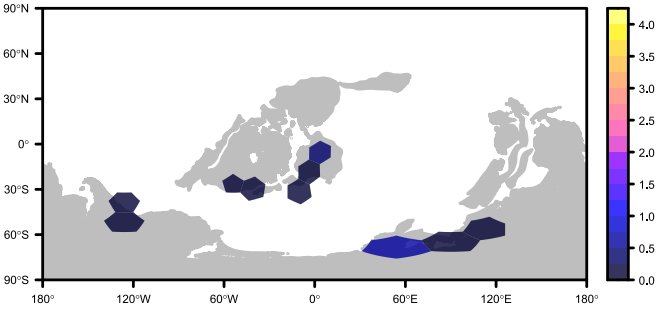
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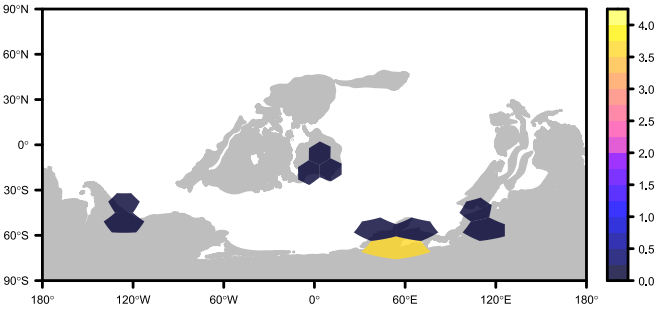
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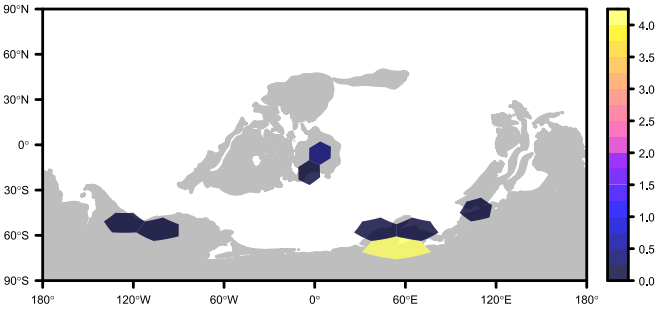
Homerian



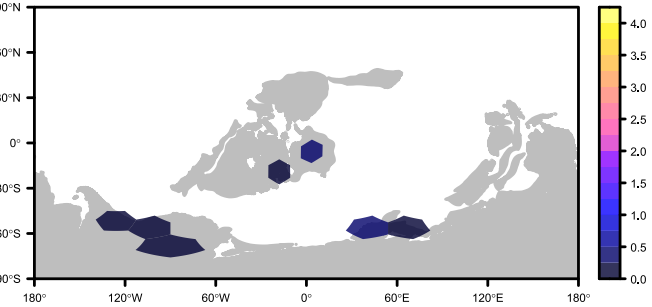
Gorstian



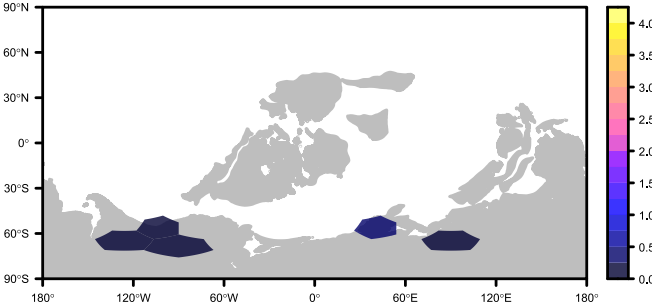
Ludfordian



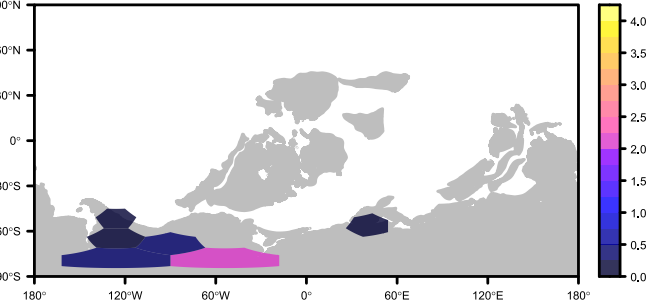
Pridoli



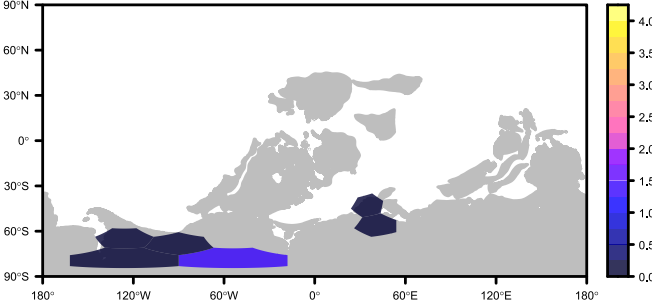
Lochkovian



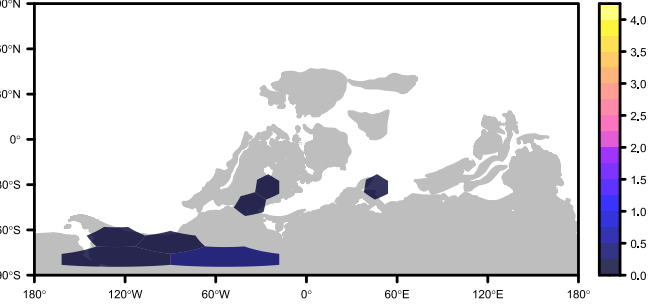
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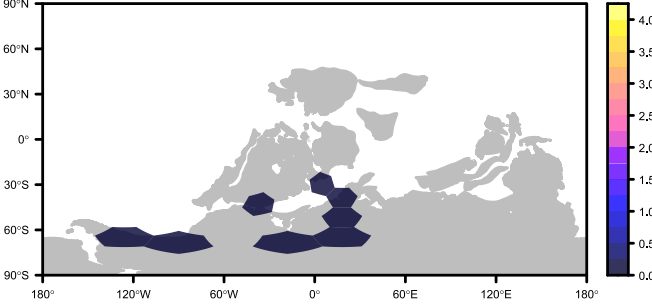
Emsian



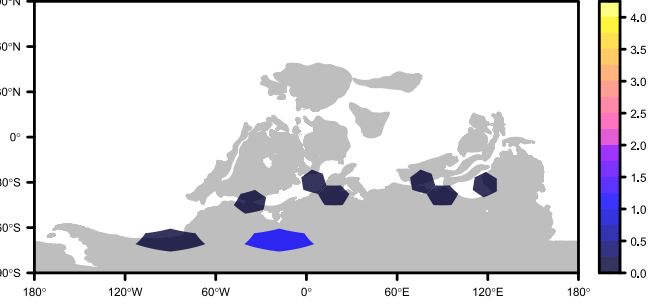
Eifelian



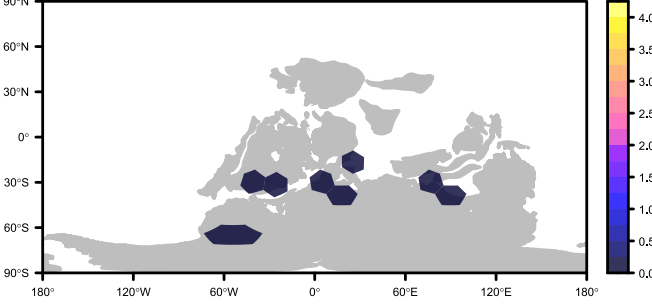
Givetian



Frasnian

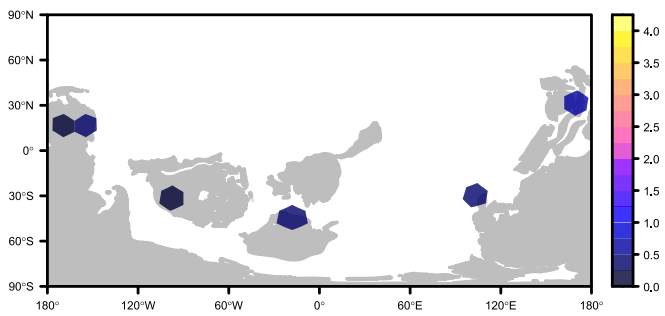


Famennian

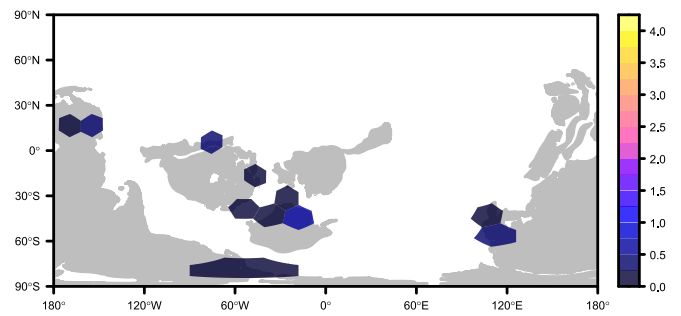


Appendix 10. Total turnover per grid cell. The color bar represents the sum of the origination and extinction rates.

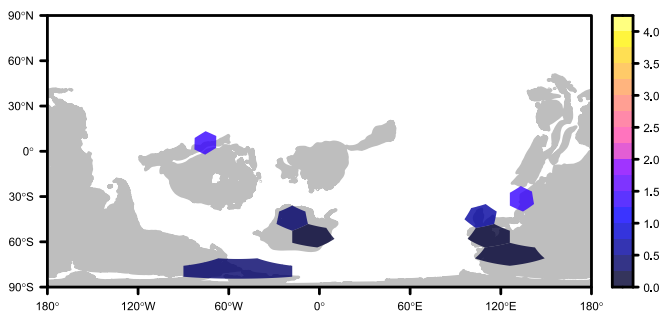
Terreneuvian



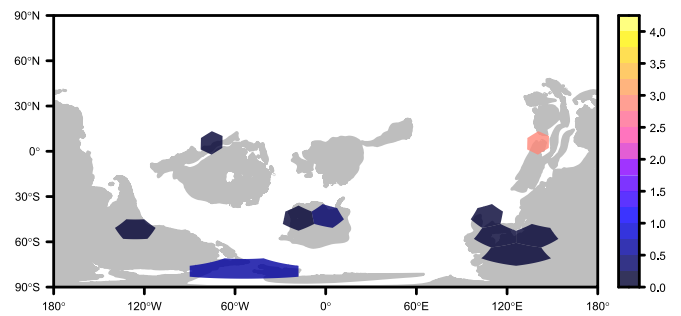
Cambrian series 2



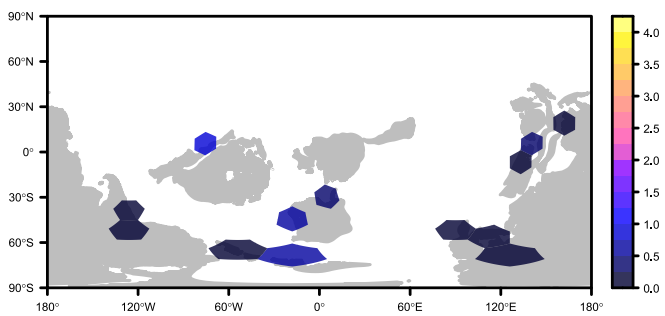
Miaolingian



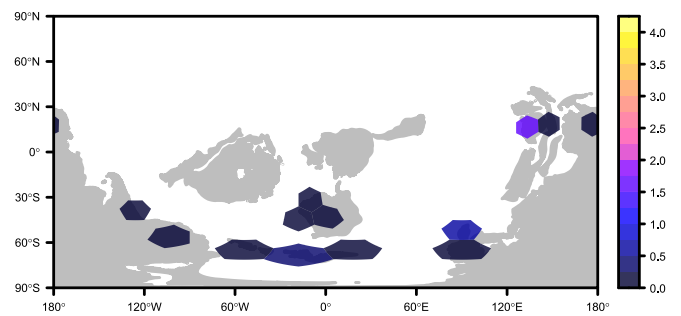
Furongian



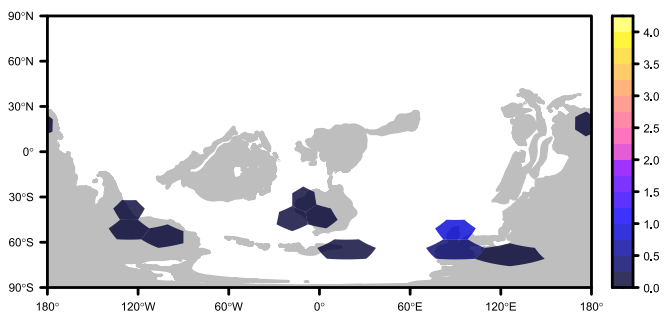
Tremadocian



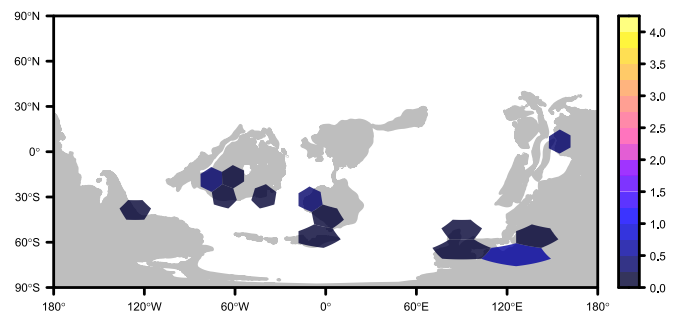
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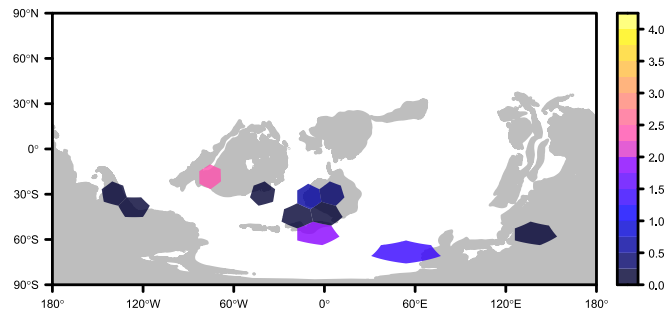
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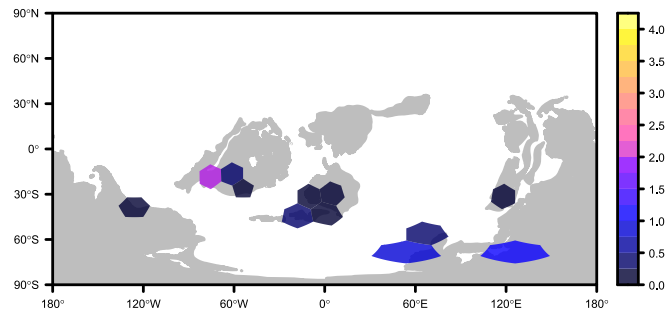
Darriwilian



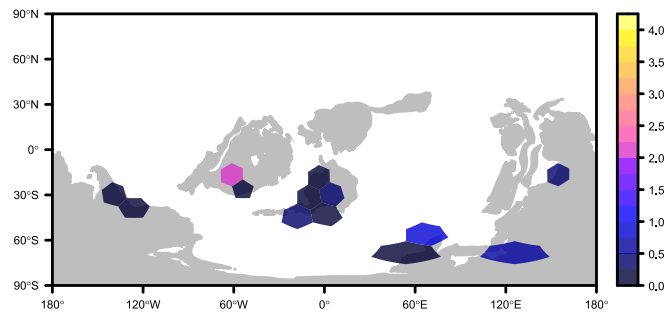
Sandbian



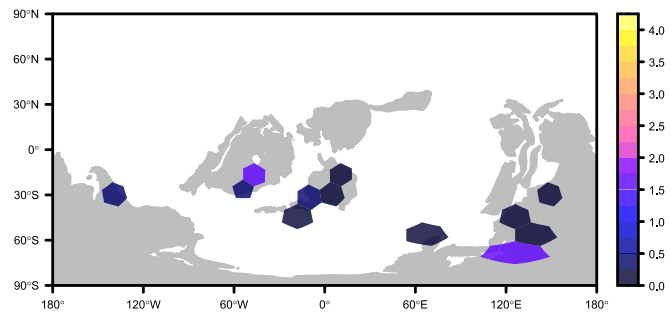
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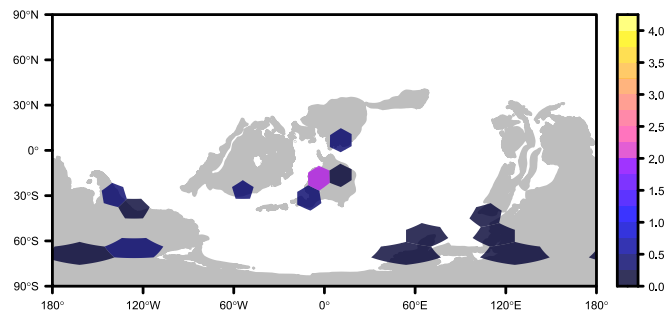
Hirnantian



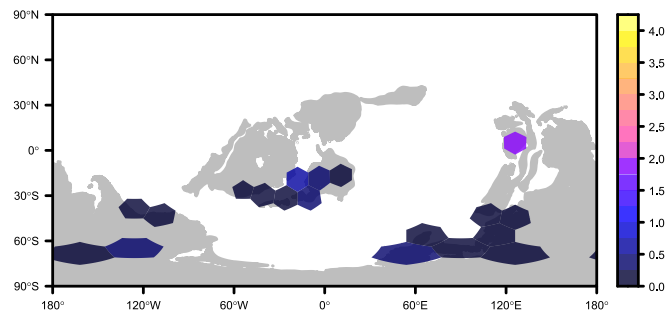
Rhuddanian



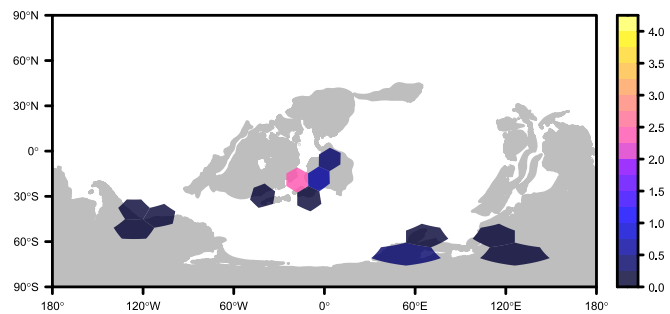
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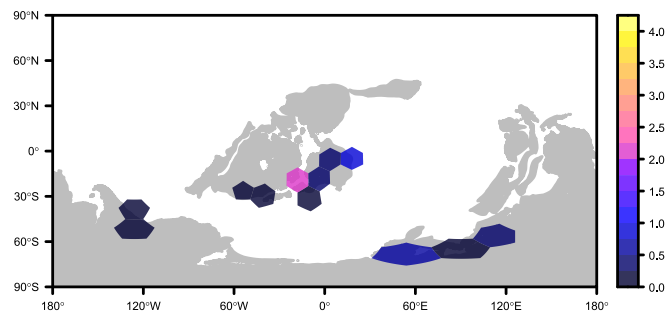
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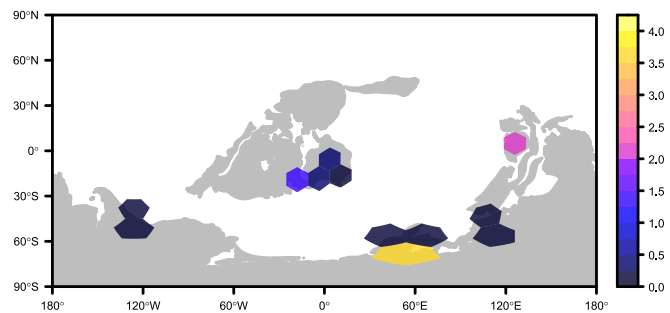
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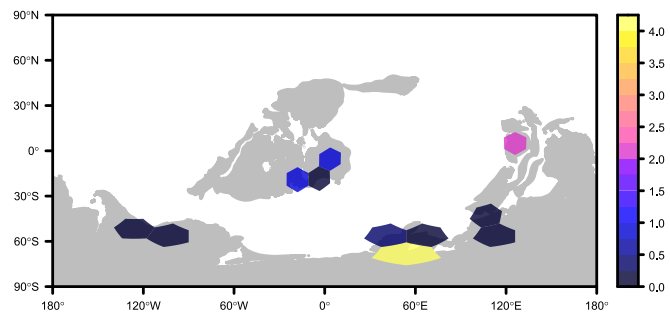
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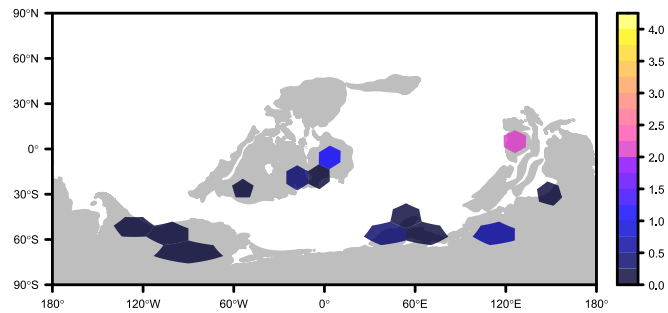
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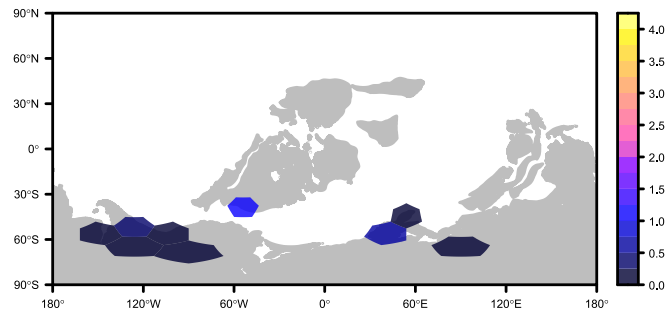
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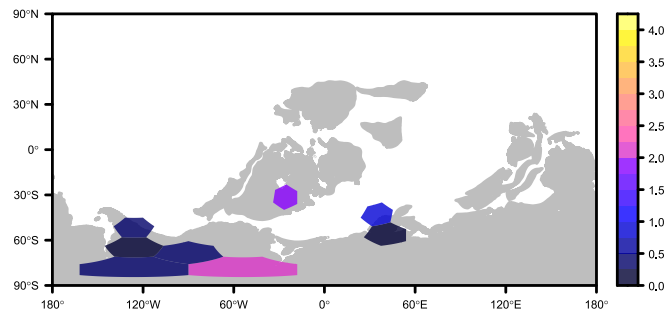
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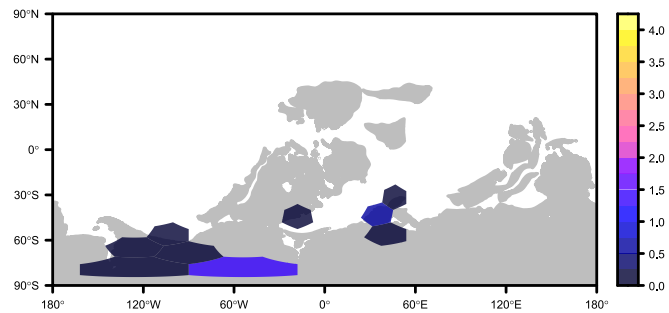
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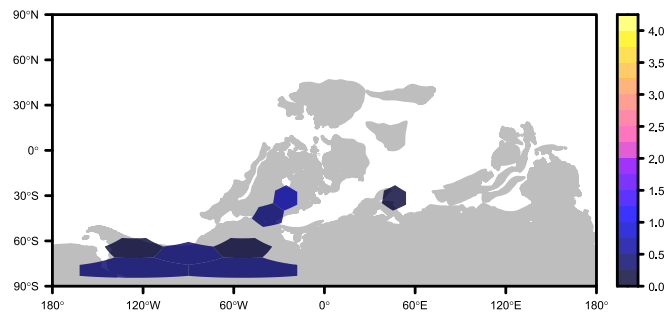
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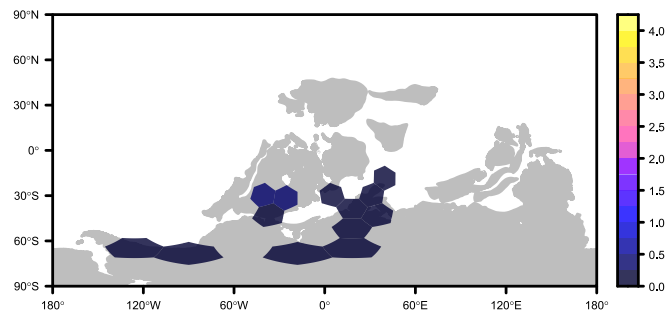
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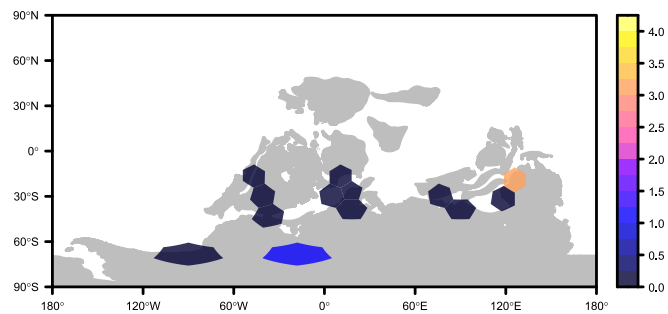
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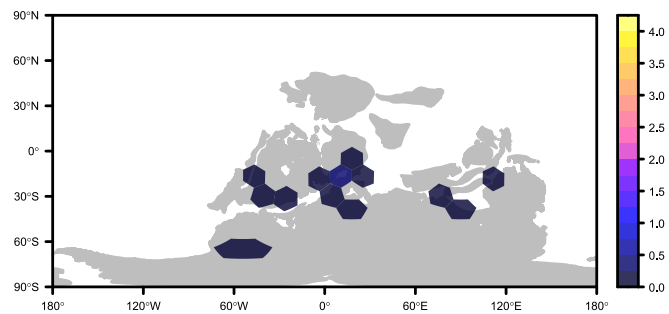
Givetian



Frasnian

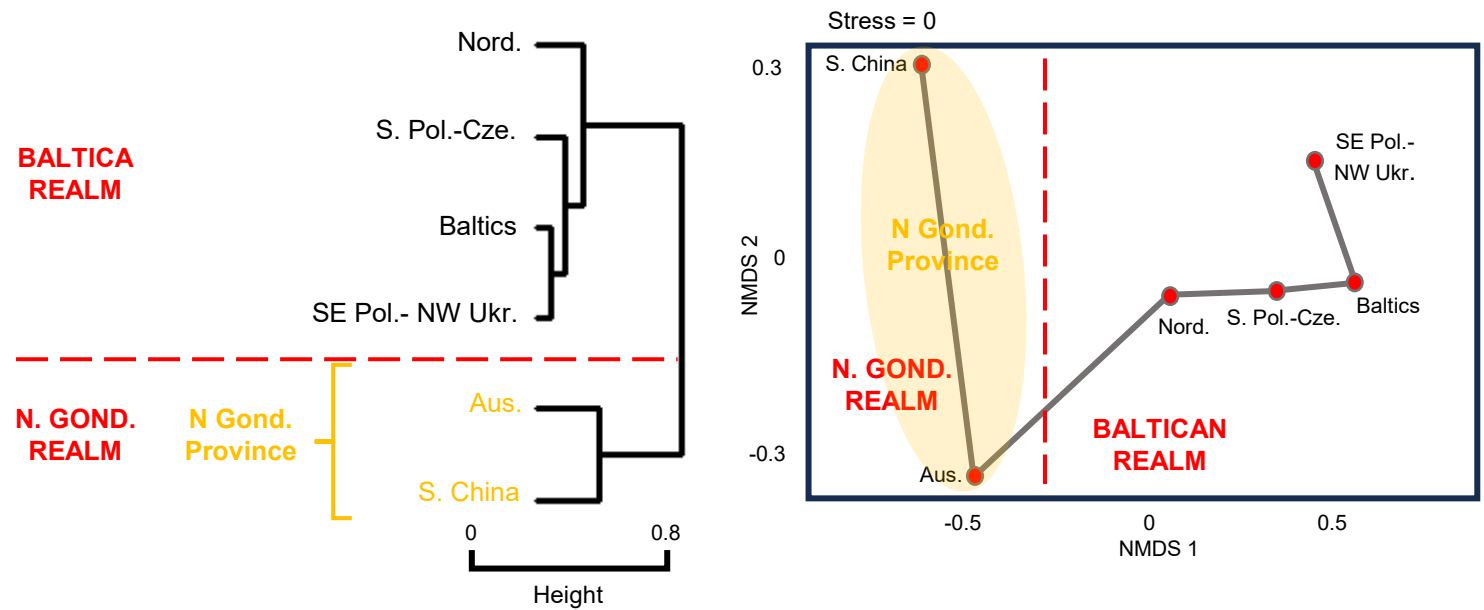


Famennian

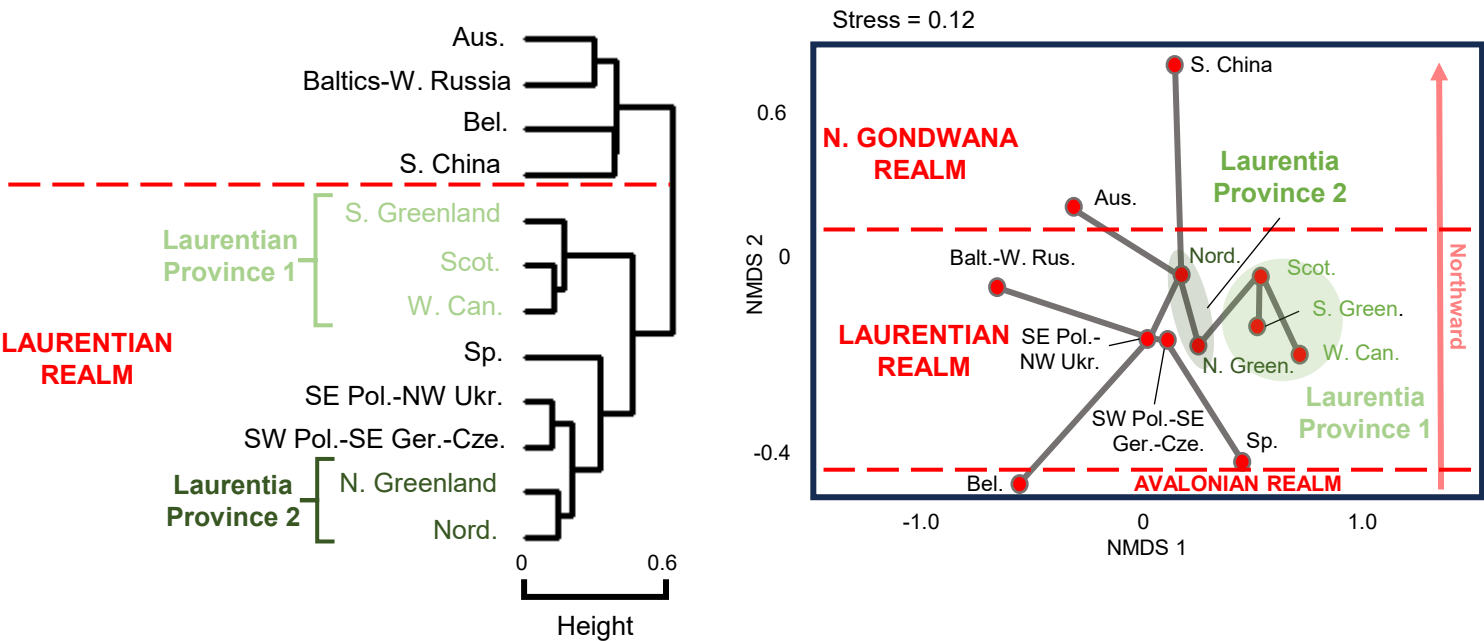


Appendix 11. Multivariate analysis results for each time interval. To the left is the hierarchical cluster analysis (HCA) dendrogram while to the right is the non-metric multidimensional scaling (NMDS) plot, with associated stress values.

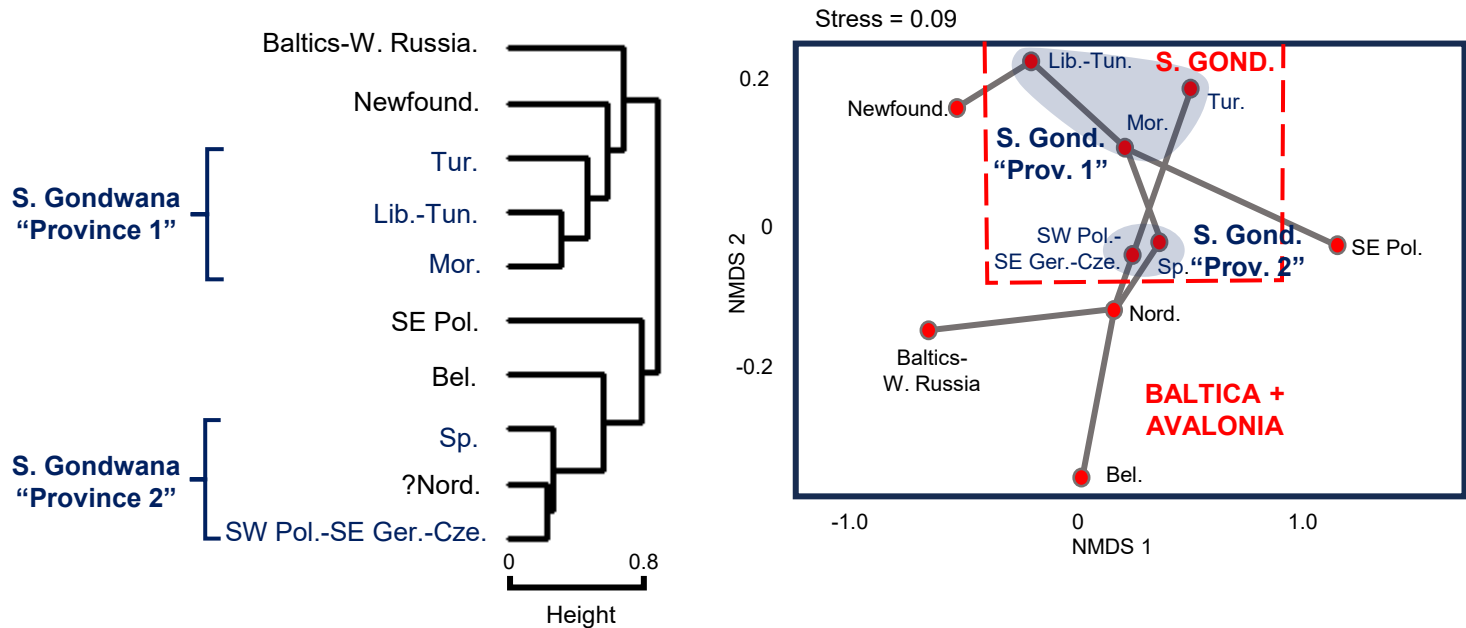
A. TERRENEUVIAN



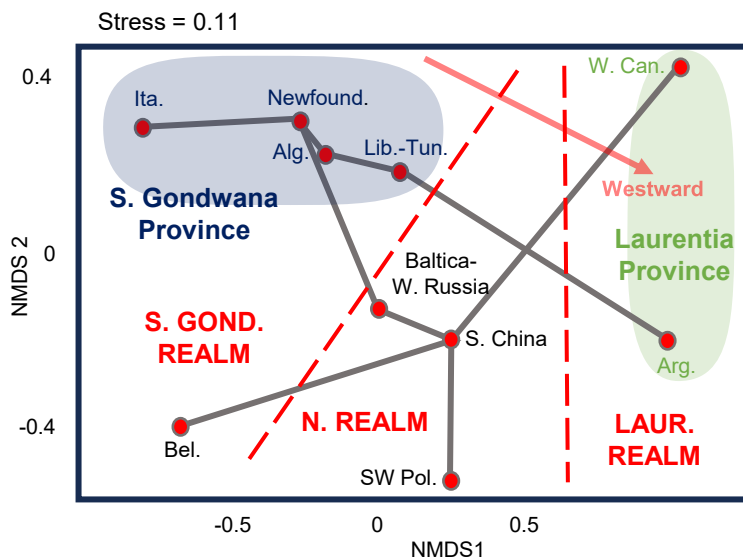
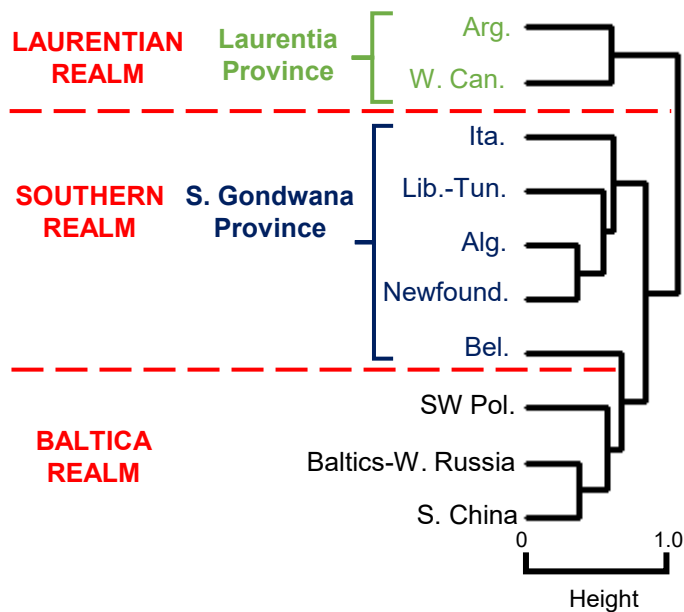
B. CAMBRIAN SERIES 2



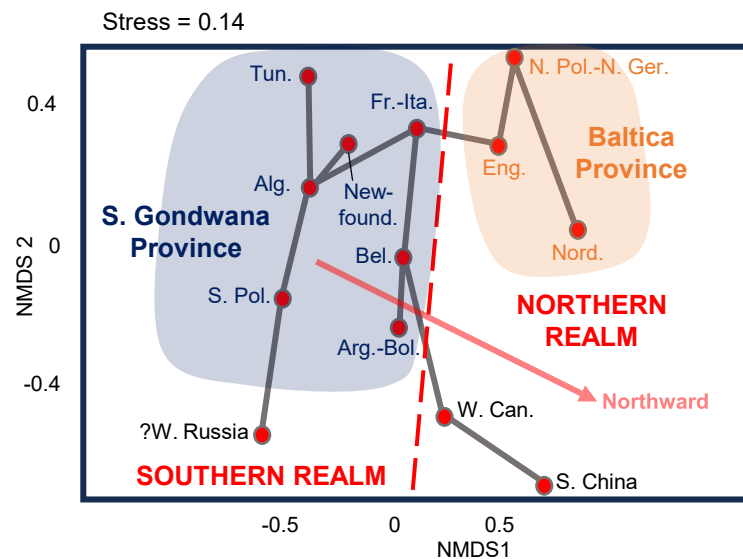
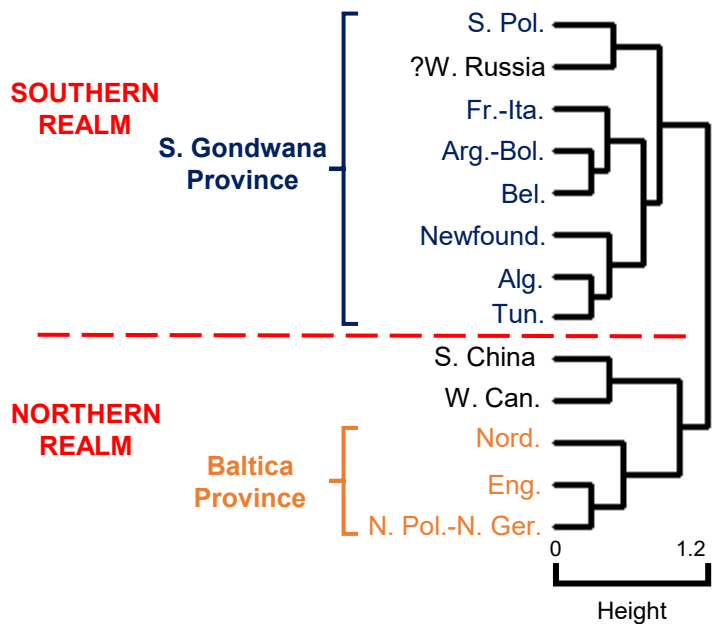
C. MIAOLINGIAN



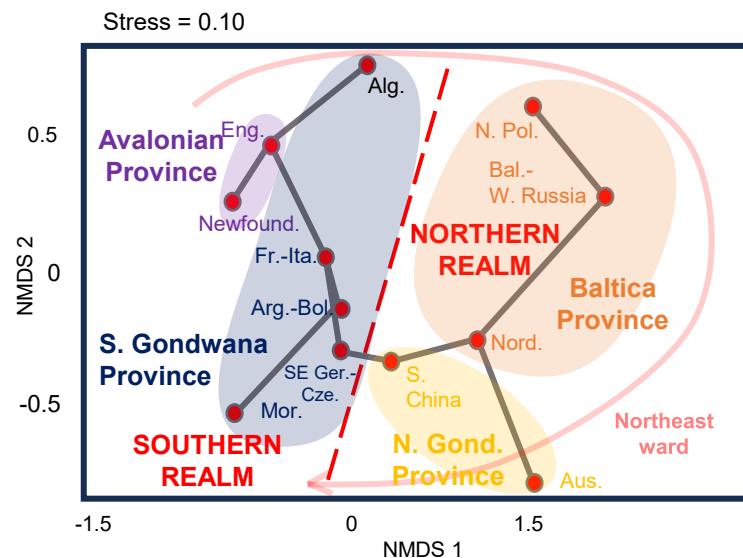
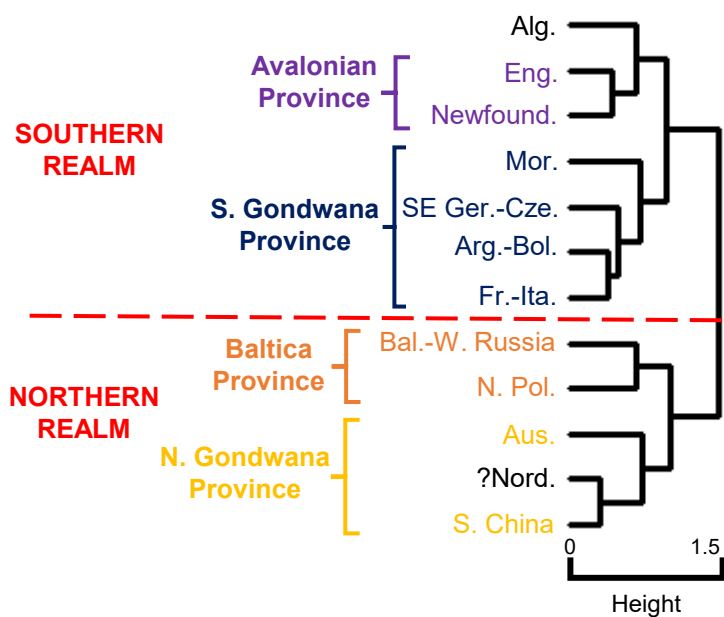
D. FURONGIAN



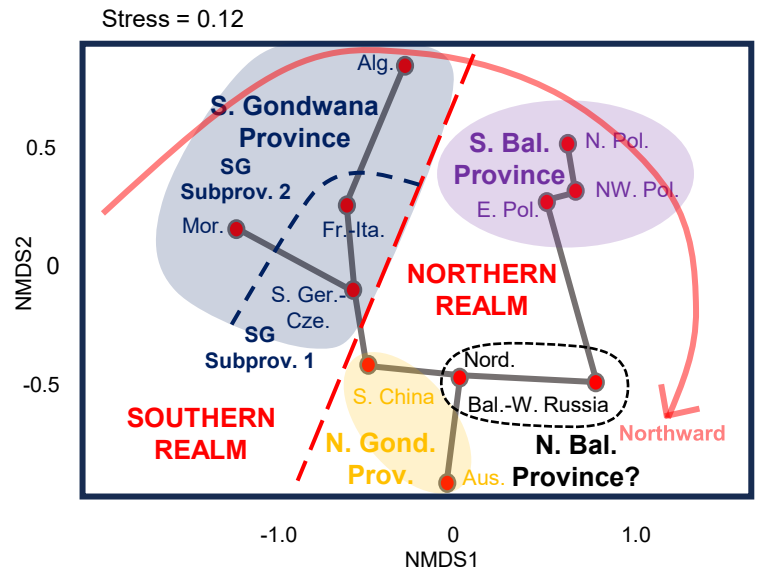
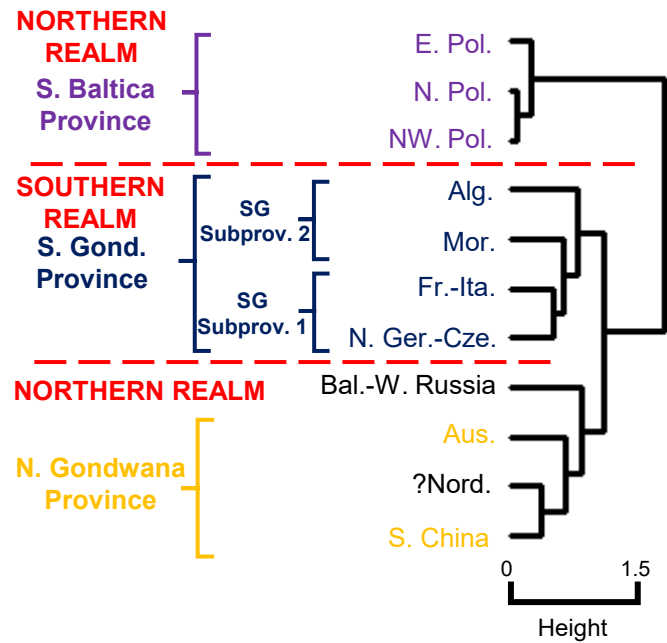
E. TREMADOCIAN



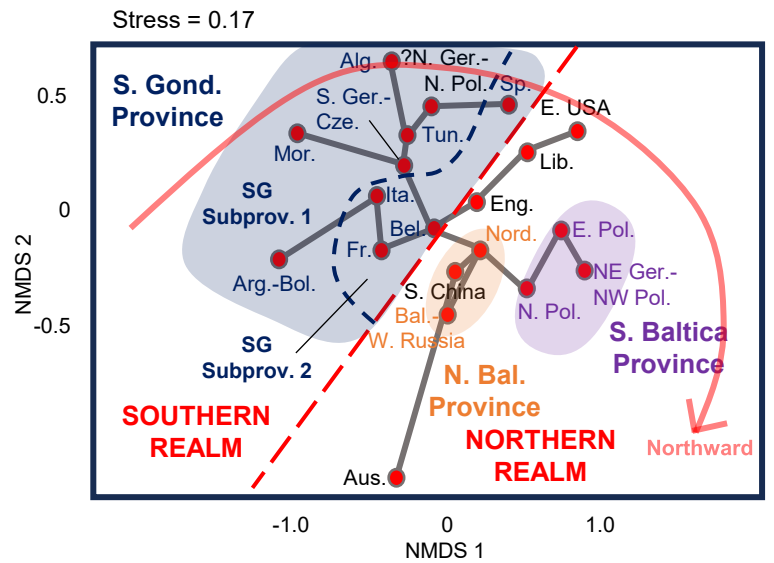
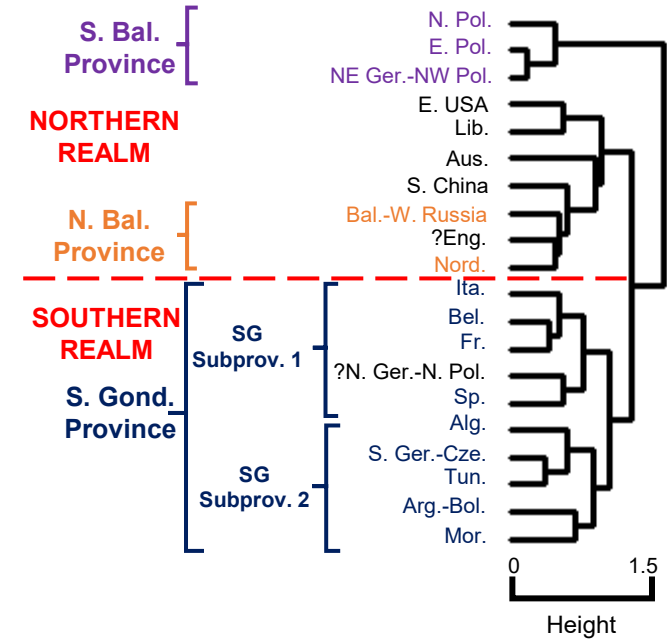
F. FLOIAN



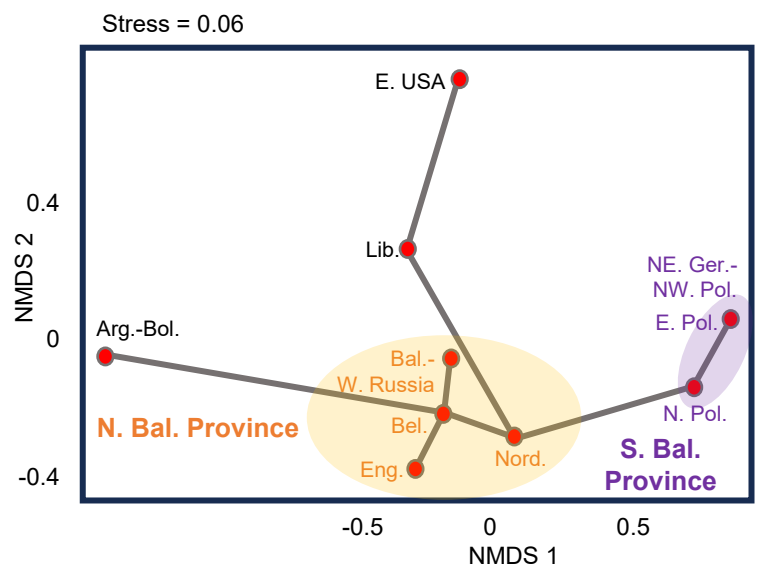
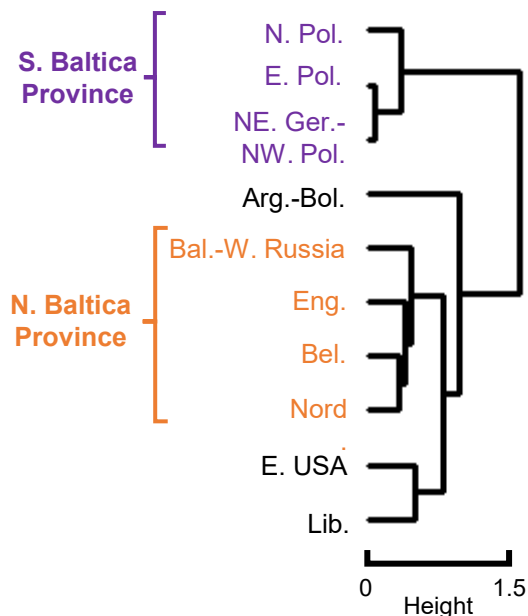
G. DAPINGIAN



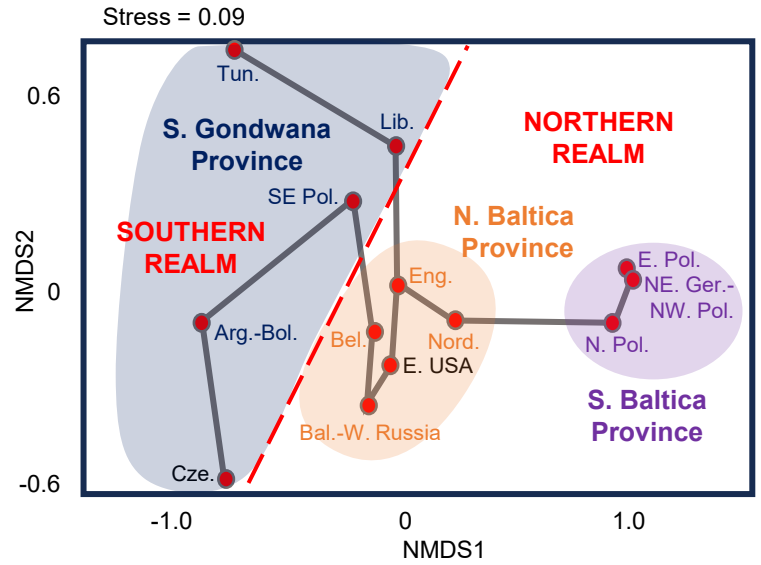
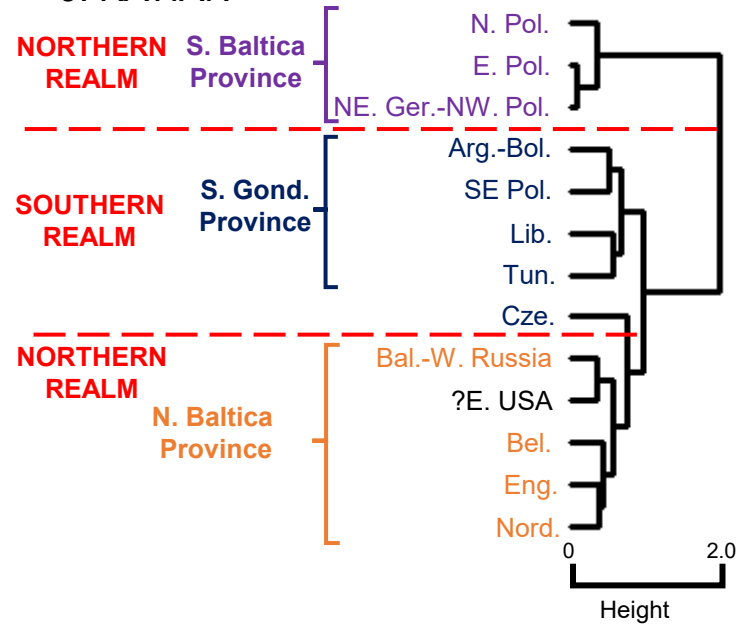
H. DARRIWILIAN



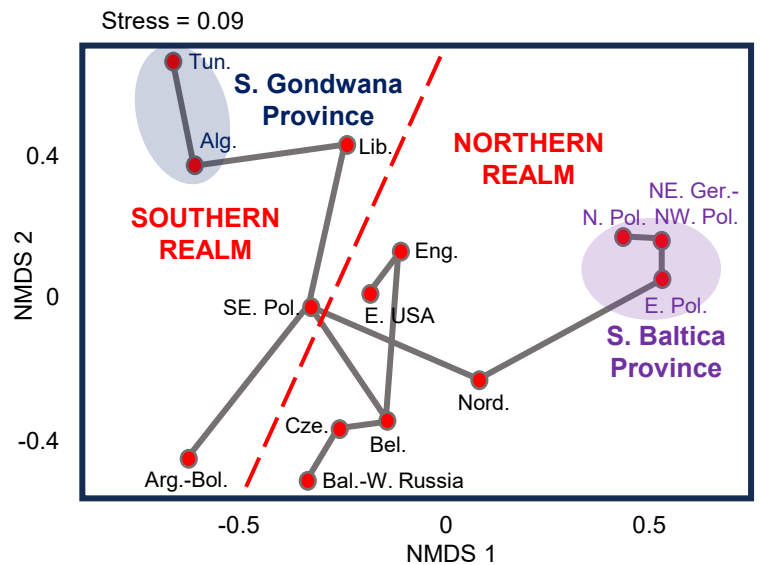
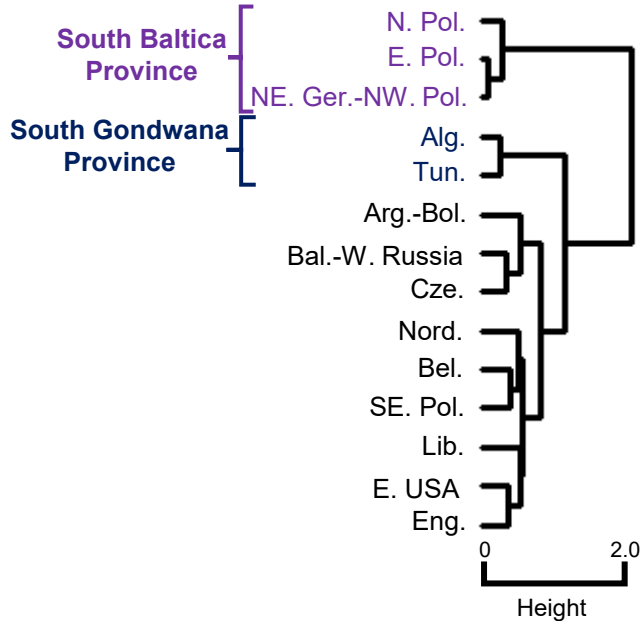
I. SANDBIAN



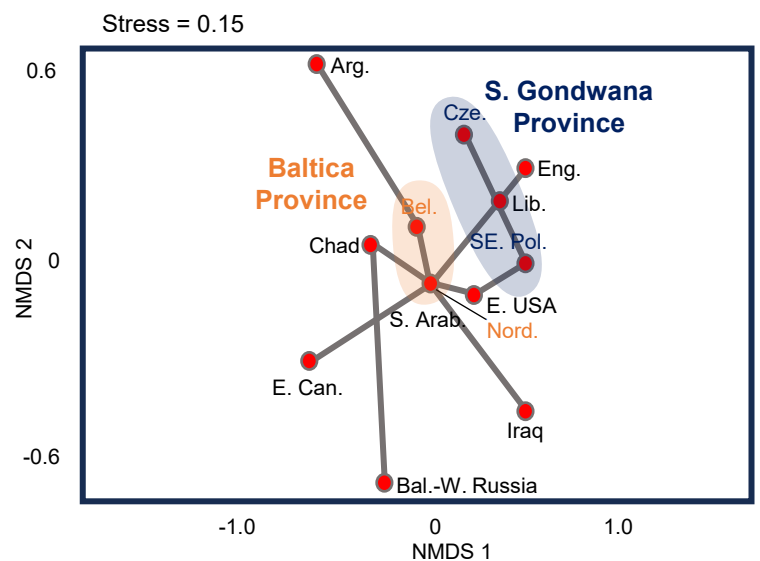
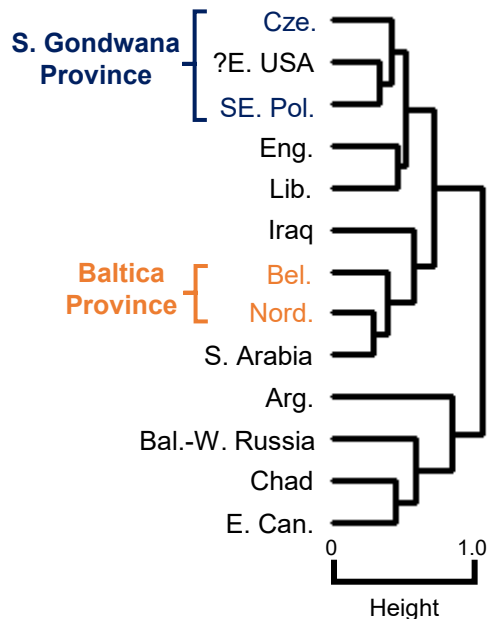
J. KATIAN



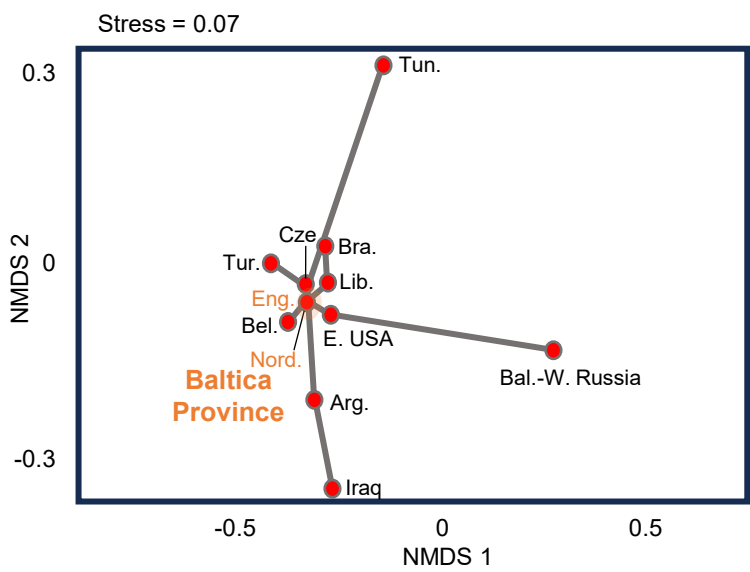
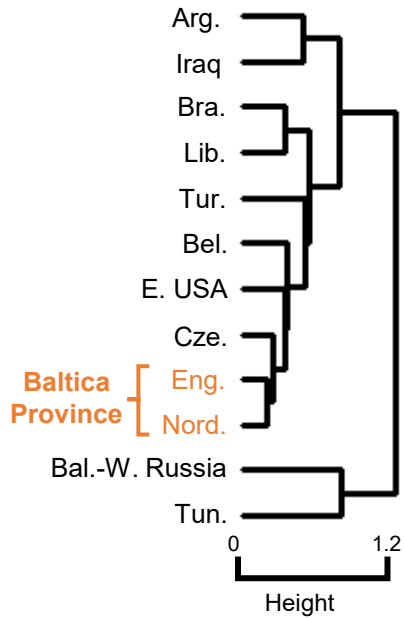
K. HIRNANTIAN



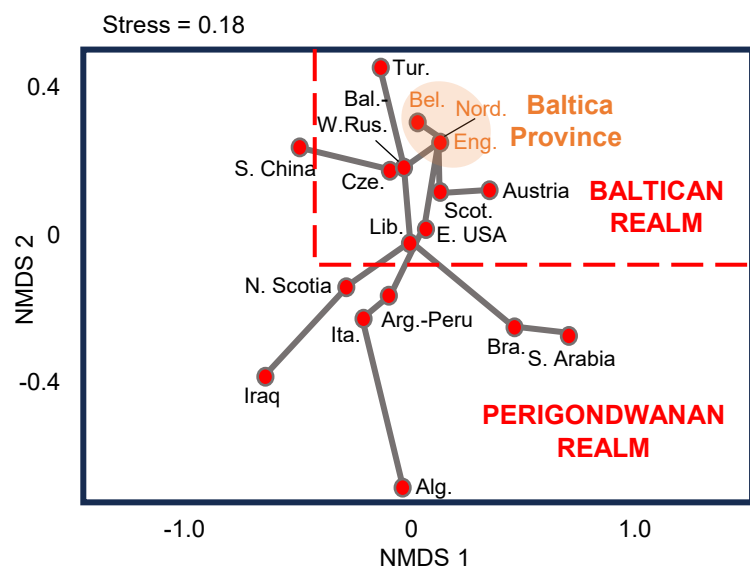
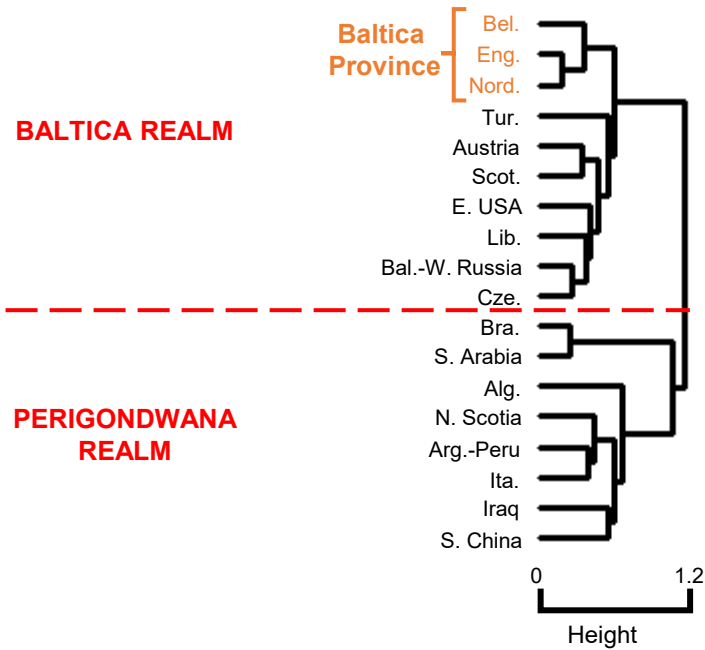
L. RUDDANIAN



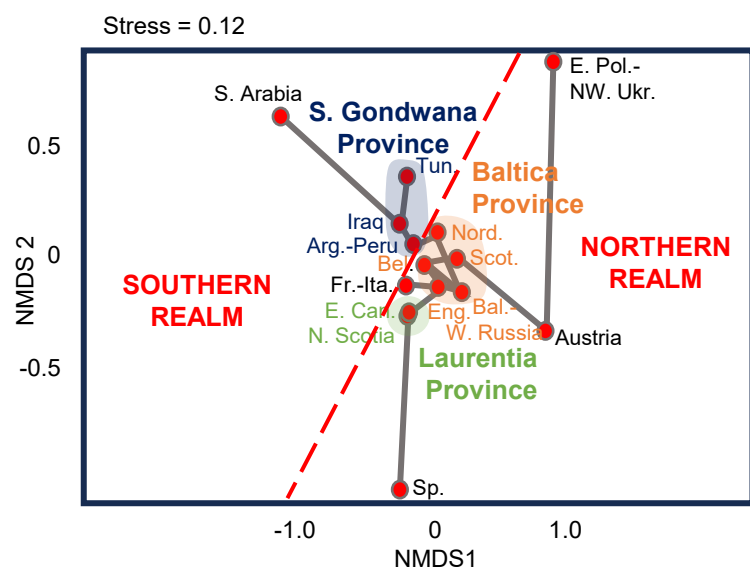
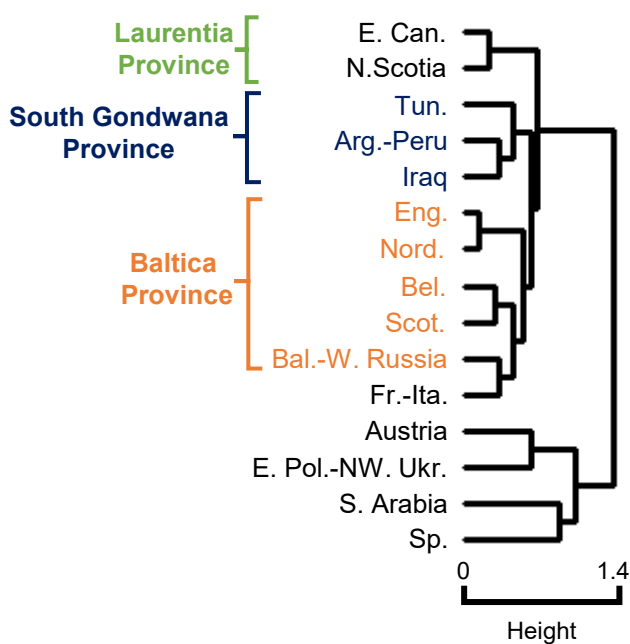
M. AERONIAN



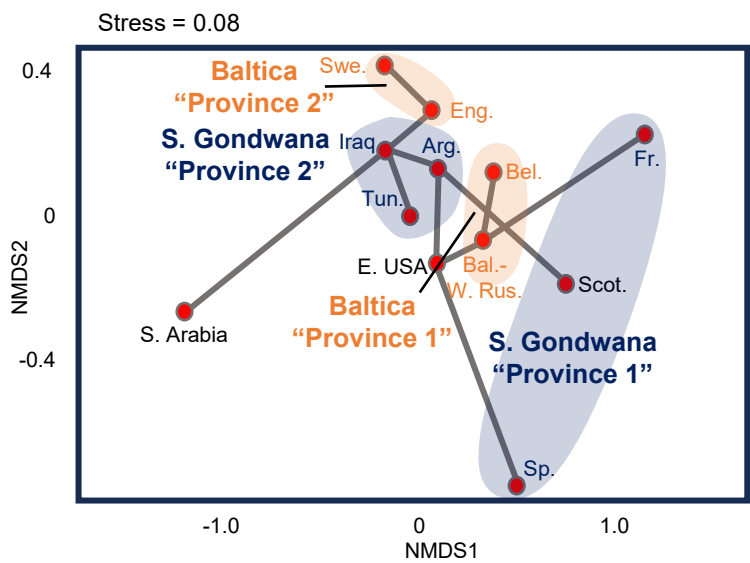
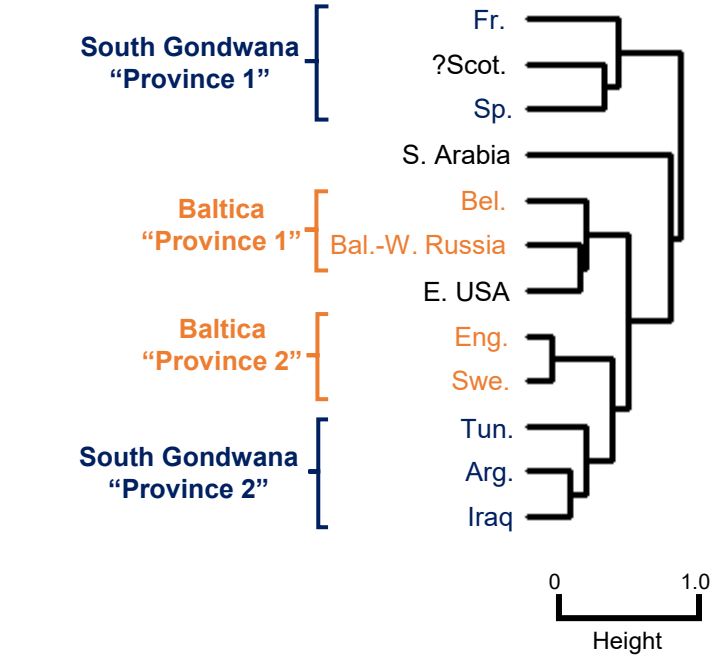
N. TELYCHIAN



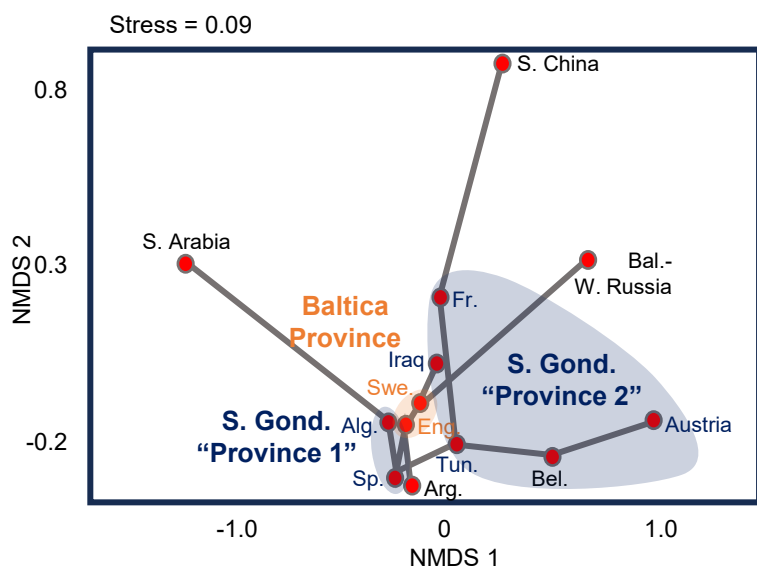
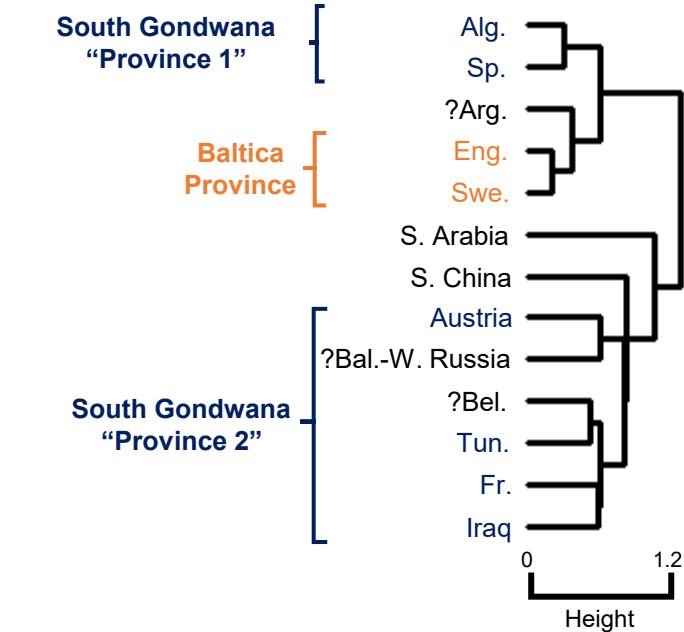
O. SHEINWOODIAN



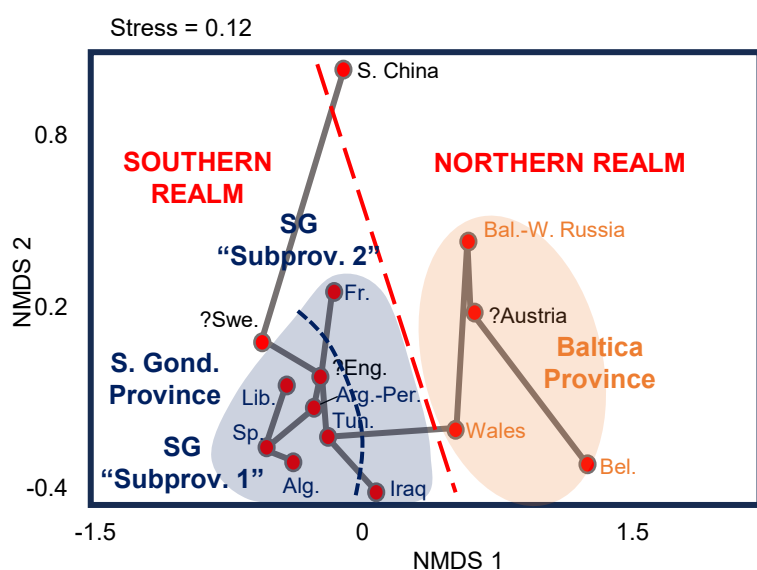
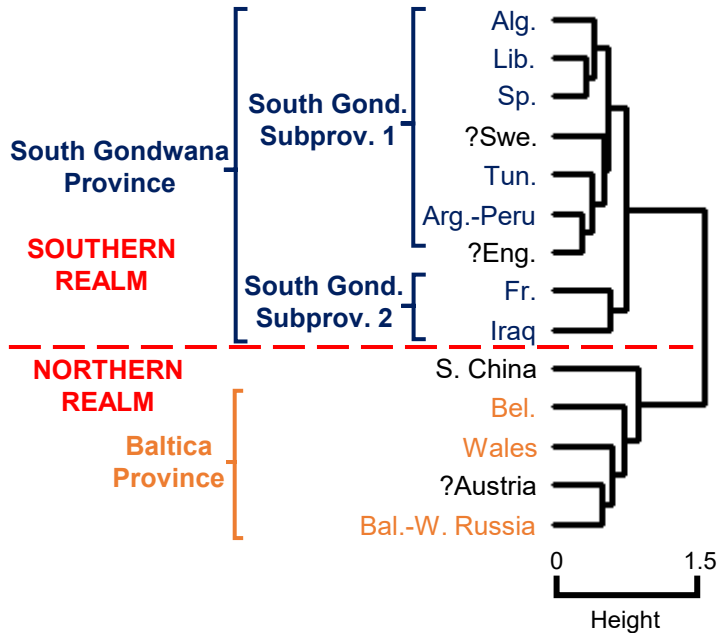
P. HOMERIAN



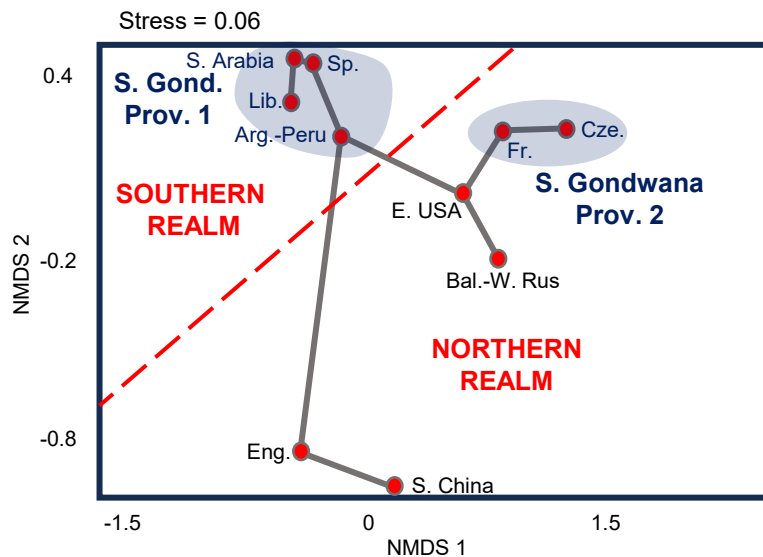
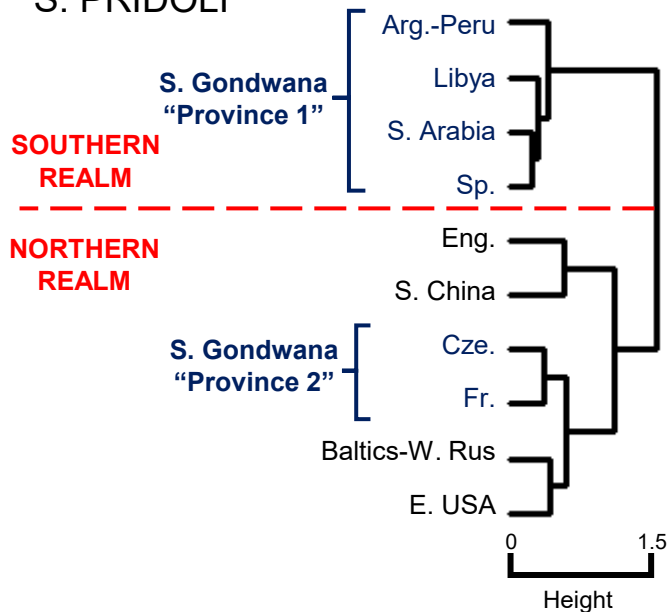
Q. GORSTIAN



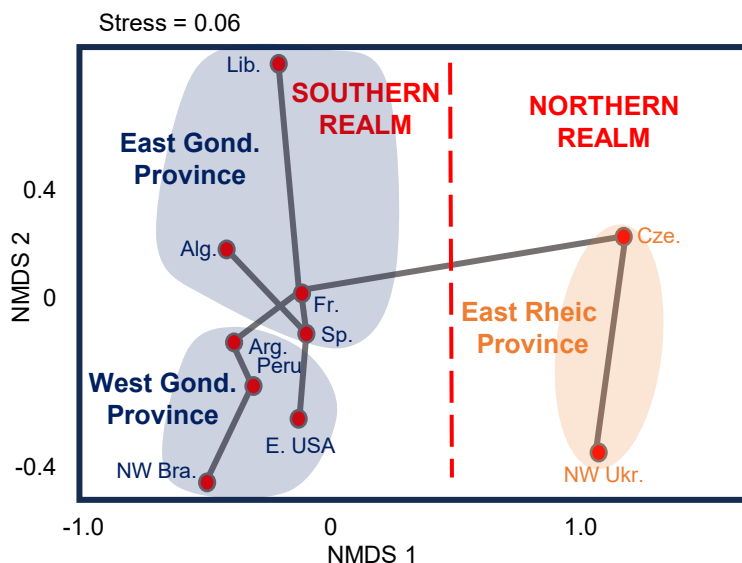
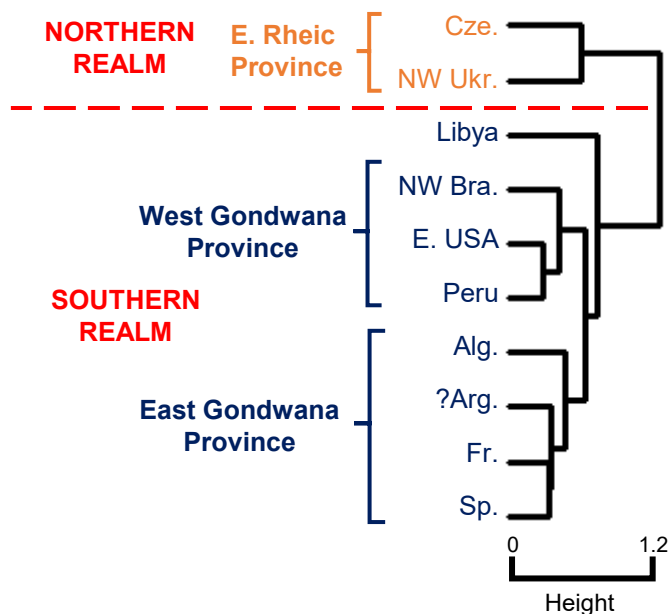
R. LUDFORDIAN



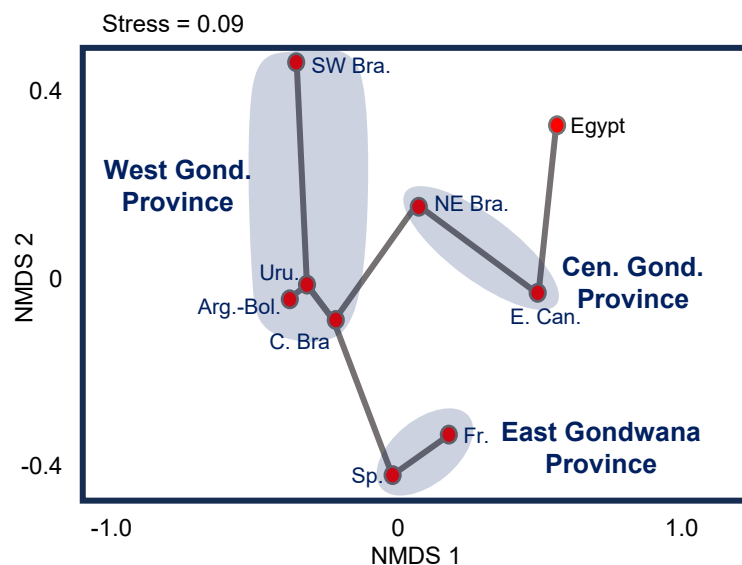
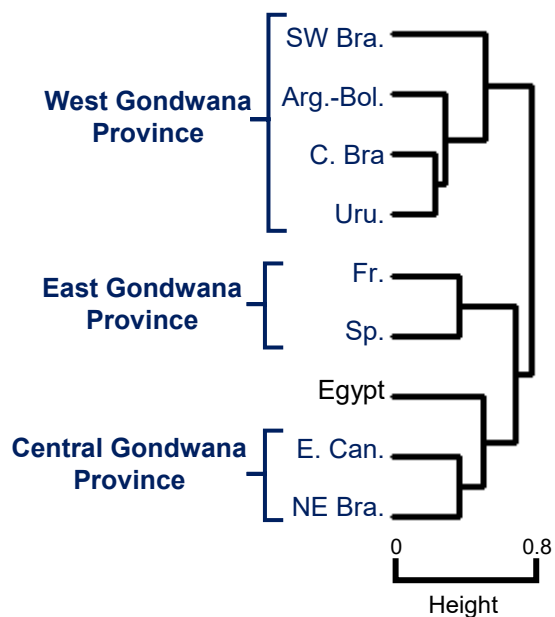
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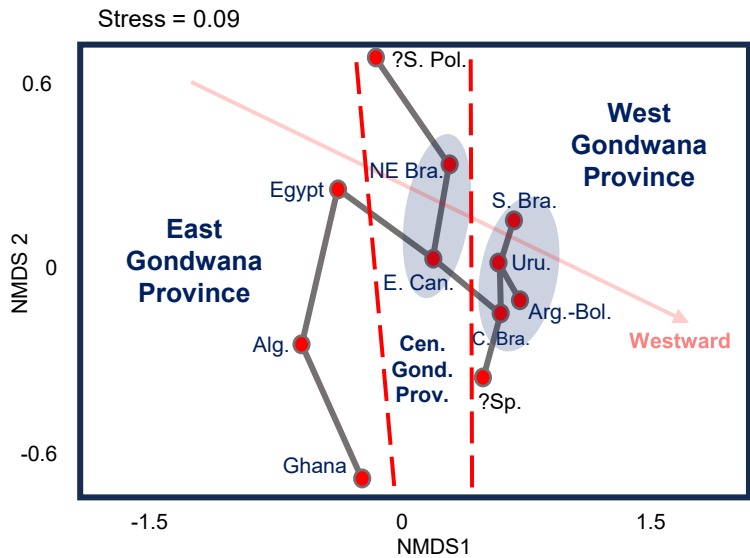
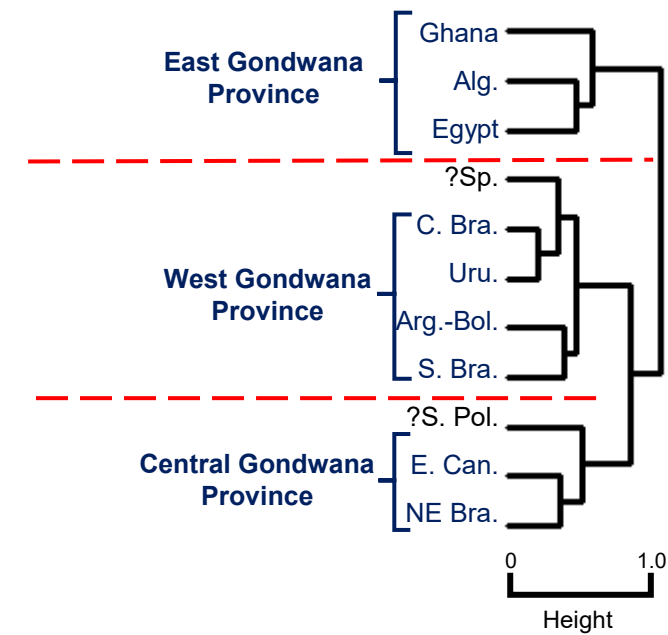
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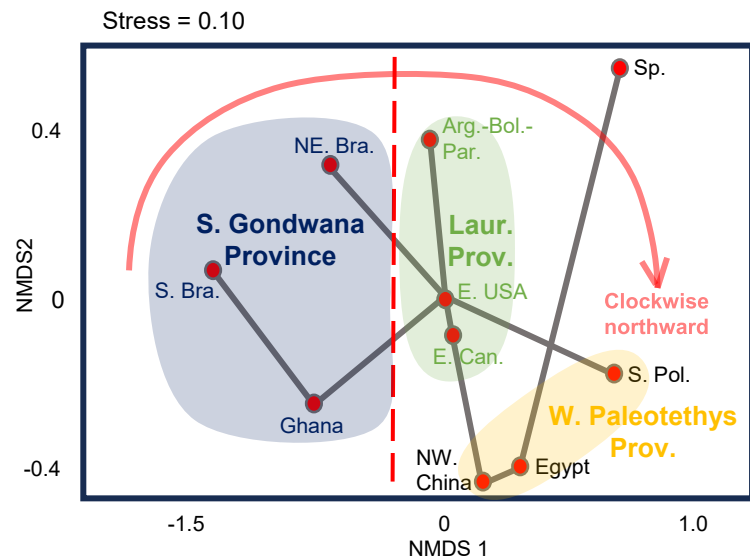
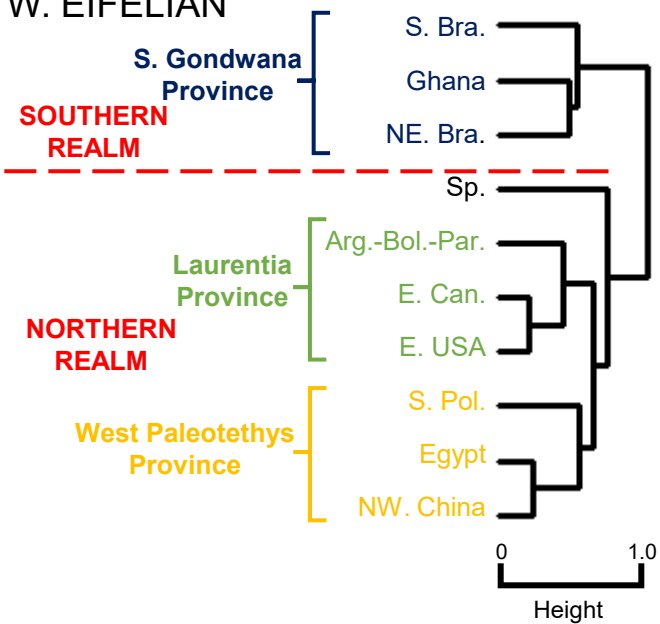
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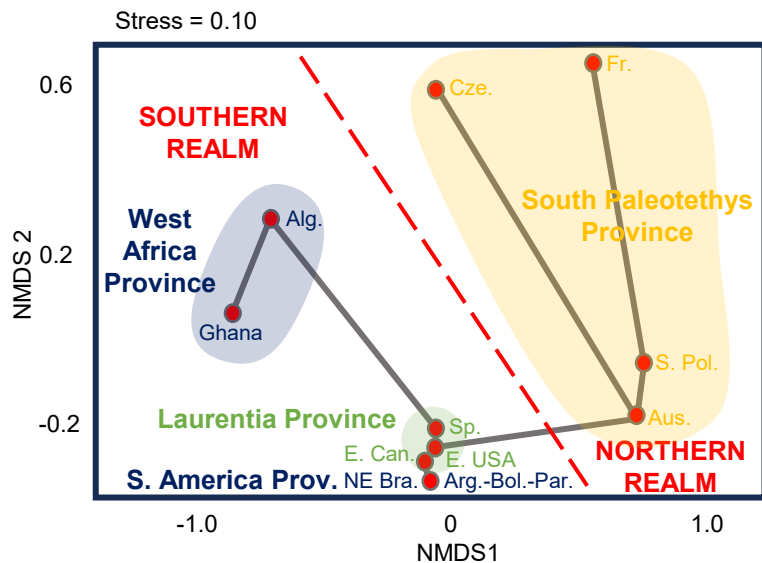
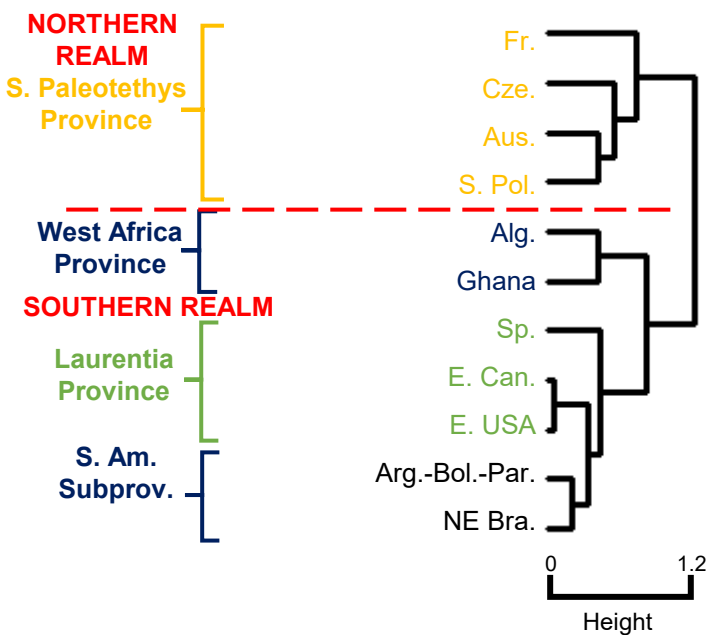
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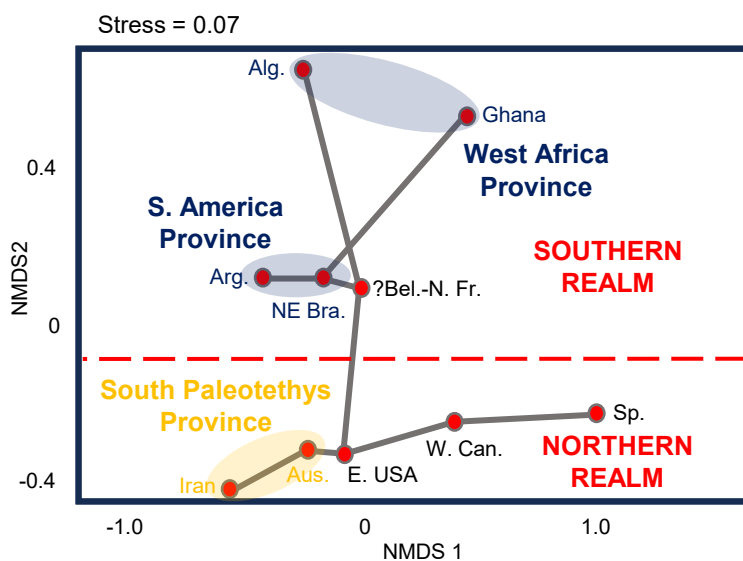
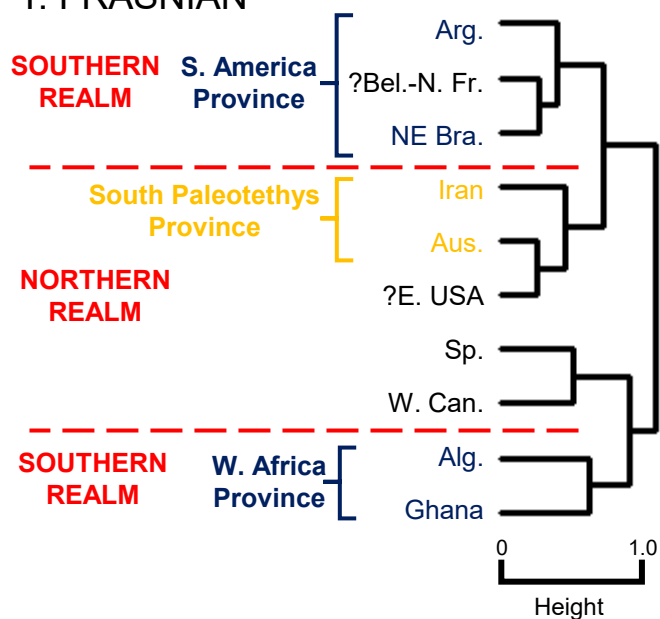
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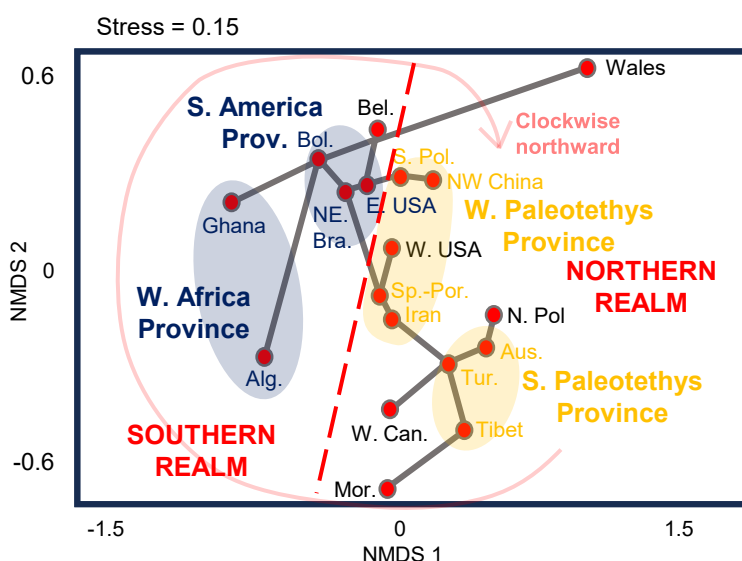
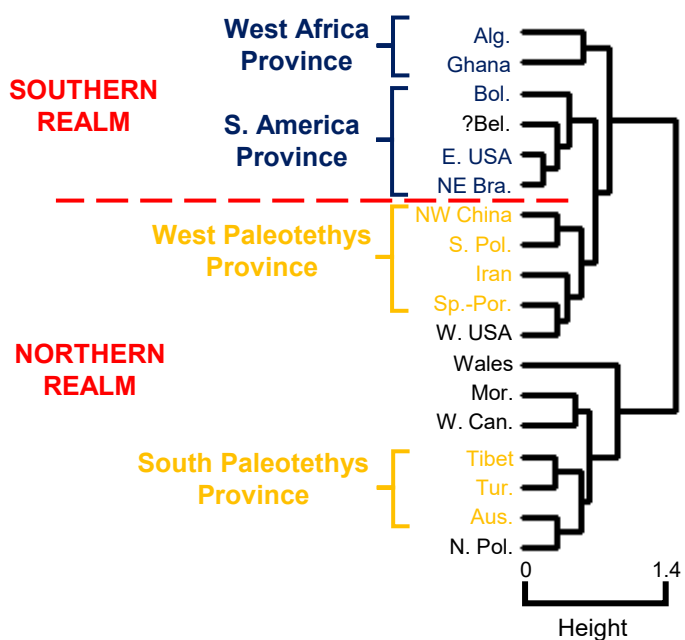
X. GIVETIAN



Y. FRASNIAN



Z. FAMENNIAN



Title: Diversity of phytoplankton in space and time in the early and middle Paleozoic

Abstract:

The present work traces the evolution of phytoplankton diversity and distribution in the early to middle Paleozoic (Cambrian to Devonian) and attempts to elucidate environmental factors which affect diversity dynamics. In order to do so a database was created based on the work of previous authors, expanded with more recent literature and georeferenced.

Proper and meaningful reconstruction of paleodiversity and paleobiogeography warrants a review of taxonomic bias and thus the author engaged in two published studies related to this bias: the first reviews an acritarch subgroup, the netromorphs, proposing a system for classifying genera and reassigning related morphotypes while the second revisits morphological plasticity in Middle Ordovician acritarch assemblages in Öland, Sweden.

The study approached diversity from three perspectives: global, latitudinal and grid-cell diversity. Analysis of global generic diversity shows the effect of mass extinctions, particularly after the Late Ordovician mass extinction (LOME) when there was a drastic drop in diversity, but this trough persisted nearly throughout the whole of the Silurian and possibly attributed to positive carbon isotope events which disrupted marine carbon cycles and lowered phytoplankton resiliency. Global trends of origination and extinction rates are correlated with habitat availability. Latitudinal diversity shows the migration of diversity peaks with the changing climate, and a stronger latitudinal diversity gradient was observed for very high polar-tropical temperature differences. The results also showed an out-of-the-tropics scenario for early to middle Paleozoic phytoplankton. Grid-cell diversity revealed the occurrence of phytoplankton diversity hotspots, but further investigation is needed to ascertain causative factors.

For the biogeographic analysis the present author also participated in two studies (submitted and published respectively) with different approaches: a qualitative description of southern Gondwana paleobiogeography during the Floian (part of a study of the Cabrières biota), using taxa to mark provinces; and a quantitative approach to the Famennian (end-Devonian) using multivariate analysis.

For the main work, multivariate analysis was performed on the phytoplankton database to determine biogeographical patterns. Results showed broad differentiation into latitudinal realms; roughly equated to warm-water (equatorial to sub-equatorial) and cold-water (high southern paleolatitudes) assemblages. Provincialism weakened in the Hirnantian, which is attributable to the LOME and the glaciations, but this situation persisted until the late Silurian at the same time there was low global generic diversity. Continental rearrangement in the Devonian fragmented and reconfigured the cold-water realm into several provinces and formed new ones at the margins of the Paleotethys Ocean.

Overall, this thesis shows how various factors can affect the diversity and distribution of phytoplankton. Future work will need to address two main issues: better spatial and temporal representation; and the application of other spatial corrections to better constrain diversification patterns.

Keywords: *acritarchs, biogeography, diversity, macroecology, netromorphs, Paleozoic, phytoplankton*

Titre : Diversité du phytoplancton dans l'espace et dans le temps au Paléozoïque inférieur et moyen

Résumé :

Le présent travail retrace l'évolution de la diversité et de la répartition du phytoplancton du Paléozoïque inférieur au Paléozoïque moyen (du Cambrien au Dévonien) et tente d'élucider les facteurs environnementaux influençant la dynamique de la diversité. Pour ce faire, une base de données a été créée à partir des travaux d'auteurs précédents, enrichie par une littérature plus récente et géoréférencée.

Une reconstitution correcte et pertinente de la paléodiversité et de la paléobiogéographie nécessite une révision des biais taxonomiques. Ainsi, l'auteur a participé à deux études publiées sur ce biais: la première porte sur un sous-groupe d'acritarches, les netromorphes, en proposant un système de classification des genres et une réaffectation des morphotypes apparentés ; la seconde revisite la plasticité morphologique des assemblages d'acritarches de l'Ordovicien moyen sur l'île d'Öland, en Suède.

L'étude aborde la diversité sous trois angles : global, latitudinal et par mailles (cellules de grille). L'analyse de la diversité générique globale met en évidence l'effet des extinctions massives, notamment après l'extinction massive de la fin de l'Ordovicien (LOME), période durant laquelle la diversité chuta drastiquement. Ce creux se prolongea presque tout au long du Silurien, probablement en raison d'événements positifs d'isotopes du carbone qui perturbèrent les cycles marins du carbone et réduisirent la résilience du phytoplancton. Les tendances globales des taux d'apparition et d'extinction sont corrélées à la disponibilité des habitats. La diversité latitudinale révèle une migration des pics de diversité en fonction du climat changeant, et un gradient de diversité latitudinale plus marqué a été observé lorsque l'écart de température entre les pôles et les tropiques était très important. Les résultats montrent également un scénario de type « sortie des tropiques » pour le phytoplancton du Paléozoïque inférieur à moyen. La diversité par cellule de grille a révélé l'existence de points chauds de diversité du phytoplancton, mais des recherches supplémentaires sont nécessaires pour en identifier les causes.

Pour l'analyse biogéographique, l'auteur a également participé à deux études (l'une soumise, l'autre publiée), adoptant des approches différentes : une description qualitative de la paléobiogéographie du Gondwana sud pendant le Floien (dans le cadre d'une étude du biote de Cabrières), en utilisant les taxons pour marquer les provinces ; et une approche quantitative du Famennien (fin du Dévonien) basée sur une analyse multivariée.

Pour le travail principal, une analyse multivariée a été réalisée sur la base de données du phytoplancton afin de déterminer les schémas biogéographiques. Les résultats ont montré une différenciation large en domaines latitudinaux, correspondant grossièrement à des assemblages d'eaux chaudes (équatoriales à subéquatoriales) et d'eaux froides (hautes paléolatitudes australes). Le provincialisme s'est affaibli durant l'Hirnantien, phénomène attribuable à la LOME et aux glaciations ; cette situation a perduré jusqu'à la fin du Silurien, période marquée par une faible diversité générique globale. Le réarrangement continental au Dévonien a fragmenté et reconfiguré le domaine des eaux froides en plusieurs provinces, tout en en formant de nouvelles en bordure de l'océan Paléotéthys.

Dans l'ensemble, cette thèse montre comment divers facteurs peuvent affecter la diversité et la répartition du phytoplancton. Les travaux futurs devront aborder deux enjeux principaux : une meilleure représentation spatiale et temporelle ; ainsi que l'application d'autres corrections spatiales pour mieux cerner les schémas de diversification.

Mots-clés: *acritarches, biogéographie, diversité, netromorphes, macroécologie, Paléozoïque, phytoplancton*